Re-validation of *Otocinclus arnoldi* Regan and reappraisal of *Otocinclus* phylogeny (Siluriformes: Loricariidae)

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*Otocinclus arnoldi* from the La Plata basin is resurrected from the synonymy of *O. flexilis* described from the rio Jacuí drainage, based on three distinguishing features: the possession of five branched pectoral-fin rays, the larger number of enlarged odontodes on the tip of the parieto-supraoccipital posterior process, and having the prootic involved in the contact with the hyomandibular articular condyle. These species are also compared to *O. mimulus*, a third species described from the Paraná River basin, and the three species are re-diagnosed. A reassessment of the phylogenetic relationships of all species of *Otocinclus* shows a well-supported clade composed of (*(O. xakriaba (O. mimulus, O. arnoldi) (O. affinis, O. flexilis))* from the eastern-draining river basins of the Brazilian Shield as sister-group to a clade including all remaining *Otocinclus* species which are distributed on a wide lowland area of the Amazonas, Paraguay, and Orinoco basins.

*Otocinclus arnoldi* da bacia do rio da Prata é revalidada da sinonímia de *O. flexilis*, descrito da bacia do rio Jacuí, baseado em três características distintivas: a presença de cinco raios ramificados na nadadeira peitoral, o maior número de odontódeos hipertrofiados na ponta do processo posterior do parieto-supraoccipital, e por ter o próotico envolvido no contato com o côndilo articular do hiomandibular. Essas espécies são também comparadas com *O. mimulus*, outra espécie descrita da bacia do rio Paraná, e as três espécies são re-diagnosticadas. Uma nova análise filogenética de todas as espécies de *Otocinclus* revelou um clado bem suportado composto por (*(O. xakriaba (O. mimulus, O. arnoldi) (O. affinis, O. flexilis))* dos rios do escudo Brasileiro que drenam para leste, como grupo-irmão a um clado incluindo todas as demais espécies de *Otocinclus* que são distribuídas em uma grande área baixa das bacias do Amazonas, Paraguai e Orinoco.

**Key words**: La Plata, Synonymy, Hypoptopomatinae, Taxonomy, Catfish, Cascudinho.

**Introduction**

*Otocinclus flexilis* Cope, 1894 was described from the rio Jacuí, Rio Grande do Sul State, Brazil, based on a syntype series with two lots and 17 specimens, collected by Herbert H. Smith in 1882 and deposited in the Academy of Natural Sciences of Philadelphia under catalog numbers ANSP 21622-21626 and ANSP 21756-21767. Cope (1894: 97) diagnosed *O. flexilis* from *O. affinis* Steindachner, 1877, mentioning the presence of six branched pectoral-fin rays and describing the color pattern as “light yellowish brown, with a row of about six oblong dusky spots along the lateral line, which become obscure anteriorly. A series of corresponding spots along the dorsal region. Dorsal and caudal fins light colored with numerous dusky spots. A black spot at the base of caudal fin in some specimens”.

In the same publication, *Otocinclus fimbriatus* Cope, 1894 was described from the same type locality of *O. flexilis*, based on differences “… in the tubercular and fringed lip … more brightly colored and with less numerous lateral spots. The ventral fins are relatively longer, and the dorsal fin originates above their base, and not behind it, as is the case in *O. flexilis*”. Schaefer (1997) examined the syntype series of *O. fimbriatus* (ANSP 21585-21597, 21752-21755, 17 specimens) and concluded that it does not present consistent differences from *O. flexilis* and, therefore, *O. fimbriatus* was synonymized with *Otocinclus flexilis*, as already suggested by Regan (1904) and Aquino (1996), and maintained by Schaefer (2003).

*Otocinclus arnoldi* Regan, 1909 was described from “La Plata” based on a single aquarium specimen donated by J. P. Arnold. The rather short original description does not state the number of pectoral-fin rays. Aquino (1996), based on a morphometric and meristic comparison, and also on the color pattern, synonymized *O. arnoldi* with *O. flexilis*. More recently, *Otocinclus mimulus* Axenrot & Kullander, 2003 was described from the rio Paraná drainage in Paraguay, being diagnosed from *O. flexilis* by possessing elevated, enlarged odontodes at the posterior parieto-supraoccipital tip and distinct modal number of premaxillary and dentary teeth and caudal vertebrae.

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**Otocinclus** is the only genus among the Hypoptopomatinae that received strong phylogenetic attention by previous authors. Schaefer (1997) produced the first phylogenetic analysis including all species of *Otocinclus* known to date. After that, Britto & Moreira (2002) described *O. tapirape* and reassessed the phylogenetic relationships among *Otocinclus* species. Axenrot & Kullander (2003) described *O. mimulus* and again reassessed the phylogeny of *Otocinclus* species, adding one character to the matrix of Schaefer (1997). Reis (2004) and Lehmann (2006) described *O. cocama* and *O. batmani*, but did not provide updated phylogenetic analyses of the genus.

In this paper we present the results of a reassessment of the validity of *Otocinclus arnoldi*, and reassess the phylogenetic relationships among all *Otocinclus* species.

### Material and Methods

The specimens examined belong to the following institutions: Natural History Museum, London (BMNH); Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá (ICNHN); Museo de Ciencias Naturales, Guanare (MCNG); Museu de Ciências e Tecnologia, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP); Museo Nacional de Historia Natural del Paraguay, Asunción (MNHN); Museu de Zoolgia da Universidade de São Paulo, São Paulo (MZUSP); Swedish Museum of Natural History, Stockholm (NRM); Universidad Federal do Rio Grande do Sul, Porto Alegre (UFRGS); Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ); and National Museum of Natural History, Smithsonian Institution, Washington (USNM). Measurements were calculated as interlandmark distances based on homologous landmarks acquired with a video digitizer, using the same set of landmarks as Schaefer (1997). An additional landmark was digitized at the end of the hypural plate and standard length was calculated as the interlandmark distance from this point to the snout tip. The software LMDIS (by R. E. Reis, 1996) was used to extract interlandmark distances. Counts and anatomical terminology follow Schaefer (1997), Arratia (2003) and Axenrot & Kullander (2003). Specimens studied were cleared and stained (c&s) using the methods of Taylor & van Dyke (1985). Osteological terminology follows Schaefer (1997) and Arratia (2003).

