

A new species of *Ammoglanis* (Siluriformes: Trichomycteridae) from Venezuela

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A new miniaturized species of the trichomycterid genus *Ammoglanis* is described from the Río Orinoco basin in Venezuela. It is distinguished from its only congener, *A. diaphanus*, by: a banded color pattern formed by internal chromatophores; 5 or 6 pectoral-fin rays (7 in *A. diaphanus*), 5/5 principal caudal-fin rays (6/6 in *A. diaphanus*), ii+6 dorsal-fin rays (iii+6+i in *A. diaphanus*), 30 or 31 vertebrae (33 in *A. diaphanus*), six or seven branchiostegal rays (five in *A. diaphanus*), subterminal mouth (inferior in *A. diaphanus*) and by the lack of premaxillary and dentary teeth. The two species also differ markedly in a number of internal anatomical traits. Synapomorphies are offered to support the monophyly of the two species now included in *Ammoglanis*, as well as autapomorphies for each of them. *Ammoglanis pulex* is among the smallest known vertebrates, the largest known specimen being 14.9 mm SL. It is a fossorial inhabitant of shallow sandy sections of clear- and light blackwater streams, and probably feeds on interstitial microinvertebrates.

Introduction

Miniaturization is a frequent phenomenon in the evolution of neotropical freshwater fishes, and it seems to have occurred independently numerous times in that biogeographical region (Weitzman & Vari, 1988). Among the many yet undescribed species of neotropical freshwater fishes, a disproportionately large number is composed of small to minute forms. The obvious reasons for this situation is that small species have attracted less attention than larger-sized components of the fish fauna, and also that they have been less frequently collected with standard sampling methods. It also happens that, when collected,

they have often been superficially mis-identified as juveniles of other fish.

Miniature species are particularly abundant in the catfish family Trichomycteridae, and expectedly there appears to be more undescribed taxa in that group than in most other neotropical fish families. This is particularly true for the subfamilies Sarcoglanidinae and Glanapteryginae, most species of which are miniaturized cryptic inhabitants of sandy environments. The new miniature species described herein was found in sand beaches of the Río Orinoco basin in Venezuela.

The phylogenetic position of the new taxon is somewhat problematic. Some derived characters

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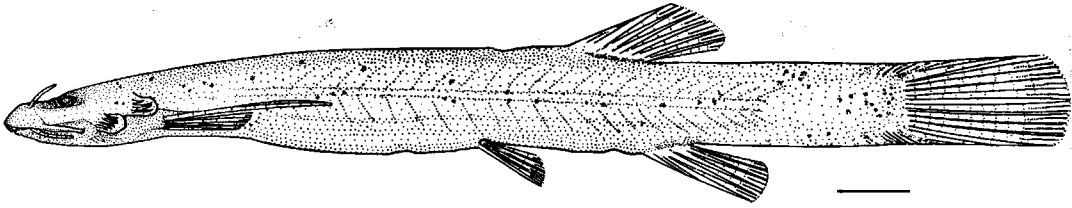


Fig. 1. *Ammoglanis pulex*, holotype, MBUCV-V-29040, 12.4 mm SL. Scale bar 1 mm.

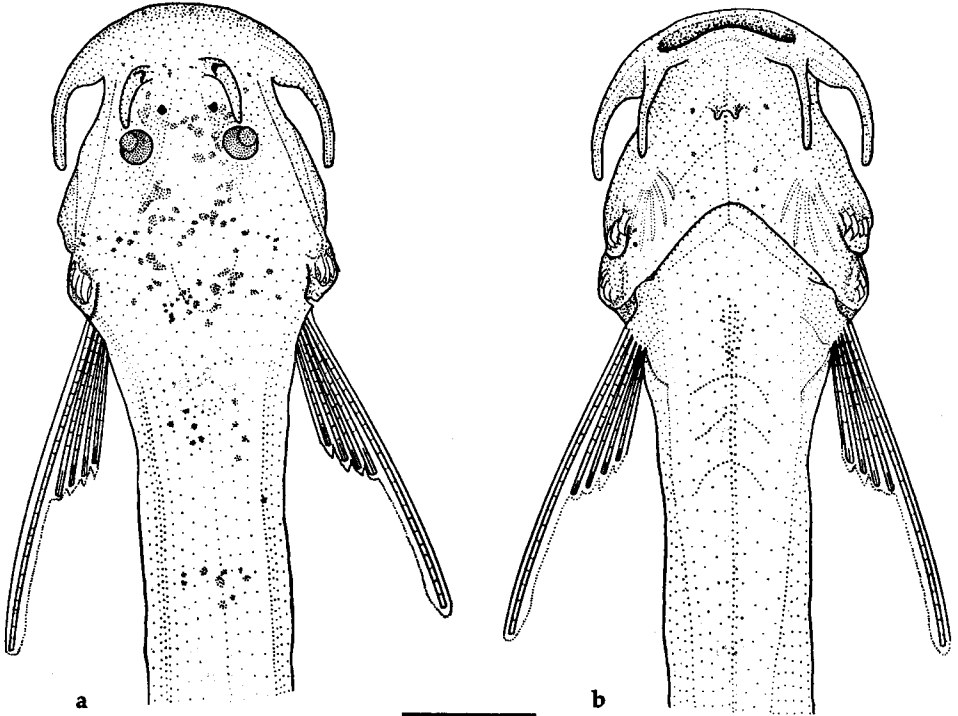


Fig. 2. *Ammoglanis pulex*, holotype, MBUCV-V-29040. a, dorsal view of head; b, ventral view of head. Scale bar 1 mm.

