

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3437, 23 pp., 14 figures, 1 table

May 14, 2004

The Second Ural Centrum in Siluriformes and Its Implication for the Monophyly of Superfamily Sisoroidea (Teleostei, Ostariophysii)

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ABSTRACT

A well-developed second ural half-centrum is a peculiar characteristic of the caudal skeleton of certain siluriforms, not seen in other Recent ostariophysans. Although the character has been previously recorded in the literature, its exact taxonomic distribution, structure, ontogeny, and phylogenetic meaning within siluriforms are not yet determined. In this paper, the degree of development of the second ural half-centrum is surveyed across the order. The ontogeny of the relevant axial structures in the posterior region of the vertebral column is reported in representative siluriform taxa. The condition where the second ural centrum is well formed and forms a complete intervertebral joint anteriorly with the compound caudal centrum is considered derived within siluriforms, a character state homoplastic with the primitive state in more distant teleostean outgroups. Various catfishes display that derived condition, which is informative about relationships at different levels within the group. The most inclusive of those clades is the superfamily Sisoroidea, including the families Amblycipitidae, Akysidae, Sisoridae, Erethistidae, and Aspredinidae. The placement of the neotropical Aspredinidae into an otherwise exclusively Asian clade has important biogeographical implications and the structure of the second ural centrum provides additional support to that hypothesis. Based on the currently available knowledge on the relationships among catfishes, a well-developed second ural centrum is hypothesized to be a result of six different events in siluriforms.

INTRODUCTION

The caudal skeleton has been a rich source of taxonomically informative variation for

the Teleostei and its subgroups. Numerous papers have documented and interpreted the structure of the internal supports of the caudal fin in bony fishes, both before and after

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the advent of phylogenetic thinking (see Monod, 1968; Schultze and Arratia, 1989 and references therein). This long record of investigation has made the caudal skeleton one of the most important sources of characters for elucidating phylogenetic relationships among teleostean fishes. Lundberg and Baskin (1969) were the first to study in detail the large degree of variation in the caudal skeleton of the order Siluriformes, and found many morphological patterns diagnostic for monophyletic groups therein. Since then, caudal skeleton characters have been regularly used in studies of relationships among catfishes. Despite relatively intense research focusing on the caudal skeleton and its variations within Siluriformes, it appears to us that a number of additional potentially informative characters still await discovery in that complex.

The aim of this paper is to report on a survey of a specific part of the caudal skeleton of siluriforms, namely the degree of development of the second ural centrum (U_2). The full development of the anterior half of that centrum, where it forms a complete intervertebral joint anteriorly and has a well-defined ossification center, occurs consistently in the adults of a few groups of catfishes, as first reported by Lundberg and Baskin (1969). This feature is unusual in siluriforms and unique among other Recent ostariophysans, yet it remains poorly understood as to its exact distribution and phylogenetic implications. Accordingly, we here conduct a comparative survey of the U_2 in various representatives of all siluriform families, aiming at documenting the distribution of the trait in as much detail as possible. On the basis of that, we propose that the degree of development of the second ural centrum is a well-defined character informative at various levels in the phylogeny of siluriforms.

This study started as an evaluation of the significance of the second ural centrum for the monophyly of the superfamily Sisoroidea, defined by de Pinna (1996) to include the Asiatic catfish families Amblycipitidae, Akysidae, Erethistidae, and Sisoridae, plus the neotropical Aspredinidae. The possible affinities of Aspredinidae with Asiatic taxa has important biogeographic implications, since it is the first case of a trans-Pacific re-

lationship in South American freshwater fishes. Although a number of trans-Pacific relationships are known for the North American freshwater fish fauna, including both Recent and Fossil taxa (Grande, 1994: 68–74), no such case was known for South America. In the process of the study, taxonomic coverage was expanded to encompass the whole Siluriformes, and revealed data relevant also for understanding relationships of other subgroups within the order.

MATERIALS AND METHODS

Comparative material representing all currently recognized families of Siluriformes was examined as cleared and stained preparations, listed in appendix 1. Representatives chosen included the genera considered primitive or basal in their respective families, whenever that information is known and specimens were available. Most specimens were prepared according to the method of Taylor and Van Dyke (1985), which stains cartilage and bone, but some were prepared previously and were stained for bone only. The embryonic specimen of *Pterobunocephalus* was prepared inside the egg, by puncturing the egg case before the clearing and staining procedure. Illustrations were prepared with the aid of a microvideo system attached to a stereomicroscope. Images taken by the video system were printed with a color video printer and then traced by hand, against comparison with the actual specimen. Anatomical terminology follows Lundberg and Baskin (1969) and, for terms not treated therein, Monod (1968).

