

Phylogenetic systematics and historical biogeography of the Neotropical electric fish *Sternopygus* (Teleostei: Gymnotiformes)

Kevin G. Hulén^{1,2}, William G. R. Crampton¹ & James S. Albert^{1,2*}

¹Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504-2451, USA

²Department of Zoology, University of Florida, Gainesville, Florida, 32611 USA

submitted January 2004

accepted November 2004

Contents

Abstract	407
Introduction	408
History of the classification	408
Nomenclature	410
Materials and methods	412
Data acquisition	412
Phylogenetic methods	415
Results	415
Descriptive morphology	415
Pigmentation	415
Body proportions	416
Neurocranium	418
Oral jaws	419
Suspensorium	420
Pectoral girdle	420
Axial skeleton	420
Interrelationships of <i>Sternopygus</i>	421
Key to the adults of <i>Sternopygus</i> species	424
Discussion	424
Historical biogeography	424
Historical ecology	425
Continuous traits as phylogenetic characters	426
Acknowledgements	426
References	426
Appendices	428

Abstract Interrelationships among 10 extant species of the Neotropical electric fish *Sternopygus* are inferred from phylogenetic analysis of 66 morphological characters, including features of pigmentation, body proportions, meristics and osteology. A total of 287 lots containing 677 specimens were examined. The important findings of this study are: (1) *S. branco* is the most basal species unique among congeners in being restricted to whitewater rivers in the Central Amazon Basin, (2) *S. sp. 'cau'* from the Rio Caura of Venezuela is the sister taxon to (*S. obtusirostris* + *S. astrabes*), (3) *S. castroi* is a junior synonym of *S. astrabes*, (4) *S. macrurus* is the sister taxon to (*S. arenatus* + *S. xingu* + *S. aequilabiatus* species group) and (5) *S. arenatus* is the sister taxon to (*S. xingu* + *S. aequilabiatus* species group). A key to the adults of *Sternopygus* species is provided. Several features of *S. astrabes* previously thought to be plesiomorphic are now considered derived, including: short body cavity, paedomorphic cranial osteology, and the habitat restriction to terra firme streams. *Sternopygus* species assemblages in the Pacific (trans-Andean) and Atlantic (cis-Andean) slopes of northwestern South America are not monophyletic and do not result exclusively from local or regional radiations. The clade

*Corresponding author. Email: jxa4003@louisiana.edu

composed of *S. macrurus*, *S. arenatus*, *S. xingu* and the *S. aequilabiatus* species group is inferred to predate the Middle Miocene uplift of the Eastern Cordillera (c. 11.8–12.2 Ma). As currently recognized *S. macrurus* is the most widely distributed and most eurytopic gymnotiform species, inhabiting all hydrogeographical regions of tropical South America and most lowland aquatic habitats. Other *Sternopygus* species have much more restricted geographic and ecological distributions. Perceptions of phylogenetic patterns in *Sternopygus* are shown to be highly sensitive to taxon sampling.

Key words biodiversity, classification, comparative osteology, evolution, South America, ontogeny

Introduction

Neotropical electric fishes (Gymnotiformes) are a diverse group of ostariophysan fishes found throughout Neotropical freshwaters and are represented by at least 131 species belonging to 31 genera (Albert, 2001, 2003; Albert & Crampton, 2003; Crampton & Albert, 2005). Gymnotiformes are readily distinguished from other Neotropical fishes by their ‘eel-like’ culteriform body shape, highly elongate anal fin with more than 100 rays (Albert, 2001), absence of dorsal and pelvic fins, reduced eyes and central visual pathways, and the ability to generate and detect electric fields used in communication and navigation (Ellis, 1913; Fink & Fink, 1981; Albert, 2001). Gymnotiformes provide unique materials for studies of the evolution of specialized sensory systems and the diversification of animals species in tropical ecosystems (Crampton, 1998; Albert 2001, 2002; Crampton & Albert, 2005). Gymnotiformes possess a combined electrogenic-electroreceptive system which is employed for both active electrolocation, and electrocommunication. Active electroreception allows gymnotiforms to communicate, navigate, forage and orient themselves relative to the substrate at night and in dark, sediment-laden waters, and contributes to their ecological success in Neotropical aquatic ecosystems. The derived and highly specialized features of electrosensory and electrogenic structures notwithstanding, patterns of diversity in gymnotiform fishes are similar to those of many diverse tropical taxa (Albert *et al.*, 2005b). For example, most gymnotiform clades are thought to be ancient and many genera are distributed in polyphyletic regional species assemblages (Albert *et al.*, 2005a).

The family Sternopygidae is represented by five genera: *Sternopygus* (Müller & Troschel, 1849), *Eigenmannia* (Jordan & Evermann, 1896), *Rhabdolichops* (Eigenmann & Allen, 1942), *Archolaemus* (Korringa, 1970), and *Distocyclus* (Mago-Leccia, 1978). Within gymnotiform fishes, sternopygids share the following unique combination of characters: (1) multiple rows of small, villiform (brush-like) teeth on dentary, (2) relatively large eyes (diameter equal to or greater than distance between nares), (3) large bag-like infraorbital bones with expanded bony arches, (4) anterior nares located outside gape, (5) anal-fin origin at isthmus, (6) absence of urogenital papilla, (7) no caudal fin or dorsal organ (Albert, 2001), and (8) a weak (less than one volt) tone-type electric organ discharge, characterized by a monophasic hyperpolarization from a negative baseline (Crampton, 1998).

The genus *Sternopygus* is distributed throughout the humid Neotropics, from Panama and the Pacific Slope of

Colombia to the Paraguay–Paraná Basin of Paraguay (Table 1; Fig. 1). *Sternopygus* species attain medium to large body sizes (18–140 cm max. total length), with a straight to rounded, or strongly concave snout (Fig. 2). *Sternopygus* is monophyletic and is unambiguously diagnosed by the following unique combination of characters (modified from Albert, 2001): (1) large gape (Mago-Leccia, 1978); (2) large branchial opening (Mago-Leccia, 1978); (3) long, evenly curved maxilla; (4) anterior process of maxilla extends as a narrow hook-like process (Lundberg & Mago-Leccia, 1986); (5) dorsal portion of ventral ethmoid elongate (Albert & Fink, 1996); (6) post-temporal fossa present between pterotic and epioccipital bones (Lundberg & Mago-Leccia, 1986); (7) gill rakers composed of three bony elements, the middle one with 3–10 small teeth (Mago-Leccia, 1978); (8) gill rakers not attached to branchial arches (Albert & Fink, 1996); (9) gap between parapophyses of second vertebra; (10) unossified post cleithrum (Albert & Fink, 1996); (11) long body cavity, with 18–30 precaudal vertebrae (Albert & Fink, 1996); (12) long anal fin with more than 220 rays (Albert & Fink, 1996), (13) unbranched anal-fin rays (Fink & Fink, 1981), (14) developmental origin of adult electric organ from both hypaxial and epaxial muscles (Unguez & Zakon, 1998; Albert, 2001), (15) absence of jamming avoidance response (Heiligenberg, 1991; Albert, 2001), (16) presence of a ‘medial cephalic fold’ (Triques, 2000), a ridge of ectodermal tissue extending from the ventral limit of the opercular opening anteromedially to the branchial isthmus.

History of the classification

The genus *Sternopygus* was established by Müller & Troschel (1849) to place species of ‘Gymnotini’ with ‘hackle-shaped (long and slender) teeth’, ‘head laterally compressed’, and ‘anterior nostrils on the upper side of the head’. Eigenmann & Ward (1905) later regarded *Sternopygus* as a junior synonym of *Gymnotus*, based on several characters now regarded to be of ambiguous polarity. *Sternopygus* was reinstated by Ellis (1913) to place Gymnotiformes with a free orbital margin (i.e. eye not subdermal).

The locality of the type species *S. macrurus* (Bloch & Schneider, 1801) is unknown, although the syntypes were probably described from materials obtained from the Dutch colonies, in either Recife (Brazil) or Surinam (Lönnberg, 1896; Wheeler, 1991). As currently recognized *S. macrurus* is the most widely distributed gymnotiform species, occurring west of the Andes from the Pacific slope and Magdalena Basins

Species	MA	PS	NW	GO	WA	EA	NE	SE	PA
<i>S. aequilabiatus</i>			X						
<i>S. arenatus</i>		X							
<i>S. astrabes</i>				X	Y	Y			
<i>S. branco</i>					X	Y			
<i>S. dariensis</i>	X	Y	Y						
<i>S. macrurus</i>		Y	Y	Y	Y	Y	Y	Y	Y
<i>S. obtusirostris</i>					X	Y			
<i>S. pejeraton</i>			X						
<i>S. sp. 'cau'</i>				Y					
<i>S. xingu</i>						X			
Total	1	3	4	3	4	5	1	1	1

Table 1 Geographic distributions of nine *Sternopygus* species. Hydrogeographic regions modified from Albert (2001). X, region of type locality; Y, specimens from other region(s); Abbreviations: EA, Amazon Basin east of Purus Arch and tributaries below fall-line of Guyana Shield (2 985 000 km²); GO, Guyanas–Orinoco Basin, incl. island of Trinidad and Upper Negro drainages above fall line (1 843 000 km²); MA, Atlantic and Pacific slopes of Middle America from the Motagua to Tuyra Basins (393 000 km²); NE, coastal drainages of northeast Brazil incl. Parnaíba, Piauí, São Francisco and Jequitinhonha Basins (1 357 000 km²); NW, Northwestern South America incl. Atrato, Magdalena and Maracaibo Basins, and north slope of Venezuela (471 000 km²); PA, Paraguay–Paraná Basin including Dulce-Salí and Salado Basins of Argentina (3 185 000 km²); PS, Pacific slopes of Colombia and Ecuador, from Baudó to Guayaquil Basins (200 000 km²); SE, coastal drainages of southeast Brazil and Uruguay from Docé to Lagoa Mirim Basins (628 000 km²); WA, Amazon Basin west of Purus Arch, below c. 500 m elevation (3 556 000 km²). Distribution data from Appendix 1.

Species	Albert & Fink (1996)	Albert		This paper
		(2001)	(2003)	
<i>S. aequilabiatus</i>	X	X	X	X
<i>S. arenatus</i>		X	X	X
<i>S. astrabes</i>	X	X	X	X
<i>S. branco</i>				X
<i>S. castroi</i>		X	X	
<i>S. dariensis</i>			X	X
<i>S. macrurus</i>	X	X	X	X
<i>S. obtusirostris</i>			X	X
<i>S. pejeraton</i>			X	X
<i>S. xingu</i>	X	X	X	X

Table 2 Summary of *Sternopygus* species recognized in recent literature reports.

of Colombia, throughout the Amazon-Orinoco Basins, in the arid northeast of Ceará (Brazil), the Atlantic coast of southeast Brazil and the Paraguay-Paraná Basin of Paraguay (Table 1, Fig. 1a). The family name Sternopygidae was coined by Cope (1871) to place the taxa recognized as all Gymnotiformes. Mago-Leccia (1978) was the first to use the name Sternopygidae in its modern sense.

Albert & Fink (1996) proposed the only previous hypothesis of phylogenetic interrelationships among *Sternopygus* (Table 2) recognizing four species: (1) *Sternopygus astrabes* (Mago-Leccia, 1994) from terra firme streams and rivers of Venezuela and Brazil (Table 1, Fig. 1b), as the most basal taxon; (2) *S. macrurus* as sister taxon to remaining *Sternopygus* species; (3) *Sternopygus xingu* (Albert & Fink, 1996)

from the Rio Tocantins and Xingu Basins of Brazil (Table 1, Fig. 1b); and (4) *Sternopygus aequilabiatus* (Humboldt & Bonpland, 1811) from the Magdalena Basin (Table 1, Fig. 1b). *Sternopygus arenatus* (Eydoux & Souleyet, 1841) from the Rio Guayaquil and Esmeraldas Basins of Ecuador (Table 1, Fig. 1b), *S. dariensis* (Meek & Hildebrand, 1916) from Panama and the Pacific slope of Colombia (Table 1, Fig. 1b), and *S. pejeraton* (Schultz, 1949) from the Maracaibo basin of Venezuela and Colombia (Table 1, Fig. 1b) were considered junior synonyms of *S. aequilabiatus*. *Sternopygus obtusirostris* (Steindachner, 1881) from the Central Amazon, Brazil (Table 1, Fig. 1b) was synonymized with *S. macrurus*. Albert (2001) recognized six species of *Sternopygus* (Table 2), maintained the synonymy of *S. macrurus* and *S. obtusirostris*, and regarded *S. dariensis*,



Figure 1 Map of South America showing the distribution of *Sternopygus* constructed from 168 museum lots containing 298 specimens. (a) *S. macrurus* (closed triangles). (b) *S. branco* (closed circles, a = type locality), *S. obtusirostris* (open squares, b = type locality), *S. astrabes* (closed diamonds, c = type locality), *S. sp. 'cau'* (open diamonds, d), *S. xingu* (closed squares, e = type locality), *S. arenatus* (stars, f = type locality), *S. dariensis* (inverted open triangles, g = type locality), *S. pejeraton* (open triangles, h = type locality), *S. aequilabiatius* (inverted closed triangles, i = type locality).

S. pejeraton and *S. aequilabiatius* as members of the *S. aequilabiatius* species group. Albert (2003) recognized nine species of *Sternopygus* (Table 2).

Nomenclature

We recognize nine valid species of *Sternopygus* (Table 2), which includes *S. branco* (Crampton *et al.*, 2004), a new species described from the Amazon River between its confluences

with the Rios Japurá and Negro and the lower 100 km of the Rio Negro (Fig. 1b, Table 1). The taxonomic status of *S. aequilabiatius*, *S. dariensis* and *S. pejeraton* are not fully understood (Mago-Leccia, 1994; Albert & Fink, 1996; Albert, 2001), so are still referred to as the *S. aequilabiatius* species group.

Examination of four specimens in the type series of *S. castroi* (Triques, 2000) from the Rio Negro tributary of the Amazon basin shows they are indistinguishable from *S. astrabes*. Triques (2000) diagnosed *S. castroi* by the

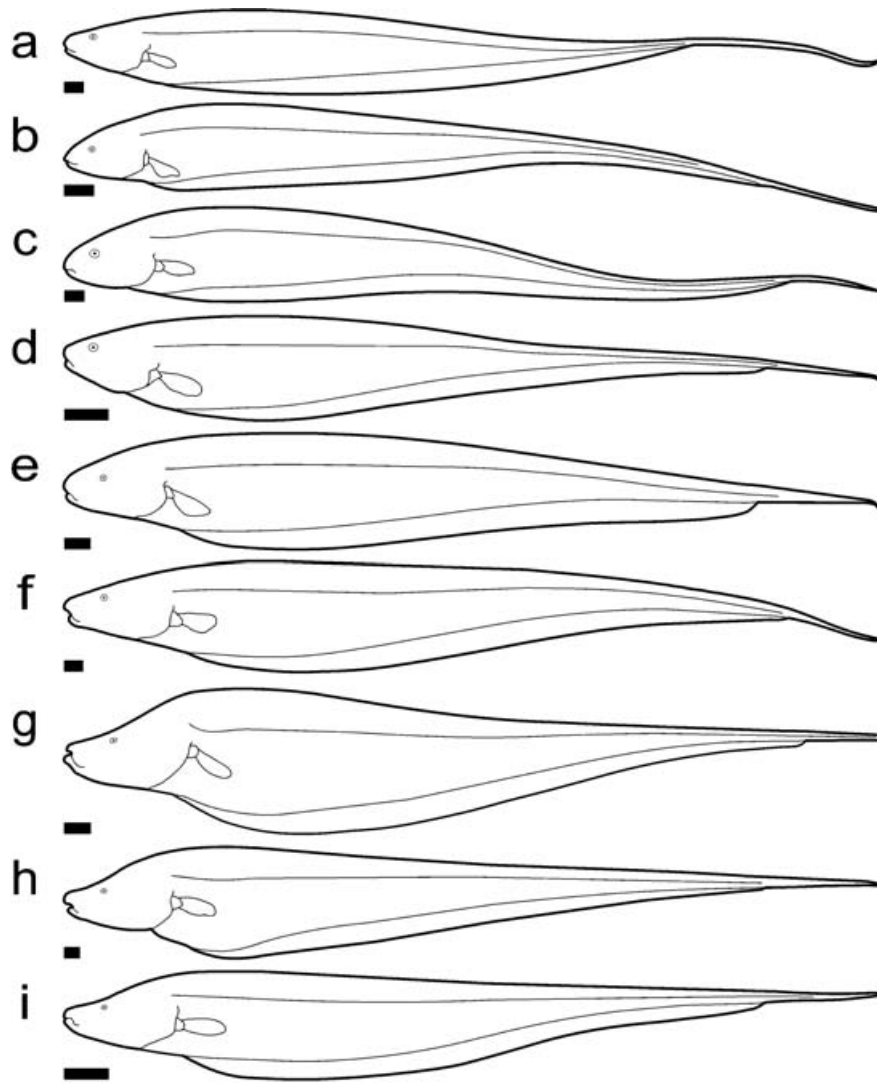


Figure 2 Shape differences in nine adult *Sternopygus* species. (a) *S. branco* (MCP 32451), (b) *S. sp. 'cau'* (AMNH 58643), (c) *S. obtusirostris* (MCP 32262), (d) *S. astrabes* (MCP 32235), (e) *S. macrurus* (ANSP 172171), (f) *S. arenatus* (MCZ 48804), (g) *S. xingu* (INPA 6425), (h) *S. dariensis* (UF 15451), (i) *S. pejeraton* (UMMZ 157671). Scale bars equal 10 mm.

simultaneous absence of an intraopercular fold and presence of a humeral spot. In the specimens examined for the present study neither of these features were determined to be diagnostic of *S. castroi*. Like many features of soft surface anatomy, the intraopercular fold is highly variable in appearance within and among *Sternopygus* species depending on preservation quality and body size. The type specimens of *S. castroi* do possess a slightly darkened humeral region, but such a distorted pattern of enhanced pigmentation in the humeral region is also observed in specimens of *S. astrabes* and *S. pejeraton*. The appearance of this slightly darkened patch is distinct from the dark humeral spot defined in character 4 as a well-defined black patch with sharp margins, which is observed in *S. sp. 'cau'*, *S. macrurus*, and *S. xingu*. In addition, the type specimens of *S. castroi* possess the principal diagnostic feature of *S. astrabes* (Mago-Leccia, 1994): two broad dark wide vertical bands in adults (visible in Triques, 2000, Fig. 1). The available meristic data (i.e. anal and pectoral fin rays) from the type specimens

of *S. castroi* are well within the range observed in populations of *S. astrabes* from throughout the Guyanas and Amazon basin.

In addition to the nine valid *Sternopygus* species we recognize *S. sp. 'cau'* as an undescribed species. Two paratype specimens of *S. astrabes* from the Rio Caura in the Venezuelan state of Bolivar were discovered to have different morphometric and meristic values than those from other populations, including the holotype from near Porto Ayacucho in the Venezuelan state of Amazonas. The specimens from the Rio Caura have a larger adult body size (mean 215 vs. 121 mm) and a non-overlapping higher range in pre-caudal vertebrae (mode 24 vs. 19). A formal description of this species will be presented elsewhere.

Sternopygus species recognized in this phylogenetic review are listed below. Square brackets contain modern or corrected spellings for river or place names.