of internal anatomy indicate that it is the sister group to the recently described *Ammoglanis diaphanus* (Costa, 1994), but its obviously paedomorphic features and scarcity of study material of *A. diaphanus* prevent a conclusive assessment of its relationships. Higher-level problems in trichomycterid phylogeny also renders its subfamilial inclusion tentative. Ongoing phylogenetic studies by MP indicates that *Ammoglanis* along with other yet undescribed forms are the sister group to a large intrafamilial clade composed of several genera and subfamilies. This implies that some modifications of the current classification

of the family are necessary so that it conforms to strict phylogenetic criteria. In the interim, however, we include the new species in Sarcoglanidinae, following current allocation of *Ammoglanis* by Costa (1994). Despite limitations on the phylogenetic knowledge about these fishes, it is necessary to describe the peculiar new species treated herein, in order to make the name available for faunal surveys and biodiversity inventories, particularly in view of the environmental impact the habitat of the species is presently undergoing.

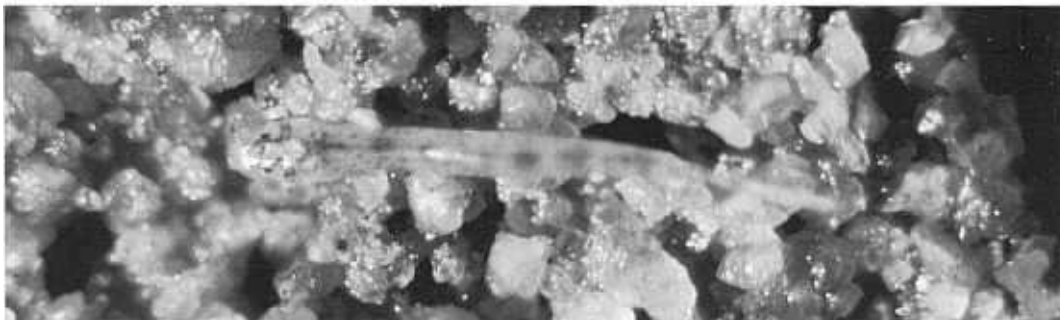


Fig. 3. *Ammoglanis pulex*. Live fish in the sand of its natural habitat. Specimen not preserved (photograph by K. Winemiller).

Material and methods

Measurements were straight-line, using a dissecting stereomicroscope with a micrometer eyepiece. Definition of measurements followed de Pinna (1989) and Tchernavin (1944), except that caudal peduncle depth was taken at its midlength. Cleared and counter-stained specimens were prepared following a slightly modified version of Taylor & Van Dyke (1985). Vertebrae, ribs and branchiostegal rays were counted on cleared and stained specimens only. Vertebral counts do not include those involved in the Weberian and caudal complexes. Institutional abbreviations are: CAS, California Academy of Sciences, San Francisco; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MBUCV, Museo de Biología, Universidad Central de Venezuela, Caracas; MCNG, Museo de Ciencias Naturales de Guanare, Guanare; and MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo. Comparative material examined is listed at the end of the paper.

Ammoglanis pulex, new species (Figs. 1-3)

Holotype. MBUCV-V-29040, 12.4 mm SL; Venezuela: Estado Amazonas: Río Paria Grande at bridge on road between Pto. Ayacucho and Samariapo (5°23'N 67°37'W); A. Barbarino & K. Winemiller. 20 Mar 1991.

Paratypes. MZUSP 42471, 26 ex., 11.9-13.8 mm SL (5 of which cleared and double stained for bone and cartilage); CAS 98921, 3 ex, 11.9-12.8 mm SL; collected with holotype. – MCNG 11172, 6 ex.,

13.9-14.4 mm SL; MZUSP 42472, 6 ex., 13.9-14.9 mm SL; Venezuela: Bolivar State: Caño Garapata at bridge on road between Caicara and Pto. Ayacucho (6°19'20"N 67°07'00"W); K Winemiller, 17 Apr 1984. – MCNG 35298, 1 ex., 13.7 mm SL; Venezuela: Amazonas State: Río Pamoni, (approx. 2°50'N 65°54'W); D. Jepsen & K. Winemiller. 2 Feb 1997.

Diagnosis. A minute trichomycterid distinguished from all other members of the family by the following autapomorphic characters: 1) dark chromatophores in interior of the body, forming a banded pattern visible from both sides by transparency in the living fish; 2) lack of dentary teeth; and 3) scythe-shaped lacrimal with an anterior facet articulating with the anterior palatine cartilage. *Ammoglanis pulex* is further distinguished from its only congener, *A. diaphanus* by: 1) lack of premaxillary teeth (vs. teeth present and well-developed); 2) pectoral-fin rays i+4 or i+5 (vs. i+6); 3) lack of metapterygoid (vs. metapterygoid small but present); 4- 30 or 31 vertebrae (vs. 33); 5) principal caudal-fin rays 5/5 (vs. 6/6); 6) dorsal-fin rays ii+6 (vs. iii+6+i); 7) rectal barbel slightly longer than soft portion of maxillary barbel (vs. the reverse); 8) 6 or 7 branchiostegal rays (vs. 5); 9) mouth subterminal (vs. mouth ventral); 10) narrow anterior cartilage of palatine, its anteroposterior width less than half the maximum width of premaxilla (vs. cartilage wider than premaxilla); and 11) tip of first pectoral-fin ray reaching to about midway between bases of pectoral and pelvic fins (vs. nearly to base of latter). Other characters, plesiomorphic or of uncertain polarity, but useful to identify the species include: 1) first pectoral-fin ray prolonged as a filament, almost twice as long as other rays;