ANATOMICAL ABBREVIATIONS

EP	epural
HS	hemal spine
HY _n	hypural <i>n</i>
LHP	lower hypural plate
NS	neural spine
PH	parhypural
PU _n	preural centrum <i>n</i>
U _n	ural centrum <i>n</i>
UN	uroneural
UHP	upper hypural plate

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
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ANSP	Academy of Natural Sciences, Philadelphia
BMNH	The Natural History Museum, London
CAS	California Academy of Sciences, San Francisco
CMK	Collection Maurice Kottelat, Cornol
DUVC	Vertebrate Collection, Duke University, Durham
FMNH	Field Museum, Chicago
MCP	Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHN	Museum National d'Histoire Naturelle, Paris
MRAC	Musee Royal de l'Afrique Centrale, Tervuren
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo
NRM	Swedish Museum of Natural History, Stockholm
RUSI	South African Institute for Aquatic Biodiversity, formerly the JLB Smith Institute of Ichthyology, Grahamstown
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C.
ZSM	Zoologische Staatssammlung, Munich

THE SECOND URAL CENTRUM IN SILURIFORMES AND OTHER TELEOSTEI

The ural centra in the caudal skeleton of adult teleosts are often compound structures formed ontogenetically by the fusion of auto- and chordacentra precursors corresponding to multiple individual centra. It has been argued that the so-called second ural centra in adult teleosts can be formed ontogenetically in markedly different ways and are not necessarily homologous in various lineages (Schultze and Arratia, 1988). A structure identifiable as a second ural centrum (U_2) is well developed in adults of the majority of lower teleosts, and this is probably the primitive condition for the group. Such is the case in most, or at least basal members of, osteoglossomorphs, elopomorphs, clupeomorphs, and esocoids (Monod, 1968; Schultze and Arratia, 1988; Arratia and Schultze, 1992), as well as most basal fossil teleosts (Patterson and Rosen, 1977). In Recent clupeo-

morphs, U_2 is most markedly developed in *Denticeps clupeoides*, sister group to all other Clupeiformes and sole Recent representative of suborder Denticipitoidei. The centrum is also well differentiated in the majority of other clupeomorphs, though usually smaller in relative size than that observed in *Denticeps*. The degree of development of U_2 is variable in most groups of lower Neoteleostei, including groups such as aulopiforms and protacanthopterygians (*sensu* Johnson and Patterson, 1996). A second ural centrum is not differentiated (or not independent) in adult acanthopterygians. Among ostariophysans, a well-developed autogenous second ural centrum is present in some fossil gonorynchiforms, such as *Dastilbe*, *Tharrhias*, and *Parachanos* (Poyato-Ariza, 1996), but not in Recent adult gonorynchiforms. *Chanos* has bilateral flanges extending dorsoposteriorly from its complex centrum (illustrated in Poyato-Ariza, 1996: fig. 19 and labeled "postero-lateral process of caudal terminal complex"). Topological similarities suggest that these structures may be remnants of the urostyle (*sensu* Monod, 1968) of a primitive U_2 , itself fused or greatly reduced and adpressed to the posterior margin of $PU_1 + U_1$. A well-developed U_2 is also present in some siluriforms, as detailed in this paper, but not in other otophysans.

Lundberg and Baskin (1969) recognized for the first time that a few Siluriformes have a well-developed U_2 as adults. In those cases, the centrum forms a normal vertebral joint anteriorly with the compound caudal centrum ($PU_1 + U_1$), with a clearly recognizable conical articular surface intermediated with cartilage. Since its discovery, the presence of a well-developed U_2 has been considered to be of phylogenetic significance. Lundberg and Baskin observed that all other adult ostariophysans lack a U_2 autocentrum, and that its presence in some catfishes indicates that "the potential for its independent redevelopment has not been lost, at least in Siluriformes" (Lundberg and Baskin, 1969: 17). In light of the phylogeny currently accepted for ostariophysans (Fink and Fink, 1996) and lower teleosts (Johnson and Patterson, 1996; Arratia, 1997a, 1997b), it seems certain that the presence (or the redevelopment) of a well-developed U_2 in some catfishes should be in-