Principal component analysis (PCA) was used to assess morphometric variation among studied *Otocinclus* populations. A total of 18 morphometric variables (Table 1) was taken from 70 specimens representing comparable size ranges: 30 specimens from the rio Jacuí basin, type-locality of *Otocinclus flexilis* (29.4-40.3 mm SL), 27 specimens from the rio Uruguai and lower rio Paraná drainage, type-locality of *O. arnoldi* (26.2-44.4 mm SL), and 13 paratypes of *O. mimulus* from the middle rio Paraná basin in Paraguay (30.9-36.3 mm SL). The analysis was performed on the covariance matrix of the 18 log_{10}-transformed measurements.

For the phylogenetic analysis we used the original data matrix of Schaefer (1997) with the addition of *Otocinclus arnoldi*, *O. tapirape*, *O. mimulus*, *O. cocama*, *O. batmani*, and another undescribed species from the rio Madeira basin provisionally called *Otocinclus* sp. “madeira”. We also included one character from Axenrot & Kullander (2003) on a mimetic association of *Otocinclus* with the callichthyid *Corydoras*, and six additional new characters. We submitted the data matrix to 10,000 replications of Random Addition Sequence (RAS) followed by TBR branch swapping using the software NONA (by P. Goloboff, 1993) and WinClada (by Nixon, 2002). Trees were rooted on *Microlepidogaster perforatus*. All multistate characters were set as unordered. Bremer branch support was calculated with NONA.

### Results

A direct comparison of proportional measurements between specimens of *Otocinclus flexilis* from the laguna dos Patos basin and specimens from the rio Paraná and rio Uruguai drainages (Table 1) reveals no differences, as already demonstrated by Schaefer (1997). The principal component analysis also failed to reveal unambiguous differences among the three populations analyzed. The first principal component included a large proportion of the total variance (78.3%) and all variable loadings were negative and varied little in magnitude, indicating that it represents a general size factor. Plots of factor scores of principal components 2 versus 3 and 2 versus 4 both grouped specimens into three broadly overlapping clusters (Fig. 1). PC 2, 3, and 4 included 7.5, 3.3, and 2.4% of the total variance, respectively.

Lateral trunk coloration in these populations is also similar, as the three groups have either a row of 3-6 distinct dark blotches or a distinct dark stripe, extending from the compound pterotic to the caudal-fin base, or a diffuse mixture of those two color patterns (Figs. 2, 3 and 4). On the other hand, however, there is an important difference in the pectoral-fin ray counts among these fishes, as already demonstrated by Schaefer (1997). All examined specimens from the La Plata basin (285 specimens, including the holotype of *O. arnoldi* and the 13 paratypes of *O. mimulus*) have five branched rays in the pectoral fin (except for one specimen each in lots MCP 25254, UFRGS 7180, and USNM 176023 which have six branched rays in one side), and all 226 specimens examined from the laguna dos Patos basin (in addition to the entire syntype series of *O. flexilis* and *O. fimбриatus* examined by Schaefer, 1997) have six branched rays in the pectoral fin, except for one specimen in UFRGS 4963 and nine juveniles from MCP 15068, with five rays in one or both sides.

Schaefer (1997: 107) described a raised tuft of odontodes forming a raised crest on the parieto-supraoccipital tip as a juvenile character of hypoptopomatines, and regarded the presence of enlarged parieto-supraoccipital crest odontodes in mature adult specimens within *Otocinclus* as a derived condition representing paedomorphosis, and therefore
synapomorphic for *O. affinis* and *O. xakriaba*. The same tuft of enlarged, raised odontodes is present in *O. mimulus*, which was coded as having the derived state in the analysis of Axenrot & Kullander (2003).

Contrary to the three species above, however, mature adult specimens of *Otocinclus* from the Jacuí and La Plata drainages do not have a raised crest of odontodes on the parieto-supraoccipital tip. However, most of the examined specimens present a patch of hypertrophied odontodes on the parieto-supraoccipital tip which are not raised to form a crest, but instead are laid on the bone surface and cannot be visualized laterally. These odontodes are 2-5 times larger than the surrounding odontodes and are present in both juveniles and adults. The population in the rio Jacuí basin has 0-10 (mode = 0, mean = 3.0) enlarged odontodes, while the fishes from the Uruguai and lower Paraná basins possess 2-23 (mode = 7, mean = 8.3) enlarged odontodes (Table 2).

The incorporation of the prootic in the contact with the hyomandibular articular condyle was described by Schaefer (1997: 104) as an autapomorphic trait of *O. xakriaba*. This feature, however, is also present in the *Otocinclus* populations from the La Plata basin, including *O. flexilis*, but not in *O. flexilis* from the rio Jacuí basin, in which only the compound pterotic contacts the hyomandibular articular condyle.

Based on the differences in pectoral-fin count, number of hypertrophied odontodes on the parieto-supraoccipital, and the involvement of the prootic in the contact with the hyomandibular articular condyle, *O. arnoldi* is resurrected from the synonymy of *O. flexilis*.

In a similar manner, a direct comparison of proportional measurements and meristics between *Otocinclus arnoldi* and a series of 13 paratypes of *O. mimulus* (Table 1) shows no differences, as already mentioned by Axenrot & Kullander (2003: 255). In the original description, *O. mimulus* was distinguished from *O. arnoldi* (*O. flexilis* of Axenrot &

### Table 1. Descriptive morphometrics of *Otocinclus* species. Values are given as percents of standard length or of head length. SD = standard deviation. Numbers in brackets correspond to landmarks of Schaefer (1997).

