AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2950, 39 pp., 25 figs., 1 table August 9, 1989

A New Sarcoglanidine Catfish, Phylogeny of Its Subfamily, and an Appraisal of the Phyletic Status of the Trichomycterinae (Teleostei, Trichomycteridae)

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ABSTRACT

Stauroglanis gouldingi is described as new genus and species of the Trichomycteridae. Characters traditionally used to delimit subgroups of trichomycterids would include *Stauroglanis* in the subfamily Trichomycterinae. Nevertheless, similarities between *Stauroglanis* and trichomycterines cannot be considered as derived characters for the two taxa. Instead, a number of other newly proposed characters constitute unequivocal synapomorphies supporting monophyly of *Stauroglanis* plus the Sarcoglanidinae. Further analysis indicates that *Sarcoglanis* and *Malacoglanis* (the two previously known sarcoglanidines) form a monophyletic group, with *Stauroglanis* as its sister group.

All characters used until the present to define the Trichomycterinae are either synapomorphies for the whole family (i.e., symplesiomorphies for the subfamily) or features of uncertain polarity. *Scleronema* and two species of *Trichomycterus, T. boylei* and *T. santaeritae,* are tentatively proposed to be more closely related to the Sarcoglanidinae than to the Trichomycterinae. In addition, it is suggested that *T. hasemani* and *T. johnsoni* are more closely related to the Tridentinae than to any Trichomycterinae. These cases are given as positive evidence that the Trichomycterinae is nonmonophyletic as presently constituted.

By current criteria, *Stauroglanis* can be considered as one more miniature trichomycterid. In view of new data, three miniaturization events are proposed within the family: at the base of Glanapteryginae/Sarcoglanidinae clade (including *Trichomycterus santaeritae*), at the base of Tridentinae clade (including *Trichomycterus hasemani* and *T. johnsoni*) and inside Vandelliinae (*Paravandellia*).

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 ISSN 0003-0082 / Price $4.70

INTRODUCTION

The subfamily Sarcoglanidinae was established by Myers and Weitzman (1966) to include two new genera and species, *Sarcoglanis simplex* and *Malacoglanis gelatinosus.* The new subfamily was characterized, among other things, by the toothless upper jaw, the presence of an adiposelike fin, and the pectoral-fin rays projecting beyond the fin membrane. The description of *S. simplex* was based on a single specimen from the upper Rio Negro below São Gabriel rapids (Amazon Basin, Brazil), whereas *M. gelatinosus* was known from two examples collected in a small side channel of the Río Orteguaza (tributary of the Río Caquetá, Amazon Basin, Colombia). The Sarcoglanidinae have to date been known only from the three specimens originally studied by Myers and Weitzman (1966), and by two additional examples of *Malacoglanis* reported by Stewart et al. (1987). Myers and Weitzman (1966) suggested that, in spite of their scarcity in collections, it is probable that the Sarcoglanidinae occur throughout the entire Amazon Basin, as well as in the Orinoco Basin.

The present paper is based on material collected by Dr. Michael Goulding in the Rio Negro (Amazon Basin), and deposited in the fish collection of the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil. Two specimens included within this material, from separate localities, represent a distinctive new taxon so far completely unknown, here proposed as a new genus and species, *Stauroglanis gouldingi.*

The relationships of the new taxon are not immediately evident. Characters traditionally used to delimit subgroups of Trichomycteridae place it in the subfamily Trichomycterinae. Nevertheless, a comparative anatomical survey of *Stauroglanis* and other trichomycterids revealed additional characters in disagreement with that initial subfamilial placement. The apomorphies relevant for intrafamilial relationships indicate that the new taxon is mostly closely related to the Sarcoglanidinae, rather than to any Trichomycterinae, as this subfamily is presently constituted. This situation led to an examination of all characters so far used to define the Trichomycterinae, in terms of their potential value as indicators of monophyly. This analysis showed that there is no known character that conflicts with the inclusion of *Stauroglanis* within the Sarcoglanidinae. None of the characters previously used to diagnose the Trichomycterinae can be considered as apomorphic at the level of this intended assemblage, thus, no evidence supports monophyly of the subfamily. On the other hand, the derived characters shared by *Stauroglanis* and sarcoglanidines are unique to them, and represent unambiguous synapomorphies indicating that they form a monophyletic group.

Although evidence supporting the proposed relationship of *Stauroglanis* with the remaining Sarcoglanidinae was not scarce, the analysis was limited by the lack of access to material of *S. simplex* and *M. gelatinosus.* As noted above, known material of the Sarcoglanidinae consists only of the holotype of *S. simplex* and the holotype and single paratype (previously cleared and stained) of *M. gelatinosus,* all of them deposited in the California Academy of Sciences. This material was loaned several years ago, subsequent to its use by Myers and Weitzman, and never returned. Since I was unable to examine these specimens for the present paper, comparisons relative to them were limited to the data in the original description (Myers and Weitzman, 1966), to the osteological sketches provided in Baskin (1973, unpubl. thesis) of the single cleared and stained paratype of *M. gelatinosus,* and to some osteological drawings of the same specimen made for me by Dr. Scott Schaefer.

ACKNOWLEDGMENTS

A previous version of this work was a dissertation submitted in partial fulfillment of a bachelor's degree in biology (major in zoology), at the Universidade Federal do Rio de Janeiro, Brazil. The final version of the manuscript was prepared at the Department of Ichthyology of the American Museum of Natural History. Support by both institutions to the author is gratefully acknowledged. I further wish to thank Dr. Heraldo Britski, the advisor of this study, for his continuous help and encouragement, and Prof. Mario Brum

and Drs. Naércio Menezes and José Figueiredo for valuable advice. I owe much, in both academic and personal grounds, to Drs. Érica Caramaschi, Ricardo Castro, and Wilson Costa, and I am pleased for their friendship. Dr. Carl Ferraris shared with me his knowledge of catfish anatomy and systematics, in many enjoyable conversations. Dr. Gareth Nelson has been most helpful in various aspects of my permanence at the American Museum. I am also indebted to Dr. Gloria Arratia for her attention and interest in my work. Dr. Silvina Menu-Marque kindly provided specimens of *Trichomycterus boylei* for study. Dr. Scott Schaefer sent useful anatomical information on the cleared and stained paratype of *Malacoglanis gelatinosus*. My special recognition is extended to Dr. Michael Goulding, for depositing his material in the collections of the MZUSP, where *Stauroglanis* ultimately became available for study. Various versions of the manuscript benefitted from reviews by Drs. Gloria Arratia, Heraldo Britski, Érica Caramaschi, Ricardo Castro, Wilson Costa, Carl Ferraris, John Lundberg, Naércio Menezes, Gareth Nelson, Scott Schaefer, Richard Vari, and Stanley Weitzman.

Financial support was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brazilian Federal Government. Travel support was also provided by Fundação de Amparo à Pesquisa no Estado do Rio de Janeiro (FAPERJ), Government of the State of Rio de Janeiro. Preparation of the final version of the manuscript was also financially supported by a grant (Graduate-Undergraduate Research Program) by the American Museum of Natural History.

Materials and Methods

All measurements were point-to-point, taken with calipers on the left side of specimens. The caudal peduncle depth was measured at the vertical through the insertion of principal caudal-fin rays. The caudal peduncle length was from the base of the last anal-fin ray to the middle of the caudal fin base. Lengths of the dorsal- and anal-fin bases were measured from the first visible ray to the point of posterior attachment. Remaining measurements followed Tchernavin (1944: 251–252). Dorsal- and anal-fin ray counts for *Stauroglanis* included all rays and splints. Dorsal- and anal-fin ray counts for taxa other than *Stauroglanis* included two anterior unbranched rays plus all following rays. The two posteriormost closely positioned rays, when present, were counted separately. Principal caudal-fin ray counts included all branched rays plus one unbranched ray in each lobe. Counts are given for each lobe (upper first), separated by a plus sign. All values in parentheses are those of the paratype.

Osteological preparations were cleared and counterstained for cartilage and bone, according to a modified version of the method of Dingerkus and Uhler (1977). A considerable part of the osteological material examined was prepared prior to this study, and part of it is stained only for bone.

Drawings were sketched with the aid of an Aus Jena stereomicroscope and camera lucida. Data checking and addition of details were accomplished by means of an Olympus stereomicroscope at greater magnifications. In all osteological illustrations (except in diagrammatic drawings), bony tissue is represented by stipple and cartilage is represented by open circles.

Only two specimens of *Stauroglanis gouldingi* are known, with the one in better condition chosen as holotype. The paratype, in a very poor state of preservation, was made into an osteological preparation. In spite of its fragile condition, the paratype cleared well and stained satisfactorily for both bone and cartilage. Its bones are, however, more loosely connected and the cleared tissues less firm than is usual for well-preserved fishes subsequently cleared and stained. Morphometric data for the paratype were taken prior to the clearing and staining of the specimen.

Anatomical Abbreviations Used in Figures

b	basioccipital
ba	basibranchials
c_{1-5}	ceratobranchials 1 to 5
e	epioccipital
e_{1-4}	epibranchials 1 to 4
el	lateral ethmoid
ex	exoccipital

f	frontal
h	hyomandibula
hb_{1-3}	hypobranchials 1 to 3
hy_{1-5}	hypurals 1 to 5
i	interopercle
l	lacrimal
m	maxilla
me	mesethmoid
mt	metapterygoid
o	orbitosphenoid
op	opercle
p	pterotic
p_{3-4}	pharyngobranchials 3 and 4
pa	parasphenoid
pal	palatine
ph	parhypural
pm	premaxilla
po	preopercle
pr	prootic
ps	pterosphenoid
pu_1+u_1	preural centrum 1 plus ural centrum 1
q	quadrate
s	sphenotic
sc	supracleithrum (posttemporosupracleithrum?)
so	supraorbital (antorbital?, frontolacrimal tendon bone?)
su	supraoccipital
tp	toothplate of pharyngobranchial 4
u	uroneural
ub	unnamed submaxillary bone
v	vomer
w	Weberian complex and capsule

Material Examined

Comparative material examined for this study is listed below. The number of specimens given (ex.) refers to the number of specimens examined, not to the total number of specimens available in the respective lot. Unless otherwise noted, specimens are undissected, alcohol preserved. The symbol CS indicates that the specimens were available as cleared and stained preparations; CS (b & c) refers to material stained for both cartilage and bone, CS (b) refers to material stained only for bone. CS (b & c) indicates that at least one of the specimens is stained for cartilage, not necessarily the whole sample. Genera and species are listed alphabetically within each suprageneric taxon.

Abbreviations for institutions are: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP); California Academy of Sciences, San Francisco (CAS); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu Nacional, Rio de Janeiro (MNRJ); National Museum of Natural History, Washington, D.C. (USNM); Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP); Museu Anchieta, Porto Alegre (MAPA—collections now under the care of researchers working at MCP).

Additional comparative data for taxa of the subfamily Trichomycterinae were obtained from Arratia et al. (1978), Arratia and Menu-Marque (1981), Arratia and Menu-Marque (1984), Arratia (1983), and Arratia and Chang (1975).

Trichomycteridae			
Trichomycterinae			
Eremophilus mutisii	MZUSP 35409	1 ex.	CS (b & c)
Hatcheria macraei	MZUSP 35687	1 ex.	CS (b)
Scleronema minutum	MCP 9315	2 ex.	CS (b & c)
Scleronema sp.	MAPA 2409	1 ex.	CS (b & c)
Scleronema sp.	MAPA 1864	1 ex.	CS (b & c)
Trichomycterus amazonicus	MZUSP 37763	1 ex.	CS (b & c)
Trichomycterus brasiliensis	MZUSP 37145	2 ex.	CS (b & c)
Trichomycterus boylei	MZUSP uncat.	2 ex.	CS (b)
Trichomycterus florensis	MZUSP uncat.	2 ex.	CS (b)
Trichomycterus hasemani	MZUSP uncat.	5 ex.	CS (b)
Trichomycterus johnsoni	MZUSP uncat.	1 ex.	
Trichomycterus quechuorum	AMNH 20351	1 ex.	CS (b)
Trichomycterus reinhardti	MZUSP uncat.	2 ex.	CS (b)
Trichomycterus tiraque	AMNH 39740	2 ex.	CS (b)
Trichomycterus vermiculatus	MZUSP uncat.	2 ex.	CS (b)
Trichomycterus sp.	MZUSP 36966	1 ex.	CS (b)

Glanapteryginae			
Listrura nematopteryx	MZUSP 37138	5 ex.	CS (b & c)
Glanapteryx anguilla	MZUSP 36530	2 ex.	CS (b & c)
Pygidianops eigenmanni	CAS 11121	1 ex.	CS (b & c)
Typhlobelus ternetzi	CAS 11119	1 ex.	CS (b)
Vandelliinae			
Paracanthopoma sp.	MZUSP 29524	1 ex.	CS (b)
Paravandellia bertonii	MZUSP 27707	1 ex.	CS (b)
Paravandellia sp.	MZUSP uncat.	2 ex.	CS (b & c)
Vandellia sp.	MZUSP 29155	2 ex.	CS (b)
Tridentinae			
Tridensimilis sp.	MZUSP 36302	2 ex.	CS (c & b)
Tridentopsis sp.	MZUSP 36303	2 ex.	CS (b & c)
Stegophilinae			
Haemomaster venezuelae	AMNH 10194	1 ex.	CS (b)
Henonemus sp.	MZUSP uncat.	1 ex.	CS (b)
Homodiaetus anisitsi	MCP uncat.	2 ex.	CS (b)
Ochmacanthus alternus	MZUSP 30467	2 ex.	CS (b)
Ochmacanthus orinoco	MZUSP 30473	1 ex.	CS (b)
Ochmacanthus reinhardti	AMNH 27693	1 ex.	CS (b)
Parastegophilus maculatus	MZUSP 35736	1 ex.	CS (b)
Pseudostegophilus nemurus	MZUSP 30427	2 ex.	CS (b)
Trichogeninae			
Trichogenes longipinnis	MZUSP uncat.	6 ex.	CS (b & c)
Nematogenyidae			
Nematogenys inermis	MZUSP 36956	1 ex.	CS (b & c)
	AMNH 55329	1 ex.	CS (b & c)
Callichthyidae			
Brochis coeruleus	AMNH 43411	2 ex.	CS (b & c)
Callichthys callichthys	AMNH uncat.	3 ex.	CS (b)
Corydoras aeneus	AMNH 21772	1 ex.	CS (b)
Hoplosternum punctatum	AMNH 11580	4 ex.	CS (b)
Scoloplacidae			
Scoloplax dicra	AMNH 10204	1 ex.	CS (b)
Scoloplax sp.	MZUSP 37489	2 ex.	CS (b & c)
Astroblepidae			
Astroblepus grixalvii	USNM 167876	2 ex.	CS (b & c)
Astroblepus sp.	AMNH 20873	1 ex.	CS (b)
Loricariidae			
Farlowella sp.	AMNH 21813	1 ex.	CS (b & c)
Hypoptopoma carinatum	AMNH 39828	2 ex.	CS (b & c)
Hypostomus sp.	AMNH 43453	1 ex.	CS (b & c)
Loricaria cataphracta	AMNH 40081	1 ex.	CS (b & c)
Pterygoplichthys sp.	AMNH uncat.	3 ex.	CS (b & c)
Diplomystidae			
Diplomystes chilensis	AMNH 55318	1 ex.	CS (b & c)
Diplomystes sp.	MZUSP 36953	1 ex.	CS (b & c)
Pimelodidae			
Chasmocranus rosae	ANSP 137968	2 ex.	CS (b & c)
Microglanis sp.	AMNH 20878	1 ex.	CS (b & c)
Rhamdia hypselurus	AMNH 24870	2 ex.	CS (b)

Pimelodus pictus	AMNH uncat.	2 ex.	CS (b & c)
Sorubim lima	AMNH 42128	1 ex.	CS (b)
Auchenipteridae			
Asterophysus batrachus	ANSP 158294	1 ex.	CS (b & c)
Auchenipterus demerarae	AMNH 55352	2 ex.	CS (b & c)
Trachycorystes fisheri	AMNH 5332	1 ex.	CS (b)
Aspredinidae			
Aspredinichthys tibicen	AMNH 7094	1 ex.	CS (b)
Bunocephalus coracoideus	AMNH 21815	1 ex.	CS (b & c)
Hypophthalmidae			
Hypophthalmus edentatus	AMNH 55396	2 ex.	CS (b & c)
Helogenidae			
Helogenes marmoratus	AMNH 7113	1 ex.	CS (b)
	AMNH 13332	1 ex.	CS (b)
Ariidae			
Genidens genidens	AMNH 20725	2 ex.	CS (b)
Bagridae			
Bagrus bayad	USNM 229884	1 ex.	CS (b & c)
Chrysichthys auratus	USNM 229728	1 ex.	CS (b & c)
Pseudobagrus fluvidraco	AMNH 10438	2 ex.	CS (b & c)
Ictaluridae			
Ameiurus nebulosus	AMNH 37682	1 ex.	CS (b)
Amblycipitidae			
Amblyceps mangois	ANSP 59316	1 ex.	CS (b & c)
Siluridae			
Kryptopterus bicirrhis	AMNH 43171	1 ex.	CS (b & c)
Sisoridae			
Glyptosternon sinense	AMNH 10265	2 ex.	CS (b & c)
Exostoma kishinouyei	AMNH 15261	1 ex.	CS (b & c)
Amphiliidae			
Amphilius pictus	AMNH 12314	1 ex.	CS (b)
Phractura scaphirhynchura	AMNH 6622	2 ex.	CS (b)

SYSTEMATIC ACCOUNTS

Stauroglanis, new genus

TYPE SPECIES: *Stauroglanis gouldingi,* n. sp.