2) body depth practically even from nape to base of caudal fin; 3) nasal barbel short, its posterior tip reaching at most the center of eye, in some specimens not reaching its anterior margin; and 4) presence of two short finger-like barbels on mentonian region.

Description. The general aspect of the new species is seen in Figures 1-2. Morphometric data are presented in Table 1. Body moderately elongate, round in cross section close to head and progressively more compressed towards caudal fin. Body in lateral view least deep close to head, reaching its maximum depth immediately anterior to pelvic fin. No median fin-fold on either dorsal or ventral profiles. Caudal region compressed, with nearly even depth, slightly expanded posteriorly due to accessory caudal-fin rays. Head nearly triangular in dorsal view, widest at opercular region. In lateral view, head very depressed, snout flattened. Mouth subterminal and small, with thin lower lip. Branchiostegal membranes narrowly attached to isthmus, branchial openings wide. Maxillary, rictal and nasal barbels short and thick, with blunt tips. Internal cores iridescent under direct light, clearly visible in all three pairs of barbels. Maxillary barbels as long as their bony base, extending slightly posterior to posterior margin of eyes. Rictal barbels slightly longer than soft portion of maxillary barbels, but not extending as far posteriorly because of pres-

ence of large bony base in latter. Nasal barbels shortest and difficult to see on head, reaching anterior margin of eyes, their origin equidistant from anterior margin of eye and anterior tip of snout. Chin region with two finger-like projections, resembling pair of very short mental barbels, one on each side of midline. (elsewhere in trichomycterids, similar structures are seen only in the stegophiline *Parastegophilus maculatus* and in the sarcoglanidines *Microcambeva barbata*, *Malacoglanis gelatinosus*, and some specimens of *Stenolicmus sarmientoi*). Eyes located slightly anterior to middle of HL, with well-formed lens directed antero-laterally in dorsal view. Opercular and interopercular odontodes well-developed and prominent externally on head. Seven opercular and six interopercular odontodes.

Pectoral fin narrow, with i+4 or i+5 rays, all segmented. First unbranched ray nearly twice as long as others. Pelvic fin origin located approximately at midlength of SL, with 4 rays (second and third branched; one specimen with 5 rays in one side) plus a pelvic splint. Tip of pelvic fin nearly a fin's length short of anal opening. Origin of dorsal fin located slightly posterior to vertical through tip of pelvic fin. Dorsal-fin rays ii+6, all segmented. Seven dorsal-fin pterygiophores. Small adipose bodies at midline anterior to dorsal fin. Origin of anal fin shortly posterior to anal opening, slightly posterior to vertical through posterior point of dorsal-fin base. Anal-fin rays iii+5, all segmented except for first. Six anal-fin pterygiophores. Adipose fin absent. Caudal fin long and rectangular in shape, not deeper than rest of caudal peduncle. Principal caudal-fin rays 5/5, all segmented. Procurrent caudal-fin rays 6 to 8 dorsally and similar range ventrally. Vertebrae 30 or 31, all with well-developed neural spines. Two or three pairs of pleural ribs, directed posteroventrally on anterior two or three free vertebral centra. Six or seven branchiostegal rays.

Pigmentation. Dark pigmentation very reduced in surface of preserved fish. Scattered dark chromatophores along sides, slightly more concentrated along lateral midline and sometimes forming a vertical band on base of caudal fin and posterior portion of caudal peduncle. Melanophores concentrated at regular intervals along dorsum, forming eight poorly-defined bands visible in dorsal view. Dark coloration on dorsal part of head formed mainly by brain pigment seen by transparency, but some integumentary

Table 1. Morphometric data for holotype and nine paratypes of *Ammoglanis pulex*.

	holotype	range	mean
Standard length (mm)	12.4	11.5-14.7	13.1
Percentage of standard length			
Total length	120	118-121	120
Pectoral-fin length	20	17-21	19
Predorsal length	65	62-68	65
Prepelvic length	53	49-54	52
Preanal length	72	68-75	71
Body depth	11	10-14	12
Caudal peduncle length	22	21-25	23
Caudal peduncle depth (max.)	9	8-10	9
Head length	18	16-18	17
Percentage of head length			
Head width	83	75-94	85
Head depth	43	39-57	46
Mouth width	33	28-40	33
Interorbital	22	20-23	22
Eye diameter	10	10-13	11

dark chromatophores present on snout and at base of opercular patch of odontodes. Ventral surface of head with sparse dark chromatophores, mainly in region between interopercula. Eyes very dark, sharply visible in external aspect. Barbels white. Fins mostly hyaline, except for few dark chromatophores scattered on caudal fin and at base of dorsal and anal fins. Dark chromatophores also present in interior of fish, mostly invisible in opaque preserved specimens, but visible in unbleached cleared and stained specimens and also in the translucent living fish. The interior chromatophores form a pattern of vertical bands matching those formed by integumentary chromatophores in the dorsum of fish, but visible in lateral view from both sides, assuming transparency of the lateral trunk musculature in the living fish.