| Character                      | Otocinclus arnoldi n = 27 | Otocinclus flexilis n = 30 | Otocinclus mimulus n = 13 |
|-------------------------------|----------------------------|-----------------------------|---------------------------|
| Standard length (mm)          | Low 26.2                   | High 44.4                   | Mean 32.8                 |
| Percents of standard length   | Low 18.8                   | High 25.8                   | Mean 22.5                 |
| Body depth [8-10]             | 1.45                       |                             |                           |
| Trunk depth at anal-fin origin [11-12] | 1.14                       |                             |                           |
| Caudal peduncle depth [13-14] | 0.76                       |                             |                           |
| SOC to dorsal-fin origin [7-8] | 0.85                       |                             |                           |
| Cleithrum to pelvic-fin origin [9-10] | 0.93                       |                             |                           |
| Pelvic-to anal-fin origin [10-12] | 1.00                       |                             |                           |
| Trunk length [11-13]          | 2.20                       |                             |                           |
| Head length [16-20]           | 1.25                       |                             |                           |
| Predorsal length [1-8]        | 2.26                       |                             |                           |
| Prepelvic length [1-10]       | 2.10                       |                             |                           |
| Preanal length [1-12]         | 3.01                       |                             |                           |
| Percents of head length       | Low 27.4                   | High 38.3                   | Mean 33.9                 |
| Snout width [17-23]           | 0.56                       |                             |                           |
| Interorbital width [19-21]    | 0.81                       |                             |                           |
| Internasal width [24-25]      | 0.44                       |                             |                           |
| Nares diameter [22-24]        | 0.21                       |                             |                           |
| Orbit length [3-15]           | 0.25                       |                             |                           |
| Prenasal length [16-18]       | 0.40                       |                             |                           |

**Fig. 1.** Plots of factor scores of principal component analysis of three populations of *Otocinclus*. Dot, *Otocinclus arnoldi*, rio Paraná basin; Circle, paratypes of *O. mimulus*, upper rio Paraná basin; triangle, *O. flexilis*, laguna dos Patos basin.
Kullander, 2003, who only examined specimens from the La Plata basin), based on the elevated tuft of enlarged odontodes at tip of parieto-supraoccipital. The tuft is distinctly conspicuous in Otocinclus mimulus because the predorsal plates immediately posterior to the parieto-supraoccipital are slightly sunk below the level of the parieto-supraoccipital border, making the tuft clearly apparent. Other meristic characters originally used to diagnose Otocinclus mimulus include modal number of premaxillary and dentary teeth, which are variable and largely overlapping, and caudal vertebrae, which suggest a distinction between the two species (Table 2). The PCA also failed to separate the two species, but showed a trend towards separation, especially on PC 4, and the two species are maintained and recognized as valid in this study.

Otocinclus flexilis Cope, 1894

Fig. 2

Otocinclus flexilis Cope, 1894: 97, pl. 8, fig. 13. Type locality: rio Jacuhy, Rio Grande do Sul [rio Jacui, Brazil]. Lectotype: ANSP 21756, 40.0 mm SL, designated by Schaefer (1997: 53).

Otocinclus fimbriatus Cope, 1894: 98, pl. 9, fig. 16. Type locality: rio Jacuhy, Rio Grande do Sul [rio Jacuí, Brazil]. Syntypes: ANSP 212752 (4) and ANSP 21585-97 (14).

Diagnosis. Otocinclus flexilis is distinguished from all other Otocinclus (except for Otocinclus xakriaba, Otocinclus affinis, Otocinclus arnoldi, and Otocinclus mimulus) by possessing an iris operculum and (except for Otocinclus xakriaba, Otocinclus arnoldi, and Otocinclus mimulus) by having a lateral trunk coloration consisting of a series of 3-6 diffuse pigment blotches (Fig. 2). An inconspicuous and not elevated patch of 0-10 (mode = 0, mean = 3.0) enlarged odontodes on the postero-dorsal parieto-supraoccipital tip, the pectoral skeleton with closed arrector fossae, and the presence of a triangular pigment mark at the dorsal-fin base distinguishes Otocinclus flexilis from Otocinclus xakriaba, which possesses an elevated patch of enlarged odontodes on the parieto-supraoccipital, has an open arrector fossae, and lacks the dorsal-fin mark. From Otocinclus arnoldi and Otocinclus mimulus it is easily distinguished by having six branched pectoral-fin rays (vs. five branched rays) and few (0-10, mode = 0, mean = 3.0) not elevated enlarged odontodes on the postero-supraoccipital tip (vs. 2-23, mode = 7, mean = 8.3) not elevated enlarged odontodes in Otocinclus arnoldi and 5-14, mode = 7, mean = 8.4 conspicuously elevated odontodes in Otocinclus mimulus).

Distribution. Otocinclus flexilis is restricted to the laguna dos Patos drainage basin (Fig. 5).

Otocinclus arnoldi Regan, 1909

Fig. 3

Otocinclus arnoldi Regan, 1909: 234. Type locality: La Plata, South America. Holotype: BMNH 1908.12.5:13, 43 mm SL.

Diagnosis. Otocinclus arnoldi is distinguished from all other Otocinclus species except Otocinclus mimulus, by having five branched rays in the pectoral-fin (vs. six branched pectoral-fin rays), and except from Otocinclus mimulus and O. xakriaba by having the prootic involved in the contact with the hyomandibular articular condyle (vs. only compound pterotic contacting the hyomandibular articular condyle). It is distinguished from Otocinclus mimulus by having a not elevated patch of enlarged odontodes on the postero-dorsal parieto-supraoccipital tip and 15 caudal vertebrae (vs. having an elevated patch of enlarged odontodes on the parieto-supraoccipital and typically having 16-17 caudal vertebrae - see Table 2). It is further distinguished (except for Otocinclus affinis, Otocinclus hasemani, Otocinclus xakriaba, Otocinclus mimulus, and Otocinclus xakriaba) by having a not elevated patch of enlarged odontodes on the postero-dorsal parieto-supraoccipital tip. It is also distinguished from all remaining Otocinclus species (except for Otocinclus xakriaba, Otocinclus flexilis, and Otocinclus mimulus) by having a lateral trunk coloration composed of either a row of 3-6 distinct dark blotches or a distinct dark stripe extending from the compound pterotic to the base of the caudal fin, or a diffuse mixture of those two color patterns (Fig. 3).

Distribution. Otocinclus arnoldi occurs in the tributaries of the lower rio Paraná drainage, lower and middle rio Uruguay, and the rio de La Plata (Fig. 5).