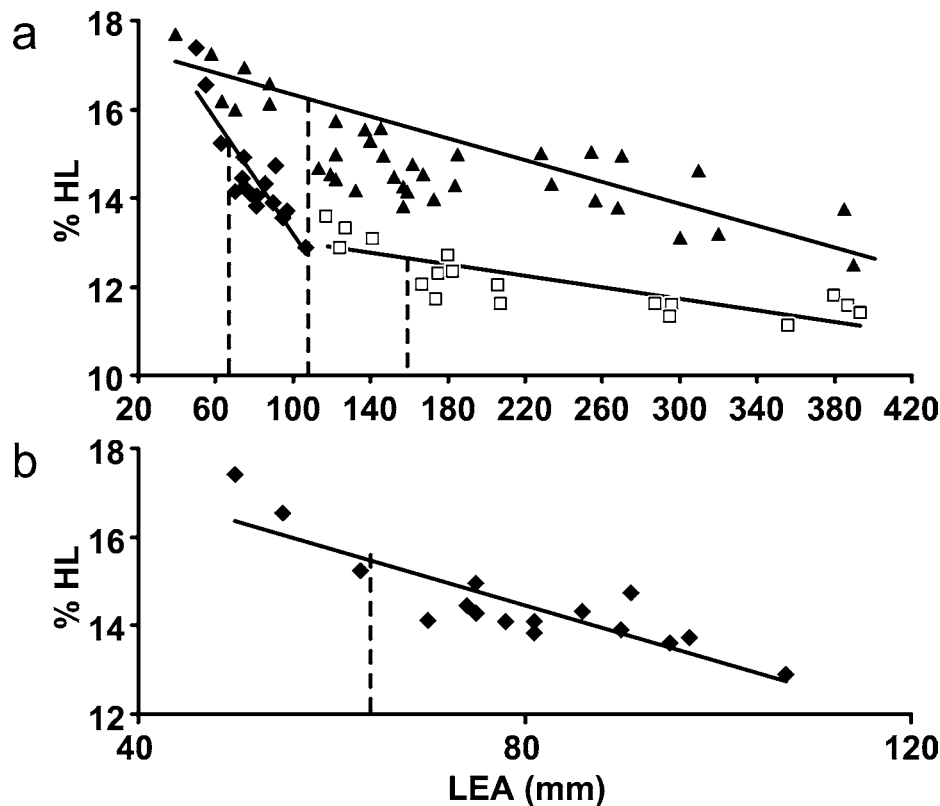


Figure 3 Allometric growth of relative head length (HL%) in three species of *Sternopygus* illustrating method of estimating size of maturity. Plot of length to end of anal fin (LEA) and head length as a percentage of LEA (HL%) for three *Sternopygus* species: (a) *S. macrurus* (closed triangles) and *S. obtusirostris* (open squares). (a, b) *S. astrabes* (closed diamonds). Dashed lines represent point where specimens are at or near asymptotic value of HL% are considered to have attained adult size.

- Sternopygus macrurus* (Bloch & Schneider, 1801)
Gymnotus macrurus Bloch & Schneider, 1801: 522 (Brazil).
Sternopygus marcgravi Reinhardt, 1852: 146 (Rio das Velhas, Brazil).
Carapus sanguinolentus Castelnau, 1855: 85, 94, Pl. 46, fig. 1. (Río Urubamba, Upper Río Ucayali, Peru).
Hildatia brasiliensis Fernández-Yépez, 1968: no pagination, fig. (unlabelled) (Sarapo, Piauí [Piauí], Brazil).
- Sternopygus aequilabiatus* (Humboldt & Bonpland, 1811)
Gymnotus aequilabiatus Humboldt, in Humboldt & Bonpland, 1811: 79, P. 10, fig. 1 (Río Magdalena, Colombia).
- Sternopygus arenatus* Eydoux & Souleyet, 1841: 143, Pl. 8, fig. 2 (Río Guayaquil, Ecuador).
- Sternopygus obtusirostris* Steindachner, 1881: 143, Pl. 2, fig. 3 (Rio Amazonas [Solimões] at Tefé [Tefé], Lago Alexo [Aleixo] and Manacapouru [Manacapuru], Rio Puty [Poti], Rio Madeira, all from Thayer Expedition).
- Sternopygus dariensis* Meek & Hildebrand, 1916: 309, Pl. 26, fig. 21 (Marrigante, Río Tuyra, Panama).
- Sternopygus pejeraton* Schultz, 1949: 60–61, Pl. 1A (Río Apón, Maracaibo basin, Venezuela).
- Sternopygus astrabes* Mago-Leccia, 1994: 79–80, Pl. 87 (Caño Pozo Azul, Agua Linda, 23 km NE. Puerto Ayacucho, tributary of Río Orinoco, Amazonas, Venezuela).
- Sternopygus castroi* Triques, 2000: 19–26, figs 1–2 (Igarapé Jaradá, Rio Cueiras, tributary of Rio Negro, Brazil).
- Sternopygus xingu* Albert & Fink, 1996: 85–102, figs 7–9 (Rio Batovi, Mato Grosso do Sul, Brazil).
- Sternopygus branco* Crampton, Hulen & Albert, 2004 (Amazon River between its confluences with the Rio Japurá and Rio Negro, Lower Rio Negro, Brazil).
- Sternopygus* sp. 'cau', undescribed (Rio Caura, Bolívar, Venezuela).

Materials and methods

Data acquisition

A total of 287 lots containing 677 specimens were examined (Appendix 1). Due to growth allometry, morphometric data are reported as mean adult values. Adult morphology was determined from plots of head length as a percentage of length to the end of anal fin (Fig. 3), and from examination of neurocranial shape from radiographs (Figs 4, 5). Sexual maturity and sex in *Sternopygus* can only be assessed through dissection of gonads. In mature specimens, testes are pinkish-white and ovaries are packed with yellow eggs. Immature specimens cannot be sexed reliably. Sexual dimorphism of morphology has not been observed in *Sternopygus*.

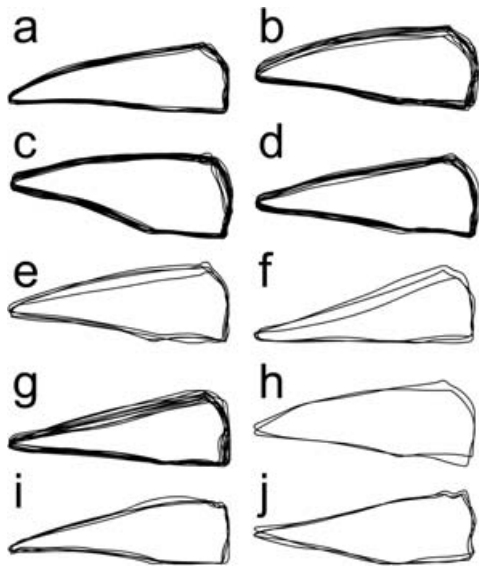


Figure 4 Tracings of adult neurocranial outlines for nine sternopygids, superimposed in lateral view. (a) *S. branco* ($n = 9$), (b) *S. obtusirostris* ($n = 10$), (c) *S. astrabes* ($n = 13$), (d) *S. macrurus* ($n = 11$), (e) *S. arenatus* ($n = 4$), (f) *S. xingu* ($n = 3$), (g) *S. aequilabiatius* ($n = 12$), (h) *S. sp.* 'cau' ($n = 2$), (i) *A. blax* ($n = 4$), (j) *D. conirostris* ($n = 3$).

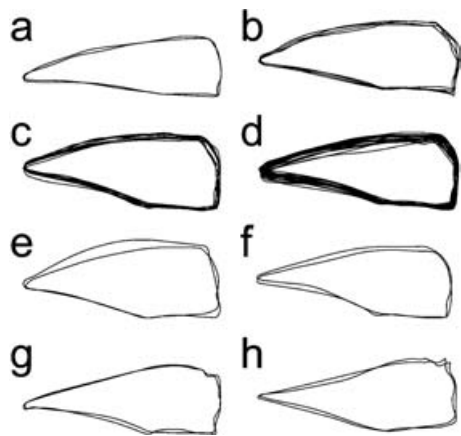


Figure 5 Tracings of juvenile neurocranial outlines for nine sternopygids, superimposed in lateral view. (a) *S. branco* ($n = 2$), (b) *S. obtusirostris* ($n = 4$), (c) *S. astrabes* ($n = 9$), (d) *S. macrurus* ($n = 10$), (e) *S. arenatus* ($n = 2$), (f) *S. aequilabiatius* ($n = 3$), (g) *A. blax* ($n = 2$), (h) *D. conirostris* ($n = 2$).

Morphometric techniques used to measure body proportions were adapted from Albert & Fink (1996). Digital calipers were used to measure point-to-point linear distances from standard landmarks to the nearest 0.1 mm (Fig. 6). Small specimens were measured using an ocular micrometer and an Olympus SZX12 dissecting microscope. Measurement accuracy and precision were estimated by comparing the standard deviation of ten repeated measures of each morphometric variable. All unilateral measurements were taken on the left side of the fish. Measurements of body size include: (1) length to the end of the anal fin (LEA), measured from the tip of snout (anterior margin of upper jaw at mid-axis of body) to end of

anal fin (where membrane posterior to last ray contacts the ventral surface of body); (2) anal-fin length (AFL), from origin of anal fin to posterior end of anal fin; (3) caudal appendage (CA), measured as the distance from the last anal-fin ray to the distal end of the caudal filament, which is often damaged and not fully regenerated, so was selectively excluded from the analysis; (4) body depth (BD), vertical distance from origin of anal fin to dorsal body border; (5) body width (BW), maximum body width at origin of anal fin; (6) head length (HL), measured from posterior margin of the bony opercle to tip of snout (anterior margin of upper jaw at mid-axis of body); (7) postorbital head length (PO), from posterior margin of the bony opercle to posterior margin of eye (at edge of the free orbital margin); (8) preorbital head length (PR), from anterior margin of eye (at edge of the free orbital margin) to tip of snout (anterior margin of upper jaw at mid-axis of body); (9) eye diameter (ED), horizontal distance between anterior and posterior margin of eye (at edge of free orbital margin); (10) interorbital length (IO), between dorsomedial margins of eyes (at edge of free orbital margin); (11) inter-narial distance (NN), from posterior margin of the anterior nares to the anterior margin of the posterior nares; (12) mouth width (MW), horizontal distance of gape at rictus; (13) branchial opening (BO), from postero-dorsal to anteroventral extent of fold along anterior margin; (14) head depth (HD), vertical distance at nape to ventral body border with lateral line held horizontal; (15) head width (HW), width at nape; (16) preanal distance (PA), from origin of anal fin to posterior margin of anus; (17) pectoral-fin length (P1), from dorsal border of fin base where it contacts cleithrum to tip of the longest ray.

Neurocranium measurements were obtained from 71 radiographs of adult sternopygids. Adults were distinguished from juveniles based on the convexity of the parasphenoid and frontal bone, with adults achieving straighter margins (Figs 4, 5). Radiographs were developed on Kodak diagnostic film (Ektascan EM-1) and analysed with the aid of an Olympus SZX12 dissecting microscope. Distinct landmarks identified along margins of bones were digitized using tpsDig 1.37 (Rohlf, 2003) and the distances between them calculated. Neurocranium measurements include: neurocranium length (NL), from ventro-posterior margin of basioccipital to anterior margin of mesethmoid; neurocranium depth (ND), from dorso-posterior margin of supraoccipital to ventro-posterior margin of basioccipital; and basioccipital length (BaL), from ventro-posterior margin to ventro-anterior margin of basioccipital.

Meristic protocols follow Albert & Fink (1996). Skeletal counts obtained from 146 radiographs include: precaudal vertebrae (PCV), which include those of the Weberian apparatus and are a good measure of body cavity length (Albert, 2001); and anal-fin rays (AFR). Additional meristics include: pectoral-fin rays (PIR); lateral line scales (LLS), from posterior edge of opercle to end of tail; scales above lateral line (SAL), from a point three times head length back from the tip of the snout at the lateral line to dorsomedial margin; scales below lateral line (SBL), from same point as SAL to base of anal-fin pterygiophores, (7) scales over pterygiophores (SOP), from same point as SAL at base of anal-fin pterygiophores to anal fin ventral border.

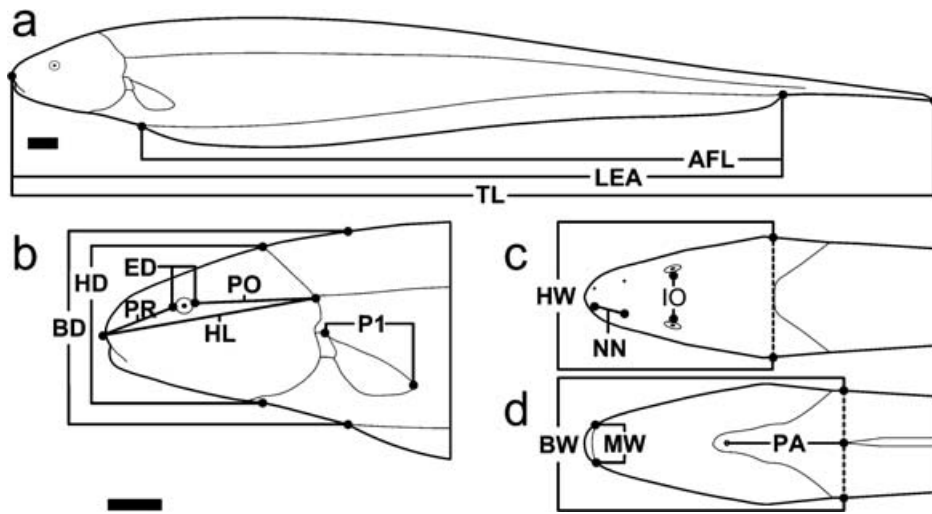


Figure 6 Measurements used for morphometric analysis of *Sternopygus*. Body proportions shown for *S. macrurus* (ANSP 172171). (a) Body, lateral view, (b) Head, lateral view, (c) Head, dorsal view, (d) Head, ventral view. Scale bars equal 10 mm.

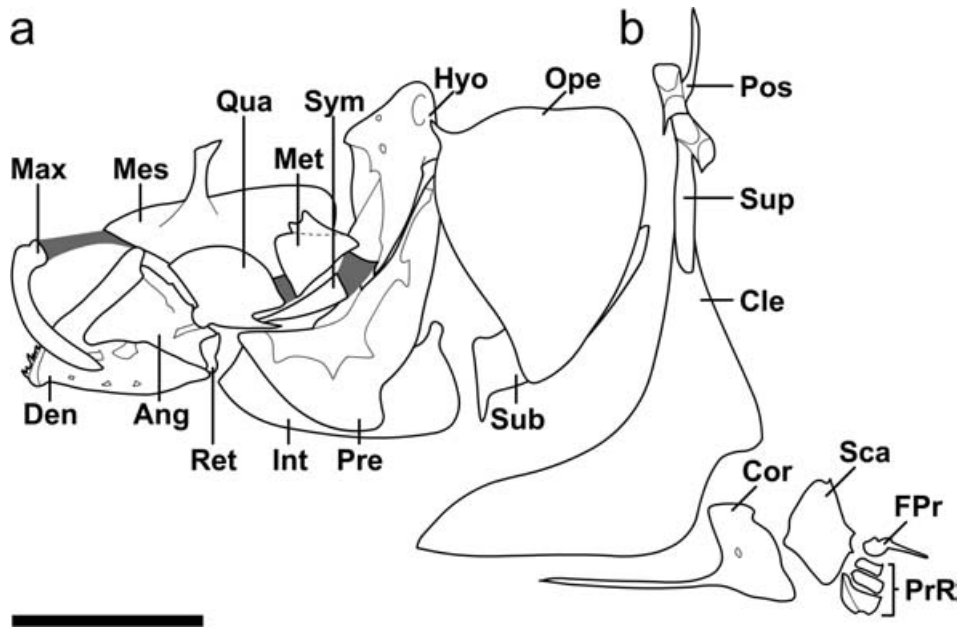


Figure 7 Articulated suspensorium and pectoral girdle of *S. macrurus* (MCP 32254), in lateral view. Cartilage represented by gray shading. (a) Suspensorium, (b) Pectoral girdle. Abbreviations: Max, maxilla; Den, dentary; Ang, anguloarticular; Ret, retroarticular; Mes, mesopterygoid; Met, metapterygoid; Sym, symplectic; Hyo, hyomandibula; Int, interopercle; Pre, preopercle; Sub, subopercle; Ope, opercle; Pos, posttemporal; Sup, supracleithrum; Cle, cleithrum; Cor, coracoid; Sca, scapula; FPr, first pectoral ray; PrR, proximal radials. Scale bar equals 10 mm.

Osteological data were obtained from 33 cleared and stained specimens representing 19 lots of sternopygid species. One large and small mature specimen of each species was cleared and stained using the enzyme technique of Taylor & Van Dyke (1985) with reagent concentrations and reaction times adjusted for each specimen. The neurocranium, suspensorium, and pectoral girdle were removed from all specimens using standard methods for small teleosts (Weitzman, 1974; Albert, 2001). Bone nomenclature follows Fink & Fink (1981) for the skeletal system (Fig. 7) and Patterson (1975) for bony elements of the skull (Fig. 8). Additionally, eight adult

specimens of a single population of *S. macrurus* from the state of Apure, Venezuela (LEA 203–298 mm) were cleared and stained for information on population-level osteological variation. The morphology used in coding osteological characters was not noticeably different in these specimens. Specimens of *S. pejeraton* and *S. aequilabiatius* were not available for osteological examination. For osteological descriptions the *S. aequilabiatius* group is represented by *S. dariensis*. Outlines of articulated and disarticulated bones were sketched with the aid of an Olympus SZX12 dissecting microscope equipped with a camera lucida. Sketches were then

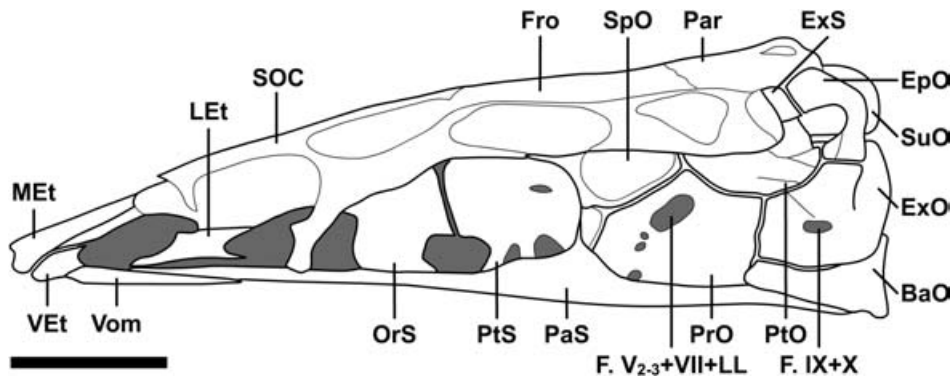


Figure 8 Neurocranium of *S. macrurus* (MCP 32254), in lateral view. Foraminae and other non-ossified areas represented by gray shading. Abbreviations: F. V2–3, foramen of some trigeminal and lateral line nerve rami; F. VII + LL, foramen of facial nerve and lateral line nerves; F. IX + X, foramen of glossopharyngeal and vagus nerves; SOC, supraorbital canal; MEt, mesethmoid; VET, ventral ethmoid; LET, lateral ethmoid; Vom, vomer; Fro, frontal; PaS, parasphenoid; OrS, orbitosphenoid; PtS, pterosphenoid; SpO, sphenotic; PrO, prootic; PtO, pterotic; Par, parietal; ExS, extrascapular; EpO, epioccipital; SuO, supraoccipital; ExO, exoccipital; BaO, basioccipital. Scale bar equals 5 mm.

traced into FLASH MX (Macromedia) to create line art figures.

