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A new genus of trichomycterid catfish (Siluroidei, Glanapteryginae), with comments on its phylogenetic relationships

by

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with 6 figures

ABSTRACT

Listrura gen. n. is described to include two species from Southeastern Brazil, *L. nematopteryx* sp. n. and *L. camposi* (Miranda Ribeiro, 1957). The new genus is uniquely characterized by the extreme reduction of the latero-sensory canals on skull and by the structure of the pectoral fin. Various synapomorphies are given indicating that *Listrura* forms a monophyletic group with the subfamily Glanapteryginae. A previously proposed hypothesis concerning the relationships between Glanapteryginae and Sarcoglanidinae is reexamined. A previously cited locality for *L. nematopteryx* is corrected.

INTRODUCTION

Neotropical catfishes of the family Trichomycteridae, commonly referred to as "parasitic catfishes", exhibit an enormous diversity of forms and habits which is for the great part poorly studied and far from being totally described. The present paper identifies a monophyletic subunit clearly distinct from all known genera of the family, and proposes a new genus to delimit it.

Listrura gen.n. includes two species, *L. camposi* (Miranda Ribeiro, 1957) and *L. nematopteryx* sp. n. The former is known only from the holotype (recent collecting trips to the type-locality failed to locate any more specimens) and this scarcity of material

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prevented its exact systematic position from being discovered previously. In 1983, nine examples of a distinct but related species were collected by Marco T. C. Lacerda, Luiz E. Rulff and Luiz E. M. Cardoso in the vicinity of Rio de Janeiro. More extensive collections of this newly discovered population provided enough material for a detailed morphological description and comparisons.

The new genus is particularly noteworthy in forming a monophyletic group together with the Glanapteryginae, a rare subfamily first described by MYERS (1944) and so far known only from the upper Rio Negro of the Amazon basin. The character set it displays is also noteworthy in calling into question the naturalness (here meaning monophyly in the strict sense) of the subfamily Trichomycterinae as presently defined.

METHODS

All measurements were made point-to-point, taken with dial calipers. Measurements were on the left side of specimens whenever possible. Body depth was taken just in front of the base of anal fin (not including the base of dorsal); caudal peduncle depth included accessory rays and was measured at the vertical through the insertion of principal caudal rays. Caudal peduncle length is from the last anal-fin ray to the middle of the caudal fin base. Internarial width is the distance between the bases of the inner rims of the posterior nares. Dorsal and anal-fin base lengths were measured from the first visible ray to their point of posterior attachment. Remaining measurements followed TCHERNAVIN (1944: 251-252). Cleared, alizarin and alizarin-alcian blue stained specimens were prepared using modified techniques of WASSERSUG (1976) and DINGERKUS & UHLER (1977). All detectable splints and segmented rays were included in anal and dorsal-fin ray counts. Principal caudal-fin rays include all branched rays plus one unbranched ray in each lobe; these counts are given for each lobe (upper first), separated by a plus sign. Fin ray counts were taken on stained and unstained specimens. The numbers of vertebrae and ribs were determined on cleared and stained preparations and from radiographs in the case of holotypes. Number of vertebrae includes five in the Weberian complex and two in the compound caudal centrum ($PU_1 + U_1$). Opercular and interopercular odontodes were counted only in holotypes and in stained specimens.

Abbreviations of institutions are: Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu Nacional do Rio de Janeiro, Rio de Janeiro (MNRJ); Muséum d'Histoire naturelle, Genève (MHNG); Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP); Museu Anchieta, Porto Alegre (MAPA) and Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam (ZMA).

Listrura, gen. n.

Type species. — *Listrura nematopteryx* sp. n.

Diagnosis. — Small, slender, burrowing Trichomycteridae with non-parasitic habits. Body very elongate, roughly rounded in cross section. Pectoral fin very narrow, with much reduced number of rays (3 or less) but relative length normal when compared to most other trichomycterids. No vestige of pelvic fins. Caudal fin rounded or very slightly pointed, showing reduced principal ray counts (4+4, 4+5, 5+4, 5+5,

or 5 + 6); continuous above and below with numerous well developed accessory rays. The numerous accessory rays on tail make the caudal region shovel-shaped. Dorsal and anal fins small, with reduced ray counts (D: 6 to 8, A: 7 or 8), and adjacent to accessory caudal rays, very posteriorly on body (in last third of standard length). All dorsal, anal and pectoral-fin rays unbranched. Small number of odontodes on opercle (4 to 7) and interopercle (5 to 9). Maxillary, rictal and nasal barbels present. Mouth subterminal and not sucker-like. Teeth conical, unspecialized and few in number, arranged in two irregular rows on dentary and premaxilla. Pectoral (axillary) organ conspicuous. Orbital margin not free. Two large sensory pores (openings of pterotic sensory canal) near upper border of opercle. Sensory canal system extremely reduced on skull, ending at temporal canal openings (no branch extending into sphenotic or frontal). High number of vertebrae (55 to 59). Cranial fontanel completely closed. Only 2 to 3 pairs of ribs. Elements of the caudal skeleton with great degree of fusion, including between hypurals 2 and 3.

E t y m o l o g y . — Derived from greek *listros* (shovel) and *ura* (tail), in reference to the form of the tail. Gender feminine.

***Listrura nematopteryx*, sp. n.**

(Figs 1-2)

Eremophilus camposi (not Miranda Ribeiro 1957); MIRANDA RIBEIRO 1962.

Holotype: MZUSP 36974, 26.9 mm SL, small marsh which is source of creek later joining Ribeirão Imbariê, tributary of Rio Estrela, near 58 km mark of old road leading to Petrópolis (“Antiga Rio-Petrópolis”, also called “Estrada Automóvel Club”), Município de Magé, Localidade de Piabetá, Rio de Janeiro, Brazil (22°36’36’’S, 43°11’26’’W), U. Caramaschi, M. T. C. Lacerda, M. C. C. Pinna and L. E. Rulff, 30 Mar 1985.