Otocinclus mimulus Axenrot & Kullander, 2003

Fig. 4

Otocinclus mimulus Axenrot & Kullander, 2003: 251. Type locality: Paraguay: Departamento Caaguazú: rio Paraná drainage, small stream (arroyo) at Estancia Maria Belén, 8 km from Colonel Patricio Colman; 25°40'13"S 55°5'52"W. Holotype: MNHN uncatalogued (ex NRM 43480), 34.1 mm SL [Holotype originally cited as MNHN uncat.].

Diagnosis. Otocinclus mimulus is distinguished from all other Otocinclus species except Otocinclus arnoldi, by having five branched rays in the pectoral-fin (vs. six branched pectoral-fin rays), and except from Otocinclus arnoldi and Otocinclus xakriaba by having the prootic involved in the contact with the hyomandibular articular condyle (vs. only compound pterotic contacting the hyomandibular articular condyle). It is distinguished from Otocinclus arnoldi by having an elevated patch of enlarged odontodes on the postero-dorsal parieto-supraoccipital tip and typically having 16-17 caudal vertebrae (vs. having a not elevated patch of enlarged odontodes on the parieto-supraoccipital and having 15 caudal vertebrae). It is further distinguished (except for Otocinclus affinis, Otocinclus hasemani, Otocinclus xakriaba, Otocinclus mimulus, and Otocinclus xakriaba) by possessing an iris operculum, and (except for Otocinclus affinis and Otocinclus xakriaba) by having an elevated patch of enlarged odontodes on the postero-dorsal parieto-supraoccipital tip. It is also distinguished from all remaining Otocinclus species (except for Otocinclus xakriaba, Otocinclus arnoldi, and Otocinclus mimulus), by possessing an iris operculum, and from Otocinclus xakriaba, Otocinclus mimulus, and Otocinclus xakriaba by having a not elevated patch of enlarged odontodes on the postero-dorsal parieto-supraoccipital tip.
flexilis) by having a lateral trunk coloration composed of either a row of 3-6 distinct dark blotches or a distinct dark stripe extending from the compound pterotic to the base of the caudal fin, or a diffuse mixture of those two color patterns (Fig. 4).

**Distribution.** *Otocinclus mimulus* is only known from the río Mondai in Paraguay, a left-bank tributary of the lower río Paraná (Fig. 5).
Table 2. Frequency distribution of variable counts of *Otocinclus* species. Caudal vertebrae counted in clear and stained specimens only. *Five specimens counted and 13 from radiographs by S.O. Kulander; **Data from radiographs by S. O. Kulander.

| Pored lateral line plates | Unpored lateral line plates | Teeth on right premaxilla |
|---------------------------|-----------------------------|---------------------------|
|                           | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
| Otocinclus flexilis       | 1 | 2 | 12 | 8 | 1 |   |   | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| Otocinclus arnoldi        | 11 | 12 | 4 | 1 | 1 |   |   |   |   |   |   |   |   |   |   |   |
| Otocinclus mimulus        | 1 | 4 | 6 | 1 |   | 1 | 1 | 4 | 4 |   |   |   |   |   |   |   |
|                           | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |   |   |   |

Phylogenetic relationships

The phylogenetic position of *Otocinclus arnoldi*, *O. batmani*, *O. cocama* and *Otocinclus* sp. “madeira” were never investigated. In order to test their phylogenetic position we added to the 27-character data matrix of Schaefer (1997) the character proposed by Axenrot & Kulander (2003) on a mimetic association with *Corydoras*, and six additional characters (Table 3), which are described below.

**Character 28:** Mimetic association with a species of *Corydoras*. According to Axenrot & Kulander (2003) “*Otocinclus mimulus, O. flexilis, O. affinis, and O. xakriaba* are considered to be mimics of particular sympatric *Corydoras* species (*C. dIPHERY, C. paleatus, C. nattereri, and C. garbei, respectively*). This interpretation of mimetic association is based on the sympotypically co-occurrence and on the shared color pattern of the *Otocinclus-Corydoras* species pair. We add to this list *O. arnoldi*, which has the same color pattern of *O. flexilis* and *C. paleatus* and also shares the sympotopic co-occurrence with *C. paleatus* (nine of the 23 MCP lots of *O. arnoldi* were collected sympotypically with *C. paleatus*).

**Character 29:** Position of pleural ribs. In loricariids the pleural ribs posterior to the well-developed rib of the sixth vertebral centrum are thin and delicate, and variably occur in the first centra posterior to the sixth centrum. In basal loricariids, most neoplecostomines, and most hypoptopomatines the first pleural rib posterior to the sixth centrum is associated with the seventh or eighth centrum (state 0). In *Otocinclus bororo, O. mariae, O. affinis, O. caxarari, O. flexilis, O. arnoldi, O. xakriaba, O. mimulus,* and *Otocinclus* sp. “madeira” the first delicate rib is associated to the ninth vertebral centrum (state 1). Contrastingly, in *Hisonotus notatus, Microlepidogaster perforatus, O. hoppei, O. huaorani, O. macrospilus, O. vittatus, O. tapirape, O. cocama,* and *O. batmani* the first delicate rib is associated with the tenth vertebral centrum (state 2). *Otocinclus mura* and *O. hasemani* have no pleural ribs, and this character is thus not applicable. The character is highly variable among the genera of the *Hypoptopoma* group, but the tribe was coded as having state 0.

**Character 30:** Shape of the ventral process of the complex centrum (VPCC). In basal loricariids and most hypoptopomatines the VPCC has the shape of a rectangular arch attached to the ventral surface of the complex centrum and contacting the swim bladder capsule by means of a thin, dorsolaterally directed splint. Among species of *Otocinclus* this state is only shared by *O. xakriaba* (state 0). In all remaining species of *Otocinclus* the VPCC lost the dorsolaterally splint, being straight, curved or shaped as a golf-stick, but never forming a complete arch (state 1).