DIAGNOSIS: A member of subfamily Sarcoglanidinae, of the Trichomycteridae. The following features distinguish *Stauroglanis* from other taxa of the family: (1) premaxilla with narrow lateral process, extending parallel to maxilla, of about same length as basal portion of premaxilla; (2) premaxilla with ventral flat expansion near distal limit of premaxillary teeth distribution; (3) small irregular-shaped bone below posterior articular process of maxilla; (4) two paired dorsal openings on neurocranium, each one framed by supraoccipital, sphenotic, and frontal; (5) vomer roughly rhombus shaped, with deep necklike constriction at point of articulation with palatine; (6) single ossified basibranchial element, crucifix shaped, with two lateral articular processes. None of these characters has been checked in *Sarcoglanis simplex* (known only from the holotype), and characters 2, 3, and 6 have also not been checked in *Malacoglanis gelatinosus.* All six characters are otherwise unique to *Stauroglanis* within trichomycterids. Other characters useful for the identification and systematic placement of *Stauroglanis* include: maxilla greatly enlarged, longer than premaxilla; cartilaginous head of palatine with thick anterior

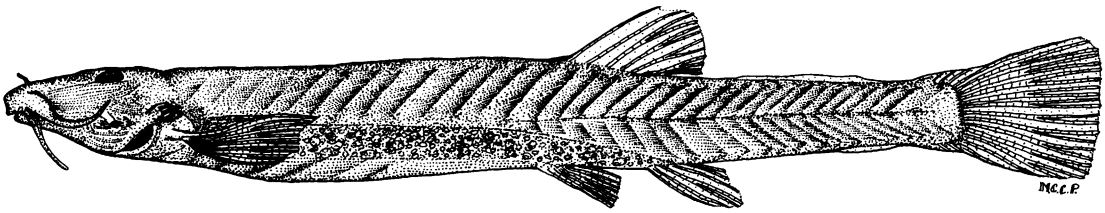

Fig. 1. Lateral view of *Stauroglanis gouldingi,* n. gen. et sp., holotype, MZUSP 31088. Scale = 5 mm.

ossification; quadrate with very long and wide anterodorsal process, distally directed backward; metapterygoid very reduced in size, partly surrounded by anterodorsal process of quadrate; interopercle reduced, with very narrow odontode attachment facet and only about three odontodes; opercle with only two large odontodes; palatine anteroposteriorly elongate; lacrimal elongate; number of teeth on premaxilla reduced (about six); size of anal fin reduced (six rays); eyes large and conspicuous; nasal barbel present but very short; snout region of head elongate; mouth subterminal, not suckerlike; all teeth conical, without evident specializations in shape; no lateral saclike adipose organ dorsoposterior to pectoral fin insertion.

ETYMOLOGY: From the Greek *stauros* (cross) and *glanis* (the catfish of Aristotle), in allusion to the crucifix shape of the single ossified basibranchial element. Gender masculine.

INCLUDED SPECIES: Only one known species, *Stauroglanis gouldingi,* n. sp.

Stauroglanis gouldingi, new species
(Figures 1–3)

HOLOTYPE: MZUSP 31088, 23.3 mm SL, Brazil, Estado do Amazonas, Rio Daraá (Rio Negro drainage system), Cachoeira do Aracu, near waterfall; coll. Michael Goulding, 10 Feb. 1980.

PARATYPE: MZUSP 30411, 23.8 mm SL, Brazil, Estado do Amazonas, Rio Negro, Island of Cumuru, near Rio Arirará; lake on island, muddy beach; coll. Michael Goulding, 1 Feb. 1980, 14:00 hr. Specimen stored in glycerol, partly dissected, cleared, and stained for cartilage and bone.

DIAGNOSIS: See generic diagnosis.

DESCRIPTION: Morphometric data for the holotype and paratype given in table 1.

Body elongate, roughly rounded in cross section in trunk region and gradually more compressed toward caudal region. Dorsal surface of body flat along its whole length. Dorsal body profile nearly straight, gently convex along its middle third. Ventral body profile concave shortly after insertion of pectorals, slightly convex along abdominal region, and straight from pelvic-fin insertion to base of caudal fin. Body deepest at about level of pelvic-fin insertion, gradually less deep toward caudal fin. Ventral profile of caudal peduncle straight, dorsal profile very slightly convex along its anterior half. Dorsal and ventral profiles of caudal peduncle slightly

TABLE 1
Morphometric Data for Holotype (A) and Paratype (B) of *Stauroglanis gouldingi,* n. gen et sp.
(All measurements expressed in mm)

	A	B
Standard length	23.3	23.8
Total length	27.3	26.8
Head length	4.2	4.7
Body depth	2.7	3.0
Caudal peduncle length	6.4	6.2
Caudal peduncle depth	1.4	1.5
Predorsal length	13.6	13.9
Preanal length	16.1	17.0
Head width	3.2	3.0
Head depth	1.8	1.6
Interorbital	0.5	0.8
Snout length	2.1	2.3
Dorsal fin base length	2.4	2.2
Anal fin base length	1.3	1.2
Prepelvic length	12.2	11.6
Breadth of mouth	1.1	1.6

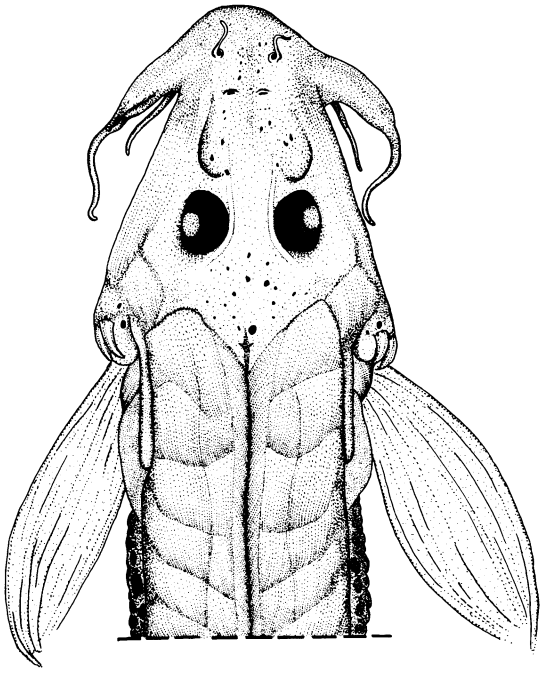

Fig. 2. Dorsal view of the head of *Stauroglanis gouldingi,* n. gen. et sp., holotype, MZUSP 31088. Scale = 1 mm.

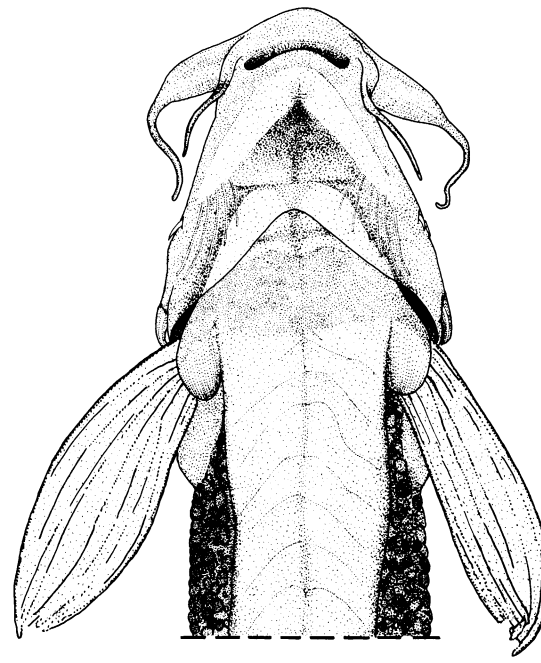

Fig. 3. Ventral view of the head of *Stauroglanis gouldingi,* n. gen. et sp., holotype, MZUSP 31088. Scale = 1 mm.

and evenly converging toward caudal fin. No dorsal or ventral expansion on caudal peduncle due to presence of procurrent rays. Dorsal profile of head flat, nearly continuous in straight line with dorsal profile of body. Ventral profile of head convex from lower lip to gular region (apparently due to expanded position of hyoid arch at time of fixation), then horizontally straight along short distance continuous with ventral trunk region.

Myotomes conspicuous, readily visible along whole body, more prominent along region from anal-fin base to middle length of caudal peduncle. Myotomes progressively narrower and more angled toward caudal fin. Deep horizontal skeletogenous septum separating epaxial and hypaxial muscle masses, deepest at about same region where myotomes are most prominent. Ventral region with easily visible muscle segments, more conspicuous anteriorly.

Long lateral band of apparently adipose tissue running from region of pectoral-fin attachment to posterior margin of anal-fin base, becoming narrower posteriorly. Band slightly hyaline, composed of large number of variously sized globular bodies, irregularly distributed in apparently more than one layer. Globular bodies with appearance of oil drops merged in water, but quite rigid to contact. Band's outer surface rough and irregular, matching contours of numerous individual globular bodies.

Integument very thin and transparent, superficial muscles, and some other internal structures readily visible. Papillae not visible on skin, even on lips and barbels of holotype, but visible in paratype as tiny alcian-blue stained dots over entire skin.

Head elongate, distinctly narrowing anteriorly, triangle shaped in dorsal view and flat. Rostral part of head very long. Anterior margin of snout rounded and convex. Mouth subterminal and narrow, lips not notably fleshy. Branchial membranes very thin and translucent, attached to isthmus only at anteriormost mesial point, gill openings unconstricted. Five to six branchiostegal rays seen without difficulty through branchial membranes. Eyes very large and conspicuous, dorsally located. Eyeball entirely visible through skin, with laterosuperior orientation. Eyes lo-

cated almost completely on posterior half of head length. Transparent areas below skin just in front of each eye, apparently filled with gelatinous matter, merging gradually with remainder of head surface. Opercular patch of odontodes small but visible in both lateral and dorsal views, partly covering pectoral fin insertion. Interopercular patch of odontodes located below each eye, extremely small and hyaline, inconspicuous on head. No fold of skin underlying interopercular patch of odontodes in holotype, very small fold present in paratype. Interopercular patch of odontodes located only slightly below horizontal through opercular patch.

Bony base of maxillary barbel very large, but more slender than in *Sarcoglanis, Malacoglanis,* and *Scleronema.* Distance between tips of bony portions of barbels approximately equal to head width, when maxillae completely protruded. Soft portion of maxillary barbel very slender, about of same length as bony section. Rictal barbel of approximately same length and diameter as soft portion of maxillary barbel. Origin of rictal barbel under anterior part of bony base of maxillary barbel. Maxillary and rictal barbels with slender central rods. Nasal barbel very short and thin, hardly visible from above, its origin at rim of anterior nare. Nares tiny and difficult to see, due to combination of reduced size and general transparency of tissues. Anterior nare surrounded by fold of skin, continuous posterolaterally with nasal barbel. Posterior nares extremely reduced and almost invisible, their openings oriented backward. Distance between anterior nares considerably greater than between posterior pair, and greater than interorbital width.

Lateral line short (less than half of head length) but very conspicuous externally, its shape strongly outlined by covering skin. Axillary organ well developed and translucent, running just below lateral line and slightly longer than it. Origin of axillary organ immediately above insertion of pectoral fin, its length less than half that of the fin.

Small rayless cutaneous folds running above and below part of caudal peduncle. Upper and lower folds with irregular margins and located on different regions of caudal peduncle. Folds extremely thin and low, very transparent and almost invisible under stereomicroscope. No predorsal fold.

Fins very damaged in preservation, original shape difficult to determine accurately, interradial membrane mostly destroyed. Reconstructed approximate outlines (from relative lengths of rays) shown in figure 1. Pectoral fin moderately elongate, approximately of same length as head. First pectoral ray (unbranched) not prolonged as filament, with same general appearance as following branched rays. Pectoral-fin rays 8 (7). Origin of dorsal fin on posterior half of standard length, behind insertion of pelvic fins. Dorsal-fin rays 8 (8). Anal-fin origin approximately below posterior half of dorsal fin base. Anal-fin base short, much shorter than dorsal-fin base. Anal-fin rays 6 (6). Pelvic fins extending beyond anal and urogenital openings, but not reaching origin of anal fin. Pelvic-fin rays 5 (5). Pelvic splint absent. All fins with some branched rays (exact proportion of branched and unbranched rays impossible to verify due to their poor condition). Principal caudal rays 6 + 6 (6 + 6). Procurrent caudal rays small, inconspicuous, and few in number; 4 dorsal and 4 ventral (data from paratype).

Pigmentation in preservative: Body almost totally white, dark pigment restricted to eyes and some isolated melanophores, forming very ill-defined pigmentation pattern. Individual melanophores very dark and quite large, of variable sizes. A group of melanophores scattered over neurocranium, over area corresponding to supraoccipital and basal portion of frontals; another on area of opercle; one on area of interopercle, and another scattered on mesial region of snout (figs. 1 and 2). Mesial ventral region from beginning of anal fin to last portion of caudal peduncle with narrow sparse scattering of melanophores. Caudal fin with scattered dark chromatophores at basal portion. Remaining fins transparent, devoid of dark pigment.

DISTRIBUTION: Known only from the localities cited for the holotype and paratype.

ETYMOLOGY: The specific name honors Dr. Michael Goulding, who collected the type specimens and all known material of *Stauroglanis,* in recognition of his contributions to the knowledge of the Amazonian fish fauna.

REMARKS: From data provided in the original description and illustration of *Trichomycterus santaeritae* (Eigenmann, 1918), it is

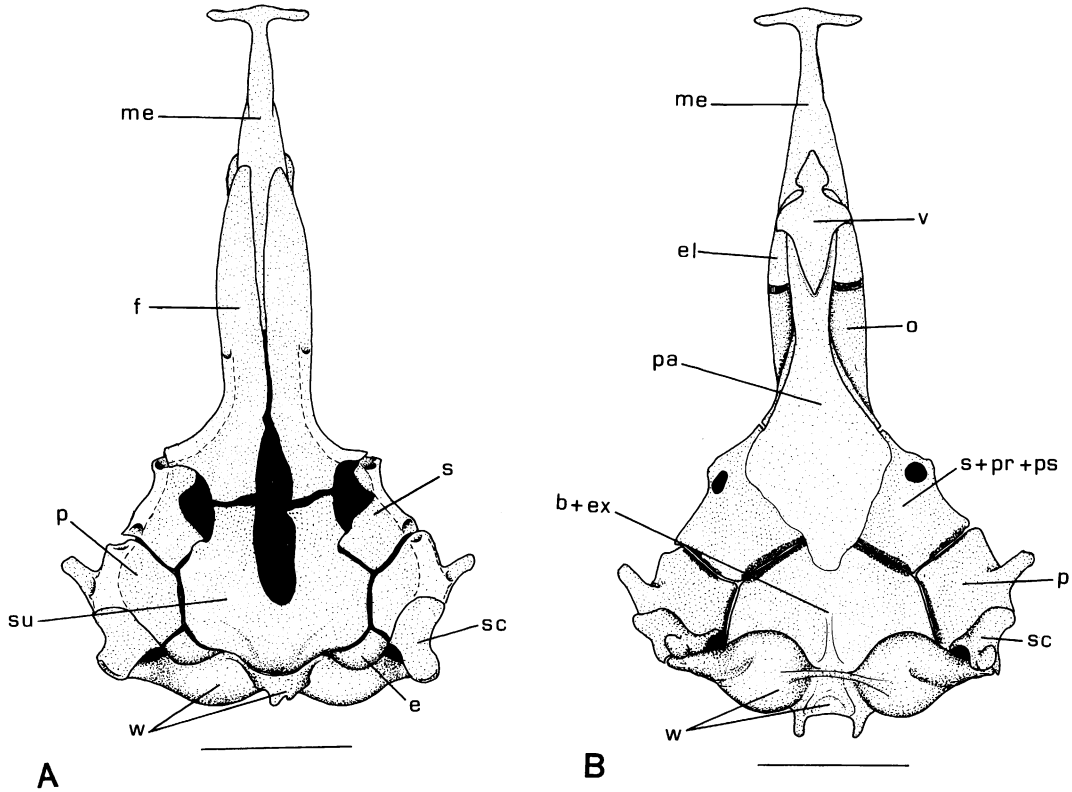

Fig. 4. Skull of *Stauroglanis gouldingi,* n. gen. et sp., paratype, MZUSP 30411. **A,** dorsal view; **B,** ventral view. Scale = 1 mm.

possible that there is a close relationship between this species and *Stauroglanis gouldingi.* While the two taxa are clearly distinct, judging from differences in color pattern, fin-ray counts, and number of odontodes, there are some notable resemblances that deserve notice. Eigenmann (1918: 341) described the teeth of *T. santaeritae* as "in a single series or in a very narrow band." This feature contrasts with the condition in most species of the genus *Trichomycterus,* and agrees with that observed in the dentary and premaxilla of *Stauroglanis* (see Osteology below). Another remarkable feature is the length of the nasal barbels, which are very short in both *S. gouldingi* and *T. santaeritae.* In the great majority of *Trichomycterus* species the nasal barbel is much longer than in those two taxa. Although not mentioned in the description, the bony base of the maxillary barbel illustrated for *T. santaeritae* seems to be very elongate, similar to the condition in *Stauroglanis* and its closest relatives (see sections Phylogenetic Relationships of *Stauroglanis* and Relationships of the Sarcoglanidinae with Other Trichomycteridae). Another noteworthy character present in *T. santaeritae* is the very large eye, which once again recalls the state in *Stauroglanis.*

These characteristics become particularly interesting when it is recognized that there are no derived characters supporting the present generic and subfamilial placement of *T. santaeritae* (see section below on the phyletic status of the subfamily Trichomycterinae). Thus, phylogenetic relationships of *T. santaeritae,* as well as of most other trichomycterine species, are a completely open question.

Unfortunately, *T. santaeritae* is so far known only from the holotype, and it was not possible to examine the internal characters necessary for an adequate comparison with *Stauroglanis.* It is thus preferable, for the time being, to maintain *T. santaeritae* in the genus *Trichomycterus.* The traits pointed

out above may serve as starting points for additional research, but are too scanty to use as a basis for a hypothesis of relationship and its consequent nomenclatural alterations.