Paratypes (7.2 to 36.6 mm SL): MZUSP 36975, 12 specimens collected with holotype; MZUSP 37137, 18 specimens, same locality as holotype, M. T. C. Lacerda, M. C. C. Pinna and K. Tanizaki, 20 Feb 1987; MNRJ 10970, 9 specimens, same locality as holotype, L. E. M. Cardoso, M. T. C. Lacerda and L. E. Rulff, 6 Aug 1983; MHNG 2385.80, 3 specimens, same locality as holotype, M. T. C. Lacerda, M. C. C. Pinna and K. Tanizaki, 20 Feb 1987; ZMA 119.463, 3 specimens collected with holotype.

D i a g n o s i s . — *Listrura nematopteryx* is readily distinguished from all other known trichomycterids by the extremely narrow, one rayed, filamentous pectoral fin. Differs further from its only congener in smaller overall size; less robust body and head; eyes less superiorly oriented; narrower and less depressed head; patches of interopercular odontodes smaller and higher on head; lateral line sensory pores on axillary organ in more vertical plane, hardly seen from above; insertion of pectoral fin higher on side of body; lower numbers of odontodes on opercle and interopercle; and mouth not as inferior.

D e s c r i p t i o n . — Morphometrics of holotype and part of paratypes given in table 1. Ventral and dorsal profiles of body smoothly curved. Trunk cylindrical, slightly higher than broad anteriorly. Body becoming gradually more compressed from pectoral region to tail. Head not noticeably depressed but relatively wide. Branchial membranes united to isthmus only at median line, wide gill openings remaining. Eye small but well formed and with distinct lens, its covering skin thin and transparent. Lips fleshy, covered with very minute numerous papillae. Upper jaw slightly longer than lower, corners of

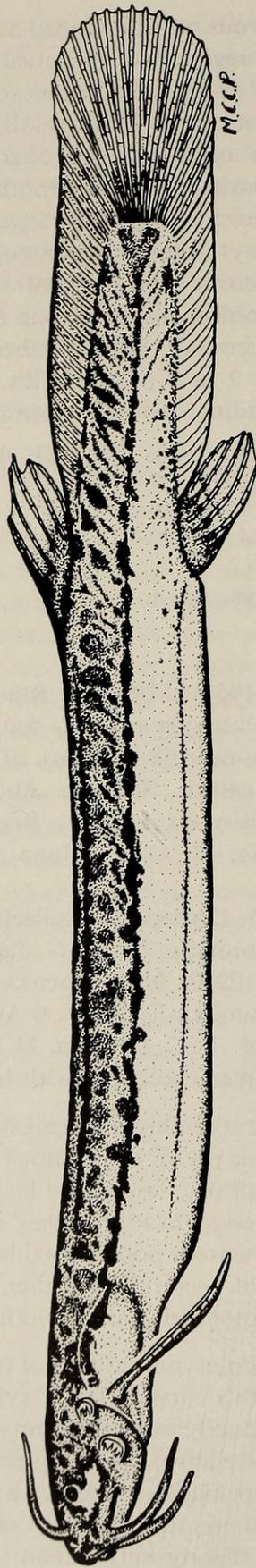


FIGURE 1.

Listrura nematopteryx. Holotype, MZUSP 36974. Lateral view. Scale 3 mm.

mouth not going far backwards. Snout with flat lateral expansion in area between eye and base of maxillary barbel. Barbels flat and well developed, their surface covered with minute papillae, similar to those on lips. All barbels with easily visible internal cores. Maxillary barbel largest, reaching little beyond base of pectoral fin. Rictal and nasal barbels shorter, extending beyond posterior tip of opercular odontodes. Posterior nares about midway between anterior ones and eyes. Anterior nares placed further apart than posterior ones. Pectoral fin flatly filamentous, with only one ray (segmented); profile gently curved, slightly constricted at base, widening towards middle and then narrowing gradually to tip. Surface of pectorals covered by papillae similar to those on lips and barbels, but less numerous. Barbels and pectorals showing great overall resemblance, with resemblance even more pronounced in living specimens, when both are stiff-looking and perfectly straight. Dorsal fin small and rounded, with 6 to 8 rays (holotype 8), fourth to sixth rays longest. In preserved specimens rays come close together distally, giving fin a slightly pointed shape. A rayless cutaneous fold preceding and continuous with dorsal fin in some individuals. Anal fin located under dorsal and of very similar shape, with 7 or 8 rays (holotype 8). Caudal rounded or very slightly lanceolate in some specimens where middle rays little longer than others. Principal ray counts variable, range as given for genus (holotype 5 + 5). Branched caudal rays dividing only once. Procurrent caudal-fin rays large and numerous (30 to 37 above and 28 to 33 below), merging gradually into principal caudal rays. A gentle depression between accessory and principal rays in some specimens (including holotype); in others caudal outline in continuous even arch. Each premaxillary with 12 to 23 teeth and each dentary with 11 to 17 teeth. Opercular odontodes 4 to 6 (holotype 5), occupying a small area and not reaching beyond rim of their underlying dermal fold. Interopercular odontodes 5 to 7 (holotype 5), occupying very slightly larger area than opercular odontodes and not reaching their underlying dermal fold rim. Variation in number of odontodes seeming at least partly due to replacement teeth. Vertebrae 57 to 59.