terpreted as apomorphic. The Diplomystidae, considered as sister group to all other fossil and Recent siluriforms (Lundberg and Baskin, 1969; Grande, 1987; Arratia, 1987; Mo, 1991; de Pinna, 1998), do not have a well-developed U_2 as adults. Likewise, species of the fossil family Hypsidoridae, considered as basal siluriforms, also lack an identifiable U_2 (Grande, 1987; Grande and de Pinna, 1998). Finally, no instances of a well-developed U_2 are known in gymnotiforms, characiforms, or cypriniforms, closest relatives of siluriforms. Within Siluriformes, Lundberg and Baskin reported the presence of a well-developed U_2 in Helogeninae (Cetopsidae), Aspredinidae, *Amblyceps* (Amblycipitidae), and some *Chiloglanis* (Mochokidae). The authors consider that each of those have closest relatives lacking a full U_2 , indicating that the structure has been redeveloped four independent times in siluriforms.

The U_2 in siluriforms, when well developed and in adults, is always entirely fused and continuous with the upper hypural plate. No siluriforms have a U_2 independent of hypural ossifications like in the primitive condition of other lower teleosts (which also include many cases of fusion). The second ural centrum in siluriforms, when present, tapers posteriorly, is fused with one or more of the upper hypurals, and does not have an articular surface on its posterior end. It should, thus, be more rigorously called a half-centrum, though for brevity in this paper it is just called a centrum. Also, it always lacks the peculiar dorsoposterior process (often tubular or semitubular) called a urostyle (in the terminology of Monod, 1968). A vestige of the urostyle may be represented by a ridge along the middorsal line of the centrum and of the associated hypural. In some aspredinids (such as *Pterobunocephalus*), the ridge may be quite deep anteriorly, indeed resembling an attenuated urostyle. This ridge accommodates the ventral margin of the uroneurals and seems to form a floor for the opisthural cavity. Overall, the condition of the caudal skeleton in catfishes with a well developed U_2 is markedly similar to that in some osteglossomorphs, such as *Pantodon*, *Scleropages*, and *Heterotis* (cf. Monod, 1968). Basal members of osteoglossomorphs, such as *Hiodon*, however, have an autoge-

nous U_2 (Hilton, 2002) similar to that in basal Elopomorphs (such as *Elops*) and quite different from the siluriform condition. Some paracanthopterygians, such as percopsiforms (Rosen and Patterson, 1969: fig. 16) also have a condition similar to that in siluriforms, though there may be some question as to the actual homology of the second ural centrum in paracanthopterygians.

The well-developed condition of the U_2 in catfishes can be associated with some interesting structural modifications. In some taxa, such as aspredinids and akysids, the U_2 and associated upper hypural plate are extremely well developed, and are oriented nearly on the horizontal axis. In such cases, it seems like the upper hypural plate is the actual caudal-fin support, while the lower hypural plate appears superficially to be a large hemal spine. This arrangement must have important, yet unexplored, biomechanical implications in the movement of the upper lobe of the caudal fin in those fishes.

The degree of U_2 development in adults varies markedly among various catfish taxa. Three basic types can be recognized: *Type 1*: there is little or no trace of U_2 ossification. Hypural 3 (or the upper hypural plate) has no obvious proximal thickening and fits into a cavity on the posterodorsal end of $PU_1 + U_1$, immediately ventral to the base of the uroneural (fig. 1). This is the condition present in most catfishes and other ostariophysans. *Type 2*: the proximal end of hypural 3 or upper hypural plate has a small bony thickening, often having a tight contact, or even forming an incipient articulation, but without a well-defined cartilage disk, with the posterior portion of $PU_1 + U_1$ (fig. 2). *Type 3*: a well-formed, obvious vertebral centrum is attached to the base of hypural 3 or a compound upper hypural plate. This centrum has a well-defined articulation anteriorly with the posterior portion of $PU_1 + U_1$, intermediated by cartilage, and a conical ossification center visible by transparency (fig. 3). In anterior view, the similarity in structure between the U_2 and a normal vertebral centrum is evident (fig. 4).