OSTEOLOGY

The aim of this section is to provide an account focusing on osteological traits of some importance for discussions of relationships, and not an exhaustive description of the whole skeleton of *Stauroglanis.* Consequently, some bones and bony complexes in which no informative variation could be detected are omitted or only very briefly mentioned. All internal osteological data are based on the single cleared and stained paratype of *Stauroglanis gouldingi.*

NEUROCRANIUM

The general shape of the neurocranium is shown in figure 4A and B. The mesethmoid is tilted downward, and the mesethmoid cornua are consequently directed ventrad. The frontals are small and slender, not contacting each other along the midline. They are closest together immediately anterior to the cranial fontanel (but do not suture), and get progressively more separate anteriorly. The space between the frontals is closed by the underlying posterior portion of the mesethmoid, which extends considerably posteriorly. The frontal bears a laterosensory canal segment along the margin of its posterior half, with one pore opening at the anterior extremity and a second immediately anterior to the cranial fontanel. In dorsal view, the sphenotic has a distinctive and almost right-angled concavity anteriorly. The anterior canal-bearing portion of the sphenotic is strongly curved laterally. The very short infraorbital sensory canal exits at the sphenotic-frontal limit, opening as a pore located just posterior to the eye. The supraoccipital is narrow anteriorly and the posterior part of the cranial fontanel extends along more than half of its length. The anterior face of the supraoccipital does not contact the posterior margins of the frontals.

There is a very characteristic dorsal opening on each side of the neurocranium, formed by concavities in the margins of the frontal, supraoccipital, and in particular the sphenotic. The openings are irregular and somewhat bilaterally asymmetrical, not closed by a cartilaginous layer. The single cranial fontanel is wide and not constricted at any point of its length. Its anterior extremity is bluntly pointed and the posterior end is rounded. The lateral ethmoids are very narrow, projecting only slightly beyond the lateral margin of the frontals and inconspicuous in dorsal view. The pterotic has a conspicuous lateral process, which apparently serves as a base for the lateral branch of the sensory canal of the pterotic (the process is damaged on the right side of the cleared and stained paratype).

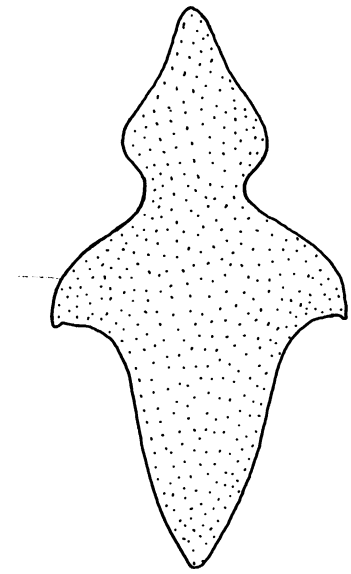

Fig. 5. Vomer of *Stauroglanis gouldingi,* n. gen et sp., paratype, MZUSP 30411. Scale = 1 mm.

The vomer (fig. 5) has a peculiar rhomboidal shape, with a necklike constriction dividing it into smaller anterior and larger posterior portions. Its broadest region is its posterior part, between the two lateral arms, whose tips are directed backward. The necklike constriction of the vomer corresponds to the site of articulation with the palatine. The parasphenoid is narrow anteriorly and wide posteriorly; its anterior extremity bifurcates around the posterior end of the vomer. Posteriorly, the parasphenoid extends to the anterior third of the basioccipital. The posterior wide portion of the parasphenoid is a very

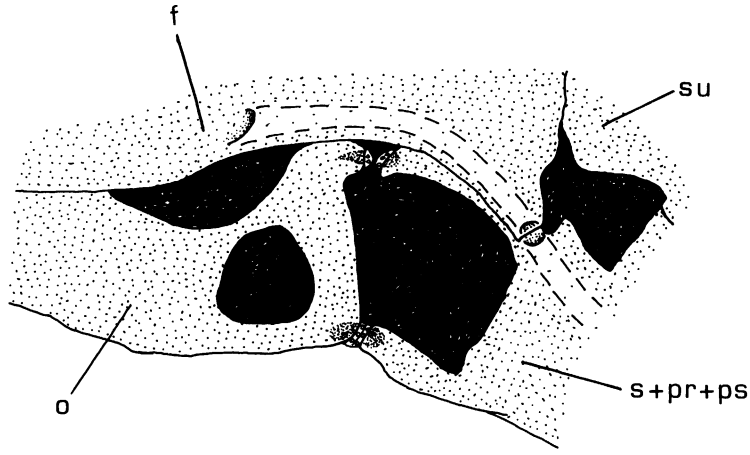

Fig. 6. Partial lateral view of the skull of *Stauroglanis gouldingi,* n. gen. et sp., paratype, MZUSP 30411. Laterosuperior view, anterior to left. Scale = 1 mm.

thin sheet, with the borders difficult to discern against the underlying bones. The prootic, sphenotic, and pterosphenoid are fused into a single ossification (as in all trichomycterids except *Trichogenes longipinnis*). The pterosphenoid portion of the compound bone can be identified as a very narrow ossification, running below and partly hidden by the canal-bearing border of the posterior part of the frontal (fig. 6). Although very narrow, the

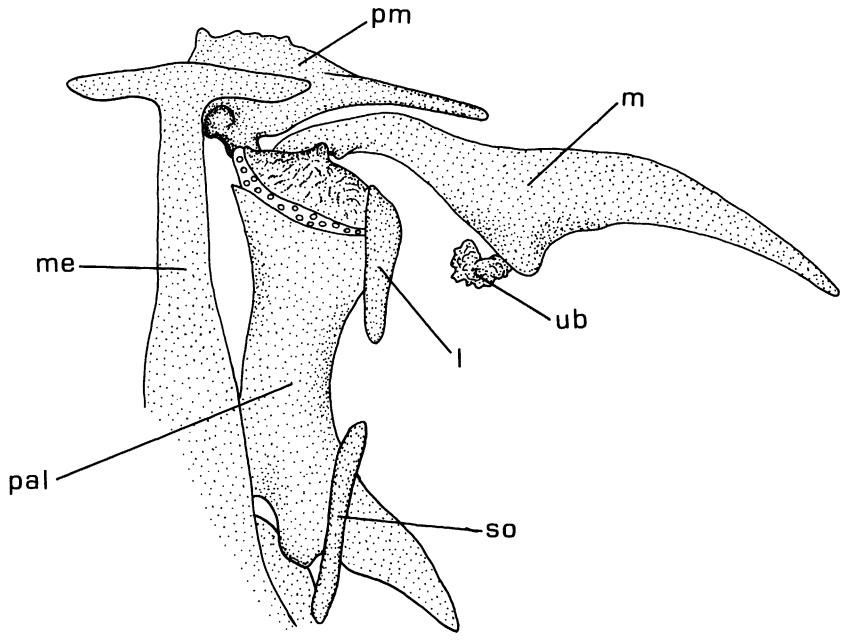

Fig. 7. Upper jaw and associated structures of *Stauroglanis gouldingi,* n. gen. et sp., paratype, MZUSP 30411. Dorsal view. Scale = 1 mm.

pterosphenoid portion still has a small but definite anterior cartilaginous facet in its contact with the orbitosphenoid.

There are three large lateral openings on the side of the neurocranium (fig. 6). The posteriormost and largest foramen (trigeminofacialis) is irregular, bordered dorsally by the portion of the compound bone corresponding to the pterosphenoid, anteriorly by the orbitosphenoid, and ventroposteriorly by the sphenotic-prootic portion of the compound bone. The second foramen (optic) is roughly rounded and is totally bordered by the orbitosphenoid. The anteriormost opening is elongate in shape, bordered dorsally by the frontal and ventrally by the orbitosphenoid; it is probably not a foramen, but an incomplete union between the orbitosphenoid and the frontal.

Jaws and Related Structures (figs. 7 and 8)

The premaxilla bears a long, toothless lateral process. The process is slightly higher than wide and extends along and parallel to the proximal portion of the maxilla. A short and stout dorsal process on the premaxilla articulates with the neck of the mesethmoid, in the region just posterior to the junction of the ethmoid cornua. The premaxillary process is small and short but well differentiated, its dorsal tip is rounded. The premaxillary teeth are simple and conical. Teeth insertion sites indicate that each premaxilla originally had between 14 and 17 teeth, disposed in two irregular rows. Teeth insertion sites cover the entire margin of the body of the premaxilla (the portion apart from the lateral process). Many premaxillary teeth seem to have been lost post mortem, and only between 6 and 9 are still attached to each bone. The attachment of the teeth to the premaxilla is very loose, with tooth bases often uncalcified. A small posterior process of the premaxilla articulates with the anterior piece of the palatine. There is a conspicuous ventral flat expansion on the premaxilla (fig. 8), at the point where the lateral process meets the body of the bone. Its shape is roughly semicircular, and it represents approximately the lateral limit of the distribution of the premaxillary teeth.

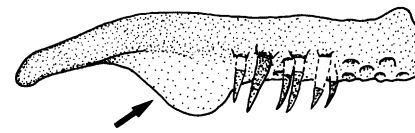

Fig. 8. Right premaxilla of *Stauroglanis gouldingi*, n. gen. et sp., paratype, MZUSP 30411. Anteroventral view. The arrow indicates the premaxillary ventral flat expansion. Scale = 1 mm.

The maxilla is very large, its length almost twice that of the premaxilla (including the lateral process). The proximal extremity of the maxilla articulates closely with the anterior piece of the palatine, and is ligamentously connected to the posterior face of the premaxilla. At about the same level as the ventral flat expansion of the premaxilla, there is a small and low frontoventral flat process on the maxilla. These flat premaxillary and maxillary processes are similar and lie in parallel planes, but do not articulate closely. The posterior process of the maxilla is proportionally enlarged, and is joined ligamentously to the lower jaw. Below this process there is a small isolated ossificiation not homologous to any known bone. The surface of this piece is rough and its shape is irregular, but it is solid and completely separate from the surrounding bones, being originally present on both sides (it is now lost in the right side of the paratype).

The palatine is elongate and most remarkable in being composed of two pieces. The larger posterior piece is apparently the autopalatine itself, homologous with the autopalatine of remaining trichomycterids and other catfishes. The anterior piece seems an anterior ossification of the cartilaginous head that covers the anterior face of the palatine, which is apparently composed of a different type of ossification, with a rough surface that contrasts with the smooth texture of the posterior piece. The anterior piece is thick and compact, with a narrow pointed anterior medial process that partly overlaps the proximal end of the maxilla. A thick layer of cartilaginous tissue remains between the anterior and posterior palatine pieces, but the resulting articulation seems to be completely immovable. The palatine (posterior piece) ar-

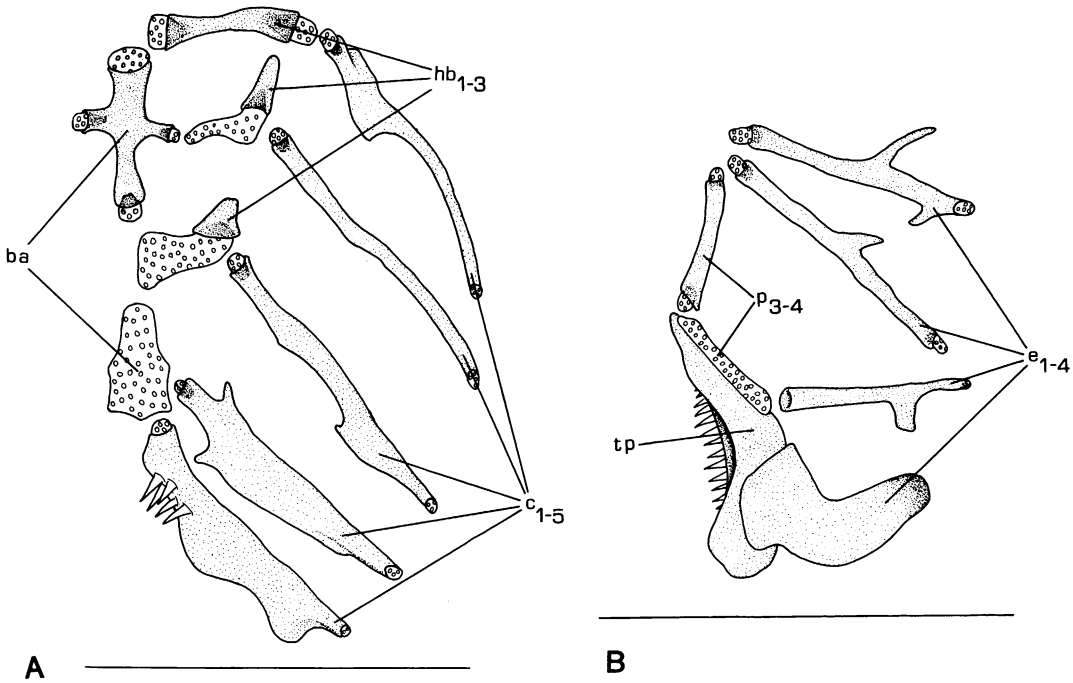

Fig. 9. Gill arches of *Stauroglanis gouldingi,* n. gen. et sp., paratype, MZUSP 30411. **A,** ventral portion under dorsal view, only right paired elements shown. **B,** dorsal portion, dorsal view of right side. Scales = 1 mm.

ticulates medially with the vomer and also with the lateral ethmoid. The anterior palatine piece articulates with the proximal portion of the maxilla and with the posterior process of the premaxilla.

The elongate lacrimal is more than half the length of the frontolacrimal tendon bone (the homologies of this bone are unclear, maybe it is the supraorbital or the antorbital; for some discussion see Baskin, 1973: 158; Britski and Ortega, 1983: 215; and Arratia, 1987: 96). The lacrimal and the frontolacrimal tendon bone are positioned in a straight line, separated by a small space (smaller than the length of the lacrimal). The position of the lacrimal is directly above the lateral limit between the two pieces of the palatine.

Branchial Arches (fig. 9A and B)

There are only two basibranchial elements. The anterior element is ossified, and has a very peculiar cross shape, with four articular facets corresponding to the tips of a crucifix. The anterior articular facet is the largest. The two lateral processes articulate with the proximal cartilaginous portions of the second hypobranchials. The disposition and orientation of the two lateral processes do not match perfectly, and the whole basibranchial bony element looks slightly asymmetrical. It is not clear whether the single basibranchial bone is a highly modified second basibranchial (with disappearance of the third basibranchial) or if it is formed by the fusion between the primitive second and third basibranchials (the first basibranchial is absent in all catfishes). No sign of a suture can be detected. Regardless, it seems certain that the second basibranchial is involved in the formation of the cross-shaped basibranchial element. The posterior basibranchial element is wholly cartilaginous. Given its topological relationships to the fourth and fifth ceratobranchials, it is inferred that it represents the fourth basibranchial of other trichomycterids. This cartilaginous piece is narrower anteriorly and has two concavities on each side of its wider posterior half, into which fit the proximal tips of the fourth and fifth ceratobranchials.

All three hypobranchials show some ossi-

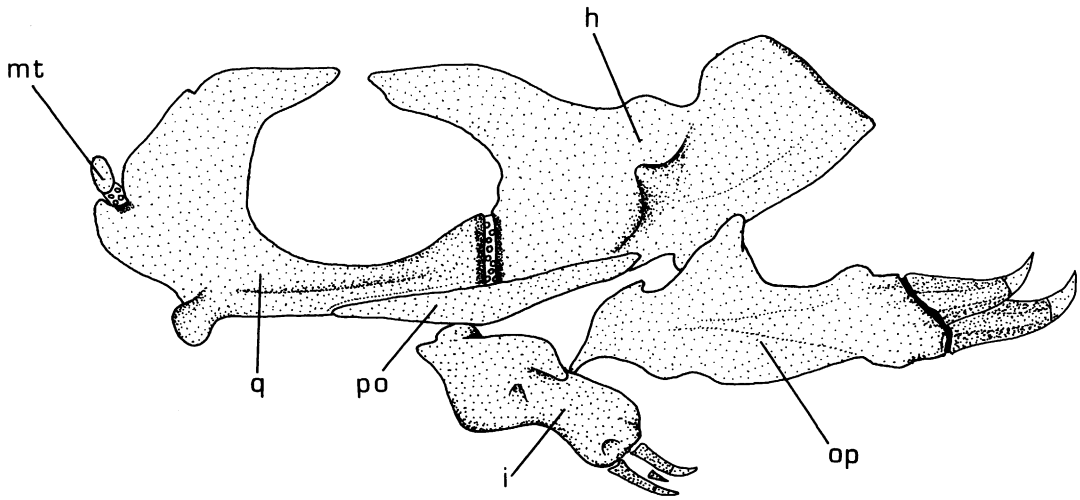

Fig. 10. Suspensorium and opercular apparatus of *Stauroglanis gouldingi,* n. gen. et sp., paratype, MZUSP 30411. Lateral view of left side. Scale = 1 mm.

fication. The first hypobranchial is cartilaginous only at the articular tips. The second has a distal, anteriorly directed conic ossification, but is largely cartilaginous. The third is similar in general shape to the second, but its bony piece is shorter and wider and its cartilaginous portion is larger.

The five ceratobranchials are elongate. The first has a conspicuous expanded proximal portion. Ceratobranchials 2 to 5 are progressively shorter and wider. The fourth has two short pointed processes (uncinate processes), the anterior directed forward and the posterior oriented posteromedially. The fifth bears about five teeth disposed irregularly on a small area on a concavity of its proximal portion. Gill rakers are completely lacking.

There are four epibranchials, the first, second and third are slender and respectively joined to the first, second, and third ceratobranchials. The fourth thicker, dorsally expanded epibranchial articulates with the fourth ceratobranchial, and is united to the fifth ceratobranchial by an elongate gently curved cartilaginous rod. Epibranchials 1 to 3 are slender and each bears a well-defined uncinatelike process, which is anteriorly located on epibranchials 1 and 2, and posteriorly placed on the third. Epibranchials 1 and 2 have convergent distal (upper) tips.

The third and fourth pharyngobranchials are present. The third is a simple ossified rod, and joins anteriorly the first and second epibranchials. The fourth pharyngobranchial is a completely cartilaginous rod joined to the anterior part of its enormous bony tooth plate. The fourth pharyngobranchial articulates anteriorly with the third, and posteriorly with the third epibranchial. The fourth epibranchial articulates only with the tooth plate of the fourth pharyngobranchial, not with its cartilaginous portion. The tooth plate of pharyngobranchial 4 is very large and much more conspicuous than the cartilaginous endochrondral portion. Approximately 14 well-developed teeth are distributed along the whole ventral extension of the tooth plate of the fourth pharyngobranchial. These tooth plate teeth are progressively larger posteriorly, where the tooth plate itself is also wider.