COLOR IN ALCOHOL. — Coloration very variable, but with following pattern constant. Overall coloration of body darker dorsally, dark mottles of various sizes and shapes along back and superior half of sides. Spots with differing degrees of intensity. Mottles partly coalescent on midlateral body surface, forming an ill-defined longitudinal stripe from opercle to base of caudal. Stripe increasingly blotched towards tail. Second longitudinal stripe, weaker, shorter and more dorsally located, close to dorsal midline. Inferior half of body unpigmented, except for lower part of caudal region and head. Spots on head smaller than on remainder of body. Snout and upper lip with uniform scattering of small chromatophores. Dorsal portion of head having, in addition to superficially located melanophores also on remainder of body, a more deeply located field of dark pigment evidently in different layer of skin. Distinct pigmentless area lateral to each eye, clearly visible as white spot on side of head, just below eye. Dorsally situated field of chromatophores extending lateroventrally onto opercular region, becoming progressively less dense ventrally. Ventral part of head with much less dense fields of chromatophores, one at base of branchiostegals, another irregularly disposed on chin region, sometimes extending onto inferior lip. Barbels white except for a few melanophores at their bases. Dorsal and anal fins hyaline. Dorsal fin with narrow dark stripe along its frontal margin. Caudal fin with few scattered melanophores near base. Superior and inferior areas of accessory caudal rays with parallel faint stripes of dark chromatophores, denser on superior area. Pectorals invariably devoid of dark pigment.

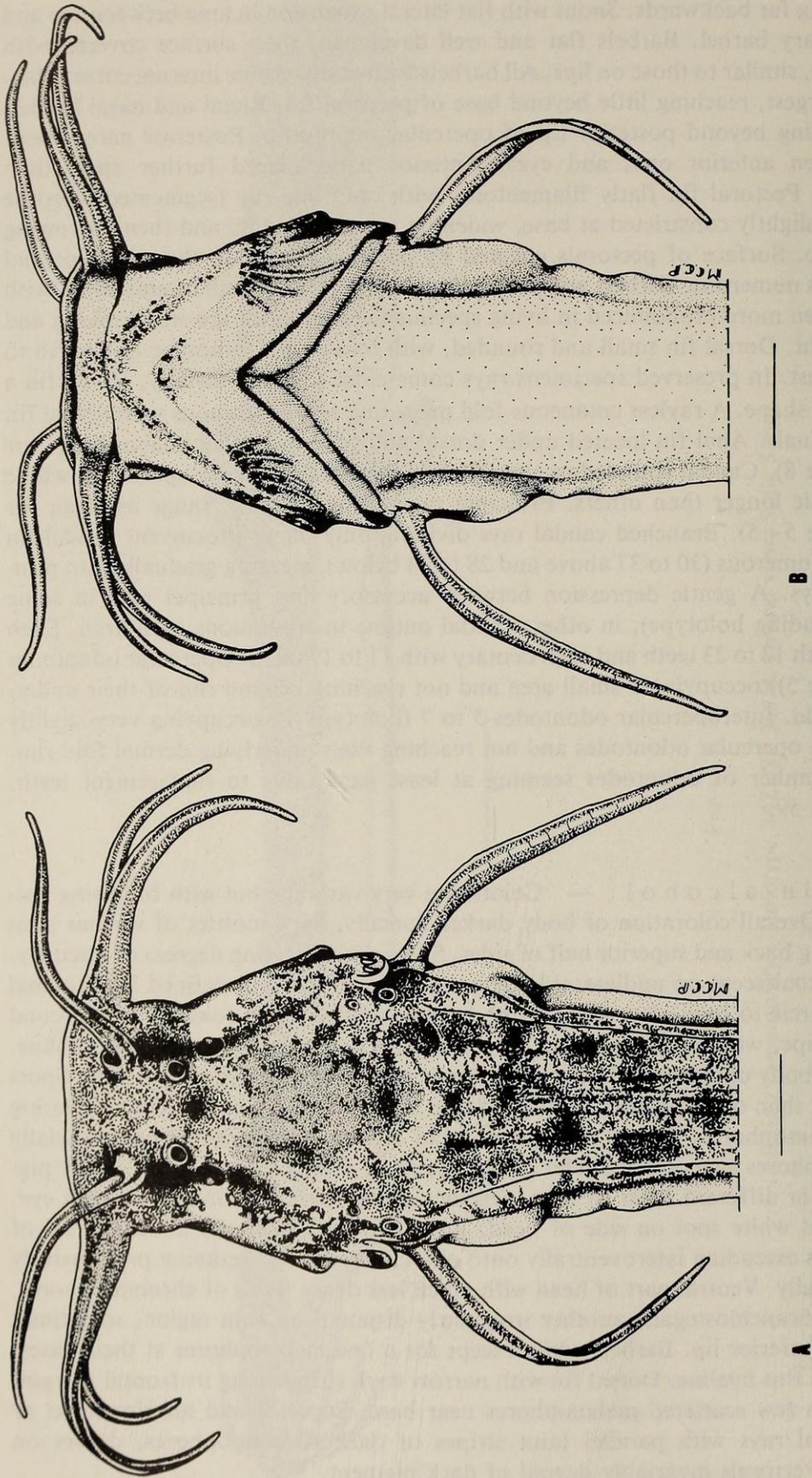


FIGURE 2.

Listrura nematopteryx. Holotype, MZUSP 36974. A-dorsal view of head. B-ventral view of head. Scales 1 mm.

Coloration of juveniles (10-19 mm SL) overall as in adults but more uniform, showing more scattered melanophores. Median lateral stripe is present and well defined, but differs in being narrower and less blotched than in larger specimens.

Distribution. — Known only from the type-locality, a single, extremely reduced marsh. The specimens of Carvalho reported by MIRANDA RIBEIRO (1962) are from the same area, but not from the same exact site (see below). This indicates that before human occupation this species probably showed a less extremely restricted range than today, although still being highly limited in distribution.