Phylogenetic methods

In selecting and coding characters we were guided by the philosophy that phylogenetic congruence among all observations is the most reliable method to assess homology (Patterson, 1982; Eernisse & Kluge, 1993). Outgroup taxa were selected based on the results of previous research (Albert, 2001). These include at least one species from each of the four non-*Sternopygus* sternopygid genera, and a non-adult member of a phylogenetically basal species (*Parapteronotus hasemani*) from the sister family Apteronotidae. Due to the derived snout shape of *P. hasemani*, morphometric measurements of an apteronotid species are reported for ‘*Apteronotus bonaparti*’. MacClade 4.03 (Maddison & Maddison, 2000) was used to construct a matrix containing 66 characters, which include previously published characters (Albert & Fink, 1996; Albert, 2001) and new observations. Pigmentation characters apply to juveniles as well as adults in species pedomorphic for those characters. Osteological and morphometric characters apply to morphologically (as opposed to reproductively) mature specimens. Morphometric and meristic traits were examined as both continuous and discrete (coded) data.

Relative mean, median or modal adult trait values were coded into multiple alternative character states and the coding scheme was selected that exhibited maximum congruence with the distributions of other characters in the data matrix (Westneat, 1993; Wiens, 2000). The alternative coding schemes differ in the number of states and range cutoffs. Tree statistics calculated from character states optimized unambiguously on a strict consensus topology of all the data, and interpreting character state changes on ‘hard’ polytomies (multiple speciation events). Congruence was assessed by values of the ‘rescaled consistency index’, which is not influenced by symplesiomorphies or autapomorphies (Farris, 1989). All characters were coded as unordered except: the multi-state

morphometric characters (char. 6, 7, 12, 30, 55), ratio of opercle dorsal margin (char. 46), rib count (char. 60), number of postcleithrae (char. 61) and body cavity length (char. 62).

The following options were employed in maximum parsimony (MP) analyses using PAUP 4.0b10 (Swofford, 2003). Heuristic searches were used with options set to save all minimum length trees. Tree-bisection-reconnection (TBR) branch swapping was performed with and without the steepest descent option. Bremer decay values (Bremer, 1994) were calculated using TreeRot (Sorenson, 1999) to generate constraint files for PAUP. Three support indices (*sensu* Wilkinson *et al.*, 2003) are reported for each internal node including branch lengths as character state changes (steps) of unambiguous optimization. Diagnoses were generated using the export branch-list option in the MacClade software with all characters optimized unambiguously on the single most parsimonious tree topology.

Results

Descriptive morphology

Characters of pigmentation are listed first, followed by those of body proportions, neurocranium, oral jaws, suspensorium, pectoral girdle, and axial skeleton. Figures 2–6 and Tables 3–5 display body proportions and counts, and Figures 7–16 display osteology, used in coding characters for the phylogenetic analysis.

Pigmentation

1. Body colour. 0: dark, with saddles or pale lateral stripe. 1: uniformly pale, no saddles or pale lateral stripe.
2. Pale lateral stripe. 0: absent from ontogeny. 1: present in juveniles. 2: present in juveniles and adults.
3. Dark saddles. 0: absent. 1: present in juveniles.
4. Dark humeral region. 0: no dark pigments. 1: well defined black patch, sharp margins.

Species	LEA			AFL			CA %		
	n	range	mean	n	range	mean	n	range	mean
<i>A. blax</i>	4	170–373	231	4	140–304	188	3	27.2–35.3	30.8
<i>A. bonaparti</i>	6	152–300	216	6	129–264	190	4	8.0–15.2	11.3
<i>D. conirostris</i>	5	150–224	197	4	139–195	173	3	31.4–44.7	37.5
<i>S. aequilabiatus</i>	16	160–390	228	16	134–335	189	12	11.0–29.0	17.8
<i>S. arenatus</i>	6	195–455	329	6	153–380	261	4	10.9–23.1	17.1
<i>S. astrabes</i>	22	81–177	121	22	64–148	102	16	23.4–43.2	34.0
<i>S. branco</i>	13	171–353	265	13	141–309	231	13	24.4–41.3	32.9
<i>S. macrurus</i>	76	140–455	265	66	114–405	224	47	10.6–28.7	18.5
<i>S. obtusirostris</i>	16	167–520	291	16	120–465	252	10	9.0–25.1	15.7
<i>S.sp. 'cau'</i>	2	200–230	215	2	171–202	187	2	14.3–33.5	23.9
<i>S. xingu</i>	5	162–446	283	5	134–371	236	3	13.3–27.2	21.0
Total	171			160			117		

Species	BD %			BW %			HL %		
	n	range	mean	n	range	mean	n	range	mean
<i>A. blax</i>	4	10.3–12.2	11.2	4	5.0–7.3	6.3	4	14.5–16.7	15.5
<i>A. bonaparti</i>	6	10.1–12.3	10.9	6	4.4–5.4	5.0	6	12.6–14.7	13.9
<i>D. conirostris</i>	4	9.8–11.9	10.8	4	4.2–5.4	4.9	4	11.6–12.3	11.9
<i>S. aequilabiatus</i>	16	10.5–13.8	12.1	16	5.3–6.3	5.9	16	13.4–16.1	15.1
<i>S. arenatus</i>	2	12.4–13.3	12.9	2	5.8–5.9	5.9	6	13.2–16.8	14.6
<i>S. astrabes</i>	22	10.4–12.4	11.5	22	4.6–6.6	5.5	22	11.7–14.7	13.3
<i>S. branco</i>	13	8.3–10.9	9.3	13	4.2–6.4	4.5	13	11.4–14.3	12.6
<i>S. macrurus</i>	66	10.3–15.2	12.8	66	4.8–8.3	6.1	66	12.5–16.8	14.3
<i>S. obtusirostris</i>	16	9.5–12.2	10.6	16	3.9–6.0	4.7	16	10.4–12.7	11.7
<i>S.sp. 'cau'</i>	2	9.4–9.8	9.6	2	4.4–4.8	4.6	2	10.3–11.3	10.8
<i>S. xingu</i>	5	13.4–16.1	14.4	5	6.2–8.2	6.8	5	16.2–19.6	17.2
Total	156			156			160		

Species	HL			PO %			PR %		
	n	range	mean	n	range	mean	n	range	mean
<i>A. blax</i>	4	26.6–62.2	36.4	4	39.4–42.1	40.6	4	44.9–48.2	47.0
<i>A. bonaparti</i>	6	22.3–42.3	29.9	6	54.9–60.5	57.9	6	36.3–39.5	37.9
<i>D. conirostris</i>	4	17.4–26.5	23.2	4	56.8–58.6	57.3	4	32.8–36.2	33.7
<i>S. aequilabiatus</i>	16	23.5–55.8	34.2	16	55.9–60.0	58.7	16	30.6–36.0	33.1
<i>S. arenatus</i>	6	32.7–62.2	47.5	6	56.3–59.1	57.6	6	32.7–37.5	35.2
<i>S. astrabes</i>	22	11.2–23.4	16.0	22	48.2–59.5	54.2	22	28.9–35.5	32.7
<i>S. branco</i>	13	24.4–41.3	32.9	13	50.8–54.9	53.0	13	36.1–40.6	38.4
<i>S. macrurus</i>	66	18.2–63.0	37.8	66	51.6–60.8	56.5	66	30.8–39.3	36.1
<i>S. obtusirostris</i>	16	20.1–54.2	33.6	16	53.4–61.2	57.3	16	31.0–35.9	34.0
<i>S.sp. 'cau'</i>	2	22.5–23.8	23.2	2	52.9–53.8	53.3	2	35.1–35.3	35.2
<i>S. xingu</i>	5	26.3–75.6	49.3	5	54.7–59.3	56.7	5	31.9–33.9	33.0
Total	160			160			160		

Table 3 Morphometrics for 10 sternopygid and one apteronotid species. Abbreviations are referenced in Materials and methods. All measurements expressed as a per cent of head length, except HL%, BD %, BW % and CA %, which are reported as a per cent of LEA.

Body proportions

5. Body depth. 0: slender, mean BD 9–11% LEA. 1: deep, mean BD 12–15% LEA.
6. Head length. 0: short, mean HL 10–13% LEA. 1: long, mean HL 14–15% LEA. 2: very long, mean 16–17% LEA.

7. Head depth. 0: deep, mean HD 76–78% HL. 1: moderate, mean HD 69–75% HL. 2: slender, mean 60–67% HL.
8. Head width. 0: narrow, mean HW 37–41% HL. 1: wide, mean HW 42–47% HL.
9. Preorbital length. 0: snout long, mean PR 36–47% HL. 1: snout short, mean PR 30–35% HL.

Species	ED %			IO %			NN %		
	n	range	mean	n	range	mean	n	range	mean
<i>A. blax</i>	4	13.9–16.8	15.6	4	15.3–18.5	16.7	4	8.6–11.3	10.2
<i>A. bonaparti</i>	6	6.6–10.8	8.0	6	15.1–18.7	17.3	6	11.9–14.7	13.0
<i>D. conirostris</i>	4	9.1–12.1	10.2	4	21.1–23.8	22.1	4	3.4–4.0	3.7
<i>S. aequilabiatus</i>	16	6.8–9.8	8.6	16	14.4–21.7	17.5	16	10.2–14.4	12.2
<i>S. arenatus</i>	2	7.4–9.8	8.6	2	22.4–33.0	27.7	2	22.0–22.9	22.5
<i>S. astrabes</i>	22	13.8–19.5	15.5	22	23.8–30.4	26.1	17	14.5–19.8	17.3
<i>S. branco</i>	13	9.8–13.5	10.7	13	22.2–25.7	24.2	13	14.9–17.4	16.0
<i>S. macrurus</i>	66	7.5–14.6	10.3	66	17.6–31.7	25.5	66	8.3–17.9	13.9
<i>S. obtusirostris</i>	16	10.1–13.5	11.9	16	22.7–28.3	24.9	16	13.5–20.0	16.9
<i>S. sp. 'cau'</i>	2	12.0–12.2	12.1	2	24.8–24.9	24.8	2	14.3–18.7	16.5
<i>S. xingu</i>	5	6.7–12.2	9.4	5	16.7–22.4	19.2	5	11.4–15.6	13.3
Total	156			156			151		

Species	MW %			BO %			HD %		
	n	range	mean	n	range	mean	n	range	mean
<i>A. blax</i>	4	8.6–12.4	10.8	4	17.1–30.9	22.5	4	56.3–62.0	59.8
<i>A. bonaparti</i>	6	13.1–21.3	16.5	6	19.7–24.0	21.7	6	73.1–79.4	75.5
<i>D. conirostris</i>	4	14.7–17.2	16.5	4	22.4–37.7	30.4	4	74.3–83.1	78.0
<i>S. aequilabiatus</i>	16	11.1–16.8	13.2	16	20.0–27.8	23.8	16	59.5–67.7	62.0
<i>S. arenatus</i>	2	11.0–13.8	12.4	2	15.7–16.5	16.1	2	68.8–73.4	71.1
<i>S. astrabes</i>	22	12.8–20.9	15.5	22	28.9–48.0	37.1	22	66.4–77.4	72.3
<i>S. branco</i>	13	12.3–13.9	12.9	13	25.9–31.1	28.2	13	57.8–68.4	64.7
<i>S. macrurus</i>	66	13.4–21.4	16.8	66	25.4–50.0	31.3	66	64.8–80.2	71.3
<i>S. obtusirostris</i>	16	14.4–17.6	15.8	16	25.4–45.3	36.9	16	68.6–79.5	73.8
<i>S. sp. 'cau'</i>	2	13.3–13.9	13.6	2	28.0–36.6	32.3	2	68.4–70.2	69.3
<i>S. xingu</i>	5	17.1–19.8	18.5	5	35.2–51.4	42.1	5	65.3–75.7	69.1
Total	156			156			156		

Species	HW %			PA %			P ₁ %		
	n	range	mean	n	range	mean	n	range	mean
<i>A. blax</i>	4	37.8–44.7	40.1	4	37.2–57.9	51.4	4	66.7–79.9	71.7
<i>A. bonaparti</i>	6	34.4–39.5	37.3	6	9.6–33.6	22.7	6	91.9–107.4	100.7
<i>D. conirostris</i>	4	42.7–45.4	43.9	4	29.3–59.8	48.4	4	78.9–87.7	83.1
<i>S. aequilabiatus</i>	16	35.9–44.6	38.8	16	40.1–56.3	47.0	16	43.7–53.3	48.8
<i>S. arenatus</i>	2	42.8–47.1	44.9	2	61.6–67.0	64.3	6	40.0–56.0	45.0
<i>S. astrabes</i>	22	37.5–51.9	46.4	22	14.3–52.6	39.4	22	43.6–67.8	58.0
<i>S. branco</i>	13	36.1–43.4	39.8	13	30.3–38.2	33.8	13	50.0–57.2	53.2
<i>S. macrurus</i>	66	33.5–59.4	46.7	66	32.7–65.1	47.6	64	37.8–64.7	48.6
<i>S. obtusirostris</i>	16	36.7–50.7	42.9	16	29.0–50.9	37.1	16	45.8–60.5	52.3
<i>S. sp. 'cau'</i>	2	44.9–45.0	44.9	2	36.9–41.2	39.0	2	52.4–57.1	54.8
<i>S. xingu</i>	5	38.8–47.3	43.4	5	32.7–42.4	36.6	5	36.8–43.0	39.7
Total	156			156			158		

Table 3 Continued.

10. Snout profile dorsal margin. 0: straight or slightly convex (Fig. 2a–e, 4). 1: strongly concave (Fig. 2f–i).
11. Interorbital distance. 0: narrow, mean IO 17–24% HL. 1: wide, mean IO 25–28% HL.
12. Internarial distance. 0: short, mean NN 4–13% HL. 1: moderate, mean NN 14–18% HL. 2: long, mean 18–23% HL.
13. Mouth width. 0: narrow; mean MW 11–14% HL. 1: broad; mean MW 16–19% HL.
14. Gape. 0: larger or equal to eye diameter. 1: smaller than eye.
15. Eye diameter. 0: small, mean ED 8–11% HL. 1: large, mean ED 12–16% HL.
16. Orbital margin. 0: covered by epidermis (Fig. 2i). 1: free (Fig. 2a–h).

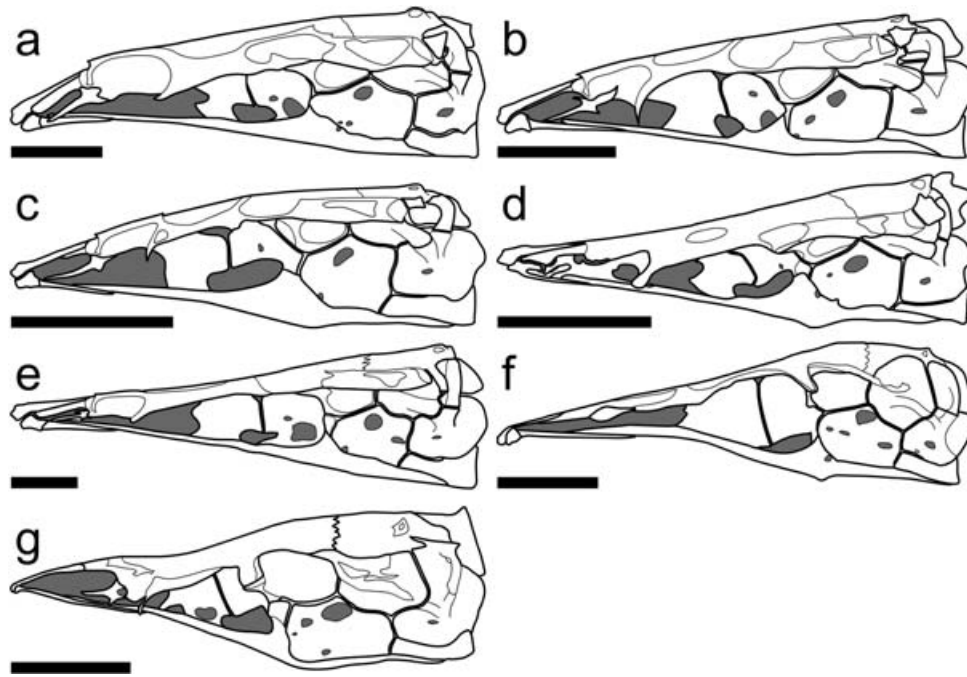


Figure 9 Neurocrania of seven sternopygids, in lateral view. Shading as in Figure 8. (a) *S. branco* (MCP 32245), (b) *S. obtusirostris* (MCP T-032), (c) *S. astrabes* (MCP 32235), (d) *S. xingu* (USNM 218830; adapted from Albert & Fink, 1996; Fig. 4.), (e) *S. aequilabiatus* (NRM 27746), (f) *A. blax* (INPA 18451), (g) *D. conirostris* (WGRC 21.020999). Scale bars equal 5 mm.

Species	n	NL		ND %		BaL %	
		range	mean	range	mean	range	mean
<i>A. blax</i>	4	16.2–16.5	16.3	25.8–29.2	27.6	12.7–18.4	16.3
<i>D. conirostris</i>	3	16.5–16.6	16.6	27.6–29.9	28.6	19.4–23.8	21.6
<i>S. aequilabiatus</i>	12	16.0–16.8	16.5	29.9–35.1	32.8	12.7–18.9	15.6
<i>S. arenatus</i>	4	16.1–16.6	16.4	31.6–38.0	35.5	10.8–22.8	17.9
<i>S. astrabes</i>	13	16.0–16.8	16.6	33.5–39.1	35.7	16.3–23.6	19.5
<i>S. branco</i>	9	16.2–16.6	16.4	31.7–34.1	33.0	14.2–18.7	16.2
<i>S. macrurus</i>	11	16.3–16.9	16.5	32.4–38.3	36.4	13.9–18.2	15.8
<i>S. obtusirostris</i>	10	16.0–16.8	16.4	35.5–39.1	37.2	16.2–24.0	19.1
<i>S. sp. 'cau'</i>	2	16.3–16.7	16.5	36.0–36.2	36.1	18.4–19.9	19.1
<i>S. xingu</i>	3	16.3–16.6	16.5	28.9–34.2	31.9	16.3–18.7	17.2
Total	71						

Table 4 Neurocranium measurements for 10 sternopygid species. Abbreviations are referenced in Materials and methods. Neurocranium depth and basioccipital length are expressed as a per cent of neurocranium length.

17. Infraorbitals 3–4. 0: tube shaped. 1: enlarged, bony.
 18. Infraorbital canals. 0: small and tubular. 1: large, open cylinders.
 19. Branchial opening. 0: wide, mean BO 31–40% HL.
 1: narrow, mean BO 16–30% HL.

Neurocranium

20. Ethmoid region. 0: well ossified (Fig. 8, 9a–e, 9g). 1: less ossified (Fig. 9f).
 21. Ventral ethmoid. 0: short (Fig. 9f, g). 1: long (Fig. 8, 9a–e).
 22. Mesethmoid. 0: gracile in lateral aspect (Fig. 9f, g). 1: robust (Fig. 8, 9a–e).
 23. Lateral ethmoid cartilage. 0: remote from maxilla. 1: contacting maxilla.
 24. Lateral ethmoid ossification. 0: independent ossification (Fig. 8, 9a–e). 1: co-ossified with frontal (Fig. 9f, g).
 25. Lateral ethmoid anterior process. 0: short, not extending to dorsal margin of vomer (Fig. 9f). 1: long, extending laterally to dorsal margin of vomer (Fig. 8, 9a–e, 9g).
 26. Vomer. 0: short, broad, length less than five times width at midlength. 1: long, narrow, length more than five times width.
 27. Antorbital process of frontal. 0: absent. 1: present (Fig. 8, 9a–g).