**Character 31:** Shape of the dorsal-fin spinelet. In basal loricariids the first dorsal-fin spine is transformed in a V-shaped spinelet, which acts with the nuchal plate as a locking mechanism for the second dorsal-fin spine (state 0). In the neoplecostomines and hypoptopomatines, however, the spinelet lost its function as a locking mechanism and is either oval or rectangular and plate-like in shape (state 1), a state shared with *Microlepidogaster perforatus* and *Hisonotus notatus*. In all species of *Otocinclus*, in contrast, the dorsal-fin spinelet is V-shaped and the dorsal-fin spine locking mechanism is functional, which represents a reversion in *Otocinclus*. All species on the *Hypoptopoma* group completely lost the dorsal-fin spinelet (state 2).

**Character 32:** Number of branched pectoral-fin rays. Most hypoptopomatines, including the *Hypoptopoma* group, *Microlepidogaster perforatus, Hisonotus notatus,* and most species of *Otocinclus* share the possession of six branched rays in the pectoral fin (state 0). Contrastingly, *O. mimulus* and *O. arnoldi* posses five branched rays in the pectoral fin (state 1).

**Character 33:** Number of predorsal plates. The number of predorsal median plates between the parieto-supraoccipital tip and the nuchal plate is variable among the hypoptopomatines. *Microlepidogaster perforatus, Hisonotus notatus, Otocinclus xakriaba, O. flexilis, O. mimulus,* and *O. arnoldi* have three or four predorsal plates (state 0). This condition is shared by the *Hypoptopoma* group, which can have three or more predorsal plates. In contrast, all the
remaining species of *Otocinclus* share the presence of two predorsal plates between the parieto-supraoccipital and the nuchal plate (state 1).

**Character 34:** Teeth on pharyngeal jaws. Hypoptopomatines generally have well developed teeth arranged in multiple series on both the upper pharyngeal tooth
plate and the fifth ceratobranchial (state 0), a condition shared by *Hisonotus notatus*, *Microlepidogaster perforatus* and the *Hypoptopoma* group. All species of *Otocinclus* share a reduction in the pharyngeal teeth, only having one series of tooth on both the upper pharyngeal tooth plate and the fifth ceratobranchial (state 1).

Besides adding the above characters, we provide modified interpretations of some of the characters as originally

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**Fig. 4.** Color variation of paratypes *Otocinclus mimulus*. All from NRM 42332, (a) SL = 34.4, (b) 31.2, (c) 35.1, and (d) 34.4 mm.
described by Schaefer (1997). His character 2 is an expansion of the subnasal lamina of the lateral ethmoid. *Microlepidogaster perforatus* and *Hisonotus notatus* share with *O. affinis*, *O. flexilis*, *O. xakriaba*, *O. mimulus*, and *O. arnoldi* the lateral ethmoid only slightly expanded medially, covering less than 20% of the nasal capsule when viewed through the nares (Fig. 6a, state 0). Contrastingly, in *O. bororo*, *O. caxarari*, *O. hasemani*, *O. hoppei*, *O. huorani*, *O. macrospilus*, *O. mariae*, *O. tapirape*, *O. vittatus*, *O. cocama*, *O. batmani*, and *Otocinclus* sp. “madeira” the subnasal lamina of the lateral ethmoid is moderately exposed and expanded medially in a concave shelf, covering 30-70% of the nasal capsule as viewed through the nares (Fig. 6b, state 1). In the *Hypoptopoma* group and in *O. mura* the lateral ethmoid is greatly expanded medially, covering 80-100% of the nasal capsule (Fig. 6c; state 2).

Schaefer’s (1997) character 21 is the midlateral dark stripe that can be solid and continuous from the compound pterotic to the caudal-fin base (state 0) or broken in a series of three or more large, diffuse blotches of irregular size and shape (state 1). To this character we added a second state where the midlateral dark stripe is not confluent with the spot at caudal-fin base, usually being interrupted one or two plates before the spot (state 2). This later condition is shared by *Otocinclus mariae*, *O. hoppei*, *O. macrospilus*, and *Otocinclus* sp. “madeira”. *Otocinclus cocama* has a very distinct lateral color pattern, but was coded as having state 1.

Some other characters that deserve comments are: Character 15 is the possession of 23 or fewer lateral plates. Despite that *O. cocama* and the undescribed species from the rio Madeira possess 21-24 lateral plates, we coded these species as presenting state 1, because the count of 24 plates is rare. Character 18 refers to the number of canal-bearing plates in the anterior field of perforated lateral line plates. Because *O. cocama* has the lateral line continuous, without a mid-body gap, we coded this character as inapplicable. Finally, the character 22 describes the paired W-shaped marks of the caudal-fin pigmentation. As both *O. cocama* and *O. batmani* have one single, wide W-shaped mark on the caudal fin, we added the state 2 for this character to code the condition shared by these two species.

The phylogenetic analysis of this expanded data matrix yielded three maximally parsimonious trees with 70 steps (CI = 60 and RI = 79), the strict consensus of which is presented in Fig. 7.

![Fig. 5. Geographic distribution of *Otocinclus flexilis* (triangles) and *O. arnoldi* (dots). Open dot represents paratypes of *O. mimulus*. One symbol may cover more than one lot or locality.](image)

**Table 3.** Data matrix of characters for *Otocinclus* species and outgroups. Characters 1-27 from Schaefer (1997), character 28 from Axenrot & Kullander (2003).