In life the fish is light translucent pink and cryptic against the sand of its natural habitat (Fig. 3).

Etymology. The specific epithet *pulex*, meaning flea in Latin, refers to the minute size of the species. A noun in apposition.

Discussion. Two of the five cleared and stained specimen are female, and have elongate gonads lightly stained in blue and visible through transparency. The gonads occupy approximately the middle third of the abdominal cavity, and have numerous differentiated ova, clearly visible under the stereomicroscope. This indicates that the specimens available of *A. pulex* are not juveniles. However, they may not be at the largest adult size. According to Manriquez et al. (1988), Arratia & Huaquin (1995) and Trajano (1997), sexual maturity in trichomycterids occurs at about 50% of maximum adult length in the species studied so far.

The degree of ossification seen in most of the skeleton in the cleared and stained specimens of *A. pulex* is typical of adult trichomycterids. All dermal, membrane and chondral elements of the skeleton are present and well ossified. Cartilage bones have only small amounts of cartilage in their centers of ossification. Such a stage in the development of the skeleton corresponds to that in nearly full-sized trichomycterids. Juvenile specimens of the family normally have membrane bones poorly calcified, or not calcified at all. Also, their chondral bones are composed largely of cartilage, a condition evident in cleared and

stained juvenile material. On the other hand, the specimens of *A. pulex* have a large area of cartilage remaining in their basipterygium and meso-coracoid, not typical for adult trichomycterids. This may indicate that the available specimens of *A. pulex*, though certainly not at very early ontogenetic stages, are not yet at the maximum size for their species.

Another relevant piece of information indicating the adult or nearly adult condition of the material of *A. pulex* currently available is that juveniles of trichomycterids and other catfishes usually have a large remnant of the embryonic fin-fold. The fold tends to be more prominent in the dorsal midline of caudal peduncle, which is also the last part of the fold to recede with growth. Some remnant of the fin-fold may extend into quite late stages of development, and sometimes is present even in paedomorphic adults, such as in the sarcoglanidines *Sarcoglanis* and *Malacoglanis* and in the glanapterygines *Pygidianops* and *Typhlobelus*. *Ammoglanis pulex* has no trace of the juvenile fin-fold.

Therefore, it seems certain that the specimens so far available of *A. pulex* are not representing particularly early ontogenetic stages, and that they are not juveniles of any currently known larger trichomycterid. Their sexual maturity at approximately 10 mm SL places the species among the smallest of all vertebrates. The smallest (here meaning shortest SL) vertebrates at sexual maturity are all gobiids, namely *Trimmatom affucius* (8 mm SL), *Eviota infulata* (8.9 mm SL) and *Pandaka pygmaea* (10 mm SL), according to Winterbottom & Emery (1981). Under a criterion of 'smallness' based on mass rather than length (Bruun, 1940), *A. pulex* would also probably rank among the lightest of all vertebrates, as judging from its elongate body shape.

Ammoglanis pulex is a miniaturized fish, falling below the 26 mm SL established by Weitzman & Vari (1988) as the cutoff for separating miniaturized from non-miniaturized fish species. Paedomorphic fishes usually have a largely cartilaginous skeleton, with a reduced degree of ossification. Paedomorphic trichomycterids depart from that general pattern, because their reduction of ossification is slight or non-existent. Definitely paedomorphic species from various subfamilies, such as *Pygidianops eigenmanni* (Glanapteryginae), *Paravandellia* sp. (Vandellinae), *Stenolicmus sarmientoi* (Sarcoglanidinae) and *Trichomycterus hasemani* (Trichomycterinae) have

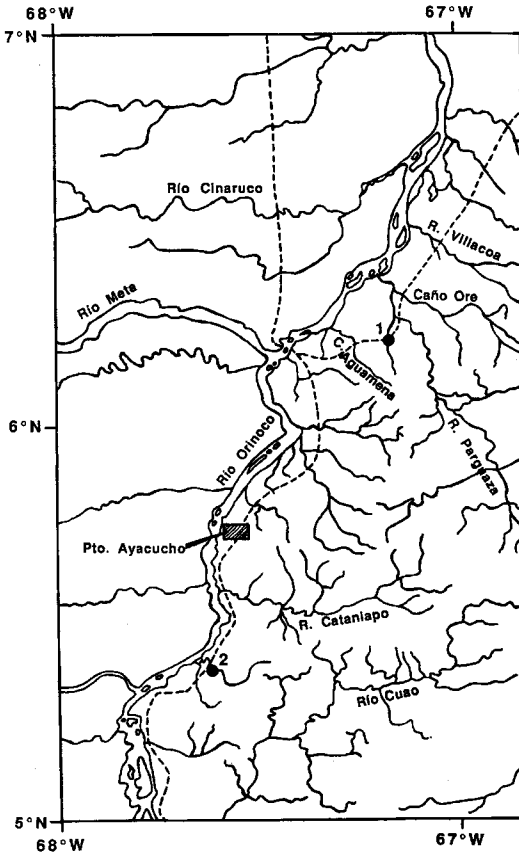


Fig. 4. Map showing the collection localities for *Ammoglanis pulex* in Venezuela. Site 1 is Caño Garrapata, Río Paraguaza drainage, Estado Bolívar (the name of the stream is now listed as Río Los Garzones). Site 2 is Río Paria Grande, tributary of the Río Orinoco, Estado Amazonas.