Suspensorium and Opercular Apparatus (fig. 10)

The articular facet for the hyomandibula with the neurocranium extends along the lateral part of the sphenotic and a small anterior portion of the pterotic. The hyomandibula has a fowardly curved conspicuous anterodorsal process, the anterior tip of which closely approaches the posterior tip of the dorsal process of the quadrate, forming a large quadrate-hyomandibular fenestra. A very strong, pointed process for muscle attach-

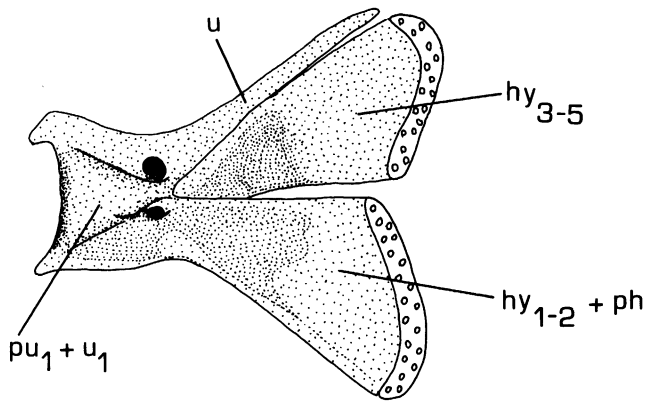

Fig. 11. Caudal skeleton of *Stauroglanis gouldingi,* n. gen. et sp., paratype, MZUSP 30411. Lateral view of left side. Scale = 1 mm.

ment on the hyomandibula is located on the middle ventral region of the bone. This process is obliquely disposed on the hyomandibula and directed markedly anteriorly. A small roundish process, articulating with the opercle, is present on the middle of the ventral margin of the hyomandibula.

The quadrate is elongate, about the same length as the longitudinal axis of the hyomandibula. A well-defined, thick process extends lateroventrally from the anterior tip of the quadrate, articulating with the lower jaw. An enormously developed dorsal process extends from the anterior dorsal region of the quadrate. This process is completely flat, shows a plain surface, and projects frontward from the dorsal margin of the quadrate and then gradually curves backward almost reaching the tip of the anterior process of the hyomandibula.

A small but well-defined concavity on the anterodorsal margin of the dorsal process of the quadrate accommodates the tiny metapterygoid. This bone is a simple oval disc, almost surrounded by the dorsal process of the quadrate. A small but well-defined cartilage links the metapterygoid with the inner surface of the concavity forming a synchondral joint between the two bones. The synchondral articulation between the hyomandibula and the quadrate is robust, provided with a very well-developed interarticular cartilage. There is no overlap of bone over the site of the articulation, i.e., no sutural articulation between the two bones. The posterior process of the palatine closely approaches the dorsal surface (the region above the attachment of the metapterygoid) of the dorsal process of the quadrate, but the two bones do not overlap. A noteworthy character is that the palatine is ligamentously linked more closely to the quadrate than to the metapterygoid.

The preopercle is an elongate bone, dorsally concave along its contact with the hyomandibula and with a short and very thin anteroventral extension closely approaching the dorsal region the interopercle. No sensory canal is associated with the preopercle. There are only two large odontodes at the posterior process of the opercle. These are inserted close together and have very broad bases. In spite of the reduced number of opercular odontodes, the width of the odontode-bearing posterior process of the opercle is not remarkably narrow.

The interopercle is very reduced when compared to the opercle. Its posteroventral, odontode-bearing, process is extremely narrow and carries only three small and weak odontodes (one of each is only partly developed). The interopercular odontodes are much less developed than those on the opercle and overlap the uppermost branchiostegal ray.

Caudal Skeleton (fig. 11)

No individual hypural elements can be discerned. The parhypural, hypural 1, and hypural 2 are represented by a single lower hy-

pural plate, continuous with the compound caudal centrum ($pu_1 + u_1$). Hypurals 3, 4, and 5 are also fused to compose a single upper hypural plate, which contacts tightly but does not fuse with the $pu_1 + u_1$. The upper and lower hypural plates tightly contact each other along their proximal limits, but no fusion or superficial ossification can be detected.

The profiles of the distal margins of the upper and lower hypural plates are curved in a peculiar way, not forming a single, even arch. The two margins turn anteriorly as they approach the midline, and they are most strongly curved at their superior (upper plate) and inferior (lower plate) distal ends. The medial corners of the upper and lower hypural plates are not at the same vertical.

The uroneural is slender and straight (very slightly turned downward distally). It reaches the dorsal margin of the bony portion of the upper hypural plate, but does not cover the distal cartilaginous layer.

The neural arch of the compound caudal centrum is open dorsally (incomplete) and does not form any rudiment of a neural spine. The epural is absent.

The hypurapophysis is small, located slightly in advance and below the opening for the caudal artery.

Other Osteological Characters

There are five abdominal or precaudal vertebrae (here counted as those without a hemal spine, not including those of the Weberian complex) and 29 caudal vertebrae (those with a hemal spine, not including the compound caudal centrum). The three anteriormost precaudal vertebrae bear pleural ribs that are similar in appearance; the first pair is only slightly shorter and thicker than those following. The rib-supporting parapophysis of the first free vertebra is much larger than those of the others.

The lateral line canal is very short; its length is less than that of a single vertebral centrum. The canal has a narrow ring of bone surrounding its anterior end, but is otherwise totally devoid of a bony covering.

There are eight dorsal-fin pterygiophores, with five distal radials (four ossified and one cartilaginous). There are six anal-fin pterygiophores, with three distal radials (two ossified and one cartilaginous). No end piece (stay) is present in either the anal- or in the dorsal-fin supports. There are two proximal radials in the pectoral girdle, both ossified, with the posterior proximal radial much larger than the anterior. Distal pectoral-fin radials are not present as either bone or cartilage.

Each dentary bears about nine loosely attached conical teeth, arranged in a single row.

The nasal bone is absent.

ON THE PAEDOMORPHIC CONDITION OF *STAUROGLANIS*

Some of the features of the skeleton of *Stauroglanis gouldingi* are similar to conditions commonly found in juvenile catfishes. The small number, loose attachment, and weak calcification of the premaxillary and dentary teeth are commonly seen in young trichomycterids of species which do not show this feature as adults. The incomplete connection between some of the neurocranial bones of *Stauroglanis,* such as between the supraoccipital and frontals, between the two frontals, or between the frontals and the orbitosphenoid, are also typical for early ontogenetic stages. The same applies to the general absence of sutural joints in the neurocranium. On the other hand, the neurocranial bones do not resemble juvenile conditions in other aspects. Usually in young stages the bones of the neurocranium lack well-defined borders, with their outer regions gradually becoming a thin cartilaginous (or dermal connective tissue) sheet. In *Stauroglanis,* in contrast, such bones have well-defined borders, lacking the cartilaginous frame. Additionally, *Stauroglanis* has three ossified hypobranchials and two ossified proximal pectoral radials, which are not usual in early ontogenetic stages of trichomycterids. These features indicate that the specimens of *Stauroglanis* studied are not juveniles, despite their small size (23.2–24.0 mm SL) and lack of clear evidence of gonadal development. The apparently juvenile condition of some skeletal traits of *Stauroglanis* are thus interpreted as paedomorphic features. The two other described sarcoglanidines are known from even smaller examples, *Malacoglanis gelatinosus* 18.2–19.9 mm SL and *Sarcoglanis simplex* 19.6 mm SL. The paratype of *M. gelatinosus*

(18.2 mm SL) is reported by Myers and Weitzman (1966: 282) as being "an adult female containing large eggs," supposedly mature eggs. Thus, at least one member of the sarcoglanidine clade can be confidently said to be sexually mature at a very reduced size. This constitutes further support for the interpretation that the juvenile state of some of the characters in *Stauroglanis* and other sarcoglanidines, as well as their small size, represents paedomorphic features.

This situation is not uncommon among South American freshwater fishes. Weitzman and Vari (1988) recently proposed that the phenomenon (called miniaturization) occurs in at least 85 species, and has evolved on at least 34 occasions in the inland fish fauna of South America. Within neotropical catfishes, miniaturization has taken place in at least 12 separate lineages, pertaining to the families Aspredinidae, Callichthyidae, Loricariidae, Pimelodidae, Scoloplacidae, and Trichomycteridae (Weitzman and Vari, 1988). Within trichomycterids, miniature members are known to occur in the subfamilies Trichomycterinae, Glanapteryginae, Vandelliinae, Tridentinae, and Sarcoglanidinae; Weitzman and Vari proposed that miniaturization events evolved at least five times within the family. The authors made this estimate based on information that the five subfamilies belong to separate and divergent clades within the family. This estimate means that the members of a given miniature lineage pertaining to one given subfamily are not the sister group of any other miniature lineage included in another subfamily, thus requiring separate miniaturization events. Weitzman and Vari's evaluation of the number of independent miniaturizations is based on the phylogenetic relationships among the groups under consideration. Some of the estimates about trichomycterid interrelationships are altered by conclusions arrived at in the present work, and need further comment. Weitzman and Vari considered *Pygidianops* the only miniature member of the Glanapteryginae, which does not reach 26 mm SL, the division between miniature and nonminiature species. Nevertheless, as they pointed out, *Glanapteryx* and *Typhlobelus* could also be consided miniatures, because of their paedomorphic features and small head sizes. These two genera were not included in their list, because their standard lengths exceeded 26 mm. Weitzman and Vari called these cases "elongate miniatures," to mean forms that are clearly miniatures in all criteria but the cutoff of 26 mm SL. Taking these factors into consideration, I think it is reasonable to consider that *Glanapteryx* and *Typhlobelus* are miniatures, as well as *Listrura* (a glanapterygine still undescribed by the time Weitzman and Vari's paper went to press). Thus, the subfamily Glanapteryginae is composed exclusively of miniature species. *Stauroglanis,* as well as *Sarcoglanis* and *Malacoglanis,* fall below the 26 mm SL limit, and can be considered a miniature according to Weitzman and Vari's criterion. Consequently, also the Sarcoglanidinae is exclusively composed of miniatures. Baskin (1973) suggested that the Glanapteryginae and Sarcoglanidinae compose a monophyletic group. Although his evidence for this hypothesis has been criticized elsewhere (Pinna, 1988), his proposal remains the only one available for intrafamilial placement of these two subfamilies. If the hypothesis that glanapterygines and sarcoglanidines are each other's closest relatives is correct, and given that both taxa are composed only of miniature species, it follows that a single miniaturization event explains the distribution of paedomorphic features in the two-subfamily clade. Another point relates to *Trichomycterus santaeritae,* listed by Weitzman and Vari as one of the miniature members of the subfamily Trichomycterinae. As mentioned above, there is some evidence indicating that this species may be related to the Sarcoglanidinae. If further investigation confirms this, then the miniature condition of *T. santaeritae* and of all members of the clade Glanapteryginae/Sarcoglanidinae is explained by the same event. The other two trichomycterine miniatures listed by Weitzman and Vari (1988) are *Trichomycterus johnsoni* and *Trichomycterus hasemani,* which are quite similar and probably each other's closest relative. Scarcity of material of *T. johnsoni* has prevented an investigation of its internal anatomy, but *T. hasemani* seems to be more closely related to the subfamily Tridentinae than to any Trichomycterinae (see discussion below on nonmonophyly of Trichomycterinae). The Tri-

dentinae are also composed exclusively of miniature species, since *Tridens melanops* (not included in Weitzman and Vari's list) can be considered an elongate miniature. Thus, similar to the situation with *T. santaeritae* and sarcoglanidines/glanapterygines, miniaturization in *T. hasemani* (and presumably also in *T. johnsoni*) is actually a result of miniaturization at the whole tridentine clade. If all the above putative hypotheses, which undoubtedly require additional corroboration, are correct, then Weitzman and Vari's consideration of five independent miniaturization events within the Trichomycteridae is an overestimation, and three such events would seem to have occurred: at the Glanapteryginae/Sarcoglanidinae clade (including *T. santaeritae*); at the Tridentinae clade (including *T. hasemani* and *T. johnsoni*); and inside the Vandelliinae (in *Paravandellia*). Independence of events in vandelliines and tridentines derives from the hypothesis of Baskin (1973), which places Vandelliinae (with only some miniature members) as the sister group to Stegophilinae (a subfamily without miniatures), and Tridentinae as the sister group to Stegophilinae plus Vandelliinae clade. Considering miniaturization at the base of the clade Tridentinae/Stegophilinae/Vandelliinae is less parsimonious, because it requires one miniaturization plus two subsequent reversals: one in stegophilines, and at least another in the nonminiature vandelliines (assuming that nonminiature vandelliines form a monophyletic group). Separate miniaturizations, in contrast, require only two steps: one event in the tridentine clade and another inside the Vandelliinae.

PHYLOGENETIC RELATIONSHIPS OF *STAUROGLANIS*

Osteological data for the two previously described Sarcoglanidinae are limited to *Malacoglanis gelatinosus,* from unpublished anatomical sketches of Baskin (1973) and from drawings provided by Dr. Scott Schaefer, both based on the single cleared and stained paratype. The illustrations of Baskin show the neurocranium (dorsal and ventral views) and the suspensorium/opercular apparatus. As the internal anatomy of *Sarcoglanis* is completely unknown at present, the following comments are based almost exclusively on the data available for *Malacoglanis.* Until further material of *Sarcoglanis* becomes available, we must assume that the characters in *Malacoglanis* are representative of the condition in *Sarcoglanis.* This assumption does not imply that the state in both taxa are identical, but only that the derived characters shared by *Stauroglanis* and *Malacoglanis* are also shared in some form by *Sarcoglanis.* This assumption presumes that *Sarcoglanis* and *Malacoglanis* compose a monophyletic group, with *Stauroglanis* as its sister taxon (see below). This working assumption seems appropriate, because *Sarcoglanis* and *Malacoglanis* share various external unequivocal synapomorphies, which make it unlikely that *Stauroglanis* is the sister group to only one of them. In agreement with this, no putatively derived character that could be checked in all three genera was found to be exclusive to *Stauroglanis* plus only one of the other two.

A separate ossification of the anterior cartilage of the palatine seems to be present in *Malacoglanis* (fig. 12). This anterior piece in *Malacoglanis* seems to differ from that described above for *Stauroglanis* in its more rounded shape and more irregular profile. One further and noteworthy distinction can be observed in the articulations shown by this anterior section of the palatine. In *Malacoglanis* it apparently articulates only with the proximal portion of the maxilla (fig. 13), while in *Stauroglanis,* as noted, it articulates also with the premaxilla (fig. 7). The relative position of the bone here called lacrimal is also distinct, in *Stauroglanis* it extends directly above the lateral margin between the two palatine pieces, but in *Malacoglanis* it is located more laterally and does not cover the palatine complex (fig. 13). In spite of these small distinctions, the state of the anterior palatine ossification in both taxa is similar, and homology of the structure is a perfectly acceptable proposal according to structural and topological criteria. Such a separate anterior palatine ossification is not present in any other member of the Trichomycteridae. A similar structure occurs in the pimelodid *Rhamdia* (Cussac and Maggese, 1988, referred to this bone as "articular ossicle," whose presence was con-

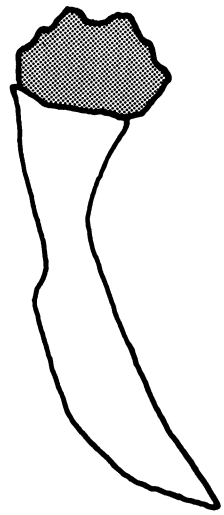

Fig. 12. Dorsal view of left palatine of *Malacoglanis gelatinosus*. Drawing inverted. Anterior piece of palatine stippled. Redrawn and modified after Baskin (1973).

firmed also in the *Rhamdia* species here examined), and in the Sisoridae examined. Considering the many branching points certainly separating *Rhamdia* and sisorids from sarcoglanidines in phylogeny, and further the absence of the structure in at least most other catfishes, it is certain that the anterior palatine ossification has evolved independently in these groups. This ossification can thus be considered a synapomorphy for the Sarcoglanidinae.

The premaxilla in *Malacoglanis* bears a very long and slender lateral process, extending half the length of the maxilla (fig. 13). This process is very similar in shape and position to that described above for *Stauroglanis* (fig. 7), showing equivalent positional relationships to the surrounding structures. In *Malacoglanis* this process is, however, much more elongate than in *Stauroglanis*. Such a long premaxillary process is unique within all trichomycterids, and is absent in *Nematogenys*, in all remaining members of the Loricarioidea and in at least most re-

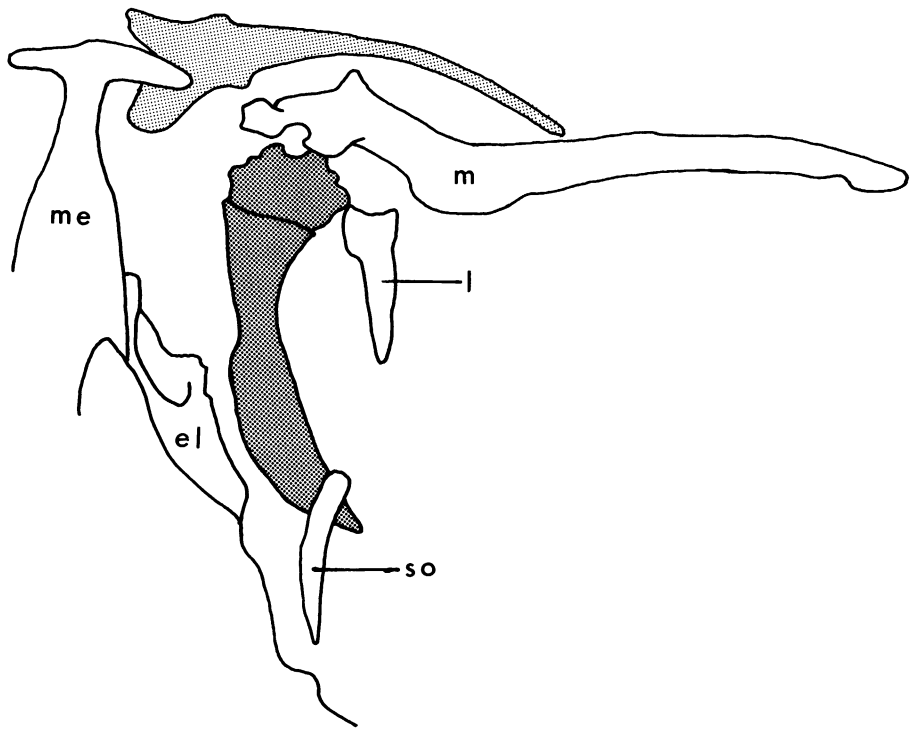

Fig. 13. Relationships among upper jaw elements and other skull structures of *Malacoglanis gelatinosus*. Dorsal view of left side, drawing inverted. Dense stippling represents the premaxilla, light stippling represents the palatine. Redrawn and modified after Baskin (1973).