Type 1 U_2 is present in outgroup ostariophysans, and is considered as the primitive state for catfishes. Type 2 seems to be subject to considerable degree of intraspecific vari-

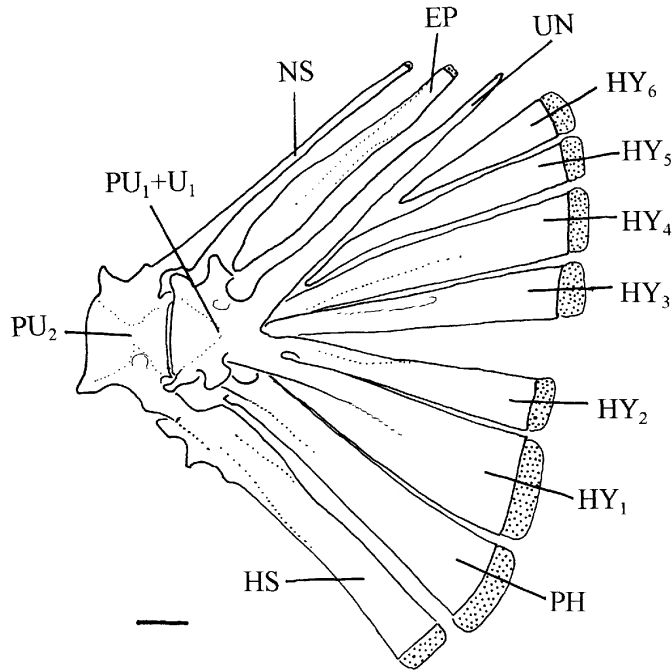


Fig. 1. Caudal skeleton of *Diplomystes mesembrinus* (Diplomystidae; MZUSP 62595, 149 mm SL). Scale bar = 1 mm.

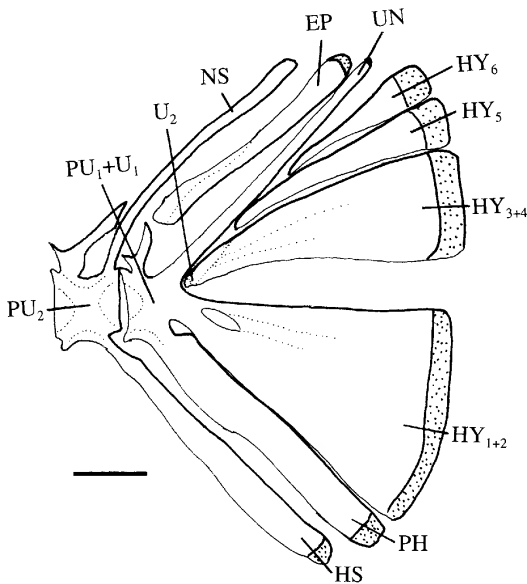


Fig. 2. Caudal skeleton of *Helicophagus waandersii* (Pangasiidae; UMMZ 186797, 77 mm SL). Scale bar = 1 mm.

ation; its delimitation as a discrete character state is difficult and we consider its phylogenetic significance to be uncertain at this point. In fact, the homology of the bony thickening at the base of the upper hypural with a ural centrum remains to be directly demonstrated by ontogenetic data. Type 3 is a condition derived within siluriforms; it seems to form a well-defined character state, with few cases of intermediate conditions and little or no relevant intraspecific variation in the samples examined. Although more in-depth studies may find a basis for considering U_2 types 1, 2, and 3 as a multistate character ordered in that sequence, we do not consider that to be warranted at present. Only type 3 can currently be considered as objective evidence of relationship.

ONTOGENETIC DATA

The ontogenetic fate of the second ural centrum seems to differ in various catfish