their skeletons very well-ossified, with relative amounts of cartilage similar to those seen in non-paedomorphic species. The skeleton of *A. pulex* is no exception to the trichomycterid condition, except for its basipterygium and mesoracoid, as mentioned above. Interestingly, miniaturized trichomycterids display other common traits of miniaturized species, such as the reduction in the latero-sensory canal system. Therefore, it seems that the effect of paedomorphosis on their skeletal system is different from that of most other fishes, and also different from the effect on other parts of their anatomy. Interestingly, miniaturized trichomycterids are found in phylogenetically distant lineages of the family, indicating that there have been several miniaturization

events in the family. Still, in all cases the degree of ossification of the skeleton is similar (not reduced), indicating that even for independent miniaturization events the peculiarity of the trichomycterid condition occurs repeatedly. The phylogenetically independent truncation of their ontogeny results in the same final configuration, itself distinct from that in most other miniaturized fish. This, in turn, may indicate that the ontogenetic timing of skeletal formation in paedomorphic trichomycterids is different from that in the majority of other teleosts.

Ecological notes. All specimens were collected from sand banks near the shorelines of clearwater, slightly tea-stained, streams draining the western Guiana highlands in northern Amazonas Territory and western Estado Bolívar, Venezuela (Fig. 4). In every instance, the fishes were found buried in coarse clear sand at the stream edge, at depths ranging from approximately 2 to at least 20 cm. The locations where fish were found were always shaded by dense tropical rain forest (gallery forest). The current was slow, pH varied between 5.5 and 6.2 and temperature between 27.5 and 28°C. The only effective means of capturing these fossorial fishes was to place handfuls of wet sand on dry ground and to carefully examine it for the tiny wiggling catfishes. A single scoop of sand (i.e., obtained with two cupped hands) from submerged sand banks yielded up to six specimens. *Ammoglanis pulex* appeared to be the numerically dominant fish species at the Caño Paria Grande site. The Caño Garrapata (= Río Los Garzones, 1991) collection site had been severely degraded by impacts from road construction and agricultural development on the watershed. During April 1984, 63 fish species were collected near the dirt trail at this site. In contrast, only six species (*Astyanax* cf. *polylepis*, *Bryconops* sp., *Copella* sp., *Hyphessobrycon* sp., unidentified Characidae, *Aequidens diadema*) were captured in the same area during March 1991. The major changes in habitat conditions at Río Los Garzones (e.g., deforestation, pollution from dumping of asphalt and other road construction materials) lead us to believe that *Ammoglanis pulex* may have been extirpated from that stream.

The species appears to be strictly fossorial by daylight (we did not attempt observe them at night). Internal and external morphological characteristics of mouth parts clearly conform with

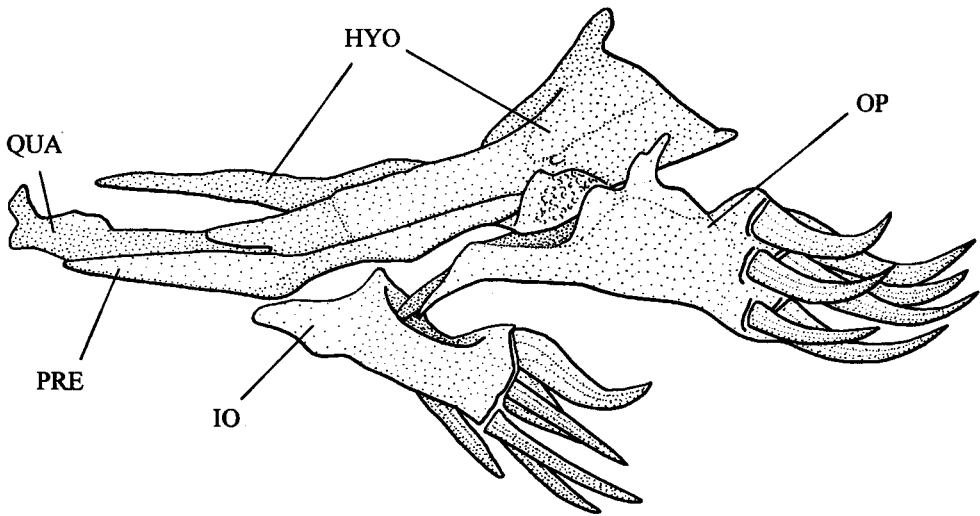


Fig. 5. *Ammoglanis pulex*, MZUSP 42471, 13.8 mm SL. Lateral view of suspensorium and opercular apparatus. Abbreviations: HYO, hyomandibula; IO, interopercle; OP, opercle; PRE, preopercle; QUA, quadrate. Scale bar 1 mm.

nonparasitic trichomycterid species, and not with parasitic taxa. The gut is relatively short and although there were no identifiable gut contents in the specimens dissected, we suspect that *A. pulex* feeds on microscopic fauna (e.g. protozoa, rotifers, nematodes) inhabiting interstitial spaces among sand grains in nutrient-poor, clear- and blackwater streams.