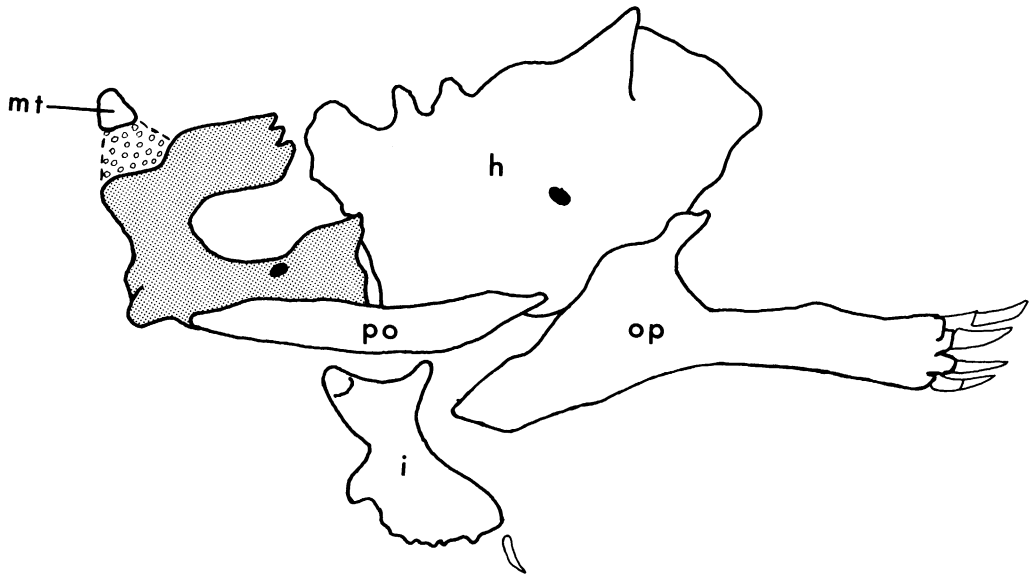

Fig. 14. Suspensorium and opercular apparatus of *Malacoglanis gelatinosus*. Lateral view of right side, drawing inverted. Stippling represents the quadrate. Redrawn and modified after Baskin (1973).

maining catfishes. In Stegophilinae and Tridentinae there is a laterally elongate premaxilla that could be interpreted as continuous with a lateral process. Nevertheless, while the premaxilla and its process in the Sarcoglanidinae are clearly distinct portions, in the Stegophilinae and Tridentinae no such separation exists. In the latter taxa, the entire bone looks like a greatly elongate premaxilla, where no distinct process can be identified. In addition, the premaxillary process is edentulous in the Sarcoglanidinae (in *Malacoglanis* and *Sarcoglanis* the entire premaxilla lacks teeth), while the elongate premaxilla of the Stegophilinae and Tridentinae bears teeth along its entire ventral surface. These structural distinctions do not preclude the possibility that the lateral premaxillary process of sarcoglanidines is homologous with the distal portion of the premaxilla in stegophilines and tridentines, and thus a synapomorphy at a level higher than that of the single subfamily Sarcoglanidinae. Nevertheless, these structural dissimilarities would require considerable further modification in one or both states for them to match a common pattern expressable as a synapomorphy (in tridentines and stegophilines there is not even a properly identifiable lateral premaxillary "process"). On phylogenetic grounds, there is also no reason to accept such a proposal. There exists no additional character supporting the clade Sarcoglanidinae plus Tridentinae plus Stegophilinae, and the only available phylogenetic hypothesis (Baskin, 1973) indicates that tridentines and stegophilines form a monophyletic group with the Vandelliinae, a subfamily with a distinct premaxillary morphology. In view of the above, the presence of a long distal premaxillary process is given as a synapomorphy at the level of the Sarcoglanidinae.

The conspicuous shape of the quadrate of *Stauroglanis* (fig. 10) occurs also in *Malacoglanis* (fig. 14). In both taxa, the anterior portion of the quadrate bears a large dorsal process that curves posteriorly and nearly reaches the anterior portion of the hyomandibula, forming a quadrate-hyomandibular fenestra. Although a dorsal process of the anterior portion of the quadrate occurs also in many other trichomycterids, the large size and posterior extension of the structure are unique to sarcoglanidines. As the state of the quadrate in sarcoglanidines is also distinct from that in the Nematogenyidae, remaining loricarioids, and other Siluroidei, it is proposed as a synapomorphy for the subfamily. A superficially similar fenestra occurs in the suspensorium of the tridentine *Tridensimilis*.

Fig. 15. Diagrammatic representation of the anterior portion of mesethmoid. Dorsal view. **A,** *Stauroglanis gouldingi,* **B,** *Malacoglanis gelatinosus.* (B) is based on a sketch provided by Dr. Scott Schaefer.

Nevertheless, the fenestra in this taxon is formed exclusively by an expansion of the hyomandibula, which has the form of a posteriorly oriented dorsal process similar to the process on the quadrate of sarcoglanidines. Thus, the structures in the two taxa are not the same at all, being formed as extensions of different bones. The conditions in sarcoglanidines and tridentines cannot be considered homologous, consequently not valid as evidence for their relationship.

Stauroglanis and *Malacoglanis* share a distinctive morphology of the anterior portion of the mesethmoid. The mesethmoid cornua in the two taxa are distinctly wider distally than basally, their dorsal profile looks expanded toward the lateral tip (fig. 15A, B). The widening results from expansion in an anteroposterior axis. In *Trichogenes* and most other trichomycterids, as well as in *Nematogenys* and most other catfishes, the mesethmoid cornua narrow uniformly from the base to the tip, without widening at their distal portion (fig. 16A–D). The condition of the mesethmoid cornua in *Stauroglanis* and *Malacoglanis* can thus be considered a synapomorphy for the two taxa. In some Stegophilinae (but not all, see fig. 17B, D), as in *Pseudostegophilus* and *Homodiaetus,* the mesethmoid cornua also looks expanded distally in general appearance (fig. 17A, C). Nevertheless, the condition in these stegophilines differs structurally from that in the comparable region of sarcoglanidines. In *Stauroglanis* and *Malacoglanis* the distal widening is the result of expansion in the anteroposterior axis. In the abovementioned stegophilines, in contrast, the widened outline apparent in dorsal view results from a flat expansion on the ventral margin of the cornua. This expansion is directed posteriorly, and its distal outline can be seen in dorsal view. As an effect of projection, the distal

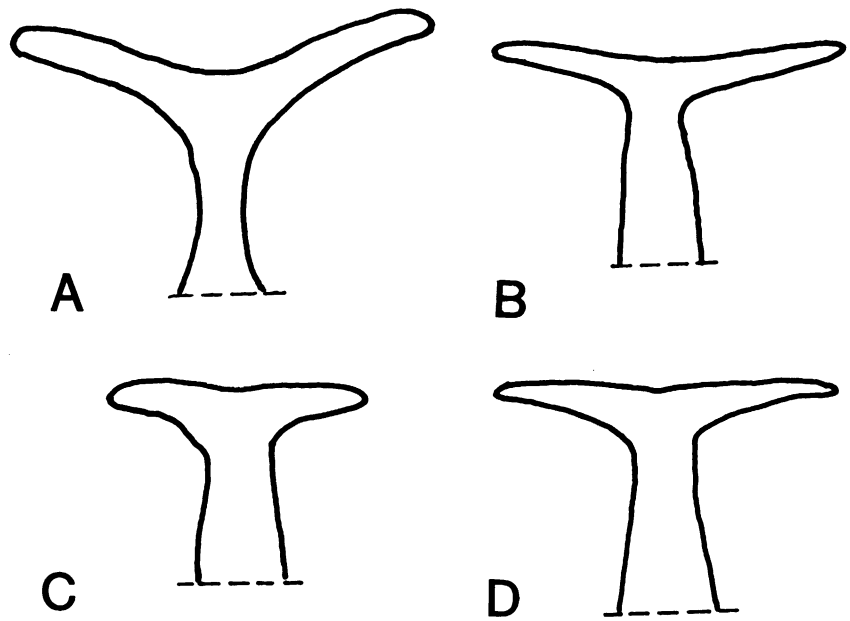

Fig. 16. Diagrammatic representation of the anterior portion of mesethmoid. Dorsal view. **A,** *Nematogenys inermis* (MZUSP 36956); **B,** *Trichomycterus quechuorum* (AMNH 20351); **C,** *Hatcheria macraei* (MZUSP 35687); **D,** *Eremophilus mutisii* (MZUSP 35409).

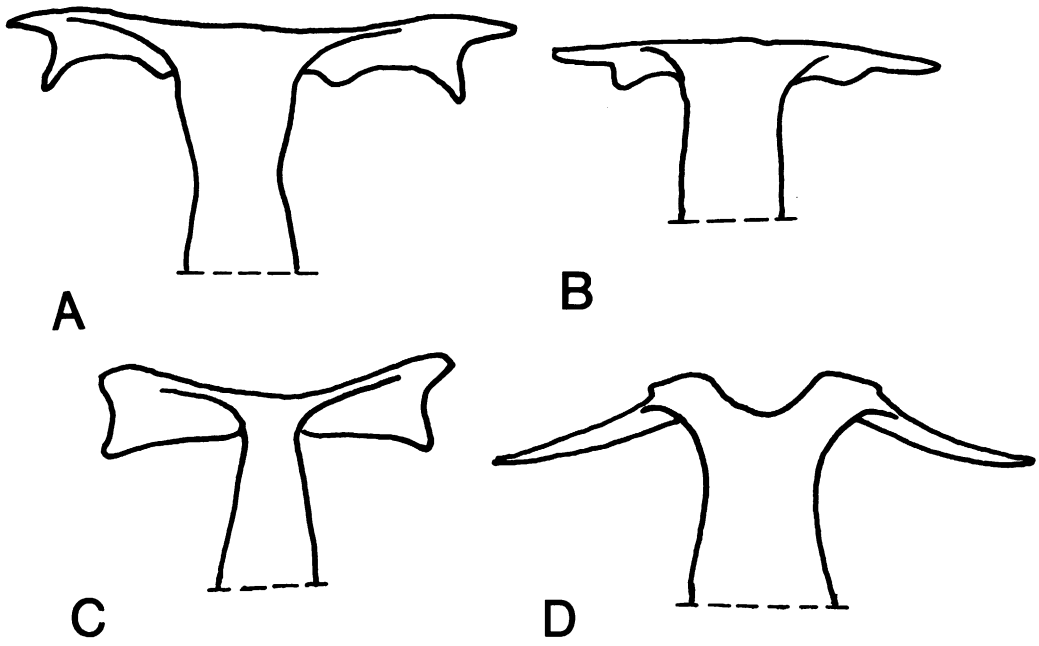

Fig. 17. Diagrammatic representation of the anterior portion of the mesethmoid in some Stegophilinae. Dorsal view. **A,** *Pseudostegophilus nemurus* (MZUSP 30427); **B,** *Ochmacanthus alternus* (MZUSP 30467); **C,** *Homodiaetus anisitsi* (MCP uncat.); **D,** *Haemomaster venezuelae* (AMNH 10194).

profile of the ventral expansion may be mistaken for the actual posterior profile of the cornua, which gives a false anteroposteriorly expanded appearance to the distal part of the cornua. Hence, the expanded distal portion of the mesethmoid cornua in sarcoglanidines and some stegophilines are not homologous.

Another noteworthy feature in the mesethmoid of *Stauroglanis* and *Malacoglanis* is the convex shape of its mesial anterior border (fig. 15A, B). In most other trichomycterids, and also in nematogenyids and in at least most other siluroids, the mesial anterior border of the mesethmoid is concave, often forming an inward angle at the site where the cornua meet (fig. 16A–D). The convex condition in *Stauroglanis* and *Malacoglanis* (more notable in the latter) can thus be given as a further synapomorphy indicating that the two forms compose a monophyletic group.

The above five characters are proposed as synapomorphies for *Malacoglanis, Sarcoglanis,* and *Stauroglanis,* being evidence for these taxa forming a monophyletic Sarcoglanidinae.

Myers and Weitzman (1966) listed six characters that uniquely characterize *Sarcoglanis* and *Malacoglanis* among trichomycterids (their numbering not followed): (1) compact, little-elongated body form; (2) very large, relatively deep head; (3) long adipose fin (high and conspicuous in one species) extending from end of dorsal fin base to almost or quite to caudal fin, and not involved with any procurrent dorsal supporting elements of the latter fin; (4) extremely large, broad pectoral fins, their length far greater than that of the large head; tips of pectoral rays not filamentous but all tips project far beyond membrane; (5) upper jaw toothless; dentary teeth uniserial, long, cylindrical, conical, and hooked inward at tip; and (6) a conspicuous, saclike, fat-filled, adipose organ on each side immediately above pectoral fins.

The six characters listed above are good diagnostic features, but not all of them are evidence for the monophyly of *Sarcoglanis* + *Malacoglanis.* A discussion of each of them is necessary to decide which ones represent synapomorphies.

1. Compact Body Form: This characteristic is very evident in *Sarcoglanis,* but not in *Malacoglanis.* The general body shape of *Malacoglanis* is similar to that in some of the

less-elongate species of *Trichomycterus* and *Scleronema,* as well as in some Stegophilinae and Tridentinae. The compact body form of *Sarcoglanis* is actually very conspicuous, and contrasts with the state in all trichomycterids and most other catfishes. The body shape of *Sarcoglanis* can, with justification, be regarded as apomorphic. Nevertheless, as it is unique to this genus, it is to be interpreted as an autapomorphy. Baskin (1973) expressed this character in terms of vertebral counts. The compact shape of *Sarcoglanis* and *Malacoglanis* would be related to a very low number of vertebrae, 30 to 31, not counting those seven involved in the Weberian complex and compound caudal centrum (Baskin did not specify to which genus each count referred). These reduced vertebral counts are unique within trichomycterids. The closest conditions are found in *Trichomycterus hasemani,* which can have as few as 32 vertebrae, and *T. duellmani* which can have as few as 33 (see Arratia and Menu-Marque, 1984). Although the difference is small, there is no overlap of counts and the reduced vertebral number in *Sarcoglanis* and *Malacoglanis* can be considered a synapomorphy for the two taxa.

2. Large and Deep Head: From the original descriptions, *Sarcoglanis* seems to have a very deep head, more so than any other trichomycterid. In *Malacoglanis,* however, this characteristic is not conspicuous and does not differ notably from that in many other trichomycterids. An adequate and precise evaluation of this character would demand exactly quantified comparative morphometric data for trichomycterids in general—which is still unavailable. In nonrigorous terms, it seems that the condition of this trait is obviously unique in *Sarcoglanis,* but in *Malacoglanis* there occurs overlap with other taxa.

3. Long Adipose Fin: The presence of an adipose fin in *Sarcoglanis* and *Malacoglanis* can be interpreted in two ways. If the adipose fin in these two taxa is considered homologous with that found in other loricarioids and remaining catfishes, it is so a symplesiomorphic feature. On the other hand, if the adipose fin is seen as a secondary acquisition (i.e., as a neomorphic character), it can be regarded as derived. Support for one or the other interpretation, in the absence of ontogenetic data, may come from two sources, structural and/or phylogenetic. At present there are no detailed anatomical studies comparing the structures of the adipose fin of *Sarcoglanis* and *Malacoglanis* to that of remaining catfishes. Based solely on superficial appearance, there is no evidence against their homology. On phylogenetic grounds, the interpretation of the adipose fin in these taxa as either a neomorph or a symplesiomorphy requires a resolved hypothesis of relationships among the outgroups to *Sarcoglanis* and *Malacoglanis* that is presently unavailable. Thus, whether the structure in *Sarcoglanis* and *Malacoglanis* is a primitive adipose fin or a secondary acquisition cannot be decided at present. Nevertheless, it is worth noting that an adiposelike fin occurs also in *Stauroglanis* (in a very reduced state) and in some other members of the Trichomycteridae, namely *Pygidianops* and *Typhlobelus* (the two genera of the subfamily Glanapteryginae) and also in *Scleronema* (a Trichomycterinae). In all these taxa the fin is not supported by procurrent caudal rays (lepidotrichia), but instead only by thin actinotrichial filaments that can be faintly discerned in transmitted light under high magnification. This structure is therefore in agreement with that known for ordinary adipose fins. The structural equivalence does not preclude the adipose fin being a secondary, hence derived, acquisition in some trichomycterids. But if this is the case, the presence of an adiposelike fin would be synapomorphic not for *Sarcoglanis* and *Malacoglanis,* but for a larger assemblage including some other trichomycterid taxa.

4. Large and Broad Pectoral Fins, Pectoral Rays Projecting Far Beyond Fin Membrane: This trait is actually two distinct and independent characters, both derived. The first, the length of the pectoral fins, lacks a precise quantitative evaluation among trichomycterids. Nevertheless, the pectoral fins in both *Malacoglanis* and *Sarcoglanis* are much longer than the head, a condition apparently not found in other members of the family. As the plesiomorphic condition is a shorter pectoral fin, found in *Trichogenes,* most other members of the family, and in the Nematogenyidae, the elongate condition in *Sarcoglanis* and *Malacoglanis* is synapomorphic. The second character, the projection of the

pectoral-fin rays beyond the fin membrane to the extent seen in *Sarcoglanis* and *Malacoglanis,* is unique within the family. It contrasts with the state most commonly found among other loricarioids and remaining catfishes, where pectoral-fin rays show little or no projection beyond the fin membrane. In the species of *Scleronema* examined, the pectoral-fin rays project considerably beyond the fin membrane. In *Stauroglanis,* in spite of the poor condition of the fins in the available material, it can be seen that the pectoral-fin rays also project considerably beyond the fin membrane. The pectoral-fin rays in *Scleronema* and *Stauroglanis* project to an extent that, aside from *Sarcoglanis* and *Malacoglanis,* is unique within the family. Nevertheless, the state in the latter two genera is much more advanced than in either *Scleronema* or *Stauroglanis,* and is evidence that *Sarcoglanis* and *Malacoglanis* are sister groups.