Species	PCV		PJR		AFR		LLS		SAL		SBL		SOP	
	n	range	n	range	n	range	n	range	n	range	n	range	n	range
<i>A. blax</i>	6	14–15	8	17–19	3	175–210	4	116–156	4	10–15	4	5–9	4	8–15
<i>A. bonapartii</i>	NA	NA–NA	6	16–18	NA	NA–NA	NA	NA–NA	5	6–7	5	12–14	5	4–6
<i>D. conirostris</i>	5	14–14	5	16–18	NA	NA–NA	NA	NA–NA	5	11–17	5	20–22	5	9–12
<i>S. aequilabiatus</i>	16	23–25	20	14–17	16	228–310	18	200–305	18	12–24	18	7–13	18	10–16
<i>S. arenatus</i>	6	21–24	9	15–17	1	215–215	5	179–245	6	15–16	6	7–9	6	15–16
<i>S. astrabes</i>	29	18–19	23	15–17	19	170–298	17	185–235	19	11–18	19	9–14	19	10–16
<i>S. branco</i>	12	25–27	13	12–15	12	250–340	10	280–340	10	17–26	10	13–17	10	13–20
<i>S. macrurus</i>	52	24–28	26	15–17	15	195–300	256	115–340	222	12–22	16	5–20	9	5–20
<i>S. obtusirostris</i>	14	22–26	25	20–15–17	15	195–312	285	190–280	240	15–21	18	7–13	11	18
<i>S. sp. 'cau'</i>	2	24–24	24	2	15–15	292	285–316	301	17–19	18	2	10–10	10	2
<i>S. xingu</i>	4	28–29	29	6	12–15	12	155–205	192	14–16	15	3	6–8	7	3
Total	146		207		115		122		145		145		145	

Table 5 Meristics for 10 sternopygid and one apteronotid species. Abbreviations are referenced in Materials and methods.

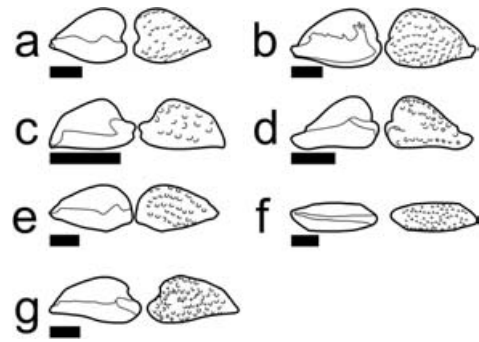


Figure 10 Dorsal (left) and ventral (right) views of the premaxilla for seven *Sternopygus* species. (a) *S. branco* (MCP 32243), (b) *S. obtusirostris* (MCP 32262), (c) *S. astrabes* (MCP 32235), (d) *S. macrurus* (MCP 32256), (e) *S. arenatus* (MCZ 58604), (f) *S. xingu* (UMMZ 228961), (g) *S. aequilabiatus* (NRM 27746). Scale bars equal 1 mm.

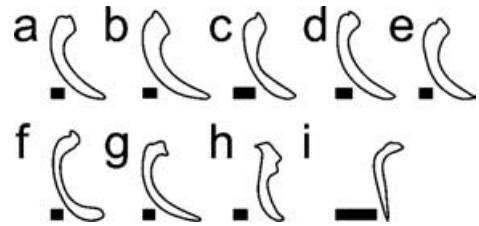


Figure 11 Maxilla for nine sternopygids, in lateral view. (a) *S. branco* (MCP 32243), (b) *S. obtusirostris* (MCP 32262), (c) *S. astrabes* (MCP 32235), (d) *S. macrurus* (MCP 32256), (e) *S. arenatus* (MCZ 58604), (f) *S. xingu* (UMMZ 228961), (g) *S. aequilabiatus* (NRM 27746), (h) *A. blax* (INPA 18451), (i) *D. conirostris* (WGRC 27.020299). Scale bars equal 1 mm.

28. Frontal margin. 0: convex dorsal to lateral ethmoid (Fig. 8, 9a–c). 1: straight dorsal to lateral ethmoid (Fig. 9d–g).
29. Sphenotic spine. 0: absent (Fig. 8, 9a–e). 1: present (Fig. 9f, g).
30. Neurocranium depth. 0: deep, mean ND 35–50% NL. 1: moderate, mean ND 30–35% NL. 2: slender, mean ND 25–30% NL.
31. Parasphenoid shape anterior portion. 0: ventral margin straight in adults. 1: ventral margin convexity retained in adults.
32. Parasphenoid width at prootic foramen. 0: narrower than PaS at PtS–OrS junction. 1: as wide or broader than PaS at PtS–OrS junction.
33. Basioccipital length. 0: Short, mean BaL 15–18% NL. 1: Long, mean BaL 18.1–22% HL.

Oral jaws

34. Premaxillary teeth. 0: conical, arranged in 1–2 regular rows. 1: villiform, arranged in multiple irregular rows (Fig. 10a–g).
35. Premaxilla shape. 0: robust, rectangular in dorsal view (Fig. 10f). 1: gracile, triangular in dorsal view (Fig. 10a–e, g).
36. Maxilla width. 0: midlength as wide as broadest area near palatine articulation (Fig. 11a–e, h). 1: midlength

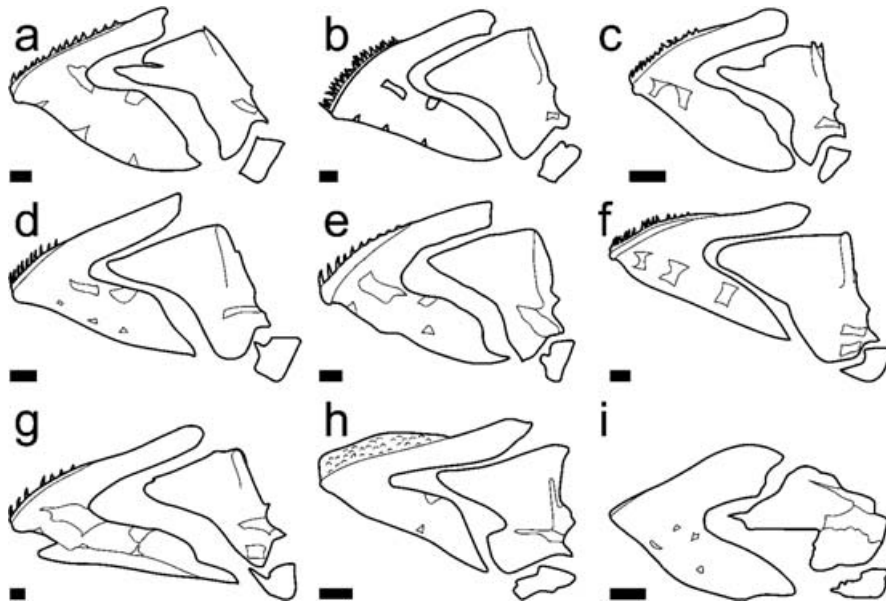


Figure 12 Dentary, anguloarticular, and retroarticular for nine sternopygids, in lateral view. (a) *S. branco* (MCP 32243), (b) *S. obtusirostris* (MCP 32262), (c) *S. astrabes* (MCP 32235), (d) *S. macrurus* (MCP 32256), (e) *S. arenatus* (MCZ 58604), (f) *S. xingu* (UMMZ 228961), (g) *S. aequilabiatus* (NRM 27746), (h) *A. blax* (INPA 18451), (i) *D. conirostris* (WGRC 27.020299). Scale bars equal 1 mm.

half width of area near palatine articulation (Fig. 11f, g, i).

37. Meckel's cartilage ossification. 0: cartilaginous in adults. 1: dorsal margin ossified completely in adults.
38. Dentary teeth. 0: present (Fig. 12a–h). 1: absent (Fig. 12i).
39. Retroarticular anterior process. 0: absent (Fig. 12a–c). 1: present (Fig. 12d–i).
40. Anguloarticular ascending process. 0: elongate, extends to or beyond dorsal margin of anguloarticular (Fig. 12a–g). 1: truncate, does not extend beyond dorsal margin of anguloarticular (Fig. 12h, i).

Suspensorium

41. Mesopterygoid process. 0: thin, not contacting neurocranium (Fig. 13i). 1: robust strut; contacting neurocranium (Fig. 13a–h).
42. Mesopterygoid dentition. 0: absent. 1: present.
43. Hyomandibular trigeminal nerve. 0: preopercular-mandibular ramus of trigeminal nerve emerging from descending limb of hyomandibula (Fig. 14h, i). 1: preopercular-mandibular ramus emerging from anterior shelf of hyomandibula (Fig. 14a–g).
44. Hyomandibular lateral ridge. 0: long, extending close to ventral margin of hyomandibula (Fig. 14a, b, d–i). 1: short, remote from ventral margin of hyomandibula (Fig. 14c).
45. Opercle posterior margin. 0: convex, evenly rounded (Fig. 15d, e, h, i). 1: straight, incompletely ossified (Fig. 15a–c, f, g).
46. Opercle, dorsal margin. 0: long, 76–90% distance of antero-ventral margin (Fig. 15e–i). 1: moderate, 70–75% distance of antero-ventral margin (Fig. 15a, d). 2: short, 67–79% distance of antero-ventral margin (Fig. 15b, c).

47. Interopercle ventral margin. 0: entire (Fig. 15a–c, e–i). 1: convex (15d).

48. Gill rakers. 0: simple, attached to gill arches. 1: complex (see text), separated by unmineralized tissue.

Pectoral girdle

49. Scapula foramen. 0: scapula small, foramen as notch in coracoid (Fig. 16a–g). 1: scapula large, with large foramen included (Fig. 16h, i).
50. Supracleithrum. 0: long and slender (Fig. 16b–h). 1: short and robust (Fig. 16a, i).
51. Posttemporal. 0: fused with supracleithrum (Fig. 16h, i). 1: not fused with supracleithrum (Fig. 16a–g).
52. Posttemporal length. 0: short, less than 50% length dorso-posterior margin of cleithrum (Fig. 16a–f, h, i). 1: long, greater than 75% length dorso-posterior margin of cleithrum (Fig. 16g).
53. Posttemporal and supracleithral canal bones. 0: small, canal and non-canal portions equal width (Fig. 16a, c–g). 1: expanded, canal portions wider than non-canal (Fig. 16b, h, i).
54. Pectoral distal radials. 0: 1–4 independent (Fig. 16a–c). 1: 3 + 4 fused (Fig. 16d–i).
55. Pectoral fin. 0: long, mean P1 61–101% HL. 1: short, mean P1 51–60% HL. 2: very short, mean P1 40–50% HL.
56. Pectoral fin rays. 0: many, mode 17–19. 1: few, mode 13–16.

Axial skeleton

57. Intermuscular bones. 0: slightly branched. 1: highly branched.
58. Dorsal myorhabdoid bones. 0: loosely packed and lightly ossified. 1: densely packed and heavily ossified.

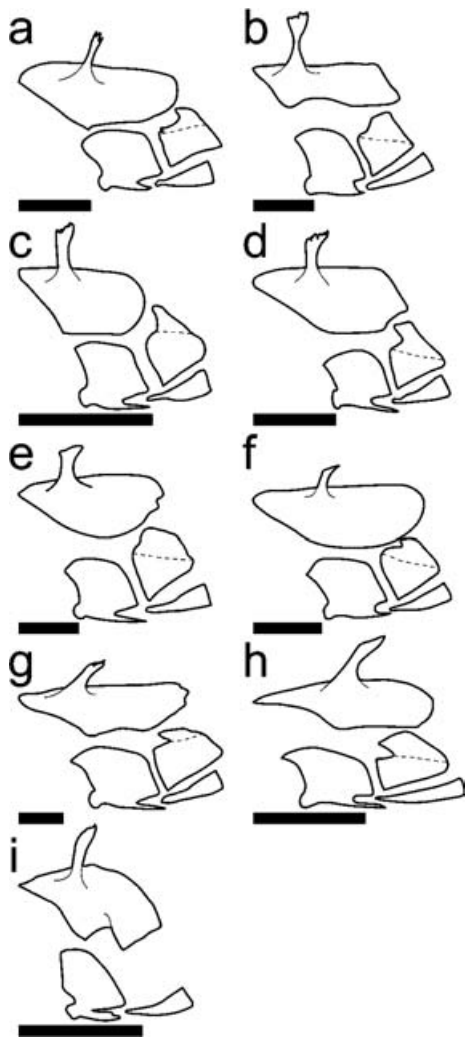


Figure 13 Quadrate, mesopterygoid, and metapterygoid for nine sternopygids, in lateral view. (a) *S. branco* (MCP 32243), (b) *S. obtusirostris* (MCP 32262), (c) *S. astrabes* (MCP 32235), (d) *S. macrurus* (MCP 32256), (e) *S. arenatus* (MCZ 58604), (f) *S. xingu* (UMMZ 228961), (g) *S. aequilabius* (NRM 27746), (h) *A. blax* (INPA 18451), (i) *D. conirostris* (WGRC 27.020299). Scale bars equal 5 mm.

59. Rib length. 0: 70–75% depth of body cavity. 1: 80–100% depth of body cavity.
 60. Rib count. 0: mode 13–20. 1: mode 8–12. 2: mode 6–7.
 61. Postcleithrae. 0: three. 1: one or two. 2: zero.
 62. Body cavity. 0: moderately long, mode PCV 18–19. 1: long, mode PCV 21–29. 2: short, mode PCV 11–15.
 63. Anterior vertebrae. 0: compressed. 1: not compressed (see text).
 64. Anal-fin rays. 0: few, median AFR 200–240. 1: many, median AFR 250–320.
 65. Anal-fin ray structure. 0: all or most rays branched about half way from base to tip. 1: all rays entirely unbranched from base to tip.
 66. Caudal rod. 0: regenerates as unossified cartilage. 1: regenerates as ossified bar.

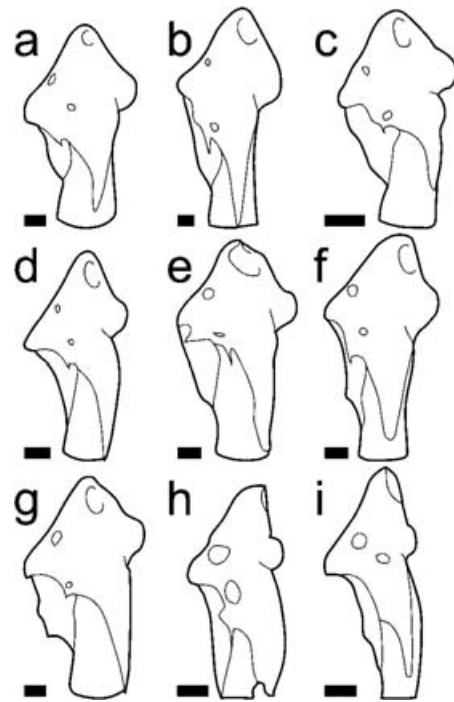


Figure 14 Hyomandibula for nine sternopygids, in lateral view. (a) *S. branco* (MCP 32243), (b) *S. obtusirostris* (MCP 32262), (c) *S. astrabes* (MCP 32235), (d) *S. macrurus* (MCP 32256), (e) *S. arenatus* (MCZ 58604), (f) *S. xingu* (UMMZ 228961), (g) *S. aequilabius* (NRM 27746), (h) *A. blax* (INPA 18451), (i) *D. conirostris* (WGRC 27.020299). Scale bars equal 1 mm.

Interrelationships of *Sternopygus*

Interrelationships of *Sternopygus* inferred in this study are depicted in Fig. 17, with Branch Lengths (BL) and Bremer Decay Indices (BDI) for all nodes provided in Table 7. Diagnoses for seven clades are provided in Appendix 2.

Sternopygus is diagnosed in having: gape larger and sometimes equal to eye diameter (char. 14); enlarged bony infraorbitals 3–4 (char. 17); robust mesethmoid (char. 22); long ventral ethmoid (char. 21); lateral ethmoid cartilage contacting maxilla (char. 23); anterior process of lateral ethmoid long, extending laterally to and sometimes beyond the dorsal margin of the vomer (char. 25); neurocranium depth moderate, mean 30.1–34.9% NL (char. 30); triangular premaxilla (char. 35); dorsal margin of Meckel's cartilage completely ossified to anguloarticular (char. 37); robust mesopterygoid process contacting the neurocranium (char. 41); preopercular-mandibular ramus of trigeminal nerve emerging anterior to the hyomandibular shelf (char. 43); length of opercle dorsal margin moderate, as measured point-to-point, 70–75% distance of antero-ventral margin (char. 46); gill rakers separated from gill arches by unmineralized tissue, not attached to ceratobranchials and epibranchials of all four branchial arches, hypobranchials of first and second arches, and the pharyngobranchials of fourth arch (char. 48). Each raker formed from three separate ossifications, two large elongate lateral ossifications, and a smaller (ovoid) central ossification; posttemporal and supracleithrum not fused (char. 51); pectoral fin length short, mean 51–60%

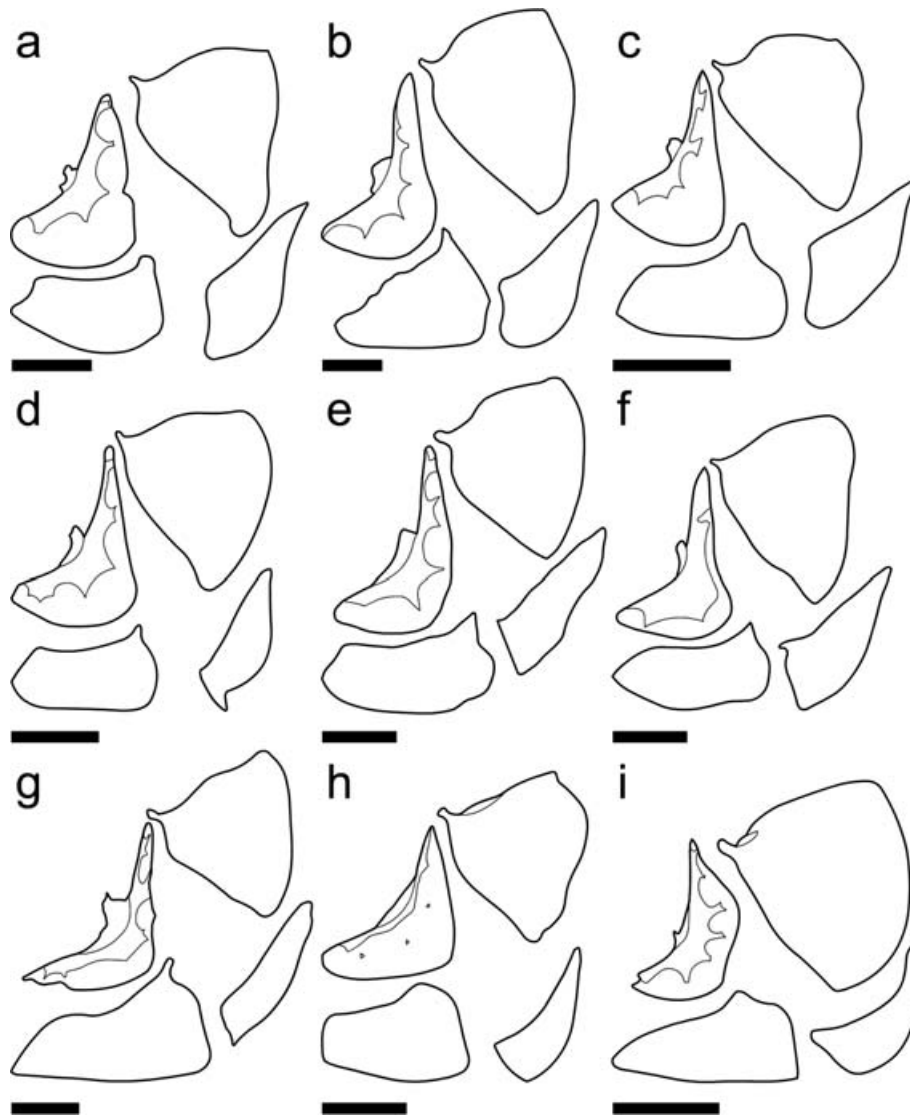


Figure 15 Opercular series for nine sternopygids, in lateral view. (a) *S. branco* (MCP 32243), (b) *S. obtusirostris* (MCP 32262), (c) *S. astrabes* (MCP 32235), (d) *S. macrurus* (MCP 32256), (e) *S. arenatus* (MCZ 58604), (f) *S. xingu* (UMMZ 228961), (g) *S. aequilabiatus* (NRM 27746), (h) *A. blax* (INPA 18451), (i) *D. conirostris* (WGRC 27.020299). Scale bars equal 5 mm.