Phylogenetic relationships

The generic allocation of *A. pulex* seems well-corroborated, because a number of derived characters indicate that the species forms a monophyletic group with *A. diaphanus*. Although direct examination of *A. diaphanus* was not possible, because the type material was not available for this study, there is enough information in the original description to permit a phylogenetically-conclusive comparison. Costa (1994) provided three autapomorphies for *Ammoglanis*: 1) slender quadrate, its maximum depth about 30% of length of its main axis; 2) expanded anterior tip of interopercle; and 3) premaxilla located posterior to mesethmoid cornu. The new species shares the first and arguably the second of those characters. Its quadrate is markedly elongate, and its deepest anterior portion is about 30% of its max-

imum length (Fig. 5). This condition seems indeed to be apomorphic in the Trichomycteridae, all other members of which have shorter and deeper quadrates. The interopercle in *Ammoglanis pulex* is somewhat extended anteriorly (Fig. 5), compared to the state in most other trichomycterids. Such elongation, however, does not seem to be as pronounced as in *A. diaphanus*, and a more precise quantification of this character, on the basis of direct examination of material of the latter species, is necessary to assess its phylogenetic significance. *Ammoglanis pulex* lacks character three above, its premaxillae are located slightly anterior to the anterior margin of the mesethmoid cornua (Fig. 6), a plesiomorphic condition corresponding to the state seen in the majority of other trichomycterids. The derived condition of this character is thus considered an autapomorphy for *A. diaphanus*, rather than a synapomorphy for *Ammoglanis*.

Although not illustrated, the description of Costa (1994: 211) indicates that *A. diaphanus* has a single and very large lozenge-shaped cranial fontanel. *Ammoglanis pulex* also has a large fontanel, which occupies most of its skull roof. This condition is certainly derived for trichomycterids, and provides further evidence that the two species in the genus form a monophyletic group. The condition, however, is not unique to them and is

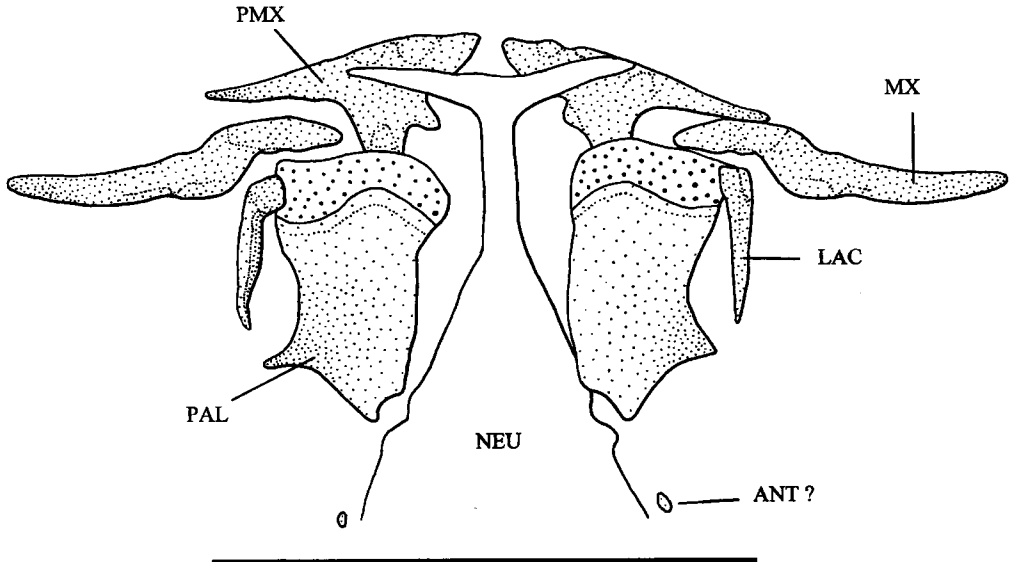


Fig. 6. *Ammoglanis pulex*, MZUSP 42471, 13.8 mm SL. Dorsal view of jaws and related structures. Neurocranium shown in outline. Larger stippling represents cartilage. Abbreviations: ANT, antorbital; LAC, lachrymal; MX, maxilla; NEU, neurocranium; PAL, palatine; PMX, premaxilla. Scale bar 1 mm.

also present in the vandelliines *Paracanthopoma* and *Paravandellia*, as well as *Trichomycterus hasemani* (de Pinna, 1989). These occurrences seem to be convergent, rather than homologous, with that in *Ammoglanis*, according to what is known about the position of those taxa in trichomycterid phylogeny (Baskin, 1973; de Pinna, 1989; Costa & Bockmann, 1993).

Another derived similarity which may indicate that *A. diaphanus* and *A. pulex* form a monophyletic group is the marked elongation of their first pectoral-fin ray. In both species the first ray is approximately twice as long as remaining rays, forming a conspicuous filament (Costa, 1994: 209 reports that the length of the ray for *A. diaphanus* varies between 40 and 100% of length of fin). Although a filamentous first pectoral-fin ray is common in trichomycterids, they are usually only approximately 30% longer than other rays in the fin. The illustration provided in Costa (1994: fig. 3) also shows a condition which may be considered as an additional autapomorphy for *A. diaphanus*, the markedly enlarged anterior cartilage of the palatine. In the primitive condition seen in other trichomycterids, including *A. pulex* and remaining loricioids, that cartilage is less than half the relative anteroposterior width seen in *A. diaphanus*.