5. Upper Jaw Toothless; Dentary Teeth Uniserial, Long, Cylindrical, Conical, and Hooked Inward at Tip: This character of Myers and Weitzman, once again, can be considered two distinct characters, one concerning the premaxillary teeth and the other the dentary teeth. The total absence of premaxillary teeth is not found in any other member of the Trichomycteridae. The closest condition is that of the glanapterygine *Typhlobelus,* which has only a single tooth on each premaxilla. Nevertheless, all other glanapterygines have higher counts of premaxillary teeth. Given the available corroboration that the Glanapteryginae is a monophyletic group (Pinna, 1988), it is more parsimonious to consider the premaxillary tooth reduction in *Typhlobelus* an independent derivation. Among loricarioid outgroups, toothless premaxillae are found only in some members of the Callichthyidae. Considering, nevertheless, that callichthyids are more closely related to the Scoloplacidae, Loricariidae, and Astroblepidae (Baskin, 1973; Howes, 1983; Schaefer and Lauder, 1986), all with numerous premaxillary teeth, it is more parsimonious to consider the loss of teeth in some callichthyids as a separate event. Consequently, the toothless premaxilla of *Sarcoglanis* and *Malacoglanis* is further evidence for their being sister groups. The statement about the dentary teeth of *Sarcoglanis* and *Malacoglanis* does not represent a synapomorphy for the two taxa, as Baskin (1973) has already noted. Uniserial dentary teeth are found also in *Stauroglanis,* in the Glanapteryginae and in some Vandelliinae. Dentary teeth that are long, cylindrical, conical, and hooked inward at the tip are found in most other trichomycterids and remaining catfishes, and are not, therefore, apomorphic for sarcoglanidines.

6. Conspicuous, Saclike, Adipose Organ Above Pectoral Fin: From the original descriptions, it seems that this adipose organ is conspicuous in both *Malacoglanis* and *Sarcoglanis,* but more so in the latter. This adipose organ is unique within the family, but unfortunately little detail is known about its structure. Even if the organ is homologous with the axillary gland found in most trichomycterids and several other catfishes (a similarly poorly known structure), it can be regarded as uniquely derived for *Sarcoglanis* and *Malacoglanis.* Its structure, size, and shape differ markedly from those seen in the axillary gland of remaining members of the family.

There are thus five synapomorphies indicating monophyly of the group formed by *Sarcoglanis* and *Malacoglanis.* I propose here that *Stauroglanis* is the sister group of those two genera, and that the derived characters uniting *Stauroglanis* and *Malacoglanis* will also be found in *Sarcoglanis,* when further material representing the genus becomes available (fig. 18).

At present there are only two characters that can be given as autapomorphic for *Stauroglanis.* These are the dorsal lateral openings on the neurocranium and the form of the vomer (see Osteology). Both traits are unique within trichomycterids and have not been recorded in any other catfish. Within the family, only in *Sarcoglanis* is the state of these structures unknown. Some other characters, such as the cross-shaped basibranchial or the unnamed bone below the maxilla, are also derived and unique within the family. Nevertheless, as these structures are completely unknown in both *Sarcoglanis* and *Malacoglanis,* it is at present uncertain whether they represent autapomorphies for *Stauroglanis* or synapomorphies for the Sacroglanidinae.

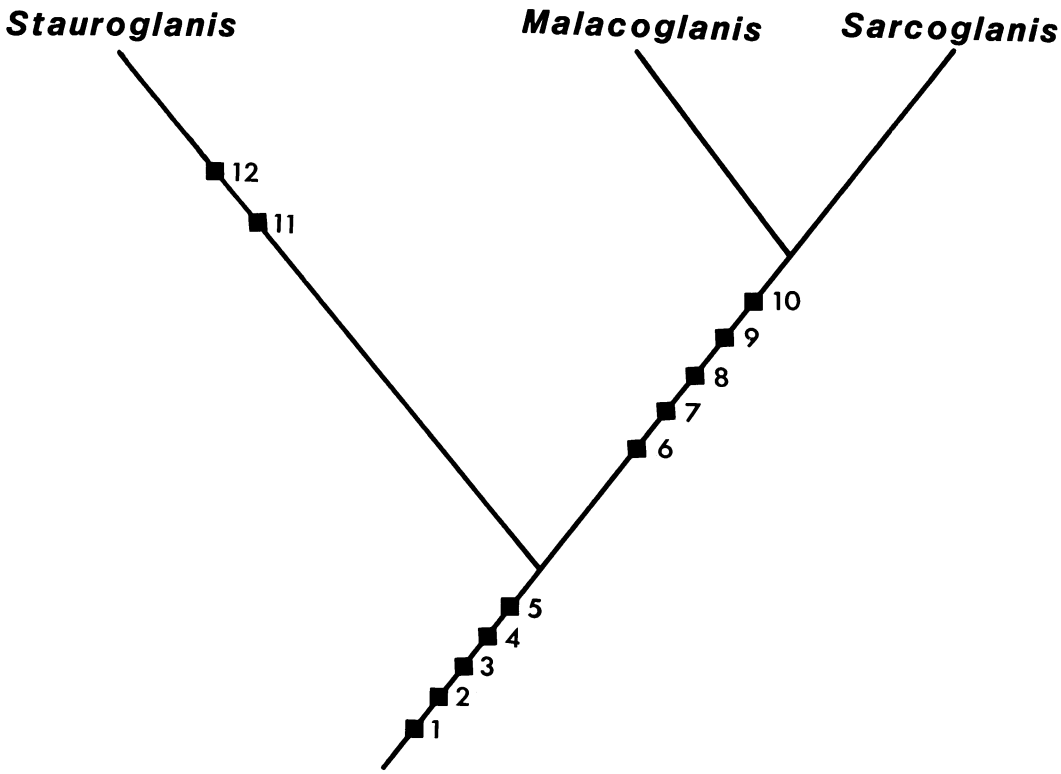

Fig. 18. Cladogram of the Sarcoglanidinae and summary of proposed characters. Characters numbered are: **1,** separate ossification of the anterior cartilage of palatine ("anterior palatine piece"); **2,** premaxilla with long and slender lateral process, extending until midway the length of the maxilla; **3,** quadrate with large dorsal process distally directed backward; **4,** mesethmoid cornua expanded distally; **5,** mesial anterior border of mesethmoid convex (all above characters predicted but not observed for *Sarcoglanis*); **6,** pectoral fins large, much longer than head length; **7,** pectoral-fin rays projecting well beyond fin membrane; **8,** absence of premaxillary teeth; **9,** conspicuous, saclike adipose organ above pectoral fin; **10,** 30 or 31 vertebrae (not including those of the Weberian complex and compound caudal centrum); **11,** lateral openings on dorsal side of neurocranium, framed by the supraoccipital, frontals, and sphenotics; **12,** vomer with posterior portion expanded laterally, lateral tips directed backward.

RELATIONSHIPS OF SARCOGLANIDINAE WITH OTHER TRICHOMYCTERIDAE

There is one evident apomorphic character shared by Sarcoglanidinae and some other trichomycterids: their enormously enlarged maxilla, which is much larger than the premaxilla (figs. 7 and 19). Such a condition contrasts with that seen in most other members of the family and with that in the Nematogenyidae and most other catfishes. The plesiomorphic state within Siluroidei is a small maxilla, with the same dimensions or smaller than the premaxilla (fig. 20A–C). The Diplomystidae have the maxilla larger than the premaxilla (Fink and Fink, 1981; Arratia, 1987), but this raises no doubt about the derived polarity of the large maxilla in some trichomycterids. Diplomystidae are the sister group of all remaining catfishes, and the structure and size of their maxilla, as well as the presence of maxillary teeth, represent a retention of the plesiomorphic condition of the maxilla within Ostariophysi (Fink and Fink, 1981; Grande, 1987). The situation in diplomystids contrasts with that seen in all other catfishes (except the fossil Hypsidoridae, the next sister group to catfishes; see Grande, 1987), in which the maxilla is toothless, reduced in size and not related to the mouth gape (it is, instead, related only to the palatine-maxillary mechanism of barbel

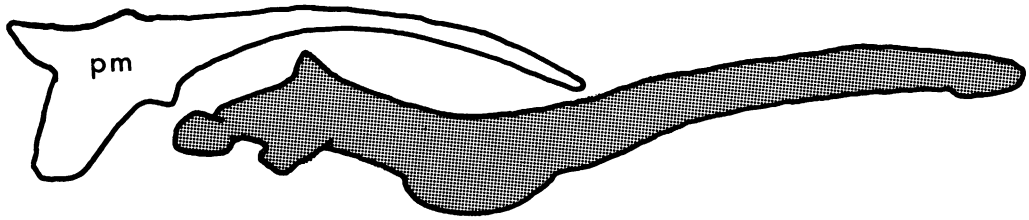

Fig. 19. Diagrammatic representation of the maxilla and premaxilla of *Malacoglanis gelatinosus*. Dorsal view of left side, drawing inverted. Maxilla stippled. Redrawn and modified after Baskin (1973).

movement; see Gosline, 1975). The morphology of the maxilla seen in the nondiplomystid (and nonhypsidorid) catfishes thus represents a uniquely derived character indicating their monophyly (Fink and Fink, 1981). The state of the maxilla in the Sarcoglanidinae does not resemble the primitive condition seen in diplomystids, it does not participate in the gape of the mouth, is not a compressed bone, and is totally related to the mechanics of the maxillary barbel movement. The maxilla of sarcoglanidines approaches the condition in diplomystids only in its relative size being larger than the premaxilla. If it is taken into consideration that the Sarcoglanidinae are part of a monophyletic Trichomycteridae, that the Trichomycteridae form a monophyletic group with the other loricarioid families, and further that the nondiplomystid catfishes form a monophyletic group, then it becomes evident that the large relative size of the maxilla in sarcoglanidines is a secondary modification. This holds true even though a large maxilla is found in diplomystids and most other noncatfish ostariophysans. Considering the large maxilla of sarcoglanidines as a posterior modification (i.e., as an apomorphic character) is more parsimonious than considering it as a symplesiomorphy with diplomystids. A more delicate situation relates to the condition in other loricarioids. All callichthyids and scoplacids examined have a maxilla much larger than the premaxilla. In loricariids and astroblepids the maxilla is also large, with the same length as, or larger than, the premaxilla. According to the presently available phylogenetic hypothesis of loricarioid phylogeny (Baskin, 1973; Howes, 1983; Schaefer and Lauder, 1986), the Loricariidae, Astroblepidae, Scoloplacidae, and Callichthyidae form a monophyletic group, which is the sister group of the Trichomycteridae. According to the same hypothesis, the Nematogenyidae is the sister taxon to the clade Trichomycteridae/Callichthyidae/Scoloplacidae/Loricariidae/Astroblepidae. *Nematogenys* has a small maxilla, the plesiomorphic condition within siluroids (fig. 20A). *Trichogenes,* the sister group of all remaining trichomycterids (Pinna, in prep.) also has the plesiomorphic condition for the maxilla (fig. 20B), similar to that of *Nematogenys.* In this scheme, the occurrence of an enlarged maxilla within the Trichomycteridae has to be considered a putative synapomorphy for the taxa sharing the trait. This reasoning involves a scheme of outgroup comparison which in general terms follows Maddison et al. (1984), and can be diagramatically appreciated in figure 21. Following the steps of the algorithm of Maddison et al. (1984) and considering the non-*Trichogenes* Trichomycteridae as an ingroup, the state at the outgroup node (i.e., the plesiomorphic state for the ingroup) is to have a small maxilla. The equivocal state assessment at the node joining trichomycterids with remaining loricarioids becomes decisive at the outgroup node, when *Trichogenes* is included in the analysis. Consequently, the large maxilla seen in a subgroup of this particular ingroup can be considered a synapomorphy for it. In view of the above, the enlarged maxilla of sarcoglanidines is an apomorphic character. It should be noticed that this polarity assessment does not change if the Nematogenyidae is placed as the sister group to trichomycterids (the traditional view before Baskin, 1973). Actually, given the position of *Trichogenes,* nontrichomycterid outgroups cannot completely change this polarity assessment, regardless of their interrelationships (see Rule 3 of Maddison et al., 1984). This observation is particularly rele-

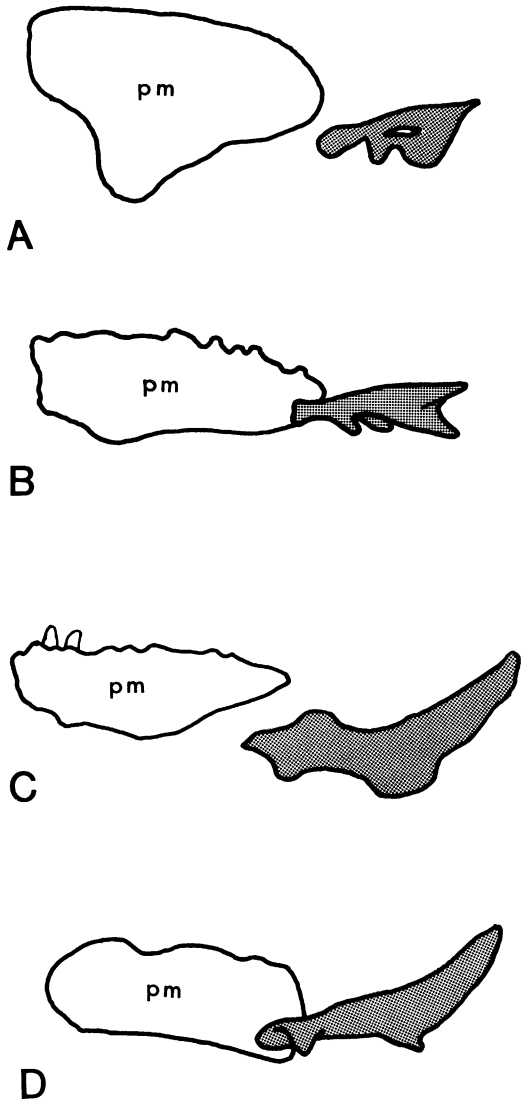

Fig. 20. Diagrammatic representation of the maxilla and premaxilla of: **A,** *Nematogenys inermis* (MZUSP 36956); **B,** *Trichogenes longipinnis* (MZUSP uncat.); **C,** *Eremophilus mutisii* (MZUSP 35409); **D,** *Trichomycterus quechuorum* (AMNH 20351). Dorsal view, right side. Maxilla stippled.

vant when it is remembered that a few other catfishes (e.g., Sisoridae) also have the maxilla larger than the premaxilla.

This apomorphic enlargement of the maxilla of sarcoglanidines is found also in some members of the subfamily Trichomycterinae, presently referred to distinct genera. The first of these is *Scleronema,* which although not studied in depth is probably monophyletic. Species of *Scleronema* share a conspicuous derived dermal opercular flap (a character traditionally used to diagnose the genus) not present in other trichomycterids nor in outgroups. Although presently supported only by this single unequivocal derived character, the monophyly of *Scleronema* stands as an acceptable proposal, since there is no evidence for an alternative hypothesis. The maxilla of *Scleronema* is similar, in relative size to the premaxilla and other upper jaw elements, to that seen in the Sarcoglanidinae (fig. 22A). As occurs in the latter taxon, the huge dimensions of the maxilla in *Scleronema* can be detected externally, as a large and conspicuous bony base for the maxillary barbel. This character was noted by Myers and Weitzman (1966), who first suggested that *Scleronema* might be related to Sarcoglanidinae.

Another form sharing the derived enlargement of the maxilla is a species presently included in the genus *Trichomycterus,* namely *T. boylei* (Nichols). This species was redescribed by Arratia and Menu-Marque (1984), who provide much anatomical data not contained in the original description. In contrast to the condition in the Sarcoglanidinae and *Schleronema,* the enlarged maxilla of *T. boylei* is not evident externally. The condition in *T. boylei* (fig. 22B) is much less conspicuous than in *Scleronema* and sarcoglanidines, but even so it is distinctly enlarged relative to the plesiomorphic state outlined above (compare figs. 20 and 22).

Thus, the Sarcoglanidinae, *Scleronema,* and *T. boylei* share a uniquely derived enlargement of the maxilla indicating that they form a monophyletic group. This assemblage, placing together one subfamily and two noncongeneric members of another subfamily, might seem at first hardly acceptable, if one assumes that the nomenclatural status reflects some phylogenetic information. Nevertheless, as shown in the next section, proposal of a group in disagreement with the present Trichomycterinae does not require any putative synapomorphy to become homoplastically distributed, because monophyly of this subfamily is not supported by any such evidence.