HL (char. 55); few pectoral fin rays, mode 13–16 (char. 56); anterior vertebrae not compressed (char. 63); anal-fin rays unbranched from base to tip (char. 65) (Clade A: Appendix 2; Fig. 17).

Sternopygus branco, sister taxon to all other species of *Sternopygus* (Appendix 2; Fig. 17), is distinct in having: a uniformly pale body with no dark saddles or pale lateral stripe (char. 1); a slender head, mean HD 60–67% HL (char. 7); a short and robust supracleithrum (char. 50).

Sternopygus sp. ‘cau’ is sister taxon to clade containing *S. astrabes* and *S. obtusirostris* (Appendix 2; Fig. 17) and an undescribed species identified by the presence of a well defined dark humeral spot with sharp margins (char. 4). *Sternopygus* sp. ‘cau’ shares with *S. astrabes* and *S. obtusirostris* the presence of dark saddles as juveniles (char. 3), and a large eye, mean ED 12–16% HL (char. 15).

Sternopygus obtusirostris and *S. astrabes* are sister taxa (Clade D: Appendix 2; Fig. 17) sharing the following charac-

ters: short head, mean HL 10–13% LEA (char. 6); moderate head depth, mean HD 69–75% HL (char. 7); internarial distance long, mean NN 19–23% HL (char. 12); broad mouth, mean MW 16–19% HL (Char. 13); short pectoral fin, mean P1 51–60% HL (char. 55). *Sternopygus obtusirostris* is distinguished from *S. astrabes* by not having a pale lateral stripe as a juvenile (char. 2). *Sternopygus astrabes* is distinguished from other species of *Sternopygus* in having a moderately long body cavity, mode PCV 18–19 (char. 62); short hyomandibular lateral ridge not descending to ventral margin of hyomandibula (char. 44); many anal-fin rays, median AFR 250–320 (char. 64).

Sternopygus macrurus is the sister taxon to the clade containing the remaining species of *Sternopygus* (Appendix 2; Fig. 17) sharing with them the following characters: deep body, mean BD 12–15% LEA (char. 5); long head, mean HL 14–15% LEA (char. 6); pectoral distal radials 3 and 4 fused (char. 54); very short pectoral fin, mean P1 40–50% HL (char.

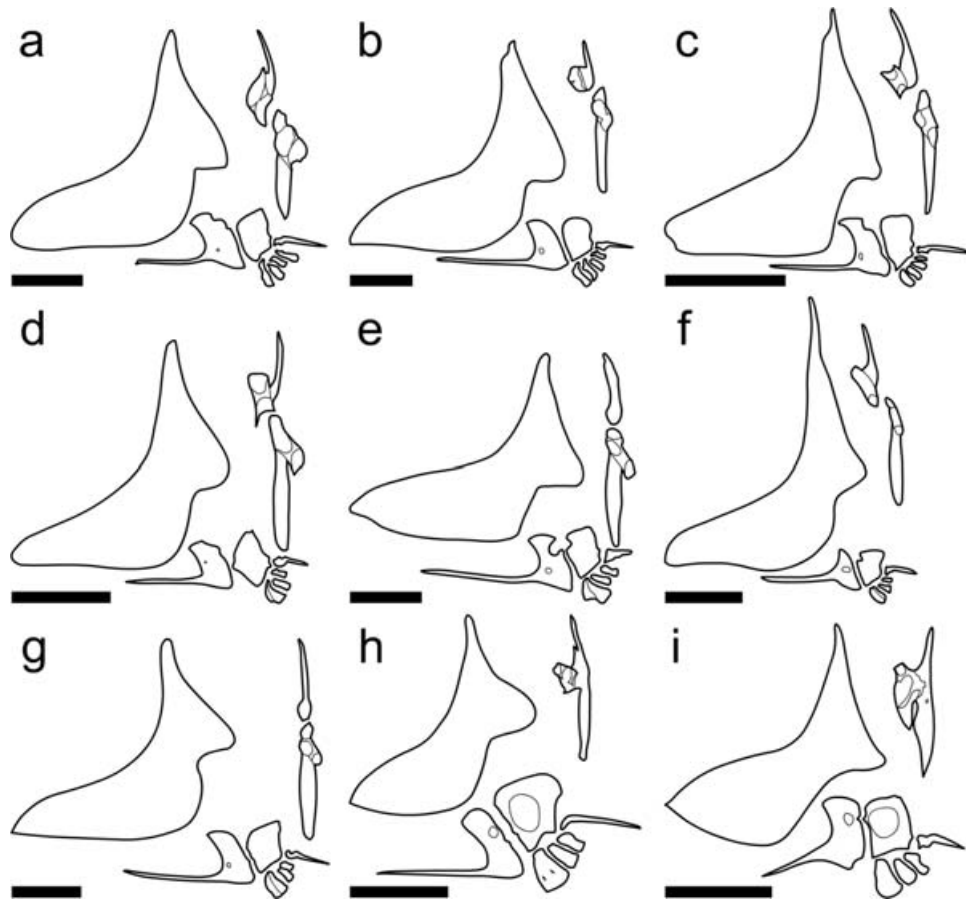


Figure 16 Pectoral girdle for nine sternopygids, in lateral view. (a) *S. branco* (MCP 32243), (b) *S. obtusirostris* (MCP 32262), (c) *S. astrabes* (MCP 32235), (d) *S. macrurus* (MCP 32256), (e) *S. arenatus* (MCZ 58604), (f) *S. xingu* (UMMZ 228961), (g) *S. aequilabiatius* (NRM 27746), (h) *A. blax* (INPA 18451), (i) *D. conirostris* (WGRC 27.020299). Scale bars equal 5 mm.

	1–10	11–20	21–30	31–40	41–50	51–60	61–66
<i>Parapteronotus hasemani</i>	0000000000	0101000010	0000000002	00100000?0	0000000000	0000000000	000100
<i>Archolaemus blax</i>	0000012000	0111110110	0001011112	1001000001	1100000010	0010001011	120001
<i>Distocyclus conirostris</i>	1000000111	0001000111	0000101112	0011010101	1000000011	0011001012	120101
<i>Eigenmannia virescens</i>	0000?00110	???1000111	0000001010	0011000000	01?0010010	0011??1012	120001
<i>Rhabdolichops electrogrammus</i>	0000000110	???1001111	0000001010	0011000001	1110110010	0001?11112	120101
<i>Sternopygus branco</i>	1000002000	0100011110	1110101001	0001101010	1110110101	1010110000	211111
<i>Sternopygus</i> sp. 'cau'	0211001110	110011??0?	??????0?0	??1???????	???????????	????11??00	?11111
<i>Sternopygus obtusirostris</i>	0010001110	1210111100	1110101000	1011101010	1110120100	1000110000	211111
<i>Sternopygus astrabes</i>	0210001110	1210111100	1110101000	1011101010	1111120100	1000110000	201011
<i>Sternopygus macrurus</i>	0201111100	1110011100	1110101000	0001101000	1110011100	1001210000	211111
<i>Sternopygus arenatus</i>	0200111110	1200011110	1110111100	0001101000	1110000100	1001210000	211011
<i>Sternopygus xingu</i>	0201121111	0110011100	1111111101	0101011000	1110100100	1001210000	211111
<i>Sternopygus aequilabiatius</i>	0200112011	0100011110	1110111101	0101111000	1110100100	1101210000	211111

Eigenmannia virescens also coded from *Eigenmannia* sp., MBUCV 7509 (Mago-Leccia, 1978, Figs 10–18).

Parapteronotus hasemani coded from mature females and non-mature males. *Parapteronotus hasemani*: head length (HL%), *A. bonaparti* = 0; head width (HW%) juveniles and adults = 0; also *A. bonaparti* juveniles and adults; gape juveniles and adults = 0; also *A. bonaparti* juveniles and adults; vomer with no ascending process; basioccipital length (BaL) juveniles = 0; also *A. bonaparti* juveniles and adults. *Rhabdolichops electrogrammus*: head length (HL%), *R. sp. 'nig'* = 0; opercle ratio of long axes, *R. sp. 'nig'*. *Sternopygus macrurus* also coded from MBUCV 7515 (Mago-Leccia, 1978, Figs 24–28). *Sternopygus xingu*, hyomandibular lateral ridge UMMZ 228961, c. 250 mm.

Table 6 Matrix of 66 characters coded for seven *Sternopygus* species, and five outgroup taxa including four sternopygids and one apteronotid. Missing data indicated by '?'. Character descriptions are referenced in Descriptive morphology.

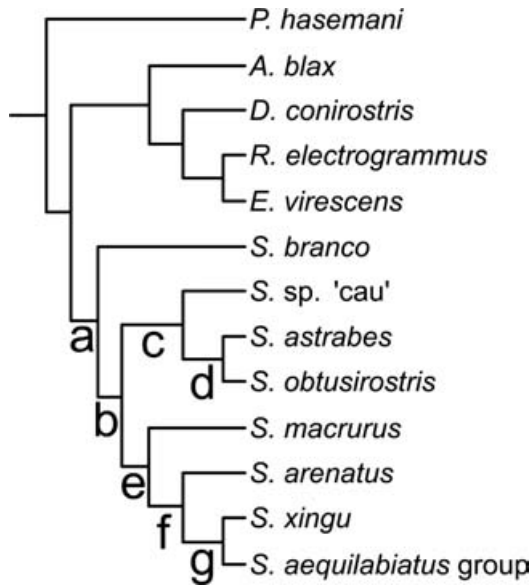


Figure 17 Interrelationships of *Sternopygus* species inferred from maximum parsimony analysis of 66 characters coded from features or pigmentation, body proportions, meristics and osteology. Terminal taxa include eight species of *Sternopygus*, four other sternopygid species and one apteronotid species. The topology is a single most parsimonious tree, with 127 steps, from data in Table 2 (CI = 0.58, RI = 0.70, RC = 0.41). Letters adjacent to nodes represent clades listed in Appendix 2.

Clade	Name	BL	BDI
A	<i>Sternopygus</i>	17	15
B	unnamed clade	4	2
C	unnamed clade	2	2
D	<i>S. obtusirostris</i> group	2	2
E	unnamed clade	4	3
F	unnamed clade	3	2
G	<i>S. aequilabiatu</i> group	5	4

Table 7 Clade names and support indices for *Sternopygus* species. Clade names from Fig. 17. The topology is a single most parsimonious tree, with 127 steps, from data in Table 2 (CI = 0.58, RI = 0.70, RC = 0.41). Steps calculated for polytomies assuming hard-polytomy option. BL, Branch length; BDI, Bremer Decay Index.

55). *Sternopygus macrurus* is distinguished in having: a well-defined dark humeral spot with sharp margins (char. 4); broad mouth, MW 16–19% HL (char. 13); ventral margin of interopercle convex (char. 47).

Sternopygus arenatus is the sister taxon to the clade containing *S. xingu* and the *S. aequilabiatu* species group (Appendix 2; Fig. 17), sharing with them the following characters: long narrow vomer, length more than five times width (char. 26); frontal margin straight at the point dorsal to lateral ethmoid (char. 28); dorsal margin of opercle long, 76–90% distance of antero-ventral margin (char. 46). *Sternopygus arenatus* is distinguished in having a long internarial distance, mean NN 18.1–23% HL (char. 12) and few anal-fin rays, median AFR 200–240 (char. 64).

Sternopygus xingu and the *S. aequilabiatu* species group are sister taxa (Clade G: Appendix 2; Fig. 17), sharing the following characters: dorsal margin of the snout profile strongly concave (char. 10); narrow interorbital distance, IO 17–24% HL (char. 11); moderate neurocranium depth, ND 30–35% NL (char. 30); width of parasphenoid at a vertical with the anterior margin of the prootic foramen as broad or broader than width of parasphenoid at vertical with the pterosphenoid – orbitosphenoid junction (char. 32); width of maxilla at its midlength narrow, less than or equal to half the width of the maxillary at area near palatine articulation (char. 36). *Sternopygus xingu* is distinguished in having: a well-defined dark humeral spot with sharp margins (char. 4); very long head, HL 16–17% LEA (char. 6); broad mouth, MW 16–19% HL (char. 13); lateral ethmoid co-ossified with frontal (char. 24); premaxilla rectangular and robust from dorsal view (char. 35).

The *S. aequilabiatu* species group is characterized in having: a slender head, HD 60–70% HL (char. 7); narrow head, HW 37–41% HL (char. 8); and long post-temporal, greater than 75% dorso-posterior margin of cleithrum (char. 52).

Key to the adults of *Sternopygus* species

- 1a. Dorsal margin of snout profile straight or convex 2
- 1b. Dorsal margin of snout profile strongly concave 6
- 2a. Body uniformly coloured with pigmentation; pale lateral stripe along the base of the anal fin pterygiophores; head depth (HD) 69–79% head length (HL) 3
- 2b. Body colour uniformly pale with no pigmentation or pale lateral stripe; HD 58–68% HL *S. branco*
- 3a. Eye diameter large, 12–16% HL; pectoral fin length (P1) 50–60% HL 4
- 3b. Eye diameter small, 7–15% HL; P1 40–50% HL 5
- 4a. Two to four dark vertical saddles on body of adults and juveniles; caudal appendage (CA) 23–43% length to end of anal fin (LEA); HL 12–15% LEA *S. astrabes*
- 4b. Dark vertical bands absent in adults only (LEA > 140 mm); CA 12–25% LEA; HL 10–13% LEA *S. obtusirostris*
- 5a. Distinct dark humeral spot; dorsal margin of snout profile slightly convex; branchial opening large (BO) 25–50% HL *S. macrurus*
- 5b. Dark humeral spot absent; dorsal margin of snout profile straight; BO small, 16–17% HL *S. arenatus*
- 6a. Distinct dark humeral spot; P1 37–43% HL; HL 17–20% LEA; BO 35–51% HL *S. xingu*
- 6b. Dark humeral spot absent or very diffuse; P1 44–53% HL; HL 13–16% LEA; BO 20–28% HL *S. aequilabiatu* species group

Discussion

Historical biogeography

Miocene tectonism in the northeastern Andes resulted in the formation of the modern watersheds of northwestern South

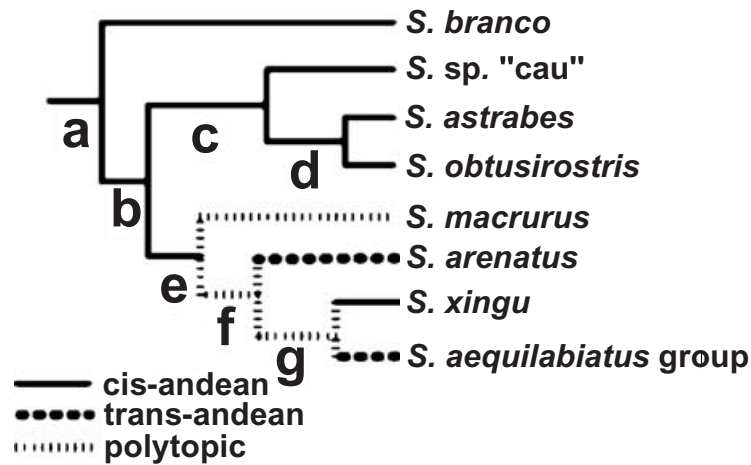


Figure 18 Historical biogeography of *Sternopygus*. ‘Polytopic’ indicates geographic distribution in both cis- and trans-Andean watersheds. This topology is consistent with a minimum divergence of Clade E before the most recent uplift of the Andean Eastern Cordillera c. 12 Ma.

America, including the Western Amazon, Orinoco, Maracaibo and Magdalena Basins (Hoorn *et al.*, 1995). Also during the Middle Miocene the Choco Block underlying the modern San Juan and Atrato Basins was accreted to the northwest corner of South America (Duque-Caro, 1990). Before the Middle Miocene most of the area of the modern Western Amazon drained northward to a delta located in the area of the modern Maracaibo Basin, and lowland Amazonian ichthyofaunas were present throughout much of northwestern South America (Lundberg, 1997; Lundberg, 1998; Lundberg *et al.*, 1998).

With the uplift of the Eastern Cordillera (c. 11.8–12.2 Ma) the Amazon-Orinoco, Maracaibo, Magdalena and Atrato-Pacific Slope regions became isolated (Hoorn *et al.*, 1995). According to a simple vicariance model this event would have separated the two (or three) cis-trans Andean sister-taxa pairs depicted in Fig. 18: *S. macrurus* (populations in the Choco and Amazon), Clade F (*S. arenatus* and Clade G) and/or Clade G (*S. xingu* and *S. aequilabiatius* group). Under this model, the origin of Clade E (Fig. 18) may therefore be inferred to predate c. 12 Ma. Such pre-Pleistocene origins of multiple *Sternopygus* taxa with cis-trans Andean distributions resemble other groups of Neotropical fishes for which species-level phylogenies have been proposed (Vari, 1988; Vari & Weitzman, 1990; Vari, 1995; Bermingham & Martin, 1998; Martin & Bermingham, 2000; Albert & Crampton, *unpubl. obs.*).

As currently recognized, *S. macrurus* is the most widely distributed gymnotiform species, and is known from all nine hydrogeographical regions of tropical South America (Table 1, Fig. 1a). These include habitats and regions as disparate as the Pacific slope of the Andes, the arid northeast of Brazil and the Pampas of Argentina. Although populations from several of these hydrogeographical regions do possess differences in the mean or modal value of morphometric and meristic features, no unambiguous diagnostic features were recovered. The conclusion that populations from throughout the continent represent a single morphospecies is based on examination of 177 lots containing 406 specimens (Appendix 1).

From comparisons with results of other studies on geographically widespread morphospecies of Neotropical fishes we expect this continental distribution will not be confirmed with other non-traditional datasets. Future work using molecular sequences, microsatellite DNA, and chromosome morphology will be used to test the hypothesis that all populations of *S. macrurus* currently recognized represent a single evolutionary lineage (Lovejoy & de Araújo, 2000).

Historical ecology

Sternopygus macrurus is the most eurytopic species of the genus, being found in most lowland aquatic habitats, including high conductivity whitewater river channels and floodplains (*várzea*) and low conductivity non-floodplain (*terra firme*) black and clearwater rivers and streams. All other *Sternopygus* species have much more restricted geographic and ecological distributions (Fig. 1b).

Sternopygus branco is unique among its congeners in being entirely restricted to whitewater rivers in the Central Amazon Basin. The capacity to inhabit large and deep (up to 25 m) Amazonian river channels is a derived feature of the Sinusoidea, a clade of gymnotiform fishes represented by two families with a high frequency wave-type EOD, Apteronotidae and Sternopygidae (Albert, 2001). Habitat utilization of Amazonian river channels is associated with a suite of behavioural, physiological and morphological traits. Many of these traits are observed in *S. branco* including reduced pigmentation and a streamlined body and head morphology (Albert, 2001). The utilization of Amazonian river channels in *S. branco* is inferred to be plesiomorphic.