| Taxon          | Character States |
|----------------|------------------|
| M. perforatus | 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 2 0 1 0 0 0 |
| H. notatus     | 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 |
| Hypoptopoma group | 0 2 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 2 0 0 0 0 |
| O. affinis     | 1 0 1 0 0 1 1 1 1 0 0 0 0 0 0 1 2 0 0 1 0 0 1 0 0 1 0 1 1 1 0 1 1 1 1 |
| O. bororo      | 1 1 1 0 1 1 1 1 1 0 1 0 0 0 1 0 0 1 0 0 1 0 0 1 0 1 1 0 1 1 1 0 1 1 1 |
| O. caxarari    | 1 1 1 0 1 1 1 1 1 1 0 0 0 1 0 0 1 0 1 1 0 0 1 0 1 1 1 0 1 1 1 0 1 1 1 |
| O. flexilis    | 1 0 1 0 0 1 1 1 1 0 0 0 0 0 0 1 2 0 0 0 1 0 1 0 1 0 1 1 1 0 1 1 1 1 0 1 1 1 1 |
| O. hasemani    | 1 1 1 0 0 1 1 1 1 0 1 1 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 1 0 0 1 1 1 1 |
| O. hoppei      | 1 1 1 0 1 1 1 1 1 1 0 0 0 0 1 0 0 1 0 0 0 2 1 0 1 1 1 0 0 2 1 0 0 1 1 1 1 |
| O. huorani     | 1 1 1 0 1 1 1 1 1 1 0 0 0 1 0 0 1 0 0 0 1 0 0 1 0 1 1 1 0 2 1 0 0 1 1 1 1 |
| O. macrospilus | 1 1 1 0 1 1 1 1 1 1 0 0 0 1 0 0 1 0 0 0 2 1 0 1 1 1 0 0 2 1 0 0 1 1 1 1 |
| O. mariae      | 1 1 1 0 0 1 1 0 1 1 1 0 0 0 1 0 0 1 0 0 2 1 0 0 1 1 1 0 1 1 1 0 1 1 1 1 |
| O. mura       | 1 2 1 0 1 1 1 1 0 1 1 0 0 0 0 0 0 0 0 0 1 2 0 0 0 1 0 1 1 1 1 0 - 1 0 0 1 1 |
| O. vestitus    | 1 1 1 0 1 1 1 1 0 1 1 1 0 1 0 1 0 2 0 0 0 0 1 0 1 0 1 1 0 2 1 0 0 1 1 1 1 |
| O. vittatus    | 1 1 1 0 1 1 1 1 0 1 1 1 0 1 0 1 0 0 0 0 1 0 1 0 0 1 1 0 0 1 0 1 1 0 2 1 0 0 1 1 |
| O. xakriaba    | 1 0 1 1 0 1 1 1 0 2 1 0 1 0 1 0 1 1 1 0 0 2 1 1 0 0 0 0 1 0 1 1 1 0 0 0 1 1 |
| O. tapirape    | 1 1 1 0 1 1 1 1 0 1 1 0 0 0 1 0 1 2 0 0 0 0 0 0 1 0 0 0 1 0 1 1 0 2 1 0 0 1 1 |
| O. mimulus     | 1 0 1 1 0 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 2 0 0 1 0 1 0 0 1 0 1 1 1 0 1 0 1 |
| O. cocama      | 1 1 1 0 0 1 1 0 1 0 1 0 0 0 1 0 0 0 0 0 1 2 0 0 1 1 1 0 2 1 0 0 1 1 1 |
| O. batmani     | 1 1 1 0 1 1 1 1 0 1 1 0 0 0 1 0 0 0 0 0 0 2 0 0 1 1 1 1 1 0 2 1 0 0 1 1 1 |
| O. arnoldi     | 1 0 1 1 0 1 1 1 0 1 0 0 0 0 0 0 0 0 0 1 2 0 0 1 1 0 1 0 0 1 0 1 1 1 0 1 0 1 |
| O. sp. “madeira” | 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 0 1 2 0 2 1 0 1 1 1 0 1 1 1 0 1 1 1 |

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Discussion

Aquino (1996) proposed that Otocinclus arnoldi is a junior synonym of Otocinclus flexilis based on overlapping results in morphometric and meristic characters, and the color pattern. However, she did not include specimens of O. flexilis from the rio Jacuí basin in the morphometric analysis, only comparing the holotype of O. arnoldi with 34 specimens (table 1, lots ILPLA 204 and 207) from the La Plata basin. Furthermore, in her table 1, the holotype of O. arnoldi is erroneously reported as having six pectoral-fin branched rays, what is contrary to our own and Schaefer’s (1997: 53) count of five branched rays. The results presented by Aquino (1996), therefore, do not provide compelling justification for considering O. arnoldi as junior synonymy of O. flexilis.

Following the synonymy of Aquino (1996), Schaefer (1997: 53) reported on the number of pectoral-fin rays present in O. flexilis, indicating that this feature is variable in this species. The reason for such variability is that specimens from both the rio Jacuí and the La Plata basin were considered to be conspecific. As shown above, all 285 specimens examined of O. arnoldi have five branched rays in the pectoral fin, contrary to all other species of Otocinclus (except O. mimulus), which retain the plesiomorphic state of having six branched rays.

In his revision of Otocinclus Schaefer (1997) reported three lots of O. affinis from the La Plata basin in Argentina (USNM 176023 and USNM 177900) and rio Uruguai in southern Brazil (MCP 9388), significantly extending the geographical range of that species from the coastal rivers of Rio de Janeiro and São Paulo to the La Plata basin. We re-examined these three lots and all 60 specimens have five branched rays in the pectoral fin, contrary to all other species of Otocinclus (except O. mimulus), which retain the plesiomorphic state of having six branched rays.

The recognition of Otocinclus mimulus as a valid species separated from O. arnoldi is based on slight differences. We preferred this course of action based on the absence of dense sampling of Otocinclus in the area between Santa Fé in Argentina and the rio Monday and other tributaries of the rio Paraná in Paraguay. Also, the restricted distribution of O. mimulus is not typical of Otocinclus species but that particular region was already detected as the area of endemism of the cichlid Gymnogeophagus setequedas. It is possible that the distribution of O. mimulus is wider than the rio Mondai alone, but like G. setequedas, it can be restricted to the tributaries of the lower rio Paraná in southeastern Paraguay and the...
Brazilian state of Paraná, between the rio Mondai and the Brazilian city of Guairá.

Despite the addition of six morphological characters, the phylogenetic relationships uncovered by the present analysis did not gain much resolution when compared to the previous analyses (Schafer, 1991; Britto & Moreira, 2002; and Axenrot & Kullander, 2003). Our results show a well-supported clade composed of \((O. \textit{xakrika}) (O. \textit{milimus}, O. \textit{arnoldi}) (O. \textit{affinis}, O. \textit{flexilis})\) as sister-group to all remaining \textit{Otocinclus} species. Inside this clade, the most basal species \textit{Otocinclus xakrika} is endemic to the rio São Francisco basin. \textit{Otocinclus milimus} and \textit{O. arnoldi} are endemic to the upper rio Parana and lower rio Parana/rio Uruguay basins, respectively. Finally, \textit{O. affinis} and \textit{O. flexilis} are endemic to coastal streams of rio de Janeiro and São Paulo in southeastern Brazil and the laguna dos Patos coastal basin in southern Brazil. This clade evolved and differentiated on the watersheds draining the Brazilian Shield, and is the sister group to the clade comprising the species inhabiting the Paraguay, Amazonas and Ornico basins.