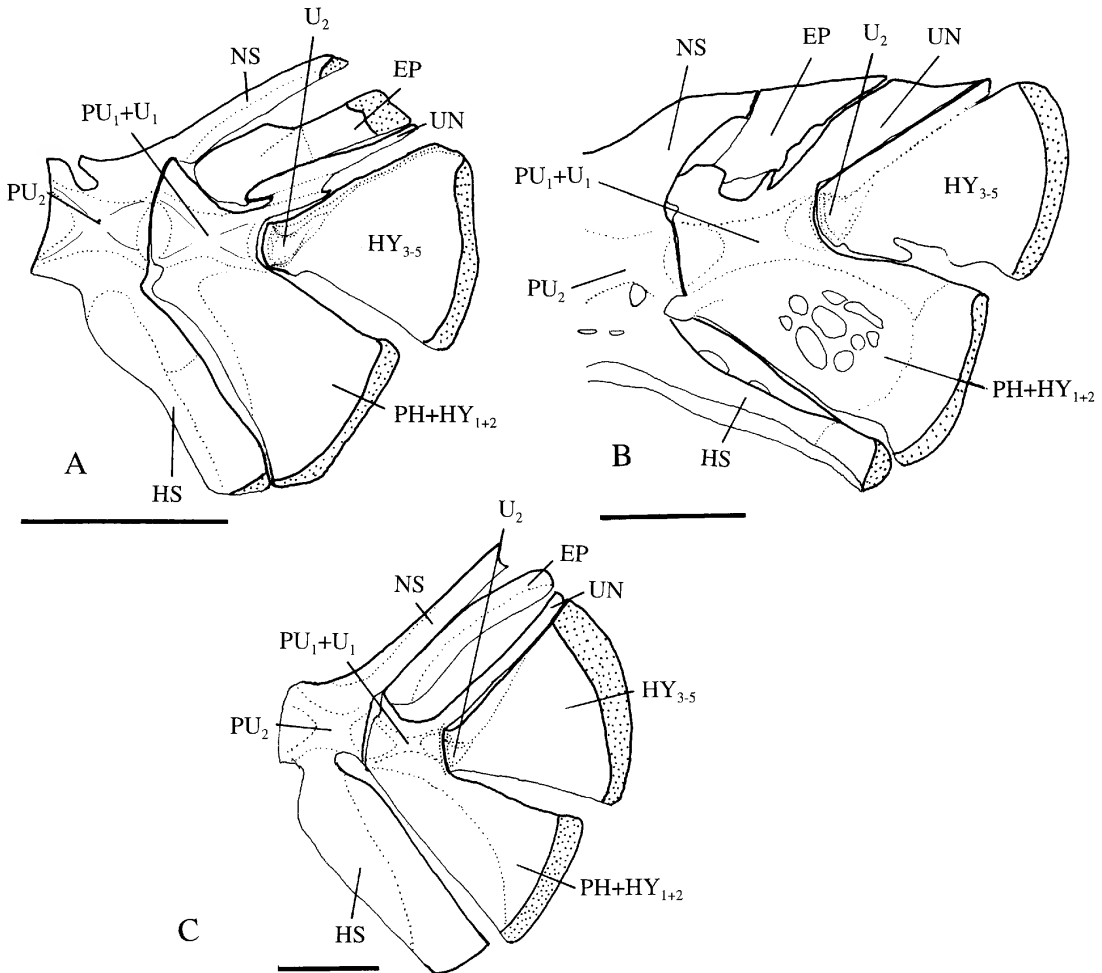


Fig. 3. Caudal skeletons in Akysidae: **A.** *Akysis recavus* (MZUSP 75128, 24 mm SL), **B.** *Breitensteinia insignis* (AMNH 58378, disarticulated adult specimen), **C.** *Parakysis grandis* (CMK 7915, 44 mm SL). Scale bar = 1 mm.

taxa. Lundberg and Baskin (1969) showed that the most common condition in siluriforms is to have a U_2 , or some remnant thereof, fused to the bases of hypurals 3 and 4, but noticed that in trichomycterids it is fused to the base of hypural 3 only. According to those authors, any remnants of the second urostyle are associated with the base(s) of upper hypurals, and not with the compound centrum. Arratia (1983) confirmed that U_2 is fused to the base of hypural 3 in some Trichomycterinae, but argued that in Nematogenyidae it is instead fused to the posterior portion of the compound centrum. An alternative interpretation, similar to Arratia's on Nematogenyidae, was advanced by

Fujita (1992) and Ichiyanagi and Fujita (1995), on the basis of observations on species of Clariidae (Siluriformes) and Cobitidae (Cypriniformes), respectively. In their view, the structure called $PU_1 + U_1$ by Lundberg and Baskin (1969) was considered to include the second urostyle as well (as $PU_1 + U_{1+2}$). Thus, the vertebral centrum material associated with hypural 3, considered by Lundberg and Baskin to be the U_2 , would actually be homologous to a more posterior urostyle (U_3). This idea was not based on direct observation of fusion, but apparently inferred on the basis of the joint association of parhypural, hypural 1, and hypural 2 to a single centrum element during