In a combined morphological and molecular analysis of all gymnotiform fishes (Albert, 2001) *S. astrabes* was inferred to retain the most plesiomorphic set of character states among extant taxa, including (among other characters): small adult body size (Fig. 2, 3); relatively short body cavity with 18–19 precaudal vertebrae (Table 4); paedomorphic features of cranial osteology (Figs 6, 15, 16). Here we recognize that the

position of *S. obtusirostris* and *S. sp. 'cau'* as members of a clade including *S. astrabes*, indicate the polarity of small body size, short body cavity length, and short anal fin length is derived. Similarly, the unique restriction of *S. astrabes* among its congeners to *terra firme* streams is inferred to be derived. This fundamental change in our perception of the evolution in *Sternopygus* highlights the sensitivity of both phylogenetic systematics and character-state reconstruction to taxon sampling.

Continuous traits as phylogenetic characters

There are many approaches to abstracting aspects of morphological diversity into hypotheses of character-state change. Empirical and theoretical challenges associated with coding continuously varying traits into discrete phylogenetic characters have been discussed extensively (e.g., Hormiga *et al.*, 2000; Weins, 2000). Here we tested the sensitivity of the tree topology to the presence of morphometric characters by excluding from the analysis those characters pertaining to body proportions (8 of 66 characters), and by employing multiple coding schemes to investigate the polarity and integrity of the characters. Excluding these characters resulted in a single most parsimonious tree topology, which differed from the total evidence analysis in one regard: *S. branco* is the sister to the clade [*S. obtusirostris* + *S. sp. 'cau'* + *S. astrabes*], and is not the sister to all other congeners. This result emphasizes the importance of the observation that *S. branco* retains the plesiomorphic slender body shape of outgroup taxa.

Acknowledgements

We acknowledge the following people for access to specimens, information and ideas; B. Brown, X. Freilich, S. Schaefer (AMNH); J. Lundberg, M. Sabaj (ANSP); J. Armbruster (AUM); O. Crimmen, D. Siebert (BMNH); D. Catania, W. Eschmeyer (CAS); L. Page, R. Robins (FLMNH); B. Chernoff, M. Rogers (FMNH); L. Rapp Y Daniel (INPA); A. Machado-Allison, F. Provenzano, R. Royero (MBUCV); R. Reis (MCP); K. Hartel (MCZ); P. Backup, R. Campos-da-Paz (MNRJ); H. Britski, M. de Pinna, J. Lima De Figueiredo, O. Oyakawa, (MZUSP); E. Ahlander, S. Kullander, A. Silvergrip (NRM); W. Fink, D. Nelson (UMMZ); S. Jewett, L. Parenti, R. Vari (USNM). We appreciate additional exchanges of data and ideas with E. Bermingham, N. Lovejoy, D. Stewart and M. Triques. Special thanks to S. Wolgemuth for assisting with translation from German. We acknowledge the Neodat project (NSF/AID DEB grant 90-24797) for collection information. Aspects of this research were supported by grants to WGRC from the Fisheries Society (UK), CNPq (Brazil), and to JSA from the U.S. National Science Foundation (NSF-DEB 0215388, 0317278, 0138633).

References

ALBERT, J.S. 2001. Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). *Miscellaneous Publications Museum of Zoology, University of Michigan* **190**, 1–127.

ALBERT, J.S. 2003. Family Sternopygidae. In: *Checklist of the Freshwater Fishes of South and Central America*, REIS, R.E., KULLANDER, S.O. & FERRARIS, C.J., JR., Eds., pp. 493–497. Edipucrs, Porto Alegre.

ALBERT, J.S. & CRAMPTON, W.G.R. 2003. Seven new species of the Neotropical electric fish *Gymnotus* (Teleostei, Gymnotiformes) with a redescription of *G. carapo* (Linnaeus). *Zootaxa* **287**, 1–54.

ALBERT, J.S., CRAMPTON, W.G.R., THORSEN, D.H. & LOVEJOY, N.R. 2005a. Phylogenetic systematics and historical biogeography of the Neotropical electric fish *Gymnotus* (Teleostei: Gymnotiformes). *Systematic and Biodiversity* **2**(4): 373–416.

ALBERT, J.S. & FINK, W.L. 1996. *Sternopygus xingu*, a new species of electric fish from Brazil (Teleostei: Gymnotoidei), with comments on the phylogenetic position of *Sternopygus*. *Copeia* **1996**, 85–102.

ALBERT, J.S., LOVEJOY, N.R., & CRAMPTON, W.G.R. 2005b. Miocene tectonism and the separation of cis- and trans-Andean river basins: Evidence from Neotropical fishes. *Journal of South American Earth Sciences*, in press.

BERMINGHAM, E. & MARTIN, A.P. 1998. Comparative mtDNA phylogeography of neotropical freshwater fishes: testing shared history to infer the evolutionary landscape of lower Central America. *Molecular Ecology* **7**, 499–517.

BLOCH, M.E. & SCHNEIDER, J.G. 1801. *Systema Ichthyologiae iconibus cx illustratum. Post obitum auctoris opus unchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider. Saxo. Berolini. Sumtibus Auctoris Impressum et Bibliopolio Sanderiano Commisum. I-lx + 1–584, pls. 1–110.*

BREMER, K. 1994. Branch support and tree stability. *Cladistics – The International Journal of the Willi Hennig Society* **10**, 295–304.

CASTELNAU, F. 1855. Poissons nouveaux ou rares recueillis pendant l'Expedition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Pará. Chez P. Bertrand, Libraire-Editeur, Paris, 112 pp.

COPE, E.D. 1871. Recent reptiles and fishes. Report on the reptiles and fishes obtained by the naturalists of the expedition. *U.S. Geological Survey Wyoming & Contiguous Territories Part 4* (art. 8), 432–442.

CRAMPTON, W.G.R. 1998. Effects of anoxia on the distribution, respiratory strategies and electric signal diversity of gymnotiform fishes. *Journal of Fish Biology* **53**, 307–330.

CRAMPTON, W.G.R. & ALBERT, J.S. 2005. Evolution of electric signal diversity in gymnotiform fishes. In: LADICH, F., COLLIN, S.P., MOLLER, P. & KAPOOR, B.G. (eds.) *Communication in Fishes*. Science Publishers Inc., Enfield, NH. In press.

CRAMPTON, W.G.R., HULEN, K.G. & ALBERT, J.S. 2004. *Sternopygus branco*, a new species of Neotropical electric fish (Gymnotiformes: Sternopygidae) from the lowland Amazon Basin, with descriptions of osteology, ecology and electric organ discharges. *Copeia* 244–258.

DUQUE-CARO, H. 1990. Major Neogene events in Panamian South America. In: TSUCHI, R., Ed., *Pacific Neogene Events, Their Timing, Nature and Interrelationships*, Tokyo University Press, Tokyo, pp. 101–114.

EERNISSE, D.J. & KLUGE, A. G. 1993. Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. *Molecular Biology and Evolution* **10**, 1170–1195.

EIGENMANN, C.H. & ALLEN, W.R. 1942. *Fishes of Western South America*. University of Kentucky, Lexington.

EIGENMANN, C.H. & WARD, D.P. 1905. The Gymnotidae. *Proceedings of the National Academy of Sciences* **7**, 157–185.

ELLIS, M.M. 1913. The gymnotid eels of tropical America. *Memoirs of the Carnegie Museum* **6**, 109–195.

EYDOUX, J.F.T. & SOULEYET, F.L.A. 1841. Poissons. *Voyage Autour du Monde Execute Pendant les Annees 1836 et 1837 sur le Corvette La Bonite* **1**, 155–216.

FARRIS, J.S. 1989. The Retention Index and the Rescaled Consistency Index. *Cladistics, The International Journal of the Willi Hennig Society* **5**, 417–419.

FERNÁNDEZ-YÉPEZ, A. 1968. Contribución al conocimiento de los peces Gymnotiformes. *Evencias* No. 20, no pagination, 5 pp. with figures.

- FINK, S.V. & FINK, W.L. 1981. Interrelationships of the ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society* **72**, 297–353.
- HEILIGENBERG, W.F. 1991. *Neural Nets in Electric Fish*. MIT Press, Cambridge.
- HORMIGA, G., SCHARFF, N. & CODDINGTON, J.A. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology* **49**, 435–462.
- HOORN, C., GUERRERO, J., SARMIENTO, G.A. & LORENTE, M.A. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene Northern South-America. *Geology* **23**, 237–240.
- HUMBOLDT, A.V. & BONPLAND, A. 1811. Poissons, pp. 17–25, 46–92 + plate 10. In: *Recueil d'Observations de Zoologie et d'Anatomie Comparee*. Vol. 1. F. Schoell Libraire et G. Dufour et Cie. Paris.
- JORDAN, D.S. & EVERMANN, B.W. 1896. The fishes of North and Middle America. *Bulletin U.S. National Museum* **47**(1), i–lx, 1–954.
- KAUP, J.J. 1856. Family Gymnotidae. In: KAUP, J.J., Ed., *Catalogue of Apodal Fishes*, pp. 124–142.
- KORRINGA, M. 1970. A new gymnotoid fish from the Rio Tocantins, Brazil. *Proceedings of the California Academy of Science* **38**, 265–271.
- LEVITON, A.E., GIBBS, R.H., JR., HEAL, E. & DAWSON, C.E. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985, 802–832.
- LÖNNBERG, E. 1896. Linnean type-specimens of birds, reptiles, batrachians and fishes in the Zoological Museum of the R. University in Upsala. Bihang Kongl. Kongliga Svenska Vetenskaps-Akademeins Handlingar **22**, 1–45.
- LOVEJOY, N.R. & ARAÚJO, M.L.G.D. 2000. Molecular systematics, biogeography, and population structure of Neotropical freshwater needlefishes of the genus *Potamorhaphis*. *Molecular Ecology* **9**, 259–268.
- LUNDBERG, J.G. 1997. Freshwater fishes and their paleobiotic implications. In: KAY, R.F., HADDEN, R.H., CIFELLI, R.L. & FLYNN, J.J., Eds., *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Press, Washington, DC, pp. 67–92.
- LUNDBERG, J.G. 1998. The temporal context for the diversification of Neotropical fishes. In: MALABARBA, L., REIS, R.E., VARI, R.P., DE LUCENA, C.A.S., & DE LUCENA, Z.M.S., Eds., *Phylogeny and Classification of Neotropical Fishes*. Museu de Ciências e Tecnologia, Porto Alegre, pp. 49–68.
- LUNDBERG, J.G. & MAGO-LECCIA, F. 1986. A review of *Rhabdolichops* (Gymnotiformes Sternopygidae) a genus of South American freshwater fishes with descriptions of four new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **138**, 53–85.
- LUNDBERG, J.G., MARSHALL, L.C., GUERRERO, HORTON, J.B., MALABARBA, M.C.S.L. & WESSELINGH, F. 1998. The stage for Neotropical fish diversification: a history of tropical South American Rivers. In: MALABARBA, L., REIS, R.E., VARI, R.P., DE LUCENA, C.A.S., & DE LUCENA, Z.M.S., Eds., *Phylogeny and Classification of Neotropical Fishes*. Museu de Ciências e Tecnologia, Porto Alegre, pp. 13–48.
- MADDISON, W.P. & MADDISON, D.R. 2000. *MacClade, Analysis of Phylogeny and Character Evolution*, 4.05. Sunderland Associates, Inc., Sunderland, Massachusetts.
- MAGO-LECCIA, F. 1978. Los Peces de la Familia Sternopygidae de Venezuela. *Acta Científica Venezolana* **29**, 1–51.
- MAGO-LECCIA, F. 1994. *Electric Fishes of the Continental Waters of America*. Biblioteca de la Academia de Ciencias Físicas, Matemáticas, y Naturales **29**, 1–206.
- MARTIN, A.P. & BERMINGHAM, E. 2000. Regional endemism and cryptic species revealed by molecular and morphological analysis of a widespread species of Neotropical catfish. *Proceedings Royal Society London Series B – Biological Sciences* **267**, 1135–1141.
- MEEK, S.E. & HILDEBRAND, S.F. 1916. The fishes of the fresh-water of Panama. *Field Museum of Natural History Publication* **191**, *Zoological Series* **10**, 217–374.
- MÜLLER, J. & TROSCHEL, F.H. 1849. *Horae Ichthyologicae*. Beschreibung und Abbildung neuer Fische. Drittes Heft. Berlin.
- PATTERSON, C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* **269**, 275–279.
- PATTERSON, C. 1982. Morphological characters and homology In: JOYSEY, K.A. & FRIDAY, A.B., Eds., *Problems of Phylogenetic Reconstruction*. Academic Press, London, pp. 21–74.
- REINHARDT, J. 1852. Om Svommeblaeren hos Familien Gymnotini. *Vidensk Meddel fra den Naturhistoriske Forening i Kjobenhavn* **9**, 135–149.
- ROHLF, J.F. 2003. *tpsDIG*. Ecology and Evolution, SUNY at Stony Brook, New York.
- SCHULTZ, L.P. 1949. A further contribution to the ichthyology of Venezuela. *Proceedings of the United States National Museum* **99**, 1–211.
- SORENSON, M.D. 1999. *TreeRot*, version 2. Boston University, Boston, MA.
- STEINDACHNER, F. 1881. Beitrage zur Kenntniss der Flussfische Sudamerikas, III. *Denkschr Akademie Wiss Wien* **44**, 103–146.
- SWOFFORD, D. 2003. *PAUP* Version 4.0 Phylogenetic Analysis Using Parsimony*. Sinauer Associates, Inc., Washington, DC.
- TAYLOR, W.R. & VAN DYKE, G.C. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybio* **9**, 107–119.
- TRIQUE, M.L. 2000. *Sternopygus castroï*, a new species of Neotropical freshwater electric fish, with new synapomorphies to the genus (Sternopygidae: Gymnotiformes: Teleostei). *Studies on Neotropical Fauna and Environment* **35**, 19–26.
- UNGUEZ, G.A. & ZAKON, H.H. 1998. Phenotypic conversion of distinct muscle fiber populations to electrocytes in a weakly electric fish. *Journal of Comparative Neurology* **399**, 20–34.
- VARI, R.P. 1988. The Curimatidae: a lowland Neotropical fish family (Pisces: Characiformes); distribution, endemism, and phylogenetic biogeography. In: VANZOLINI, P. & HEYER, W.R., Eds., *Proceedings of a Workshop on Neotropical Distribution Patterns*. Academia Brasileira de Ciências, Rio de Janeiro, pp. 343–377.
- VARI, R.P. 1995. The Neotropical fish family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): Supra and interfamilial phylogenetic relationships, with a revisionary study. *Smithsonian Contributions to Zoology* **564**, 1–97.
- VARI, R.P. & WEITZMAN, S.H. 1990. A review of the phylogenetic biogeography of the freshwater fishes of South America. In: PETERS, G. & HUTTERER, R., Eds., *Vertebrates in the Tropics*. Museum Alexander Koenig, Bonn, pp. 381–393.
- WEINS, J.J. 2000. Coding morphological variation within species and higher taxa for phylogenetic analysis. In: WIENS, J., Ed., *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press, Washington, DC, pp. 115–145.
- WEITZMAN, S.H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. *American Museum of Natural History Bulletin* **153**, 327–478.
- WESTNEAT, M.W. 1993. Phylogenetic relationships of the tribe Cheilini (Labridae: Perciformes) *Bulletin Marine Science* **52**, 351–394.
- WHEELER, A. 1991. The Linnaean fish collection in the Zoological Museum of the University of Uppsala. *Zoological Journal Linnean Society* **103**, 145–195.
- WILKINSON, M., LAPOINTE, F.J. & GOWER, D.J. 2003. Branch lengths and support. *Systematic Biology* **52**, 127–130.

Appendix 1: material

Materials examined from 287 lots containing 677 specimens of sternopygid species. Data are arranged alphabetically by species, country, state, then by museum acronym and catalogue number, followed in parentheses by number of specimens, size (mean or range) in millimeters total length, but sometimes using length to the end of anal-fin (LEA) when caudal appendage of specimen was damaged, type-status (HT, holotype; PT, paratype), specimen status (C&S, cleared and stained), summary of locality, latitude, longitude, and date of capture when available. Institutional abbreviations follow (Leviton *et al.*, 1985) with the addition of INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus). Specimens of *S. macrurus* are arranged by region alphabetically (region abbreviations described in Table 1).

Outgroup specimens

Apteronotus sp. – **Brazil:** Amazonas: MCP uncat., WGRC 03.180199 (1, 205), Rio Japurá-Solimões confluence, 3°06'44"S, 64°47'32"W, 18.I.1999. MCP uncat., WGRC 06.130199 (1, 152), Rio Japurá-Solimões confluence, 3°06'44"S, 64°47'32"W, 13.I.1999. MCP uncat., WGRC 15.110100 (1, 300), Rio Japurá-Solimões confluence, 3°06'44"S, 64°47'32"W, 11.I.2000. MCP uncat., WGRC 26.260199 (1, 230), Rio Japurá-Solimões confluence, 3°06'44"S, 64°47'32"W, 26.I.1999. MCP uncat., WGRC 38.231099 (1, 249), Rio Tefé, 3°47'19"S, 64°59'55"W, 23.X.1999. MCP uncat., WGRC 74.041299 (1, 160), Rio Japurá-Solimões confluence, 3°07'08"S, 64°47'18"W, 04.XII.1999.

Archolaemus blax. – **Brazil:** Amazonas: INPA 18451 (7, 90–202, 2 C&S), Tucuruí, Rio Tocantins, 04°25'S, 49°32'W, 22.X.1984. Pará: INPA 5064 (1, 373), Rio Trombetas, Rio Cachorro, 01°05'S, 57°02'W, 15.IV.1985.

Distocyclus conirostris. – **Brazil:** Amazonas: MCP uncat., WGRC 03.030299 (1, 216), Rio Japurá-Solimões confluence, 03°07'08"S, 64°47'18"W, 03.II.1999. MCP uncat., WGRC 06.140199 (1, 224), Rio Japurá-Solimões confluence, 03°06'44"S, 64°47'32"W, 14.I.1999. MCP uncat., WGRC 06.260199 (1, 143), Rio Japurá-Solimões confluence, 03°06'44"S, 64°47'32"W, 26.I.1999. MCP uncat., WGRC 10.030299 (1, 185), Rio Japurá-Solimões confluence, 03°07'08"S, 64°47'18"W, 03.II.1999. MCP uncat., WGRC 21.020999 (1, 150, C&S), Rio Japurá-Solimões confluence, 03°06'44"S, 64°47'32"W, 02.II.1999. MCP uncat., WGRC 27.020299 (1, 212, C&S), Rio Japurá-Solimões confluence, 03°06'44"S, 64°47'32"W, 02.II.1999.

Ingroup specimens

Sternopygus arenatus. – **Ecuador:** Esmeraldas: MCZ 54969 (4, 56–145), Rio Cayapas, 0°44'N, 78°55'W, 29.VI.1977. MCZ 58604 (1, 248, C&S), Rio Cayapas, 01°44'N, 77°55'W, 29.VI.1977. Guayas: NRM 28178 (2, 490–595), Guayaquil, 26.XI.1934. UMMZ 205390 (4, 195–455), Guayaquil, 02°10'S, 79°54'W. Los Rios: MCZ 48804 (1, 390), Quevedo, 1°S, 79°27'W, 04.XI.1971.