The other \textit{Otocinclus} clade in the present hypothesis is not well resolved, showing a large amount of polytomy and low internal branch support values. The two most basal species in that clade, however, \textit{O. tapirape} and \textit{O. hasemani}, are both endemic to the rio Tocantins, a river emptying near the mouth of the rio Amazonas but still running on rocks of the Brazilian Shield. The remaining of the species are distributed on a wide lowland area of the Amazonas, Paraguay, and Ornico basins, suggesting that the genus \textit{Otocinclus} began to differentiate on the watersheds draining the Brazilian Shield uplands and invaded lowlands of the continent only once.

\textbf{Material examined.} \textit{Acestridium discus:} Brazil: Amazonas: MZUSP 85320, 7, 2 c&s, 26.8–56.6 mm SL, igarape Barroso, tributary to rio Preto da Eva on Francisco Mendes road, 2°44'N, 59°38'W. \textit{Hisronotus notatus:} Brazil: Espírito Santo: MCP 18098, 208, 3 c&s, 31.1–41.0 mm SL, rio São José dos Torres on road BR-101, between São José dos Torres and Travessão, 21°4'43"S 41°14'2"W.

Brazilian Shield. The remaining of the species are distributed

\textbf{Material examined.} \textit{Otocinclus arnoldi} (285 specimens): Brazil: MCP 14165, 1, 26.1 mm SL, arroio Santo Antonio on road from Rosário do Sul to Santana do Livramento, 30°18′S 54°59′W. MCP 14196, 1, 34.3 mm SL, Rosário do Sul, 30°16′S 54°55′W. MCP 16189, 7, 24.5–27.6 mm SL, marginal lagoon on pâraa Formosa, São Marcos, Mato Grosso, 29°30′S 56°50′37″W. MCP 21626, 1, 33.4 mm SL, rio Uruguay and lateral pools at praira Formosa, São Marcos, Mato Grosso, 29°29′S 54°56′12″W. MCP 23086, 1, 31.7 mm SL, rio Jaguaru-Mirim, ca 5 km SE of São Francisco do Assis, 29°36′03″S 55°05′08″W. MCP 23110, 2, 33.5–53.7 mm SL, rio Inhacundá near São Francisco de Assis, 29°32′27″S 55°07′45″W. MCP 23153, 8, 30.2–39.3 mm SL, and MCP 25210, 5, 30.5–39.6 mm SL, rio Inhacundá near São Francisco de Assis, 29°32′51″S 55°08′11″W. MCP 23881, 1, 39.4 mm SL, arroio Ibicuí at Passo do Vai, Alegrete, 29°24′S 56°37′W. MCP 25234, 8, 2 c&s, 32.7–44.3 mm SL, rio Inhacundá near São Francisco de Assis, 29°32′27″S 55°07′45″W. MCP 25245, 46, 1 c&s, 30.1–42.7 mm SL, stream tributary to rio Inhacundá, São Francisco de Assis, 29°32′29″S 55°07′50″W. MCP 26766, 1, 28.1 mm SL, arroio Ibicuí da Fazixa on road BR 158, Santana do Livramento, 30°47′31″S 55°12′35″W. MCP 26814, 2, 22.1–22.9 mm SL, rio Ibicuí between São Vicente do Sul and Cacequi, 29°50′22″S 54°47′53″W. MCP 26833, 1, 26.3 mm SL, creek tributary to rio Santa Maria, Rosário do Sul, 30°10′44″S 54°51′22″W. MCP 26684, 8, 2 c&s, 20.7–31.9 mm SL, arroio do Salso, Rosário do Sul, 30°22′27″S 55°02′07″W. MCPP 26970, 2, 24.5–37.1 mm SL, rio Caxambu, Panambi, 28°35′50″S 53°27′31″W. MCP 27658, 1, 29.0 mm SL, arroio Caraí-Passo on road from São Francisco de Assis to Manoel Viana, 29°31′03″S 55°10′49″W. MCP 34613, 20, 19.9–24.5 mm SL, rio Ibicuí, São Vicente do Sul, 29°48′45″S 54°58′W. MCP 43818, 1, 29.2 mm SL, arroio Quairai-Chico at the Parque Estadual do Espinhilho, Quairai, 30°47′57″S 57′28″W. UFRRS 5297, 1, 29.2 mm SL, rio do Salso at Rosário do Sul, 30°22′27″S 55°21′00″W. UFRRS 5336, 4, 21.6–31.6 mm SL, arroio do Salso, Rosário do Sul, 30°22′27″S 55°21′00″W. UFRRS 5366, 1, 33.0 mm SL, rio Ibicuí-Mirim on road from Cacequi to São Vicente, Cacequi, 29°50′14″S 54°47′53″W. UFRRS 66388, 4, 31.7–38.2 mm SL, stream on road BR-290 ca 10 km from Rosário do Sul, 30°12′42″S 55°03′17″S. UFRRS 83339, 1, 43.5 mm SL, arroio do Salso, tributary to rio Santa Maria on road BR 293 between Bagé and Dom Pedrito. Uruguai: Rio Uruguay drainage: MCP 10003, 5, 29.9–36.5 mm SL, rio Negro, Arriera, Cerro Largo, 31°50′S 54°28′W. UFRRS 7180, 17, 31.5–47.7 mm SL, tributary to rio Yi, Durazno, 33°15′S 56′00″W. UFRRS 7181, 1, 47.8 mm SL, arroio Corrales on route 27,Tacuarembó, 31°23′35″S 55′12″W. UFRRS 7182, 2, 