A few autapomorphies have been identified

for *A. pulex*. One of them is the scythe shape of its lachrymal (Fig. 6), which has a pointed posterior tip slightly curved mesially. In other trichomycterids, the lachrymal has a blunt posterior end, not curved mesially. Another remarkable feature of the lachrymal in *A. pulex* is the presence of an anterior facet, which apparently articulates with the anterior cartilage of the palatine. Such facet is absent in other trichomycterids examined. Both the scythe shape and the facet are absent in the lachrymal of *A. diaphanus* according to Costa (1994: fig. 3). The dark chromatophores forming a banded pattern in the interior of the body (see Description) is another autapomorphy for *A. pulex*. Although not yet reported for any other trichomycterids, internal chromatophores visible on the outside of fish have been reported for other small-sized teleosts (e.g. the gobiid *Eviota*, see Lachner & Karnella, 1980), indicating that the character is likely paedomorphic. The lack of dentary teeth in *A. pulex* is also autapomorphic. Although premaxillary teeth are absent or nearly absent in some sarcoglanidines and glanapterygines (e.g., *Sarcoglanis* and *Typhlobelus*, respectively), the dentary teeth are always present in species of those subfamilies. Totally edentulous dentaries are seen elsewhere in trichomycterids only in the vandelliine *Vandellia*. However, the lack of dentary teeth in that case seems to be

independent of that in *A. pulex*, because all other Vandelliinae have dentary teeth.

The inclusion of *Ammoglanis* within the Sarcoglanidinae, suggested by Costa (1994), was based on three synapomorphies (for a detailed description and discussion of each of them, see de Pinna, 1989; de Pinna & Starnes, 1990; Costa, 1994 and Costa & Bockmann, 1994): 1) lateral process of premaxilla pointed; 2) enlarged maxilla; and 3) ventral expansion on premaxilla. The first character is certainly derived and present in all species so far included in the Sarcoglanidinae. It is evident in *Ammoglanis pulex* (Fig. 5) but according to the illustration in Costa (1994: 210), the condition is less marked in *A. diphanus*, and may be close to that in the basal glanapterygine *Listrura*. The second character, an enlarged maxilla, is derived and present in all sarcoglanidines, but also occurs in some genera and species outside the subfamily, such as the trichomycterine *Scleronema* and again the glanapterygine *Listrura*. Finally, the ventral expansion in the premaxilla, definitely an apomorphic condition, is absent in some sarcoglanidines, such as *Stenolicmus* and *Sarcoglanis*. Therefore, the relationships of *Ammoglanis* with sarcoglanidines is not yet well-established, and needs further study. If *Ammoglanis* is excluded from the Sarcoglanidinae, then the monophyly of the remaining clade is well-corroborated on the basis of other characters (de Pinna, 1989; de Pinna & Starnes, 1990; Costa & Bockmann, 1993, 1994). *Ammoglanis* also does not seem to be the sister group to the Glanapteryginae plus Sarcoglanidinae. The two subfamilies are hypothesized as sister groups by the reduction of anal-fin rays (seven or fewer); reduced number of premaxillary teeth; quadrate with a posteriorly-directed process; and anterior portion of hyomandibula modified into a long process (Baskin, 1973; Costa & Bockmann, 1993). The first and third of those characters are absent in *Ammoglanis*. The second is present, but remains a poorly-defined character (premaxillary teeth may be numerous in the glanapterygines *Listrura* and *Glanapteryx*, and few in vandelliines). The fourth character above is indeed present in both species of *Ammoglanis*, but it also occurs in vandelliines and tridentines and seems to apply at a more inclusive level of generality. The presence of the derived condition in vandelliines and tridentines is partly concealed by subsequent modifications of their suspensorium, which apparently prevented its recognition in those taxa pre-

viously. In vandelliines the process is certainly present, but it runs alongside the mesial margin of the quadrate and therefore is not visible in lateral view. In tridentines the distal portion of the process is deflected dorsoposteriorly, and may look like a different structure at first sight, but is clearly homologous according to criteria of topological correspondence, simply having a deviant shape. The absence of the hyomandibular process in stegophilines is probably due to the extensive additional expansion of the anterior portion of the hyomandibula. In stegophilines with less extreme expansions of the hyomandibula (e.g., *Stegophilus insidiosus*), there is still an anterior process, running parallel to the dorsal margin of the quadrate, probably homologous with the process in other taxa.

It is possible that *Ammoglanis* is in fact the sister group to a larger clade composed of several subfamilies. The genus shares two characters provided by Costa & Bockmann (1993) for a group composed of the subfamilies Sarcoglanidinae, Glanapteryginae, Vandelliinae, Stegophilinae and Tridentinae, plus the genus *Ituglanis*: interopercular patch of odontodes reduced and pleural ribs reduced to one to six pairs. It also shares two other synapomorphies for a more restrictive group composed of all the taxa above, except *Ituglanis*: posterior process of parasphenoid absent and metapterygoid greatly reduced or absent. If the corollaries of those characters are accepted, then *Ammoglanis* would be the sister group to a large clade composed of the Sarcoglanidinae, Glanapteryginae, Vandelliinae, Stegophilinae and Tridentinae. As a consequence of that, the genus would have to be assigned a new subfamily, because its inclusion in any of the currently-recognized ones would necessarily result in a non-monophyletic group. In the meantime, however, we provisionally choose to maintain *Ammoglanis* in the Sarcoglanidinae, while recognizing that the subject still requires further investigation and additional data.