Remarks. — In 1962, Miranda Ribeiro reported two specimens of what he then identified as new material of *Eremophilus camposi*. Although the two fishes (MNRJ 9373) are now poorly preserved, a reexamination is still informative. Their pectoral fins, even though partially destroyed, can still be verified as being one-rayed, and all their proportions and fin ray counts agree with those of *Listrura nematopteryx*. The only differences found concern the number of odontodes on opercle and interopercle and the pattern of pigmentation, two characters no longer observable (most odontodes have fallen off and the coloration is faded) but which are recorded in MIRANDA RIBEIRO's 1962 paper. Since odontodes are very difficult to visualize in unstained specimens, it is possible that the reduced recorded number (3 on opercle and 4 on interopercle) was due to one or more having been overlooked by Miranda Ribeiro. Furthermore, original teeth insertion sites indicate that intact patches of odontodes were not smaller than those here described for *L. nematopteryx*. A more significant difference is found in the main lateral stripe, which Miranda Ribeiro reports as extending only to the level of dorsal fin, whereas in *L. nematopteryx* it extends to the base of caudal. This short lateral stripe is seen in one specimen in MZUSP 36975, which is a normal *L. nematopteryx* in all remaining aspects. Thus it appears that the specimen used by Miranda Ribeiro may be a low frequency color variant. It is possible that the population from which his examples were taken differed from the one used here as the basis for *L. nematopteryx*, but in any event it can be stated with certainty that his two fishes are either *L. nematopteryx* or at least members of its closest known relative.

According to MIRANDA RIBEIRO's same work (1962), these fishes were collected by the now late Prof. Antenor Leitão de Carvalho in Caminho do Tinguá, Tinguá, Rio de Janeiro. Nevertheless, Prof. Carvalho (pers. comm. 2 Nov 1985) stated that his two specimens were actually collected very close to the present type-locality of *L. nematopteryx*, perhaps about 1 km distant, and that Miranda Ribeiro's cited locality (Tinguá) was mistaken. The MNRJ 9373 jar label was written by Miranda Ribeiro, and thus does not represent the original collection information. Since Tinguá is only about 23 km in a straight line from the type-locality of *L. nematopteryx*, its occurrence or not there could seem to be a matter of little concern. However, considering the extremely endemic distribution of this species, an enlargement of more than 20 km in its range, if true, could constitute an alteration of considerable magnitude.

***Listrura camposi* (Miranda Ribeiro)**
(Figs 3-4)

Eremophilus camposi Miranda Ribeiro, 1957.

Holotype: MZUSP 3426, 38 mm SL, coll. Antônia Amaral Campos, 1940, Ribeirão Poço Grande, tributary of right margin of Rio Juquiá, itself tributary of Rio Ribeira, Município de Juquiá, São Paulo, Brazil (approx. 24°15'S, 47°37'W).