40.4–45.5 mm SL, arroio Cuchapirou on route 27, Tacuarembó, 31°05′S 55°25′W. UFRRS 9244, 1, 19.8 mm SL, arroio Batovi at km 24 of route 27, rio Tacuarembó basin, Rivera, 31°06′38″S 55°24′56″W. Otocinclus bororo: Brazil: Mato Grosso: MCP 15721, 5 paratypes, 2 c&s, 19.1–26.6 mm SL, creek on road from Barra do Bugres to Cáceres, 15°45′S 57°20′W. Otocinclus cacaariri: Brazil: Mato Grosso: MCP 19286, 7 paratypes, 2 c&s, 21.4–25.7 mm SL, tributary to rio Guaporé, Guajarâ-Mirim, 10°48′S 65°23′W. Otocinclus cocama: Peru: Loreto: MCP 34842, 8 paratypes, 2 c&s, 29.7–40.7 mm SL, Quebrada Yanyacu, Jenaro Herrera, 04°33′55″S 73°39′00″W. Otocinclus flexilis (226 specimens): Brazil: Rio Grande...
do Sul, laguna dos Patos drainage: MCP 9628, 3, 22.1-23.1 mm SL, arroio dos Ratios, Arroio dos Ratios, 30°07’S 51°43’W. MCP 15068, 145, 9.7-46.1 mm SL, swamp of rio Gravatá near road RS 118, ca. 500m from highway BR 290, Gravatá, 29°58’S 50°56’W. MCP 17414, 13, 2 c&s, 23.5-45.1 mm SL, arroio Itaetá, Passo das Pedras, 31°50’S 52°43’W. MCP 18307, 2, 23.6-37.8 mm SL, arroio Sapucaia, Esteio, 29°52’S 51°09’W. MCP 21426, 2, 28.4-33.9 mm SL, arroio Arambaré, Pedro Osório, 31°51’S 52°49’24”W. UFRGS 2011, 2, 29.4-31.7 mm SL, creek between highway BR 290 and Santo Antônio, 29°52’S 50°35’W. UFRGS 2013, 3, 32.4-34.1 mm SL, arroio Ramos between highway BR 290 and Santo Antônio, 29°52’S 50°30’2”W. UFRGS 4963, 22, 23.5-31.0 mm SL, flood of rio Gravatá, Porto Alegre, 29°57’S 50°59’42”W. UFRGS 6325, 11 of 171, 33.3-41.5 mm SL, creek near Gravatá, 29°57’S 51°00’23”W. UFRGS 7144, 9, 33.5-43.4 mm SL, rio Gravatá at the Passo das Canoas, Gravatá, 29°57’46”S 51°0’7”W. Otocinclus hasemani: Brazil: Piáu: MCP 22547, 94, 21.0-27.9 mm SL, riacho Palo, Formosa, 05°14’27”S 42°40’19”W. Otocinclus hoppe: Brazil: Pará: MCP 22545, 26, 23.8-32.1 mm SL, igarapé tributary to rio Guamá, Castanhá, 01°18’06”S 47°59’11”W. Otocinclus huanuaro: Peru: Loreto: NRM 17994, 13, 21.8-29.0 mm SL, and NRM 37375, 3 c&s, 18.0-29.3 mm SL, quebrada at km 53, San Jacinto, 02°31’S 75°43’W. Otocinclus macrospilus: Colombia: Amazonas, Rio Amazonas drainage: ICMNHN 41555, 5, 27.3-37.3 mm SL, and ICMNHN 5213, 4, 23.6-31.2 mm SL, Quebrada Yahuaraacaca, km 8, Leticia, 04°08’05”S 69°56’32”W. ICMNHN 5030, 1, 30.3 mm SL, rio Puré, Leticia, 02°07’05”S 69°37’50”W. Peru: Loreto, Iquitos, Rio Amazonas drainage: MCP 28205, 1, 23.3 mm SL, quebrada Pintuyacu, 43 km SW of Iquitos on road to Nauta, 04°55’58”S 73°27’18”W. Otocinclus mimicus: Paraguay: NRM 42332, 13 paratypes, 30.1-36.9 mm SL, and NRM 43479, 1 paratype c&s, 36.2 mm SL, small stream at Estancia María Belén km 8 from Coronel Patricio Colman, Caaguazu, 25°40’13”S 55°05’52”W. Otocinclus mura: Brazil: Pará: MCP 22550, 19, 21.2-32.7 mm SL, igarapé Urucuré, Tomé-Açu, 02°29’13”S 48°31’31”W. Otocinclus tapirape: Brazil: Goiás: UFRJ 5421, 2 c&s, 20.1-20.3 mm SL, crío Água Parada, 11 km W of Novo Planalto, 13°17’S 49°62’W. Otocinclus vestitus: Colombia: ICMNHN 4981, 1, 23.6 mm SL, caño La Arenosa, 10 km S on road Leticia to Tarapacá, 04°8’S 69°56’W. Otocinclus vividus: Colombia: ICMNHN 1316, 1, 20.6 mm SL, laguna de Menegua, Puerto Lopez, 04°06’S 72°54’W. Venezuela: MCNG 15667, 16, 9.1-25.8 mm SL, caño Maraca, on road Guanare to Guanarito, 08°50’N 69°21’W. Otocinclus xakriaba (30 specimens): Brazil: Mato Grosso: rio São Francisco drainage: MCP 16879, 25, 4 c&s, 22.5-28.7 mm SL, rio Peru-Açu, Januária, 15°11’S 44°12’30”W. MCP 23506, 1 c&s, 30.2 mm SL, rio Paraopeba, Jatuba, 19°57’S 44°18’W. Otocinclus sp. “madeira” (49 specimens): Brazil: Amazonas: rio Madeira drainage: MCP 35594, 34, 4 c&s, 19.8-27.6 mm SL, igarapé do Doce on Transamazônica Road ca. 12 km W of Humaitá, 07°34’25”S 63°06’39”W. MCP 35595, 15, 2 c&s, 22.7-28.2 mm SL, igarapé do Vinte e Dois at Recanto do Sanarí, ca. 22 km W of Humaitá, 07°35’36”S 63°10’27”W.

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