Sternopygus astrabes. – **Brazil:** Amazonas: BMNH 1998.3.11.15a (1, 195), Rio Tefé, Lago Tefé, 03°20'08"S, 64°42'10"W, 27.VII.1996. INPA 09980 (2, 102–131), Rio Demini, 00°23'18"S, 62°51'55"W, 29.X.2000. INPA 9980 (1, 135), Lago Amanã, 2°38'47"S, 64°39'19"W, 5.I.1995. INPA 9981 (1, 166), Lago Amanã, 2°38'47"S, 64°39'19"W, 5.I.1995. MCP 32230 (1, 107), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 30.XII.1998. MCP 32231 (2, 50–55), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 24.VIII.1999. MCP 32232 (1, 63, C&S), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 21.IX.1999. MCP 32233 (1, 81, C&S), Rio Tefé, Tefé, 03°24'28"S, 64°44'16"W, 17.III.2000. MCP 32234 (1, 81), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 10.X.2000. MCP 32235 (10, 104–143, 2 C&S), Rio Demini, 00°23'18"S, 62°51'55"W, 29.X.2000. MCP 32236 (4, 75–91), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 16.X.2002. MCP 32237 (1, 97), Rio Solimões, Alvarães, 03°16'05"S, 64°47'42"W, 27.XI.2002. MCP 32238 (1, 70), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 24.I.2003. MCP 32239 (2, 74–75), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 20.II.2003. MCP 32240 (2, 78–95), Rio Tefé, Tefé, 03°24'28"S, 64°44'10"W, 26.II.2003. MZUSP 47987 (1, 130, S. castroi HT), Rio Cuieras, Igarapé Jaradá, 02°70'S, 60°40'W, 30.I.1977. MZUSP 48911 (1, 117, S. castroi PT), Rio Cuieras, Igarapé Jaradá, 02°40'S, 60°20'W, 01.II.1977. MZUSP 48912 (1, 178, HT), Igarapé Jaradá, Rio Cuieras, 1.II.1977. MZUSP 49788 (1, 142, PT), Igarapé Jaradá, Rio Cuieras, 1.II.1977. **Venezuela:** Amazonas: ANSP 162128 (1, 75, PT), Rio Orinoco, nr. Isla Temblador, 03°04'N, 66°28'W, 10.III.1987. ANSP 162663 (4, 70–177), Rio Autana, Raudal Peresa, 04°46'N, 67°19'W, 13.XI.1985. MBUCV 13896 (6, PT), Rio Orinoco, 30.III.1983. MBUCV 14182 (1, 196, HT), Rio Orinoco, 30.III.1983.

Sternopygus branco. – **Brazil:** Amazonas: INPA 12370 (1, 171), Rio Negro, Lago do Prato, 02°37'36"S, 60°57'W, 18.IX.1991. INPA 15786 (1, 492, PT), Rio Japurá, Paraná Maiana, 03°06'44"S, 64°47'32"W, 28.I.1999. INPA 18236 (1, 265, PT), Rio Solimões-Japurá confluence, 03°09'08"S, 64°47'04"W, 24.II.2000. MCP 32241 (1, 353, PT), Rio Solimões-Japurá confluence, 03°09'08"S, 64°47'04"W, 08.II.1999. MCP 32242 (3, 180–211, PT, 2 C&S), Rio Solimões-Japurá confluence, 03°07'08"S, 64°47'18"W, 07.XII.1999. MCP 32243 (1, 252, PT, C&S), Rio Japurá, Paraná Maiana, 03°04'50"S, 64°47'18"W, 12.I.2000. MCP 32244 (1, 253, PT), Rio Japurá, Paraná Maiana, 03°06'44"S, 64°47'32"W, 22.II.2000. MCP 32245 (2, 246–251, PT, 1 C&S), Rio Solimões-Japurá confluence, 03°09'08"S, 64°47'04"W, 24.II.2000. MCP 32246 (3, 319–345, PT), Rio Solimões-Japurá confluence, 03°09'08"S, 64°47'04"W, 07.II.2001. MCP 32451 (1, 333, HT), Rio Solimões-Japurá confluence, 03°09'08"S, 64°47'04"W, 07.II.2001. MZUSP 56187 (1, 421), Rio Negro, Manaus, 03°0'S, 60°24'W, 13.XII.1993.

Sternopygus dariensis. – **Colombia:** Antioquia: NRM 27742 (1, 326), Rio Atrato, Buchadó, 06°25'N, 77°46'W, 28.I.1989. NRM 27745 (1, 390), Rio Atrato, Buchadó, 06°25'N, 74°46'W, 27.I.1989. Chocó: FSUC uncat. (2, 145–252), upper Rio Nercua, Rio Truando, 28.VIII.1967. FSUC uncat. (11, 103–320), near Teresita, Rio Solando, 08.II.1968.

NRM 10697 (1, 170), Rio Saija, 1939. NRM 10698 (3), Rio San Juan, 1939. NRM 27746 (6, 210–291, 2 C&S), Rio Baudó, Boca de Pepé, 05°04'N, 77°03'W, 22.II.1989. **Panama:** Cocle: UF 27523 (5, 93–245), nr. El Valle, 08°31'N, 80°33'W, 24.IV.1965. Darien: CAS 14037 (1), Rio Tuyra, Marrigante, III.1912. FMNH 8829 (1, PT), Rio Tuyra, Marrigante, 08.III.1912. FMNH 8949 (1, HT), Rio Tuyra, Marrigante, 08.III.1912. UF 15451 (2, 348–355), Rio Pirri, El Real, 08°07'59"N, 77°43'59"W, VI.1967. Colon: USNM 329425 (2, 180–185), Rio Mebrillo, 22.III.1967. Herrera: UF 12978 (2, 226–242), nr. Chepo, 07°43'59"N, 80°48'69"W, 29.IV.1965.

Sternopygus macrurus (EA). – **Brazil:** Goiás: MCP 18204 (1, 361), Rio Araguaia, nr. Luís Alves, 13°14'S, 50°35'W. MNRJ 12189 (2, 33–126), Rio Maranhão, Rio da Mula, 14°16'S, 49°04'W, 10.VII.1985. MNRJ 12190 (2, 116–117), Rio Tocantins, Serra da Mesa, 14°50'S, 48°19'W, 20.X.1985. MNRJ 12191 (10, 115–310), Rio Tocantins, Córrego Bariguda, 14°05'S, 48°20'W, 15.X.1985. MNRJ 12208 (2, 76–168), Rio Tocantins, Córrego Lajeado, 13°31'S, 49°10'W, 29.V.1987. MNRJ 12209 (4, 104–113), Rio Tocantins, Córrego Lajeado, 13°39'S, 48°09'W, 06.I.1987. Pará: INPA 4843 (12, 114–220), Rio Tocantins, Tucuruí, 04°25'S, 49°32'W, 01.XII.1984. INPA 5739 (1, 162), Rio Trombetas, Rio Cachorro, 00°58'S, 57°02'59"W, 08.XII.1988. INPA 6409 (1, 256), Rio Tocantins, Breu Branco, 04°01'59"S, 49°40'W, 14.XI.1981. INPA 6410 (1, 382), Rio Tocantins, Igarapé Jatobal, 08°56'S, 49°46'W, 31.X.1980. INPA 6411 (2, 234–317), Rio Tocantins, Breu Branco, 04°04'04"S, 49°38'08"W, 13.VII.1982. INPA 6414 (2, 118–220), Rio Tocantins, Igarapé Jatobal, 08°56'S, 49°46'W, 08.VII.1982. INPA 6416 (1, 425), Rio Tocantins, Tucuruí, 03°42'S, 49°42'W, 26.X.1980. INPA 6431 (3, 366–495), Rio Tocantins, Tucuruí, 03°42'S, 49°42'W, 31.XXXI.1985. INPA 9092 (2, 225–271), Rio Tocantins, Laguinho, 08°56'S, 49°46'W, 11.XI.1981. INPA uncat. (6, 236–433), Rio Jarim, Cachoeira Santo Antonio, 01°09'S, 51°54'W, 9–18.VI.1987. INPA uncat. (6, 236–433), Rio Jarim, Cachoeira Santo Antonio, 01°09'S, 51°54'W, 9–18.VI.1987. MCZ 9409 (1, 320), Ilha do Marajó, Lago Arari, 00°20'S, 49°10'W, 01.III.1866. MCZ 9412 (2, 234–455), Rio Pará, nr. Belém, 01°27'S, 48°29'W, 10.VIII.1865. MCZ 9442 (2, 385–390), Rio Pará, nr. Belém, 01°27'S, 48°29'W, 10.VIII.1865. MCZ 9453 (1, 212), Lago Aleixo, Rio Negro, 27.XI.1865. MCZ 9456 (5, 310–368), Rio Pará, nr. Belém, 01°27'S, 48°29'W, 10.VIII.1865. MCZ 9829 (2, 185–448), Rio Xingu, Porto de Moz, 01°45'S, 52°10'W, IX.1865. MCZ 25708 (1, 300), Rio Xingu, Porto de Moz, 01°45'S, 52°10'W, IX.1865. MCZ 45193 (6, 119–286), Ilha do Marajó, Cachoeira do Arari, 01°11'S, 48°45'W, VII.1965. MCZ 60047 (1, 140), Rio Xingu, Porto de Moz, 01°45'S, 52°10'W, 23.VIII.1865. UMMZ 203393 (1, 355), Rio Tocantins, Belém, 19.VII.1935. Mato Grosso: INPA 11578 (1, 112), Rio Aripuanã, Dardanelos, 09°10'S, 60°38'W, 09.XI.1976. MZUSP 25136 (1), Ilha de Taiamã (Sema), Rio Paraguay, 8.VIII.1980. MZUSP 27740 (1), Rio Taquari, Coxim. MZUSP 28568 (1), Rio Taquari, junto à cidade de Coxim, X.1983. MZUSP 36339 (2), Ladá Rio Corumbá, Mato Grosso, IX.1985. MZUSP 44418 (3), Cáceres, Rio Paraguay, 11–12.VIII.1991. MZUSP 45345 (2), riacho Monjolinho, Rio Preto, São Francisco,

24.X.1992. USNM 326121 (3, 133–368), Waura, Rio Batovi, Rio Xingu, VIII.1964. USNM uncat. (6, 125–215), Waura, Rio Batovi, Rio Xingu, VIII.1964. USNM uncat. (2, 161–164), Waura, Rio Batovi, Rio Xingu, VIII.1964. Tocantins: INPA 4536 (1, 166), Rio Tocantins, Itupiranga, 05°09'S, 49°20'W, 06.VII.1980. INPA 4825 (1, 460), Rio Tocantins, Lago Grande, 05°09'S, 49°20'W, 21.XI.1981. INPA 6415 (1, 193), Rio Tocantins, Itupiranga, 05°09'S, 49°20'W, 29.VII.1982.

Sternopygus macrurus (GO). – **Brazil:** Roraima: INPA 1156 (1, 76), Rio Branco, Boa Vista, 02°49'N, 60°40'W. INPA 2046 (8, 129–525), Rio Uraricoera, Ilha Maracá, 03°02'N, 60°30'W, 12.III.1988. INPA 2060 (1, 221), Rio Uraricoera, Ilha Maracá, 03°02'N, 60°30'W, 13.III.1988. INPA 2062 (10, 70–395), Rio Uraricoera, Ilha Maracá, 03°02'N, 60°30'W, 14.III.1988. INPA 4540 (1, 159), Rio Mucajaí, Cachoeira Paredão, 02°25'N, 60°52'W, 18.II.1987. INPA 4874 (1, 132), Rio Uraricoera, Ilha Maracá, 03°02'N, 60°30'W, 11.III.1988. INPA 6412 (2, 262–361), Rio Mucajaí, Cachoeira Paredão, 02°25'N, 60°52'W, 03.X.1986. INPA 6419 (1, 317), Rio Mucajaí, Cachoeira Paredão, 02°25'N, 60°52'W, 19.II.1987. INPA 7417 (1, 113), Rio Branco, Igarapé Juruaquim, 03°22'N, 60°19'W, 27.III.1992. **Guyana:** Essequibo: UMMZ 13054 (1, 308), Botami Gardens, Georgetown. UMMZ 215184 (1, 180), Mahida Creek, Potaro River, 20.VIII.1971. UMMZ 215834 (2, 138–461), tidal canal at Anna Regina, 07°16'N, 58°30'W, 27.VIII.1971. UMMZ 215916 (1, 384), Barana River at Kokerite Village, 01.IX.1971. USNM 209204 (1, 160), Crusa Creek, Rupununi District, 15.V.1970. **Suriname:** Marowijne: UF 16268 (1, 161), Marowijne River, 05°30'N, 54°03'W, VII.1967. **Venezuela:** Apure: FMNH 100719 (1, 175), Rio Anarco near Rio Suripa, Rio Apure, 01.I.1991. FMNH 100725 (5), Caño Socopo, Rio Suripa, Rio Apure, 07.I.1991. FMNH 100726 (1, 197), Caño Socopo, Rio Suripa, Rio Apure, 12.I.1991. MCNG 3733 (10, 177–398, 8 C&S), Rio Apure, Munoz, 07°28'30"N, 69°30'50"W, 19.III.1981. UF 80888 (2, 164–195), Rio Apure, Munoz, 07°25'20"N, 69°35'40"W, 13.II.1979. Portuguesa: UF 80862 (2, 176–180), Laguna Chiriguare, 08°48'N, 68°30'W, 03.IV.1984. UMMZ 212346 (1, 36), Guarico, Rio Apure, 21.VIII.1981. USNM 194179 (1, 306), Rio Las Palmas, Barinas, 15.VI.1958.

Sternopygus macrurus (NE). – **Brazil:** Bahia: MCP 16730 (1, 338), Rio Tato, nr. Barra de Cocos, 14°14'22"S, 44°31'42"W, 16.VII.1993. MZUSP 2644 (1), Rio São Francisco, 1908. UMMZ 216316 (1, 275), Barreiras, mouth of Rio Grande, 28.III.1942. Minas Gerais: ANSP 172171 (2, 54–235), Rio Verde Grande, nr. Janauba, 16°39'01"S, 43°42'49"W, 20.VII.1993. MZUSP 39474 (3), Rio São Francisco, Barra do Rio Formoso, 8–10.II.1988. MZUSP 39640 (1), Rio Abaeté, Tiros, 18.III.1988. MZUSP 39951 (1), Água Vermelha, Rio Grande, 27.VI.1978. MZUSP 47447 (1), Rio Verde, entre Francisco Sá e Montes Claros, 23.VII.1994. MZUSP 24652 (1), Pedra Ponte, Três Marias, 23.VIII.1978. USNM 44967 (1, 354), Rio das Velhas, São Francisco, 15.II.1895. Ceará: MCZ 9418 (1, 420), Ceara, nr. Fortaleza, 03°45'S, 38°30'W, 05.VIII.1865. Piauí: AUM 20601 (1), Rio Parnaíba, Rio Gurgueia, 06°14'S, 42°37'W, 5.IX.1971. AUM 20630 (1), Rio Parnaíba, Rio Esfolado, 07°24'S, 43°38'W, 5.IX.1971. AUM 20757 (9), Rio Parnaíba,

Santa Filomena, 09°08'S, 45°55'W, 8.IX.1971. MCZ 9450 (3, 263–370), Rio Parnaíba, Rio Puty, 05°05'S, 42°49'W, XII.1865. MCZ 46859 (1, 143), Rio Parnaíba, Lagoa Seca, 03°11'S, 41°50'W, 29.VIII.1968. Rondônia: INPA uncat (polo. 1206) (2, 175–390), Rio Machado, Nazaré, 10°05'S, 62°18'W, 21.III.1987. INPA uncat (polo. 1353) (4, 119–205), Rio Jamari, UHE Samuel, 08°45'S, 63°28'W, 07.VI.1988. INPA uncat (polo. 146) (6, 164–330), Rio Machado, Rio Urupá, 10°52'S, 61°58'W, 04.VI.1984. INPA uncat (polo. 204) (1, 420), Rio Guaporé, Surpresa, 11°54'S, 64°59'W, 16.VI.1984. INPA uncat (polo. 610) (1, 155), Rio Machado, Nazaré, 10°05'S, 62°18'W, 09.XI.1983. INPA uncat (polo. 629) (4, 170–290), Rio Machado, Jiparaná, 08°03'S, 62°52'W, 16.VI.1984. INPA uncat (polo. 709) (2, 137–150), Rio Marmoré, Guajará-Mirim, 10°48'S, 65°22'W, 26.XI.1983. INPA uncat (polo. 754) (15, 135–155), Rio Machado, Rio Urupá, 10°52'S, 61°58'W, 05.VI.1984. INPA uncat (polo. 867) (1, 142), Rio Jamari, UHE Samuel, 08°45'S, 63°28'W, 04.IX.1985. INPA uncat (polo. 949) (8, 131–286), Rio Jamari, UHE Samuel, 08°45'S, 63°28'W, 10.IX.1985. Sergipe: MZUSP 24476 (1), Rio São Francisco, Propriá, 18.XII.1975.

Sternopygus macrurus (NW). – **Colombia**: Magdalena: UF 17210 (1, 192), Rio Magdalena, Cartagena, 11°01'N, 74°15'W, 18.VIII.1969.

Sternopygus macrurus (PA). – **Paraguay**: Canendiyu: UMMZ 206424 (1, 144), Rio Paraguay, 24°02'12"S, 54°19'W, 13.VII.1979. Concepcion: NRM 23196 (1, 140), Rio Paraguay, Concepcion, 23°48'S, 56°17'W, 18.VIII.1993. UMMZ 206765 (1, 450), Rio Aquidaban, Parque Cerro Cora, 22°38'12"S, 56°03'W, 25.VII.1979. UMMZ 206794 (1, 115), Rio Apa, nr. Bella Vista, 22°06'30"S, 56°30'W, 27.VII.1979. UMMZ 208004 (1, 80), Rio Paraguay, Concepcion, 23°15'18"S, 56°30'W, 11.IX.1979.

Sternopygus macrurus (PS). – **Colombia**: Chocó: NRM 27740 (4, 180–251), Rio Baudó, Boca de Pepé, 05°04'N, 77°03'W, 22.II.1989. UMMZ 179240 (1, 312) Rio Meta, 1936.

Sternopygus macrurus (SE). – **Brazil**: Rio de Janeiro: MCZ 45096 (1, 201), Rio Paraíba do Sul, nr. Rio de Janeiro, 22°53'S, 43°17'W, II.1872.