As noted in the previous section, the con-

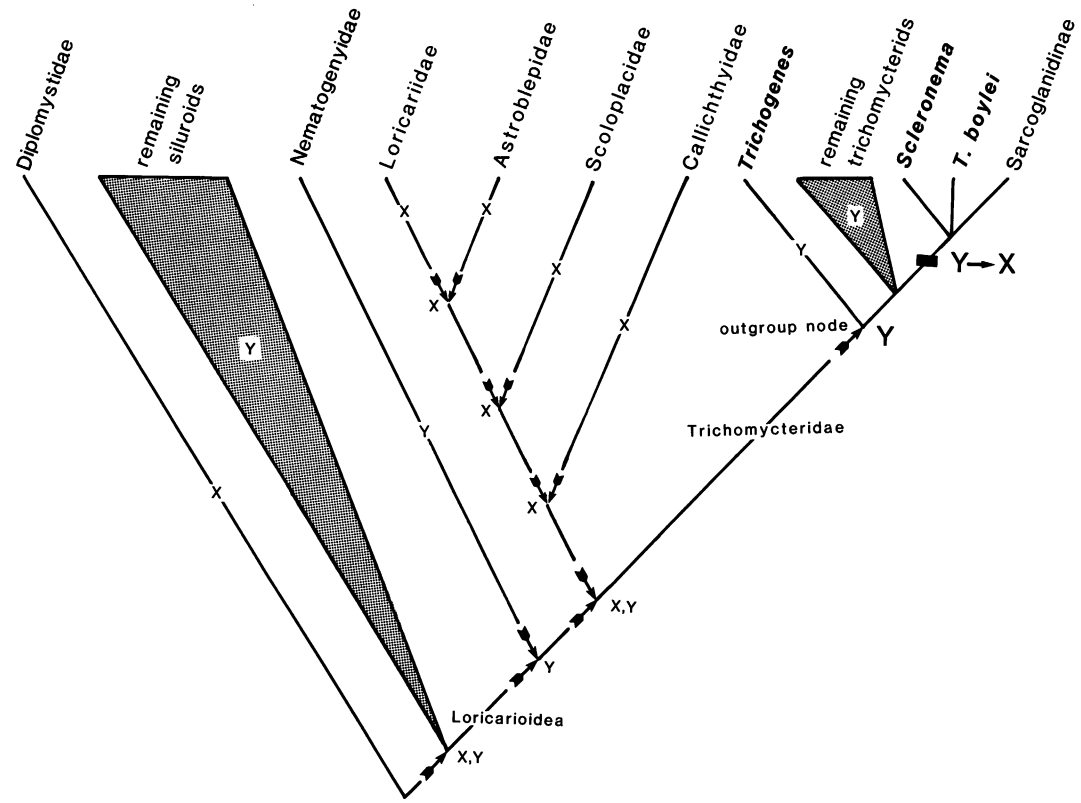

Fig. 21. Diagram explaining the polarity assessment of the large maxilla of the Sarcoglanidinae and its closest relatives, following the procedures of Maddison et al. (1984). X represents large maxilla, Y represents small maxilla. Stippled triangles (meaning polytomies at their insertion nodes) represent unresolved relationships and/or components which are not relevant for the present discussion. For further explanation see text.

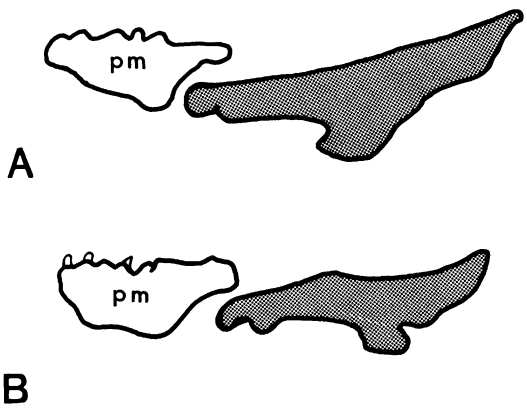

Fig. 22. Diagrammatic representation of the maxilla and premaxilla of: **A,** *Scleronema minutum* (MCP 9315); **B,** *Trichomycterus boylei* (MZUSP uncat.). Dorsal view, right side. Maxilla stippled.

vex, rounded anterior mesial border of the mesethmoid is a synapomorphy joining *Stauroglanis* with other sarcoglanidines. Indeed, the trait in *Stauroglanis* and *Malacoglanis* is developed to a degre unique for these two taxa. Nevertheless, the same trait is present, in a much less evident condition, in *Scleronema* (fig. 23A). This character, therefore, provides further corroboration that *Scleronema* is the sister group of the Sarcoglanidinae. Accordingly, presence of a convex mesial anterior border of the mesethmoid is interpreted as a synapomorphy at the clade *Scleronema*/Sarcoglanidinae, and the more extreme state of this character, in turn, is synapomorphic for a less inclusive clade (*Stauroglanis* plus remaining sarcoglanidines). In the larger of the two specimens of *T. boylei* examined (40.5 mm SL), the anterior mesial margin of the mesethmoid is also

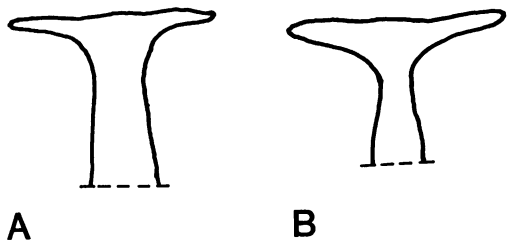

Fig. 23. Diagrammatic representation of the anterior portion of mesethmoid in: **A,** *Scleronema minutum* (MCP 9315); **B,** *Trichomycterus boylei* (MZUSP uncat.). Dorsal view.

convex, in the same style seen in *Scleronema* and sarcoglanidines (fig. 23B). In the smaller specimen (31.8 mm SL), the anterior margin of the mesethmoid is straight, not convex as in *Scleronema* and sarcoglanidines but also not concave as in the primitive condition. Possibly the convex state of the mesethmoid becomes evident only in fully grown individuals. The smallest *Scleronema* specimen examined (19.1 mm SL) has no evident convex margin, while the larger individuals have it. Even though not fully conclusive at present, the presence of a convex anterior mesial margin of the mesethmoid at least agrees with a hypothesis which places *T. boylei* in a monophyletic group with *Scleronema* and the Sarcoglanidinae.

Baskin (1973) provided five characters to support the Sarcoglanidinae plus the Glanapteryginae as a monophyletic group. Some of these characters, if accepted as valid evidence, would put into doubt the proposed monophyly of the group Sarcoglanidinae + *Scleronema* + *T. boylei.* This occurs because Baskin's characters proposed to unite sarcoglanidines with glanapterygines are absent in *Scleronema* and *T. boylei,* thus implying that the characters joining these two taxa with sarcoglanidines are homoplastic.

Three of Baskin's characters, "opercular bone with a long posterior process," "dorsal membrane present," and "reduced number of premaxillary teeth," have been discussed by Pinna (1988), who concluded that they are not valid evidence for the monophyly of Sarcoglanidinae + Glanapteryginae. Another of Baskin's characters, "anal rays fewer than eight," as Baskin himself observed, is not reliable evidence. Some other trichomycterids may have as few as eight rays (including *T. boylei*), and *Malacoglanis* has seven, which makes the difference too small for a meristic feature known to show considerable intraspecific variation. *Scleronema* may have very reduced anal-fin ray counts, but considerable variation occurs, and counts ranging from six to eight have been observed. Another character Baskin (1973) used to corroborate monophyly of sarcoglanidines plus glanapterygines was the "opercular and interopercular odontodes reduced or absent." This trait is undoubtedly apomorphic at this level within the family, and is not seen either in *Scleronema* or *T. boylei.* Nevertheless, reduction of odontodes has occurred independently in Sarcoglanidinae and in Glanapteryginae. The monophyly of *Listrura* plus remaining Glanapteryginae is a well corroborated hypothesis (Pinna, 1988), but both species of this genus have numerous opercular and interopercular odontodes. The state in *Listrura* thus retains the plesiomorphic condition within trichomycterids, and remaining glanapterygines have lost odontodes (at least in the adult stage). This means that, once monophyly of Glanapteryginae is accepted, reduction of odontodes has occurred inside the subfamily (more precisely at the *Glanapteryx* + *Typhlobelus* + *Pygidianops* clade), and not at a higher level. As a further consequence, the reduction of odontodes seen in Sarcoglanidinae, a reduction which is less marked than in Glanapteryginae, is an independent event. This conclusion involves a scheme of parsimony, in which acceptance of homoplasy in the reduction of odontodes is more parsimonious than postulating homoplasy in all other known putative synapomorphies supporting other components of relationship.

The relationship proposed here implies considerable alterations in the presently accepted classification, and would require *Scleronema* and *T. boylei* to be transferred to the subfamily Sarcoglanidinae. However, considering the still poorly known anatomy of *Scleronema, Sarcoglanis,* and *Malacoglanis,* it is better to wait for a more complete set of data, before making the necessary alterations of nomenclature. Furthermore, removing *T. boylei* from the Trichomycterinae would also imply its removal from *Trichomycterus,* which could be a premature alteration. While

phylogenetic relationships among *T. boylei, Scleronema* and sarcoglanidines remain unresolved, there can be no adequate generic placement for this species.

Baskin (1973) proposed that Sarcoglanidinae, Glanapteryginae, and Trichomycterinae comprise a monophyletic unit, referred to by him as the Trichomycterinae-group. His proposal relies on a single character, the presence of a frontolacrimal tendon bone. As mentioned above, this structure has already been proposed as homologous with the supraorbital and also with the antorbital, and its homology to structures in other catfish groups seems problematical. Schaefer (1987) reported a structure similar in shape and position in the family Loricariidae. A bone occupying the same position (but with a distinct shape) is present in *Trichogenes longipinnis,* the plesiomorphic sister group to the whole family Trichomycteridae (Pinna, in prep.). If the structures in loricariids, *Trichogenes,* trichomycterines, sarcoglanidines and glanapterygines are accepted as homologous, then their occurrence in the three latter taxa does not indicate their monophyly, because it is a symplesiomorphy at that level.

PHYLETIC STATUS OF THE SUBFAMILY TRICHOMYCTERINAE

The genera *Trichomycterus, Hatcheria, Scleronema, Bullockia, Rhizosomichthys,* and *Eremophilus* have been traditionally placed together to form the subfamily Trichomycterinae. *Trichomycterus* is by far the most speciose genus of the group (and of the family), consisting of over 100 nominal species and large numbers of undescribed forms. *Eremophilus* includes at present two species, *E. mutisii* from Colombia, and *E. candidus* from southeastern Brazil (*E. camposi* is actually a member of the Glanapteryginae, now placed in the genus *Listrura*). The two species of *Eremophilus* are brought together based on a single character, the absence of pelvic fins, and it is probable that *E. mutisii* and *E. candidus* do not form a monophyletic group. Pelvic fins have been lost at least two other independent times within the family, in the Glanapteryginae and in the Tridentinae (in *Miuroglanis*; see Baskin, 1973). Furthermore, *E. candidus* is very similar to some southeastern Brazilian species, all having normal pelvics (e.g., see illustration of *Trichomycterus brasiliensis* in Britski et al., 1986). *Scleronema* comprises *S. operculatum, S. minutum,* and *S. angustirostris,* species in need of a careful taxonomic revision. *Hatcheria* (see Arratia and Menu-Marque, 1981), *Bullockia,* and *Rhizosomichthys* are presently monotypic.

The taxa united as Trichomycterinae show a general resemblance to each other which understandably led early taxonomists to consider them as a natural group. However, as discussed below, this subfamily is not monophyletic. The problems involved with the recognition of Trichomycterinae are related to interpretation of data, and were not amenable to critical evaluation by early systematists working with the group. This fact was not due to inaccuracies in their observations, nor to lack of morphological data, but instead, was a direct consequence of the limitations of the systematic methods available at the time. This was part of a general tendency to place highly derived forms in separate high-level groups and to unite generalized forms in a taxon of equivalent rank. In present terms, the adoption of a group such as Trichomycterinae is related to acceptance of symplesiomorphies as potential indicators of monophyly, which is further related to a definition of monophyly that is not strict.

A survey of the pertinent literature provides a number of characters previously used to delimit or diagnose the subfamily Trichomycterinae. These characters are evaluated below relative to their value as potential indicators of phylogenetic kinship. The characters are extracted mainly, but not exclusively, from works with revisionary aims, namely Eigenmann (1918), Myers (1944), and Arratia et al. (1978). These works summarized most data relevant to the group, and attempted wider comparative concerns. In the two former papers, characters provided in keys were also scrutinized, since authors of that time used to express their justifications for particular groupings in the form of keys. Each character treated below is numbered and is immediately followed by a short commentary evaluating its generality.

1—Nasal Barbal Present: A nasal barbel is present in all members of the Glanapterygi-

nae and Sarcoglanidinae, in *Tridentopsis* (a genus of the Tridentinae), and (in variable degrees of development) in the Nematogenyidae (but the condition in the latter taxon may be nonhomologous; see Arratia, 1987: 91). Presence of a nasal barbel cannot consequently be considered a synapomorphy at the level of the Trichomycterinae.

2—Two Barbels at Angle of Mouth: Nearly all trichomycterids possess this trait, in no way unique to the Trichomycterinae. This character is probably a synapomorphy at the level of the whole family, considering that it is not found in other members of the Loricarioidea and remaining catfishes (the condition in Callichthyidae is nonhomologous; see Baskin, 1973: 42 and Arratia, 1987: fig. 40C).

3—Gill Membranes Free or Narrowly Connected With Isthmus: This is the plesiomorphic condition for the gill membranes at the level of the family, found in *Trichogenes* and in the Nematogenyidae. Free or narrowly united branchial membranes furthermore also found in glanapterygines and sarcoglanidines.

4—No Mental Barbels: Absence of mental (chin) barbels is characteristic of all trichomycterids. This character is possibly apomorphic at the family level, hence invalid to unite members of a subgroup.

5—Opercle and Interopercle with Odontodes ("Spines"): Mere presence of opercular and interopercular odontodes is a symplesiomorphy, since these are found also in other loricarioids. The profound modifications of shape seen in the opercle and interopercle of all trichomycterids is almost always associated with the presence of a definite restricted site of odontode attachment. These modifications are unique within catfishes and constitute an unequivocal synapomorphy for joining all trichomycterids. Thus, they do not represent evidence for monophyly of the Trichomycterinae only.

6—Anal Fin Short: This rather vague character was evidently intended to contrast Trichomycterinae with Tridentinae, which possess high number of anal-fin rays (more than 15). While the state in tridentines can be confidently regarded as apomorphic, the condition in trichomycterines (8 to 12 rays, a count also found in most other subfamilies and remaining catfishes, including nematogenyids and diplomystids) is plesiomorphic, and hence no evidence for their monophyly.

7—Mouth Subterminal, not Suckerlike: The Vandelliinae, Stegophilinae and Tridentinae all have inferior, highly specialized mouths. What characterizes the Tricomycterinae is their lack of these buccal specializations. A similar subterminal and unspecialized mouth is found also in *Trichogenes,* sarcoglanidines, glanapterygines, nematogenyids and most other catfishes. Thus, the condition in trichomycterines is a primitive character and does not indicate their exclusive common ancestry. Only if the suckerlike oral disc of some other loricarioids is considered the primitive state for loricarioids, could the unspecialized mouth of trichomycterines be considered a secondary reversal and thus a derived trait. But no evidence exists that a suckerlike mouth is the primitive condition for loricarioids. Actually, the available hypothesis for loricarioid interrelationships (Baskin, 1973; Schaefer and Lauder, 1986) indicates exactly the opposite.

8—Caudal Fin Rounded, Truncated, or Emarginate: The shapes specified above vary enormously within most subfamilies of Trichomycteridae, and do not delimit any grouping in agreement with the current Trichomycterinae.

The following characters are osteological, and were presented by Arratia et al. (1978) as diagnostic for their subfamily Pygidiinae (= Trichomycterinae).

9—Well-Developed Palatine Connected with Endopterygoid, Premaxilla, and Sometimes the Maxilla: Arratia (in litt.) informs me that there was a printing mistake in the description of this character in Arratia et al. (1978), and that the original sentence should be "well developed palatine connected with endopterygoid, *maxilla and sometimes the premaxilla.*" The comments below refer to the corrected sentence. A well-developed and wide palatine is characteristic of almost all trichomycterids, with the exception of the glanapterygine *Typhlobelus* (which has all jaw structures enormously modified). The connection of the palatine with the maxilla is a

common feature of most catfishes, and is involved with movement of the maxillary barbel. The connection of the palatine with the premaxilla, although not widespread among catfishes, is found also in most other trichomycterids. The connection of the palatine with the pterygoid bones is found in many other trichomycterid subfamilies, such as Stegophilinae and Vandelliinae, and hence is not unique to Trichomycterinae. The connection of the palatine to the suspensorium in trichomycterids is undoubtedly a remarkable feature, deserving careful comparative investigation. Nonetheless, it is clear that this character cannot be a synapomorphy for the members of the Trichomycterinae, since it is not unique to them.

10—Supraorbital Present: As noted above (see Osteology and Relationships of Sarcoglanidinae with other Trichomycteridae), there is no agreement on the nature of this bone, also proposed as an antorbital (Britski and Ortega, 1983) or an ossified frontolacrimal tendon (the "fronto-lacrimal tendon bone" of Baskin, 1973). It should be noted that absence of the supraorbital has been given as a synapomorphy for all catfishes (Fink and Fink, 1981). If this bone is really a supraorbital (an alternative which would require altering the level of universality of the character "absence of supraorbital" for siluroids), its common possession by some trichomycterids would not imply their common ancestry, since this structure would be a symplesiomorphy. A supraorbital is present in many Characiformes and remaining Ostariophysi. Evidently the presence of "supraorbital" in some trichomycterids can be interpreted as a secondary acquisition, thus a derived character. But such a proposal would necessarily rely on specific resolved relationships of the group, which are not available at present. A similar reasoning applies if the bone is proposed as an antorbital. The suggestion that the bone is a frontolacrimal tendon bone implies that it is a neomorphic feature, thus exclusively derived for the taxa sharing it (a view expressed in Baskin, 1973). Whatever be the case, the presence of a frontolacrimal tendon bone (or a secondarily acquired supraorbital or antorbital) is not exclusive to the Trichomycterinae among trichomycterids. It is also present in the Sarcoglanidinae and Glanapteryginae (see discussion above on relationships of sarcoglanidines with other trichomycterids).