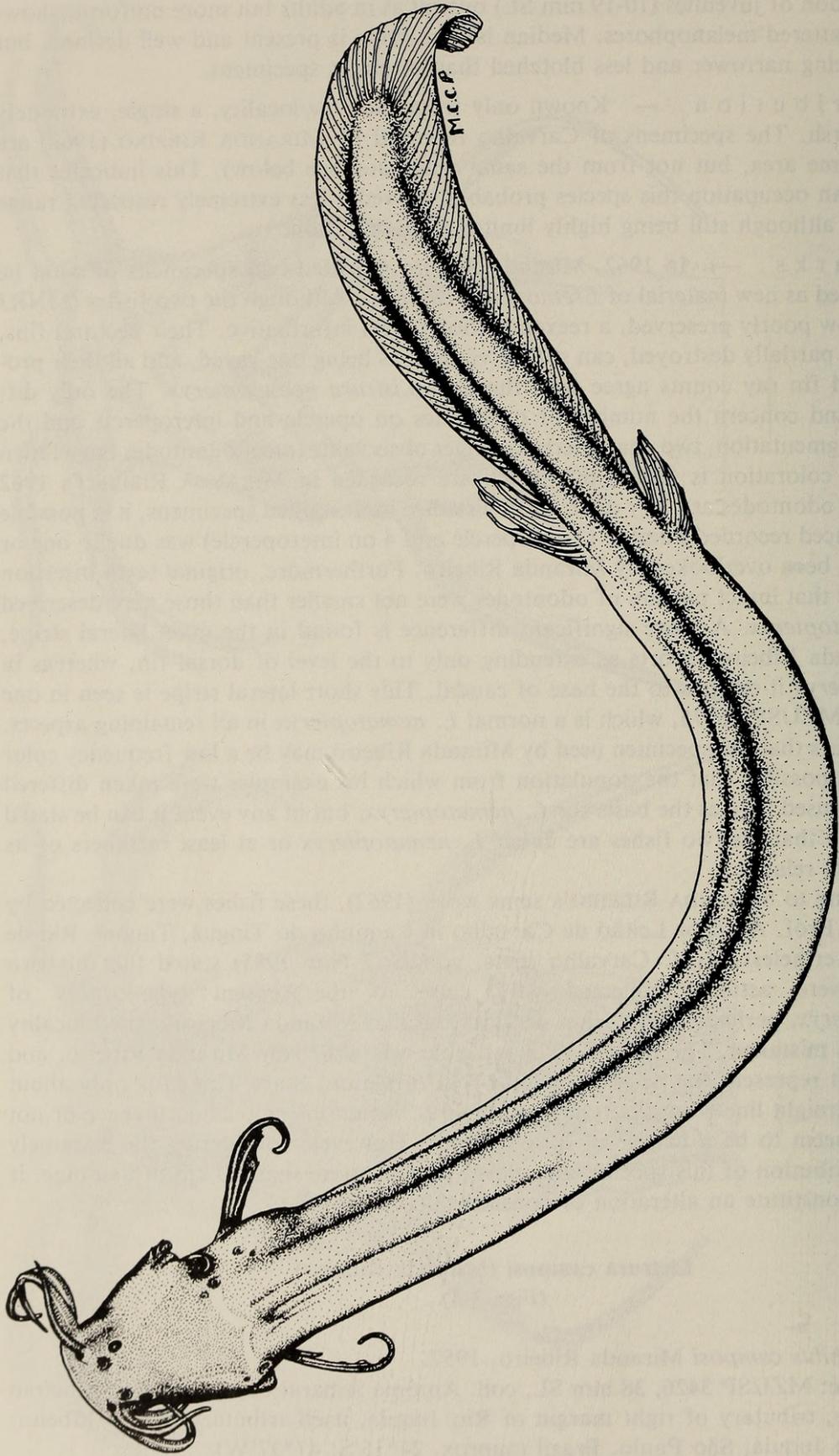
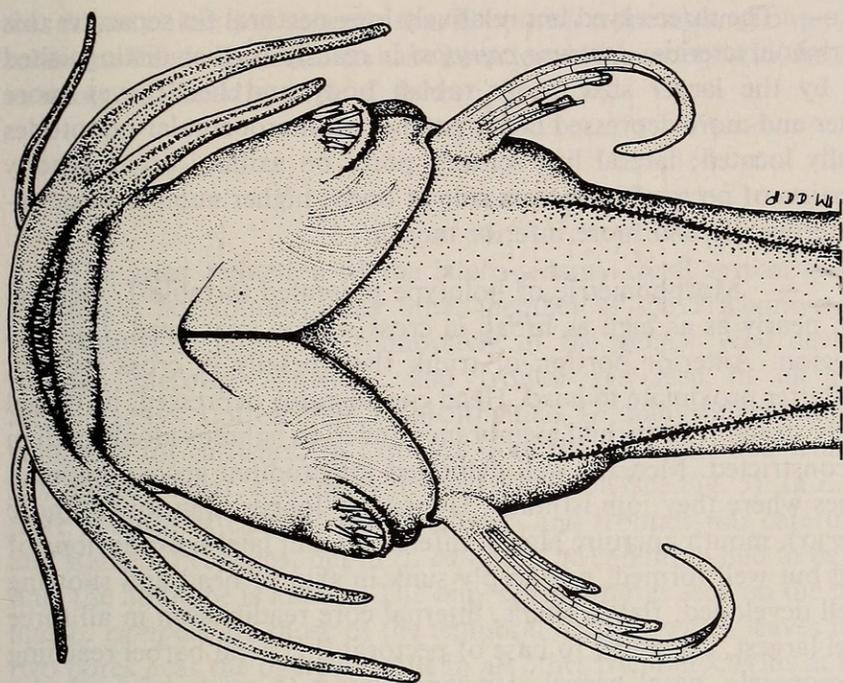
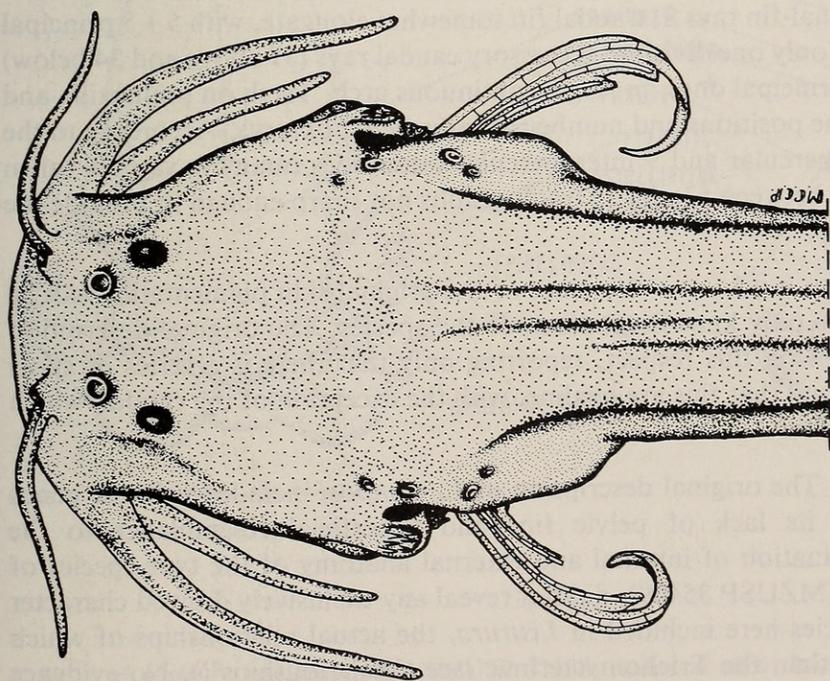


FIGURE 3.

Listrura camposi. Holotype, MZUSP 3426. Perspective drawing viewed from above. Pictured in actual preserved shape due to the fragile present condition of the specimen. Exact proportions are not to be taken from this illustration. Scale 3 mm.



B



A

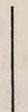


FIGURE 4.

Listrura camposi. Holotype MZUSP 3426. A-dorsal view of head. B-ventral view of head. Scales 1 mm.

D i a g n o s i s . — The three rayed but relatively long pectoral fin separates this species from all other trichomycterids. *Listrura camposi* is readily further distinguished from *L. nematopteryx* by the larger size; more robust body and head; eyes more superiorly oriented; wider and more depressed head; patches of interopercular odontodes larger and more ventrally located; lateral line sensory pores on axillary organ readily visible from above; insertion of pectorals lower on side of body; higher number of odontodes on opercle and interopercle and more inferior mouth.