Sternopygus macrurus (WA). – **Argentina**: La Plata: ANSP 78191 (1), Río de la Plata, 34°55'S, 57°57'W approx 1870s. Santiago del Estero. USNM 246086 (1), Río Dulce, 27°47'S, 64°16'W, 12.VI.1933. Bolivia: Beni: AMNH 39822 (1), Río Mamoré, Costa Marquez, 12°33'S, 64°12'W, 9.X.1964. AMNH 40159 (1), Río Mamoré, Guayaramerin, 10°51'S, 65°21'W, 20.X.1964. UMMZ 204744 (19, 124–427), Río Mamoré, Río Itenez, 12°31'S, 64°19'W, 30.IX.1964. UMMZ 204800 (2, 320–322), Río Mamoré, Río Baures, 12°34'S, 64°19'W, 3.X.1964. UMMZ 204888 (11, 145–411), Río Itenez, Río Baures, 07.X.1964. USNM 305511 (1), Río Mamoré, Río Matos, 14°55'S, 66°17'W, 28.VIII.1987. Pando: FMNH 106700 (1), Río Mamoré, Cobija, 11°26'S, 69°01'W, 4.IX.1996. Santa Cruz Dept: UF 82344 (1), Río Mamoré, Río Jorge, 17°31'S, 63°15'W, 10.VIII.1986. **Brazil**: Amazonas: BMNH 1998.3.11.02 (1, 212), Rio Solimões, nr. Alvarães, 03°06'17"S, 64°55'07"W, 29.VIII.2003. BMNH 1998.3.11.03 (1, 145), Rio Solimões, nr. Alvarães, 03°06'17"S, 64°55'07"W, 29.VIII.2003. BMNH 1998.3.11.04 (1, 150),

Rio Solimões, nr. Alvarães, 03°06'17"S, 64°55'07"W, 29.VIII.2003. BMNH 1998.3.11.05 (1, 157), Rio Solimões, nr. Alvarães, 03°06'17"S, 64°55'07"W, 29.VIII.2003. BMNH 1998.3.11.06 (1, 161), Rio Solimões–Japurá Confluence, 02°54'46"S, 64°54'26"W, 16.IX.1993. BMNH 1998.3.11.07 (1, 163), Rio Solimões, nr. Tefé, 03°16'05"S, 64°41'21"W, 05.IX.1993. BMNH 1998.3.11.10 (1, 257), Lago Tefé, 03°20'08"S, 64°42'10"W, 27.VII.1996. BMNH 1998.3.11.11 (1, 210), Lago Tefé, 03°20'08"S, 64°42'10"W, 27.VII.1996. BMNH 1998.3.11.12 (1, 187), Lago Tefé, 03°20'08"S, 64°42'10"W, 27.VII.1996. BMNH 1998.3.11.13 (1, 43), Rio Tefé, Igarapé Curupira, 03°26'01"S, 64°43'47"W, 04.II.1995. INPA 15783 (1, 418), Lago Amanã, 02°28'54"S, 64°42'48"W, 30.XI.1998. INPA 15802 (2, 286–305), Rio Solimões–Japurá Confluence, 03°07'08"S, 64°47'18"W, 15.X.1999. INPA 17143 (2, 207–242), Rio Purus, Lago Jarí, 04°54'51"S, 62°21'26"W, 08.VI.2001. INPA 17305 (1, 190), Rio Purus, Sacado de Santa Luzia, 04°42'18"S, 62°22'26"W, 04.VI.2001. INPA 18165 (1, 204), Rio Solimões–Japurá Confluence, 03°09'08"S, 64°47'04"W, 08.XII.1999. INPA 18166 (3, 172–221), Rio Japurá, Paraná Maiana, 03°04'50"S, 64°47'18"W, 15.X.1999. INPA 18188 (3, 232–283), Lago Tefé, 03°34'35"S, 64°59'19"W, 22.VI.1999. INPA 18190 (4, 360–492), Rio Japurá, Paraná Maiana, 03°04'50"S, 64°47'18"W, 13.I.1999. INPA 18233 (1, 252), Rio Tefé, 03°46'49"S, 64°59'29"W, 01.VI.2000. INPA 18234 (1, 168), Rio Solimões–Japurá Confluence, 03°09'08"S, 64°47'04"W, 08.XII.1999. INPA 18235 (1, 220), Rio Solimões–Japurá Confluence, 03°09'08"S, 64°47'04"W, 24.II.2000. INPA 18238 (1, 88), Lago Caiambé, 03°35'34"S, 64°26'37"W, 28.XII.1998. INPA 18316 (1, 345), Rio Japurá, Paraná Maiana, 03°06'44"S, 64°47'32"W, 05.XII.1999. INPA 18317 (1, 48), Rio Tefé, Igarapé Curupira, 03°26'01"S, 64°43'47"W, 07.II.2000. INPA 4736 (3, 94–147), Rio Solimões, Lago Janauacá, 03°25'28"S, 60°16'53"W, 17.III.1978. INPA 4809 (2, 212–357), Rio Solimões, Lago Janauacá, 03°25'28"S, 60°16'53"W, 07.IV.1978. INPA 4824 (1, 450), Rio Solimões, Ilha do Careiro, 03°12'S, 59°45'W, 02.XII.1985. INPA 4837 (1, 310), Rio Uatamã, Balbina, 01°53'S, 59°28'W, 24.X.1987. INPA 4841 (1, 325), Rio Solimões, Ilha do Careiro, 03°12'S, 59°45'W, 18.XI.1985. INPA 4869 (6, 33–130), Rio Solimões, Lago Janauacá, 03°25'28"S, 60°15'53"W, 25.II.1978. INPA 6428 (1, 165), Rio Solimões, Aramacá, 04°20'S, 69°55'W. INPA 6429 (2, 305–383), Rio Japurá, 30.IX.1976. INPA 6432 (3, 377–489), Rio Solimões, Ilha do Careiro, 03°12'S, 59°45'W, 26.II.1986. INPA 6433 (1, 443), Rio Solimões, Ilha do Careiro, 03°12'S, 59°45'W, 31.III.1987. INPA 9933 (1, 287), Rio Jaú, Miracutucu, 01°54'S, 61°26'W, 29.X.1994. Pará: INPA uncat. (6, 236–433), Rio Jarim, Cachoeira Santo Antonio, 01°09'S, 51°54'W, 9–18.VI.1987. INPA uncat. (6, 236–433), Rio Jarim, Cachoeira Santo Antonio, 01°09'S, 51°54'W, 9–18.VI.1987. MCP 32247 (1, 101), Rio Solimões, nr. Alvarães, 03°06'18"S, 64°55'07"W, 29.VIII.2003. MCP 32248 (2, 145–147), Rio Japurá, Nova Colômbia, 02°54'47"S, 64°54'26"W, 16.IX.1993. MCP 32249 (8, 42–75), Lago Caiambé, 03°35'34"S, 64°26'37"W, 28.XII.1998. MCP 32250 (1, 157), Rio Solimões–Japurá Confluence, 03°07'08"S, 64°47'18"W, 19.I.1999. MCP 32251

(3, 39–122), Rio Solimões–Japurá Confluence, 03°06'44''S, 64°47'32''W, 26.I.1999. MCP 32252 (1, 157), Lago Tefé, 03°34'35''S, 64°59'19''W, 22.VI.1999. MCP 32253 (4, 184–303), Lago Tefé, 03°34'35''S, 64°59'19''W, 22.VI.1999. MCP 32254 (3, 132–310, C&S), Rio Tefé, 03°46'49''S, 64°59'29''W, 13.VII.1999. MCP 32255 (1, 85), Rio Tefé, Igarapé Repararimento, 03°24'28''S, 64°44'10''W, 29.VII.1999. MCP 32256 (1, 173, C&S), Rio Tefé, Tefé, 03°24'28''S, 64°59'55''W, 22.X.1999. MCP 32257 (1, 88), Rio Tefé, Tefé, 03°24'28''S, 64°44'10''W, 22.XII.1999. MCP 32258 (1, 264), Rio Solimões–Japurá Confluence, 03°09'08''S, 64°47'04''W, 07.II.2001. MCP uncat. (1, 159), Rio Solimões, Tefé, 03°46'S, 73°15'W. NRM 14073 (1, 505), Joapoary, 30.XI.1924. **Ecuador:** Napo: FMNH 103297 (1, 230), Rio Payamino, 00°26'S, 77°2'12''W, 20.IX.1981. FMNH 103299 (3, 115–257), Rio Sardinias, 00°06'S, 77°12'30''W, 29.IX.1981. FMNH 103300 (2, 178–320), Rio Napo, 00°23'24''S, 76°37'06''W, 04.X.1981. **Peru:** Cajamarca: ROM 5228 (1, 163), Río Tabaconas, 05°23'S, 78°45'W, 7.VII.1986. Loreto: UF 116550 (1, 415), Rio Nanay, Mixana, 03°52'46''S, 73°29'33''W, 26.III.2001. UF 117121 (2, 400–401), Rio Nanay, Mixana, 03°52'46''S, 73°29'33''W, 26.III.2001. UF 122829 (1, 162), nr. Iquitos, 03°46'S, 73°15'W, 20–28.V.2002. UF 122830 (1, 167), nr. Iquitos, 03°46'S, 73°15'W, 20–28.V.2002. UF 122831 (1, 137), nr. Iquitos, 03°46'S, 73°15'W, 20–28.V.2002. UF 122832 (1, 88), nr. Iquitos, 03°46'S, 73°15'W, 20–28.V.2002. UF 122833 (1, 122), nr. Iquitos, 03°46'S, 73°15'W, 20–28.V.2002. UF 122838 (1, 113), nr. Iquitos, 03°46'S, 73°15'W, 20–28.V.2002. UMMZ 187220 (1, 185 SL), Río Purus, Río Curanja, 10°08'S, 71°13'W, VII.1966. UMMZ 228964 (2, 270–285), Buen Suceso, Rio Javari, 15.V.1993. UMMZ 228965 (1, 224), Santa Ana, Rio Tahwayo, 6.V.1993. USNM 86835 (1, 176), Rio Pichis, 1920. Madre de Dios: USNM 263888 (1), Río Madre de Dios, Tambopata, 12°49'S, 69°16'W, 20.VIII.1983. Ucayali: ROM 55540 (1, 167), Río Ucayali, Pucallpa, 08°23'S, 74°32'W, 1988.

Sternopygus obtusirostris. – **Brazil:** Amazonas: BMNH 1998.3.11.14 (1, 195), Rio Tefé, Lago Tefé, 03°20'08''S, 64°42'10''W, 27.VII.1996. BMNH 1998.3.11.15 (1, 180), Rio Tefé, Lago Tefé, 03°20'08''S, 64°42'10''W, 27.VII.1996. BMNH 1998.3.11.16 (1, 200), Rio Tefé, Lago Tefé, 03°34'35''S, 64°59'19''W, 10.VIII.1996. BMNH 1998.3.11.17 (1, 180), Rio Tefé, Lago Tefé, 03°34'35''S, 64°59'19''W, 10.VIII.1996. INPA 15787 (1, 180), Rio Tefé, Lago Tefé, 03°20'08''S, 64°42'10''W, 05.V.1996. INPA 15797 (2, 437–523), Rio Tefé, Lago Tefé, 03°34'35''S, 64°59'19''W, 28.VIII.1999. INPA 16579 (2, 167–183), Rio Jauaperi, Igarapé Cambeua, 01°25'59''S, 61°35'W, 01.XII.2000. INPA 18155 (2, 215–398), Rio Tefé, 03°47'19''S, 64°91'55''W, 23.X.1999. INPA 18232 (1, 422), Lago Amanã, 02°39'46''S, 64°39'09''W, 01.V.1994. INPA 18237 (1, 174), Lago Amanã, 02°32'31''S, 64°41'30''W, 24.XI.1998. INPA 6430 (1, 520), Rio Solimões, Ilha do Careiro, 03°12'S, 59°45'W, 31.III.1987. INPA 9072 (1, 356), Rio Negro, Anavilhanas, 02°42'S, 60°45'W, 06.III.1976. MCP 32259 (1, 121), Rio Tefé, Lago Tefé, 03°20'08''S, 64°42'10''W, 04.V.1996. MCP 32260 (1, 118), Rio Tefé, Lago Tefé, 03°20'08''S, 64°42'10''W, 05.V.1996. MCP 32261 (1, 142), Rio Tefé, Ilha Martelo, 03°46'49''S, 64°59'29''W,

26.VII.1999. MCP 32262 (6, 288–431, 1 C&S), Rio Tefé, 03°47'S, 64°59'55''W, 25.X.1999. MCP 32263 (1, 125), Rio Tefé, Ilha Martelo, 03°46'49''S, 64°59'29''W, 14.VI.2000. MCP 32264 (1, 123), Rio Tefé, Lago Tefé, Igarapé Repararimento, 03°24'28''S, 64°17'10''W, 02.II.2003. MCP T-032 (1, 180, C&S), Rio Tefé, Toco Preto, 03°47'19''S, 64°59'55''W, 24.X.1999. MCZ 9411 (1, 175), Rio Amazonas, nr. Parintins, 02°40'S, 56°45'W, 30.VIII.1865. MCZ 9413 (1, 208, ST), Rio Tefé, Lago Tefé, 03°24'19''S, 64°45'W, X.1865. MCZ 9425 (1, 295, ST), Rio Maúes, Maúes, 03°22'S, 57°38'W, 15.XII.1865. MCZ 9453 (1, 206, ST), Rio Negro, Lago Aleixo, 03°05'S, 59°53'W, 06.XII.1865. MZUSP 6100 (1, 524), Rio Puraquequara, 03°02'59''S, 59°46'W, 17.IV.1967. Pará: MCZ 2768 (1, 175), Rio Amazonas, Óbidos, 01°52'S, 55°30'W, XII.1865.

Sternopygus pejeraton. – **Venezuela:** Zulia: MCZ 37222 (1, PT), Rio Motatan, 09°28'N, 70°37'W, 17.III.1942. UF 25447 (1, 191), Rio Catatumbo, 09°22'59''N, 71°43'59''W, 17.VI.1974. UMMZ 157671 (2, 195–228, PT), Rio Palmar, 10°11'N, 71°52'W, 21.II.1942. USNM 121567 (17, 160–426), Rio Socuy, Lago Maracaibo, 24.II.1942.

Sternopygus sp. 'cau'. – **Venezuela:** Bolívar: AMNH 58643 (2, 263–267), Rio Caura, 7°38'N 64°53'W, 22.XI.1985.

Sternopygus xingu. – **Brazil:** Mato Grosso: MZUSP 48374 (1, 182, HT), Rio Batovi, 13°S, 53°30'W, 19.VIII.1964. VIII. MZUSP 48375 (4, 162–260, PT), Rio Batovi, 13°S, 53°30'W, 19.VIII.1964. VIII. UMMZ 228961 (4, 206–265, PT, 2 C&S), Rio Batovi, 13°S, 53°30'W, VIII.1964. USNM 218830 (15, 175–265, PT, 2 C&S), Rio Batovi, 13°S, 53°30'W, 19.VIII.1964. VIII. USNM 326120 (3, 380–525, PT), Rio Batovi, VIII.1964. USNM 338273 (14, 72–304, PT), Rio Batovi, VIII.1964. USNM uncat. (28, 91–240, PT, 2 C&S), Rio Batovi, VIII.1964. Pará: INPA 6418 (1, 353), Rio Tocantins, Tucuruí, 03°42'S, 49°42'W, 31.X.1980. INPA 6420 (1, 485), Rio Tocantins, Itupiranga, 05°08'05''S, 49°19'36''W, 29.VII.1982. INPA 6425 (1, 270), Rio Tocantins, Breu Branco, 04°01'59''S, 49°40'W, 11.VII.1982. INPA 6426 (1, 446), Rio Tocantins, Lago Taua, 03°42'S, 49°42'W, 31.X.1980. INPA 6427 (1, 455), Rio Tocantins, Lago Grande, 05°09'S, 49°20'W, 21.XI.1981. INPA 6918 (1, 354), Rio Tocantins, 05°01'S, 50°40'W, XI.1980.

Appendix 2: *Sternopygus* branch list

Steps in parentheses are unambiguous character-state changes on tree topology of Figure 17. Clade A–G named in Table 7. Abbreviations listed in Materials and methods. Additional abbreviations include: consistency index (CI), rescaled index (RI) and rescaled consistency (RC).

Clade A: (steps: 17)

- 14 Gape: larger or equal to eye diameter (CI: 1.00, RI: 1.00, RC: 1.00)
- 17 Infraorbitals 3–4: enlarged, bony (CI: 0.50, RI: 0.67, RC: 0.33)
- 21 Ventral ethmoid: long (CI: 1.00, RI: 1.00, RC: 1.00)
- 22 Mesethmoid: robust (CI: 1.00, RI: 1.00, RC: 1.00)

- 23 Lateral ethmoid cartilage: contacting maxilla (CI: 1.00, RI: 1.00, RC: 1.00)
- 25 Lateral ethmoid anterior process: long, extending lateral to dorsal margin of vomer (CI: 0.50, RI: 0.67, RC: 0.33)
- 30 Neurocranium depth: moderate, mean 30.1–34.9% NL (CI: 0.40, RI: 0.57, RC: 0.23)
- 35 Premaxilla shape: gracile, triangular in dorsal view (CI: 0.50, RI: 0.80, RC: 0.40)
- 37 Meckel's cartilage ossification: dorsal margin ossified completely in adults (CI: 1.00, RI: 1.00, RC: 1.00)
- 43 Hyomandibular PM opening: emerging from anterior shelf (CI: 0.50, RI: 0.50, RC: 0.25)
- 46 Opercle, ratio of long axes: dorsal margin moderate, mean 70–75% distance of antero-ventral margin (CI: 0.50, RI: 0.67, RC: 0.33)
- 48 Gill rakers: complex (see text), separated by unmineralized tissue (CI: 1.00, RI: 1.00, RC: 1.00)
- 51 Posttemporal: not fused with supracleithrum (CI: 1.00, RI: 1.00, RC: 1.00)
- 55 Pectoral fin length: short, mean P1 51–60% HL (CI: 1.00, RI: 1.00, RC: 1.00)
- 56 Pectoral fin rays: few, mode P1R 13–16 (CI: 0.50, RI: 0.50, RC: 0.25)
- 63 Anterior vertebrae: not compressed (see text) (CI: 1.00, RI: 1.00, RC: 1.00)
- 65 Anal-fin ray structure: unbranched (CI: 1.00, RI: 1.00, RC: 1.00)

Clade B: (steps: 4)

- 2 Pale lateral stripe: present in juveniles and adults (CI: 0.50, RI: 0.80, RC: 0.40).
- 8 Head: wide, mean HW 42–47% HL (CI: 0.33, RI: 0.33, RC: 0.11).
- 11 Interorbital distance: wide, mean IO 25–28% HL (CI: 0.50, RI: 0.75, RC: 0.38).
- 30 Neurocranium: deep, mean HD 35–50% NL (CI: 0.40, RI: 0.57, RC: 0.23).

Clade C: (steps: 2)

- 3 Dark bars: present in juveniles (CI: 1.00, RI: 1.00, RC: 1.00).

- 15 Eye: large, mean ED 12–16% HL (CI: 0.50, RI: 0.67, RC: 0.33).

Clade D: (steps: 2)

- 12 Internarial distance: long, NN 19–23% HL (CI: 0.67, RI: 0.50, RC: 0.33).
- 13 Mouth: broad; mean MW 16–19% HL (CI: 0.25, RI: 0.25, RC: 0.06).

Clade E: (steps: 3)

- 5 Body: deep, BD 12–15% LEA (CI: 1.00, RI: 1.00, RC: 1.00).
- 6 Head: long, HL 14–15% LEA (CI: 0.67, RI: 0.75, RC: 0.50).
- 54 Pectoral distal radials: 3 and 4 fused (CI: 0.50, RI: 0.75, RC: 0.38)
- 55 Pectoral fin: very short, P1 40–50% HL (CI: 1.00, RI: 1.00, RC: 1.00).

Clade F: (steps: 3)

- 26 Vomer: long, narrow, length more than five times width (CI: 0.50, RI: 0.67, RC: 0.33).
- 28 Frontal margin: straight dorsal to lateral ethmoid (CI: 0.50, RI: 0.67, RC: 0.33).
- 46 Opercle, ratio of long axes: dorsal margin long, mean 76–90% distance of antero-ventral margin (CI: 0.50, RI: 0.67, RC: 0.33).

Clade G: (steps: 5)

- 10 Snout profile: dorsal margin strongly concave (CI: 0.50, RI: 0.50, RC: 0.25).
- 11 Interorbital: narrow, IO 17–24% HL (CI: 0.50, RI: 0.75, RC: 0.38).
- 30 Neurocranium: moderate, ND 30–34.9% NL (CI: 0.40, RI: 0.57, RC: 0.23).
- 32 Parasphenoid width at prootic foramen: as wide or broader than (PaS) at (PtS)–(OrS) junction (CI: 1.00, RI: 1.00, RC: 1.00).
- 36 Maxilla width: midlength half width of area near palatine articulation (CI: 0.50, RI: 0.50, RC: 0.25).