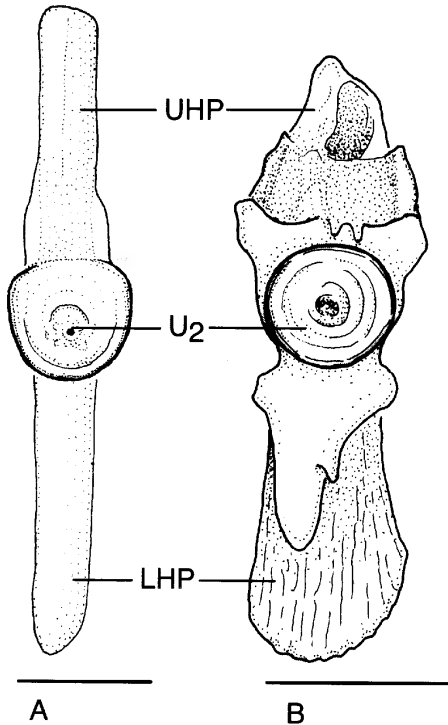


Fig. 4. Caudal skeleton in anterior view: **A.** *Parakysis grandis* (Akysidae; MZUSP 63109, 37.8 mm SL), **B.** *Agmus* sp. (Aspredinidae; AMNH 97160, disarticulated adult specimen). Scale bars = 1 mm.

ontogeny, thereby implying that this element is compound from three primitive centra. The compound nature of the teleostean U_1 has been suggested in the past (Nybelin, 1971) on the basis of its association with hypurals 1 and 2 in the vast majority of teleosts, fossil and Recent (Patterson and Rosen, 1977; de Pinna, 1996; Arratia, 1997b). Schultze and Arratia (1988) went further, and proposed not only that U_1 was formed by fusion of two centra (as U_{1+2}), but also that U_2 was formed by fusion of three other centra (as U_{3+4+5}). Such complex fusions have not been corroborated by other authors (Hilton, 2002), and have also not been confirmed in the material examined for this paper. While some of the individual ural and preural centra may indeed be compound in origin, evidence for that is controversial. Therefore, we prefer to maintain the terminology of Lundberg and Baskin until more direct evidence of the exact composition of the compound ural centrum in os-

tariophysans and other teleosts is available. We would further note that hypural 1 originates, in at least one siluriform (Fujita, 1992) and one cypriniform (Ichihanagi and Fujita, 1995), as a basal anteroventral offshoot of the cartilaginous hypural 2, rather than as an independent element (this information disagrees with Arratia, 1997b: 309, who stated that hypurals 1 and 2 are not connected by cartilage in juvenile ostariophysans). This is perhaps also the case in juveniles of many other teleosts, where cartilaginous hypurals 1 and 2 are fused at their bases at a stage when all other hypurals are independent (cf. Monod, 1968: figs. 30, 32, 61; Patterson and Rosen, 1977: figs. 26, 28). Although separate chondrification and subsequent cartilage fusion in early development has been documented for some taxa (cf. Fujita, 1994, in the cichlid *Tilapia* and Arratia and Schultze, 1992, in the Salmonid *Onchorhynchus*), it seems possible that hypural 1 in many, perhaps most, teleosts is just an ontogenetic offshoot from hypural 2. If so, it should not be expected to be associated with its own centrum in the vertebral series, and the centrum that supports hypurals 1 and 2 in the majority of teleosts would indeed be a single element. In that case, the compound centrum for the parhypural plus hypurals 1 and 2 in siluriforms and other ostariophysans would not involve three or more centra, but only two ($PU_1 + U_1$), as normally accepted. However, general conclusions along these lines need further information on early chondral differentiation of the elements of the caudal skeleton, not yet available for most relevant taxa.

The development of the second ural centrum in catfishes in general is still poorly documented, and current ideas are based on observations on few taxa. Ontogeny of U_2 in groups where it displays a type 3 degree of development is virtually unknown, in great part due to the difficulty in obtaining growth series of the relevant taxa. Juveniles of the superfamily Sisoroidea are rare in collections. For this study, we obtained juvenile sisoroid material of *Gagata* (Sisoridae) and *Aspredo* (Aspredinidae), plus late embryonic material of *Pterobuniocephalus* (Aspredinidae). Although no growth series were available, observation of juvenile conditions is nonetheless informative about the forma-