D e s c r i p t i o n . — Morphometric of holotype presented in table 1. General profile of body straight, nearly as high as broad in cross section near head, tapering laterally towards tail region. Anterior portion of trunk flat dorsally in cross section, becoming progressively flatter proximate to head. Head considerably depressed, its dorsal and ventral profiles nearly straight. Branchial membranes united to isthmus along median line, gill openings not constricted. Median, well delimited longitudinal groove between two branchial membranes where they join isthmus. Upper jaw longer than lower (more so than in *L. nematopteryx*), mouth aperture almost inferior. Small lateral expansions of snout present. Eye small but well formed, not deeply sunk in skin of head and showing distinct lens. Barbels well developed, flat in shape, internal core readily seen in all three barbels. Maxillary barbel largest, extending to base of pectoral fin, rictal barbel reaching posterior margin of interopercle, nasal barbel extending almost to origin of opercular odontodes. Posterior nares midway between anterior ones and eyes, more closely together than anterior ones. Pectoral fin with three rays, first ray much longer and thicker than other two. All rays segmented and unbranched. Original contour of pectorals damaged by long preservation. From what can be presently seen and from drawing in original description, they show a smooth profile, gently widening from base to maximum width (shortly before middle of length), then gradually narrowing to tip. Their present coiled shape is probably a consequence of fixation, since some specimens of *L. nematopteryx* also show coiled pectorals after fixation although that shape is never observed in living fish. Papillae observable only on fleshy lips. Dorsal fin small, slightly pointed, with 6 rays preceded by small cutaneous fold. Anal fin origin along same vertical as dorsal, two fins of similar appearance. Anal-fin rays 8. Caudal fin somewhat elongate, with 5 + 5 principal rays, branched rays with only one division. Accessory caudal rays (37 above and 34 below) merging gradually into principal ones, in single continuous arch. Teeth on premaxilla and dentary seemingly in same positions and number as in *L. nematopteryx*. According to the original description, 7 opercular and 9 interopercular odontodes (many have now fallen off). Vertebrae probably between 57 and 55 (radiographs not sharp enough to provide the exact count).

C o l o r i n a l c o h o l . — No trace of the original skin pigmentation can be observed at present in the only known specimen of the species. The original description is unfortunately very brief on this respect, reporting only that there is a series of spots along the lateral midline and that fins are hyaline, with the exception of the caudal, which showed some scattered spots.

R e m a r k s . — The original description of *L. camposi* included it in the genus *Eremophilus*, based on its lack of pelvic fins and superficial resemblance to the Trichomycterinae. Examination of internal and external anatomy of the type-species of *Eremophilus*, *E. mutisii* (MZUSP 35409), did not reveal any exclusively derived character shared by it and the species here included in *Listrura*, the actual relationships of which are in subfamilies other than the Trichomycterinae (see "Relationships"). No evidence

was found either that suggests that *E. mutisii* is the sister-group of *Listrura* and its closest relatives. Pelvic fins seem to have been lost independently in the two cases, as is common in many unrelated groups of fishes.

RELATIONSHIPS

The great reduction of the latero-sensory canal system seen in the two species of *Listrura* is not found in any other member of the Trichomycteridae and constitutes a synapomorphy indicating monophyly of the genus. Well developed canals extending through pterotic, sphenotic and frontal are seen in all related outgroups (e.g. *Nematogenys*, Loricariidae, Callichthyidae, Diplomystidae) and this is the plesiomorphic condition for catfishes. In *Listrura*, both the sphenotic and frontal are totally devoid of any sensory canal, a uniquely derived condition (see Fig. 5). In *L. nematopteryx* the complete absence of canals from sphenotics and frontals was carefully confirmed in cleared and stained specimens, but in *L. camposi* the condition had to be verified indirectly, since only the holotype is known. The only sensory pores seen on the head of *L. nematopteryx* and *L. camposi* are those of the temporal branch, which leaves the pterotic and opens as two pores near the opercle, while in all other trichomycterids at least one more pore (the