Comparative material. The following comparative material of Sarcoglanidinae and Glanapteryginae was examined (BC – material cleared and stained for bone and cartilage; B – cleared and stained for bone only; the designation “ex” with no specification indicates alcohol-preserved material): Sarcoglanidinae: *Sarcoglanis simplex*, INPA 8165 (13 ex, 2BC); *Stauroglanis gouldingi*, MZUSP 30411 (1 paratype, BC); *Stenolicmus sarmientoi*

USNM 301663 (1 paratype, B). Glanapteryginae: *Glanapteryx anguilla*, MZUSP 36530 (21 ex, 2BC); *Glanapteryx niobium*, INPA 12421 (holotype); *Listrura nematopteryx*, MZUSP 36975 (12ex, paratypes), uncat. (5 BC); *Pygidianops eigenmanni*, CAS 11121 (2 paratypes, 1BC); *Pygidianops* sp., INPA 12427 (6ex., 2BC); *Typhlobelus ternetzi*, CAS 56201 (2 paratypes, 1B); *Typhlobelus* sp., INPA 12929 (10 ex, 2BC). Representatives examined of other Trichomycteridae and remaining loricarioids are listed in de Pinna (1992).

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Literature cited

- Arratia, G. & L. Huaquin. 1995. Morphology of the lateral line system and of the skin of diplomystid and certain primitive loricarioid catfishes and systematic and ecological considerations. *Bonn. Zool. Monogr.*, 36: 1-110.
- Baskin, J. N. 1973. Structure and relationships of the Trichomycteridae. Unpubl. Ph.D. Dissertation, City University of New York, New York, 389 pp.
- Bruun, A. F. 1940. A study of a collection of the fish *Schindleria* from south Pacific waters. Dana Report, 21: 1-12.
- Costa, W. J. E. M. 1994. A new genus and species of Sarcoglanidinae (Siluriformes: Trichomycteridae) from the Araguaia basin, central Brazil, with notes on subfamilial phylogeny. *Ichthyol. Expl. Freshwaters*, 5: 207-216.
- Costa, W. J. E. M. & F. A. Bockmann. 1993. Un nouveau genre néotropical de la famille des Trichomycteridae (Siluriformes: Loricarioidei). *Rev. Fr. Aquariol.*, 20: 43-46.
- 1994. A new genus and species of Sarcoglanidinae (Siluriformes: Trichomycteridae) from southeastern Brazil, with a reexamination of subfamilial phylogeny. *J. Nat. Hist.*, 28: 715-730.
- Lachner, E. A. & S. Karnella. 1980. Fishes of the Indo-Pacific genus *Eviota*, with descriptions of eight new species (Teleostei: Gobiidae). *Smithson. Contr. Zool.*, 315: 1-127.
- Manriquez, A., L. Huaquin, M. Arellano & G. Arratia. 1988. Aspectos reproductivos de *Trichomycterus arcolatus* Valenciennes, 1846 (Pisces: Teleostei: Siluriformes) en Río Angostura, Chile. *Stud. Neotrop. Fauna Envir.*, 23: 89-102.
- de Pinna, M. C. C. 1989. A new sarcoglanidine catfish, phylogeny of its subfamily, and an appraisal of the phyletic status of the Trichomycterinae (Teleostei, Trichomycteridae). *Amer. Mus. Novit.*, 2950: 1-39.
- 1992. A new subfamily of Trichomycteridae (Teleostei, Siluriformes), lower loricarioid relationships and a discussion on the impact of additional taxa for phylogenetic analysis. *Zool. J. Linn. Soc.*, 106: 175-229.
- de Pinna, M. C. C., & W. C. Starnes. 1990. A new genus of Sarcoglanidinae from the Río Mamoré, Amazon basin, with comments on subfamilial phylogeny (Teleostei, Trichomycteridae). *J. Zool., London*, 222: 75-88.
- Taylor, W. R. & G. C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybiurn*, 9: 107-109.
- Tchernavin, V. 1944. A revision of some Trichomycterinae based on material preserved in the British Museum (Natural History). *Proc. Zool. Soc. London*, 114: 234-275.
- Trajano, E. 1997. Population ecology of *Trichomycterus itacarambiensis*, a cave catfish from eastern Brazil (Siluriformes, Trichomycteridae). *Env. Biol. Fishes*, 50: 357-369.
- Weitzman, S. H. & R. P. Vari. 1988. Miniaturization in South American freshwater fishes: an overview and discussion. *Proc. Biol. Soc. Wash.*, 101: 444-465.
- Winterbottom, R. & A. Emery. 1981. A new genus and two new species of gobioid fishes (Perciformes) from the Chagos Archipelago, Central Indian Ocean. *Env. Biol. Fish.*, 6: 139-149.

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