11—Quadrate, Metapterygoid, Hyomandibula, and Preopercle Incompletely Fused: There is some disagreement about the identity of the pterygoid bones of trichomycterids. Arratia et al. (1978) suggested that the metapterygoid is represented by the bony plate that partly surrounds the quadrate posterodorsally, so that the hyomandibula and metapterygoid are fused into a single bone, the anterior portion of which corresponds to the metapterygoid and the posterior portion to the hyomandibula. This view was apparently supported by the presence of a crest extending along the bone. This crest seems to have been interpreted as the primitive sutural limit between the hyomandibula and the metapterygoid, and would result from their fusion (see Arratia et al., 1978: 164, fig. 2B). An alternative view adopted here (also Arratia, 1987, and Baskin, 1973) is that the whole bony plate that articulates with the neurocranium is solely the hyomandibula. The crest seen on the outer surface of the bone is a process for muscle attachment. The anteriormost separate suspensory element, articulating ventrally with the quadrate and ligamentously joined anteriorly to the palatine, is considered the only pterygoid element. Whether this element is homologous with the metapterygoid or with the mesopterygoid of other catfishes is uncertain, as is the identity of the pterygoid bones of siluroids in general (for some discussion see Arratia, 1987; Howes, 1983; Gosline, 1975; Fink and Fink, 1981). According to Arratia (personal commun.), this pterygoid element of trichomycterids is formed ontogenetically in an endochondral fashion, which hence supports homology with the metapterygoid. If so, only the partial fusion of the quadrate, hyomandibula, and preopercle is left to be analyzed as a possible diagnostic character for the Trichomycterinae. I was not able to locate evidence of fusion between these bones in any trichomycterids examined. The quadrate, hyomandibula, and preopercle are frequently joined in a very tight union, but it is hard to say whether there is fusion involved with this

union. Arratia (in litt.) stated that limits among the hyomandibula, quadrate and preopercle are indistinguishable in adult specimens of *Trichomycterus aerolatus, T. chiltoni, T. rivulatus, T. maete, T. mendozensis, T. chungaraensis, Hatcheria macraei,* and *Bullockia maldonadoi.* Unfortunately there are no equivalent data for other trichomycterid subfamilies, thus no comparison of this detail is possible. Under gross examination of cleared and stained preparations available, however, it seems that the state of the joint between the three bones in trichomycterines does not differ from the condition in other subfamilies.

12—Occipital Crest Lacking: The medial dorsal crest on the supraoccipital, present in most catfishes, is absent in all members of the Trichomycteridae, not only in the Trichomycterinae. Thus, this character is apomorphic at the level of the family, not of the subfamily (see Baskin, 1973).

13—Pectoral Girdle with One Radial: Trichomycterines have two pectoral proximal radials, one ossified and the other cartilaginous. From the shape and position of the element illustrated by Arratia et al. (1978), it is clear that the authors refer to the ossified proximal radial, which is the larger of the two. Arratia et al. (1978) were obviously contrasting the situation in Trichomycterinae to that in Nematogenyidae (their Nematogenyinae), where three ossified proximal radials are present. Although all members of Trichomycterinae for which data are available (representatives of all genera but *Rhizosomichthys*) have only a single ossified proximal radial, this character is not exclusive to that group, but is also found in other members of the family (e.g., most Vandelliinae and some Stegophilinae). Thus, this character is not exclusive to Trichomycterinae and is not evidence for their monophyly.

14—Parhypural, Hypural 1 and Hypural 2 Fused; Hypurals 3, 4, and 5 with Different Degrees of Fusion: The parhypural, hypural 1, and hypural 2 are fused into a single unit in all members of Trichomycterinae, a condition contrasting to the separate parhypural seen in the Nematogenyidae. Lundberg and Baskin (1969) report a separate parhypural for *Eremophilus mutisii, Vandellia cirrhosa, Tricomycterus quechuorum,* and *T. vermiculatus.* The situation in these species (including *T. quechuorum,* as examined here in the same specimen used by Lundberg and Baskin) is similar to that described by Arratia (1983) for *T. mendozensis* and *Hatcheria macraei.* In these cases, only a suture remains between the tightly united parhypural and hypurals 1 + 2, a condition contrasting to that seen in nematogenyids. In the latter family, the parhypural is well separated from hypurals 1 + 2 by a space, which separates the two units until their attachment to the compound centrum (see Lundberg and Baskin, 1969; Arratia, 1983). The condition of the parhypural in *Nematogenys* reflects the primitive state for catfishes (Lundberg and Baskin, 1969) and the fusion (or near fusion) seen in trichomycterines is consequently a derived trait. Nevertheless, similar patterns of the caudal skeleton occur in most, perhaps all, remaining members of Trichomycteridae and Loricarioidea, as well as in numerous other catfishes. I have not found a single derived pattern of hypural fusion shared exclusively by the members of the Trichomycterinae. Perhaps the occurrence of separate hypurals 3, 4, and 5 in some specimens of some members of Trichomycterinae can be found only in that subfamily among trichomycterids. Nevertheless, the separate condition of the upper hypurals is found in numerous other catfishes, and is the primitive situation for these structures (Lundberg and Baskin, 1969). Besides being a plesiomorphic trait, the separate condition of the upper hypurals in trichomycterines is a difficult character to evaluate phylogenetically, due to its large intraspecific variation (Arratia, 1983).

As seen above, none of the characters used until the present to separate the Trichomycterinae from the remaining members of the family can be considered a synapomorphy for the group. My studies have failed to disclose a single derived character exclusive to the Trichomycerinae, in spite of specific efforts in this direction. This situation by itself does not directly imply that the subfamily is nonmonophyletic, but only represents a lack of evidence for its monophyly. Positive evidence for nonmonophyly of the Trichomycterinae can come only from the demonstration that some forms previously included in

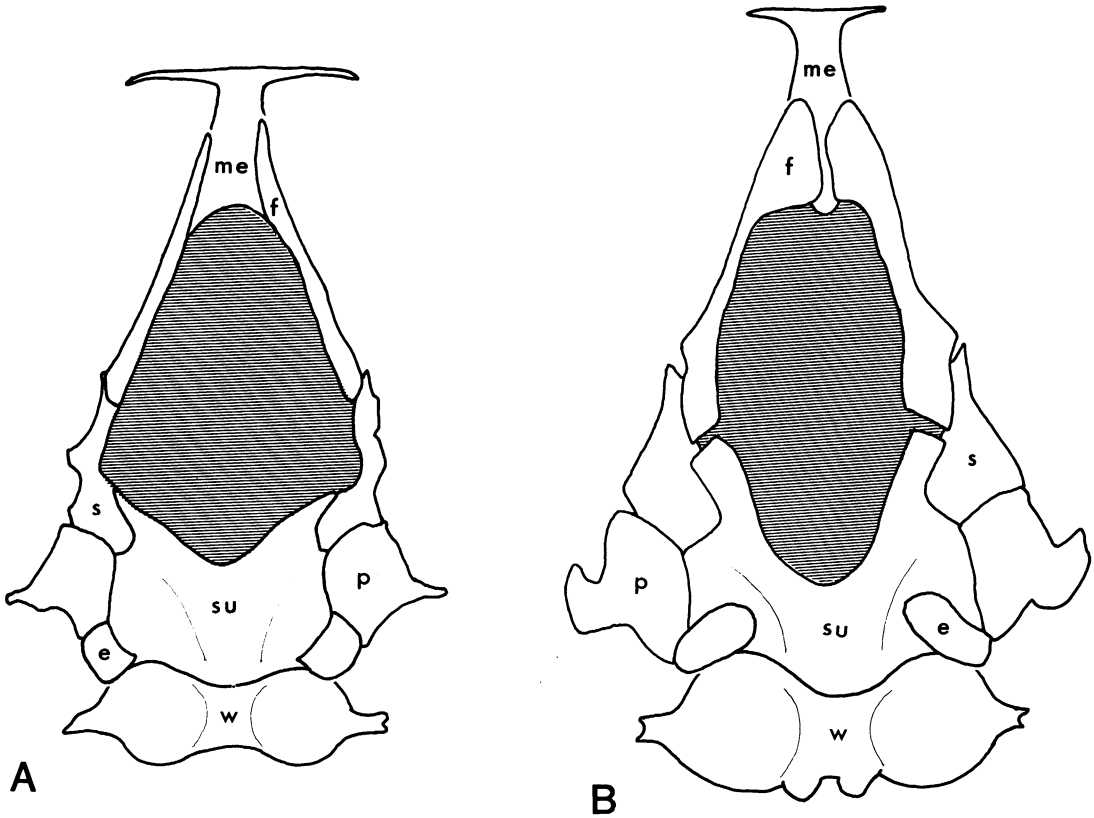

Fig. 24. Diagrammatic representation of dorsal view of skull of: **A,** *Tridentopsis* sp. (MZUSP 36303); **B,** *Trichomycterus hasemani* (MZUSP uncat.). Hatching represents the cranial fontanel.

the group are actually more closely related to other subfamilies. From this point of view, the nonmonophyletic status of the Trichomycterinae can already be considered evident. As seen above, there is evidence indicating that *Scleronema, T. boylei,* and perhaps *T. santaeritae,* all of them included in the Trichomycterinae, are actually more closely related to the Sarcoglanidinae. To these examples I would add *Trichomycterus hasemani* (and possibly also *T. johnsoni,* a distinct but seemingly very similar species, so far too poorly known to allow an adequate comparison). Baskin (1973) proposed that the enormously expanded cranial fontanel (which practically leaves the neurocranium without a roof) seen in the members of the Tridentinae (see fig. 24A) constitutes a synapomorphy for this subfamily. I agree with him about this character; such an expanded fontanel is not seen in other loricarioids or in most other catfishes. An expanded fontanel similar to that of tridentines is present also in *T. hasemani* (fig. 24B), and this constitutes a synapomorphy for the two taxa. Elsewhere within trichomycterids, a comparable situation is found only in the vandelliine *Paravandellia* (senior synonym of *Branchioica*), as shown in figure 25. But the situation in *Paravandellia* is an independent event. In other vandelliines the cranial fontanel is completely closed (except in *Paracanthopoma,* which has a complex and unique skull roof structure) and this is also the situation in all stegophilines (considered by Baskin, 1973, as the sister group of vandelliines). Consequently, it is more parsimonious to consider two separate events of fontanel expansion (one in tridentines and another in *Paravandellia*) than to put a single fontanel expansion at the base of the tridentine/stegophiline/vandelliine clade with subsequent reversals in stegophilines and non-*Paravandellia* vandelliines. Placing *T. hasemani* as the sister group exclusively of

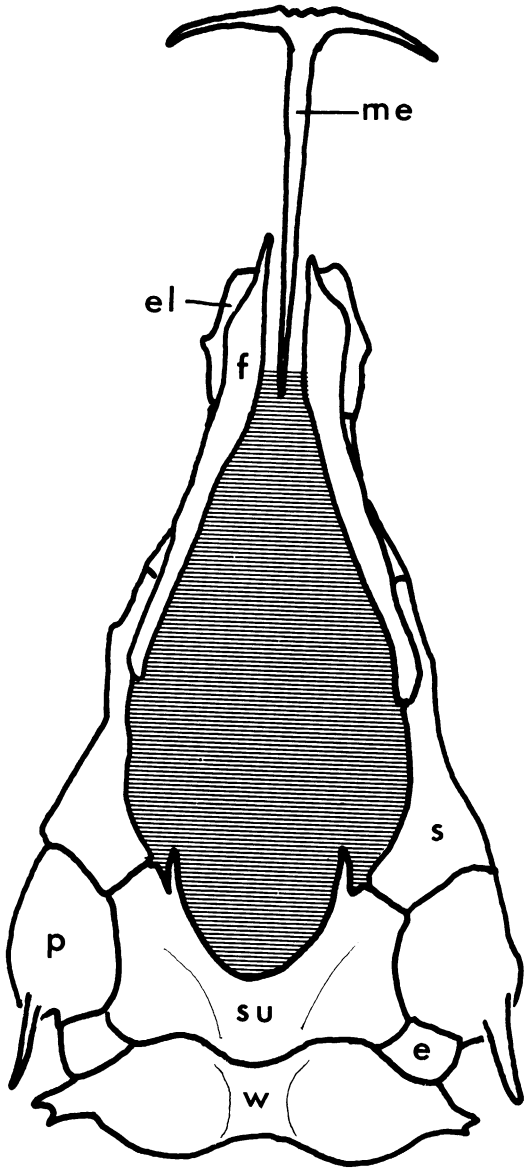

Fig. 25. Diagrammatic representation of dorsal view of skull in *Paravandellia* sp. (MZUSP uncat.). Hatching represents the cranial fontanel.

Paravandellia would be also unparsimonious, because it would require reversal in the several characters joining *Paravandellia* with other vandelliines in the lineage leading to *T. hasemani* (for some of these characters, see Baskin, 1973). It is interesting to observe that the shape of the anterior border of the supraoccipital (i.e., the posterior profile of the fontanel) in *T. hasemani* is more similar to that in tridentines than to that in *Paravandellia.* In *T. hasemani* and tridentines, the distal portions of the anterior margin of the supraoccipital are gently turned laterally. In *Paravandellia,* in contrast, the profile of the anterior margin of the supraoccipital is in a single arch. Although it cannot be determined whether the similar supraoccipital profile in *T. hasemani* and tridentines represents a derived condition (because there are no close outgroups with expanded fontanels to compare), the similarity in shape is at least an argument in favor of the homology of the fontanel expansion in the two taxa, when compared to *Paravandellia.*

An interesting observation at this point is that *Stauroglanis* would fit into the Trichomycterinae quite well, according to the available diagnostic characters for the group. Notwithstanding, as seen, *Stauroglanis* is rather related to the Sarcoglanidinae. A similar example is the genus *Listrura,* which according to traditional criteria would easily fall into the Trichomycterinae (actually one of the species, *L. camposi,* was originally described within a trichomycterine genus, *Eremophilus*), but is actually more closely related to the Glanapteryginae (Pinna, 1988).

All other subfamilies of the Trichomycteridae are probably monophyletic (some evidence is provided in Baskin, 1973), in agreement with the naturalness envisioned by early authors for the same groupings. This agreement is due to their possession of some externally evident and distinctive specializations, which made each of them seem to fit "natural" assemblages. It is not surprising that together with the recognition of obviously aberrant groups, a group was also erected to place together the forms lacking those evident specializations. This was apparently what has led to the establishment of the Trichomycterinae. After its adoption, the composition of the group remained unquestioned, a situation which largely persists today. Obviously the nonmonophyly of the Trichomycterinae does not preclude the existence of very large monophyletic subunits within the subfamily, but it only means that the subfamily as presently composed is not monophyletic.

It is possible that the forms now united as trichomycterines represent various sister

groups to different subfamilies and groups of subfamilies, and will be shown in the future to compose widely distant lineages. The numerous species at present placed as trichomycterines will possibly be scattered throughout the family, at various levels, in a complex phylogenetic pattern. Naturally the fragmentation of the Trichomycterinae involves resolution of all these relationships, a task that undoubtedly will demand detailed long-term studies.

A situation analogous to that outlined above can be seen within trichomycterines themselves. Each genus included within the subfamily is characterized by some distinctive and apparently apomorphic character, except the genus *Trichomycterus*. This genus has been, and continues to be, diagnosed exactly by the lack of specializations characterizing the remaining genera of the subfamily, a situation remarkably similar to that seen at the higher level of its subfamily. It is no coincidence that the genus *Trichomycterus* comprises the largest species assemblage of the family, a set of numerous superficially similar forms lacking evident specializations. Since the characters elucidative for relationships are probably internal anatomical details, they have remained unnoticed under the ordinary depth of character analysis. As a consequence, an enormous number of species have come to be assigned to the "unspecialized" genus. Like the subfamily Trichomycterinae, the genus *Trichomycterus* (even if *T. boylei, T. santaeritae, T. hasemani,* and *T. johnsoni* are withdrawn) is probably nonmonophyletic.

Howes (1983: 331) suggested that the expanded and dorsally concave palatine of astroblepids could be a synapomorphy joining this family with *Trichomycterus rivulatus,* which would be reason to question monophyly of *Trichomycterus*. Although I obviously agree with him about nonmonophyly of *Trichomycterus,* I do not agree with his justifications for this conclusion. Considering one species of *Trichomycterus* as the sister group of astroblepids would imply nonmonophyly not only of the genus, but also of the Trichomycteridae. This would implicate that all numerous synapomorphies for the family (Baskin, 1973) are homoplastically distributed. Further, it would also imply that all derived characters exclusively joining astroblepids with loricariids (and also those joining the two families with callichthyids) (Schaefer and Lauder, 1986) are also homoplasies. This would result in an enormously unparsimonious arrangement of loricarioid catfishes. The expanded shape of palatine of astroblepids actually resembles that in all trichomycterids, and this condition contrasts with the more slender palatine of remaining loricarioids and catfishes. Nevertheless, given the available corroboration for the other components of relationship, this similarity must be the result of convergence. I did not observe a concave palatine in any trichomycterid examined, but I did not examine the species available to Howes (*T. rivulatus*). In any event, if *T. rivulatus* and astroblepids share a derived concave palatine, this character is also more parsimoniously interpreted as convergent.

The situation outlined above does not mean that descriptions of new taxa in the genus *Trichomycterus* should be viewed as an error or in any sense undesirable. While there are no resolved relationships that could provide better generic arrangements, it is completely justified to make known the numerous species that are yet undescribed, even if their placement in *Trichomycterus* is assumedly provisory. This situation is not uncommon in neotropical freshwater fish systematics and has been consciously dealt with in other groups, for example the Curimatidae (e.g., Vari, 1987). But being aware of this situation makes evident the relevance of including new untraditional characters as part of normal taxonomic descriptions, as has been done in trichomycterids, for example, by Arratia and Menu-Marque (1984).

It is probable that the situation verified in the Trichomycterinae and *Trichomycterus* is also the case in various other groups of siluroids. A remarkably similar case has been reported in the neotropical family Loricariidae. Schaefer (1987) noticed that the loricariid subfamily Hypostominae has been traditionally diagnosed by plesiomorphic features, and that no putative synapomorphy is known to indicate monophyly of the group. Similar situations can also be observed in taxa ranked as high as family. An enormous and diverse group such as the Pimelodidae

is not supported by a single synapomorphy (see Lundberg et al., 1988), and monophyly of the family remains an assumption not supported by any evidence. Pimelodids seem to be defined by nothing but symplesiomorphies and lack of specializations characterizing other neotropical catfish families.

This state of affairs is actually part of a more general problem related to the inadequacy of traditional taxonomic schemes when viewed under a phylogenetic perspective. A broader overview of this subject is given by Weitzman and Fink (1983), in their discussion of classificatory schemes of New World Characiformes.

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