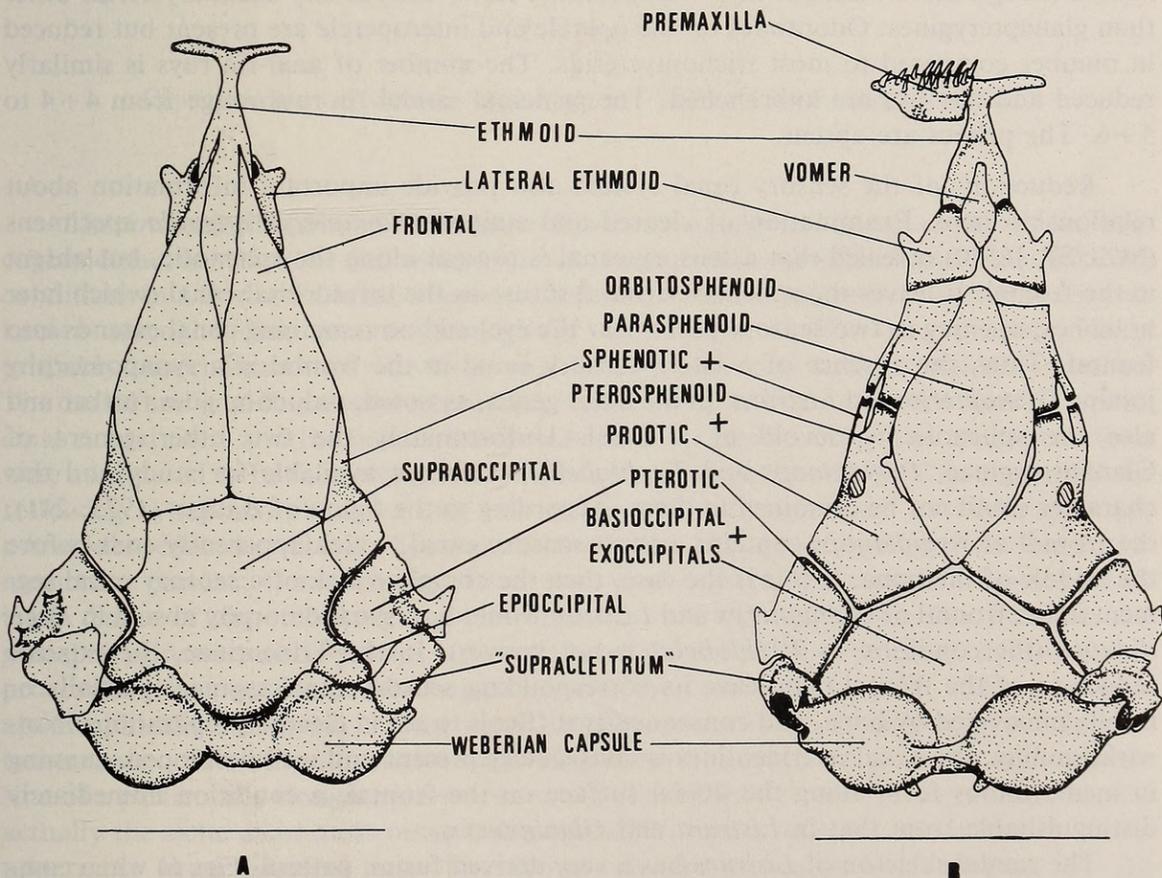


FIGURE 5.

Skull of *Listrura nematopteryx*. MZUSP 37138. A-dorsal view. B-ventral view. Scales 1 mm.

opening of the infraorbital canal) can be seen. As the infraorbital canal in trichomycterids emerges from the sphenotic-frontal suture (as in many other Siluroidei, see LUNDBERG, 1982: 36), an infraorbital sensory pore would indicate that at least the sphenotic bears a sensory canal segment. Since close examination does not reveal any sign of such pore on the head of *L. camposi*, it can be inferred that its sensory canal system is absent from, or at least greatly reduced on the sphenotic and frontal.

Many of the peculiarities found in the internal anatomy of *L. nematopteryx* are likely to be part of a derived pattern synapomorphic for both species of the genus, but presently impossible to verify in *L. camposi*. A particularly remarkable autapomorphy for *L. nematopteryx* (possibly synapomorphy for *Listrura*) is the bottle shape of the vomer (see Fig. 5B). Such a format is not found in any other member of the family, nor in any of the related outgroups, being regarded so as uniquely derived.

BASKIN (1973) gave the following derived characters for the subfamily Glanapteryginae: 1) dorsal fin absent; 2) pectoral rays one or none; 3) opercular and interopercular odontodes absent; 4) fewer than seven anal-fin rays, none segmented or branched; 5) principal caudal-fin rays 5 + 6 or fewer; 6) pelvic fins minute or absent. *Listrura* shares all these characters, either completely or at least to an extent which is unique for that genus and glanapterygines. The dorsal fin is present but with the size and number of rays reduced relative to most trichomycterids and other catfishes. The pectoral rays, although more than one in *L. camposi*, are fewer than in any trichomycterids other than glanapterygines. Odontodes on the opercle and interopercle are present but reduced in number compared to most trichomycterids. The number of anal-fin rays is similarly reduced and the rays are unbranched. The principal caudal-fin rays range from 4 + 4 to 5 + 6. The pelvics are absent.

Reductions of the sensory canal system also provide important information about relationship here. Examination of cleared and stained *Glanapteryx anguilla* specimens (MZUSP 36530) revealed that a sensory canal is present along the sphenotic, but absent in the frontal. It leaves the sphenotic-frontal suture as the infraorbital canal (which later branches, opening as two sensory pores near the eye) and no remaining canal extends into frontal. Thus, the absence of a latero-sensory canal in the frontal is a synapomorphy joining *Glanapteryx* and *Listrura*. In the latter genus, as noted, reduction goes further and also the sphenotic is devoid of a canal. Unfortunately the two other genera of Glanapteryginae, *Pygidianops* and *Typhlobelus*, were not available for study and this character could not be examined in them. According to the figure of BASKIN (1973: 241), the frontal of *Pygidianops* contains a short sensory canal, which apparently ends before the middle of the bone. If this is the case, then the complete lack of a sensory canal segment in the frontal of *Glanapteryx* and *Listrura* would be a synapomorphy absent in *Pygidianops* (the condition in *Typhlobelus* is not known). In the Tridentinae, the extreme reduction of the frontal may leave its corresponding sensory canal segment partially or totally uncovered by bone, and consequently difficult to see in cleared preparations. Notwithstanding, the canal in tridentines is consistently present and well developed, running in membranous form along the dorsal surface on the frontal, a condition immediately distinguishable from that in *Listrura* and *Glanapteryx*.

The caudal skeleton of *Listrura* has a very derived fusion pattern (Fig. 6) when compared to the primitive state of this structure in catfishes (LUNDBERG & BASKIN, 1969). Fusion occurs between all elements, only the distal part of uroneural and a small fraction of the inner rims of hypurals 2 and 3 remaining unfused (in variable degrees). Such extreme fusion is seen also in *Glanapteryx*, where fusion proceeds even further, but in no

other trichomycterid (the condition in the Sarcoglanidinae and remaining Glanapteryginae is unknown).

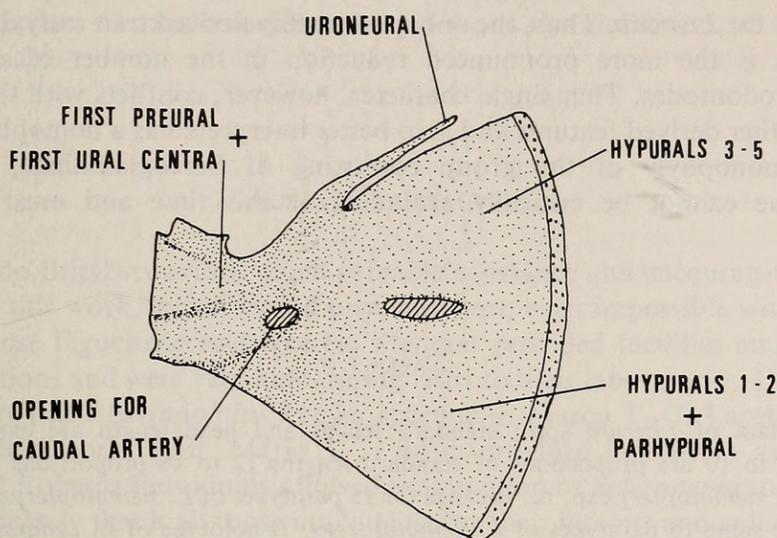


FIGURE 6.

Caudal skeleton of *Listrura nematopteryx*. MZUSP 37138. Scale 0.5 mm.

Listrura and glanapterygines seem to form a monophyletic group excluding the Sarcoglanidinae, in which the following features retain a plesiomorphic state relatively to the conditions in *Listrura* + Glanapteryginae. The dorsal fin is reduced in only one of the two known sarcoglanidine genera (*Sarcoglanis*, see MYERS & WEITZMAN, 1966), being probably a specialization of that taxon only. The pectoral rays are not reduced in number. The dorsal and anal fins always retain some branched rays. There are more than 5 + 6 principal caudal rays, and the pelvics are present with no sign of reduction. Sarcoglanidines were considered to be the sister-group of glanapterygines by BASKIN (1973), who cited the following synapomorphies for the two subfamilies: 1) opercular and interopercular odontodes reduced or absent; 2) opercular bone with a long posterior process; 3) a dorsal membrane present; 4) anal-fin rays fewer than 8; and 5) reduced number of premaxillary teeth. Some of these characters are incongruent with the hypothesis that *Listrura* and glanapterygines are sister-groups, and worthy of discussion in more detail. The posterior process of the opercular in *Malacoglanis* in the figure in BASKIN (1973: 301) seem to be apomorphically elongated, but the same cannot be said of the Glanapteryginae. In that taxon there occurs only a posterior narrowing of the opercle, what gives the false impression of a particularly elongate posterior process. The relative length of the process remains actually the same as in most other trichomycterids; extending until about the tip of the uppermost branchiostegal ray. The dorsal membrane (perhaps a remnant of the embryonic fin fold) appears to be a character of doubtful homology and polarization. The structure occurs also in adult *Scleronema* specimens (MCP 9315; MAPA 2409, 1864, 1468, 1802), in at least one species of *Trichomycterus* (*T. duellmani*, see ARRATIA & MENU-MARQUE, 1984), is absent in *Glanapteryx* and present in only a few specimens of

Listrura. Reduced anal-fin ray numbers are also present in *Listrura* and may be possibly a synapomorphy, but at a more inclusive level. The number of premaxillary teeth in *Glanapteryx* is not so reduced, the genus has about 17 teeth on each premaxilla, a value overlapping that for *Listrura*. Thus, the only presumably derived trait truly discordant with my hypothesis is the more pronounced reduction in the number of opercular and interopercular odontodes. That single character, however, conflicts with the distribution of numerous other derived features and is so better interpreted as a homoplasy. The question of the monophyly of the group consisting of Sarcoglanidinae, *Listrura* and Glanapteryginae cannot be critically evaluated at this time and must await future investigation.

TABLE 1.

Morphometric data of *Listrura* spp.; standard length and head length are expressed in mm; measurements 2 to 10 are proportions of standard length; 12 to 16 proportions of head length. A-holotype of *L. nematopteryx* sp. n.; B-range for 15 paratypes of *L. nematopteryx*; C-Average for the same 15 paratypes of *L. nematopteryx*; D-holotype of *L. camposi*.

	A	B	C	D
1. Standard length	26.90	18.21-36.60	26.13	37.15
2. Total length	1.12	1.11-1.20	1.15	1.12
3. Body depth	0.08	0.06-0.10	0.08	0.09
4. Caudal peduncle length	0.22	0.19-0.29	0.23	0.22
5. Caudal peduncle depth	0.09	0.08-0.10	0.09	0.08
6. Predorsal length	0.72	0.71-0.76	0.73	0.73
7. Preanal length	0.75	0.69-0.76	0.72	0.71
8. Dorsal base length	0.05	0.04-0.07	0.06	0.04
9. Anal base length	0.05	0.05-0.07	0.06	0.05
10. Pectoral fin length	0.15	0.11-0.15	0.13	0.08
11. Head length	3.35	2.70-3.95	3.39	4.55
12. Head width	0.87	0.76-0.91	0.84	1.00
13. Head depth	0.43	0.37-0.51	0.44	0.42
14. Interorbital	0.33	0.25-0.33	0.28	0.33
15. Rostral part of head	0.36	0.34-0.48	0.40	0.34
16. Internarial width	0.19	0.13-0.19	0.17	0.22

For the reasons given above, *Listrura* is here formally included within the subfamily Glanapteryginae, although not conforming completely with the original definition of the subfamily (MYERS, 1944). The subfamilial inclusion is justified in light of the derived characters uniting *Listrura* more closely to the original members of the Glanapteryginae than to any other known Trichomycteridae.

One important final point of note relative to the characters displayed by *Listrura*, is that it fits well the traditional definition of the Trichomycterinae (e.g. EIGENMANN, 1918; MYERS, 1944), although its actual relationships lie outside that subfamily. It is worthy of attention that traits used so far to delimit the Trichomycterinae have been clearly plesiomorphic, bringing together forms only due to their lack of the obvious specializations of the remaining subfamilies. BASKIN's (1973: 78) failure in finding synapomorphies

for trichomycterines is symptomatic of this situation. The more detailed diagnosis given by ARRATIA *et al.* (1978) for the Trichomycterinae (their Pygidiinae) also does not include any character that can be considered derived. *Listrura*, thus, demonstrates the problems with the utilization of plesiomorphic characters in the definition of the subfamily Trichomycterinae.

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