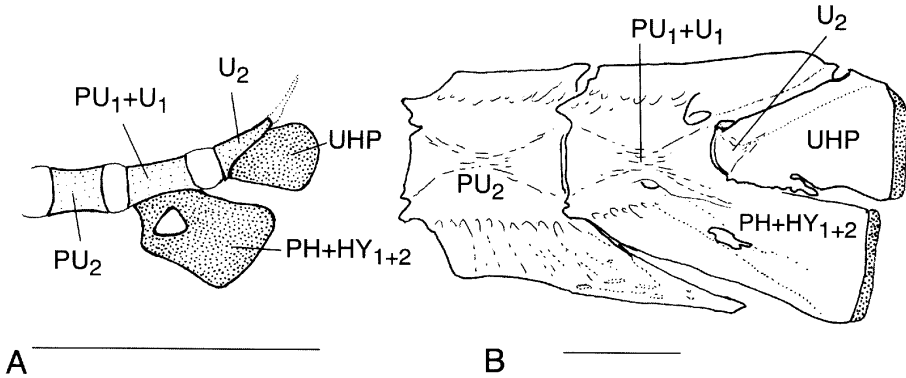


Fig. 5. Ontogenetic changes in the second ural centrum of Aspredinidae. **A.** *Pterobunocephalus* sp. (MZUSP 57208, approx. 5.5 mm SL), late embryo inside eggshell, **B.** *Pterobunocephalus* sp. (MZUSP uncat., 63.0 mm SL), adult. Heavy stippling represents cartilage, light stippling represents a thin mineralized layer, and open areas represent notochord (in A) or bone (in B). Scale bars = 0.5 mm (A) and 1 mm (B).

tion of the second ural centrum in those taxa. In the smallest specimen examined, a *Pterobunocephalus* embryo still inside an eggshell, hypurals 3 and 4 are already fused to U_2 (fig. 5A). Still, there is little doubt that the structure is actually a ural centrum, because it forms a continuous series with other centra anterior to it. Concomitantly, its homology with the respective centrum in adults is also obvious (fig. 5B). Similar situations are seen in later-stage juveniles of *Gagata* (fig. 6) and *Aspredo* (MZUSP 77694). The configurations in these specimens rule out

the possibility that the structure identified as U_2 might be a centrum-like specialization of the proximal part of the upper hypural complex, that is, not really a centrum, but simply a hypural modification gross-morphologically similar to a centrum in adults.

In catfishes without a well-developed U_2 , very little centrum material, if any, is associated with the bases of hypurals 3 and 4. In very small juvenile *Trichogenes longipinnis* (Trichomycteridae) examined, no ossifications can be clearly identified as U_2 material during the ossification of the caudal skeleton. At the earliest stage available (fig. 7A), the limits between centra can be seen as membranous separations, and the region corresponding to U_2 is independent of any hypurals. It remains so as ossification progresses (fig. 7B). Whatever little U_2 material that gets ossified seems to be incorporated into the posterior region of the compound centrum and/or the mesial surface of the uroneural. The bone thickening at the base of hypural 3 in adults is entirely composed of hypural material, since an evident thickening is already evident in the cartilaginous phase of the hypural, before the onset of ossification. The same situation holds for juvenile *Clarias gariepinus* (NRM 15319). Thus, the generally held assumption that U_2 is fused to the bases of hypurals 3 (trichomycterids) or 3 and 4 (all other catfishes) does not seem ontogenetically corroborated in the taxa exam-

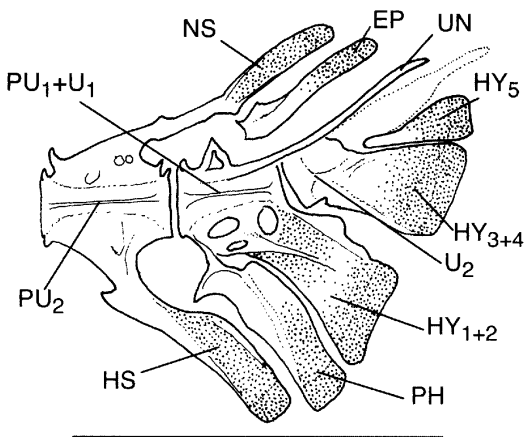


Fig. 6. Caudal skeleton of juvenile specimen of *Gagata melanopterus* (Sisoridae; MZUSP 52865, 16.0 mm SL). Stippling represents cartilage, open areas represent bone or notochord (in dotted lines). Scale bar = 1 mm.

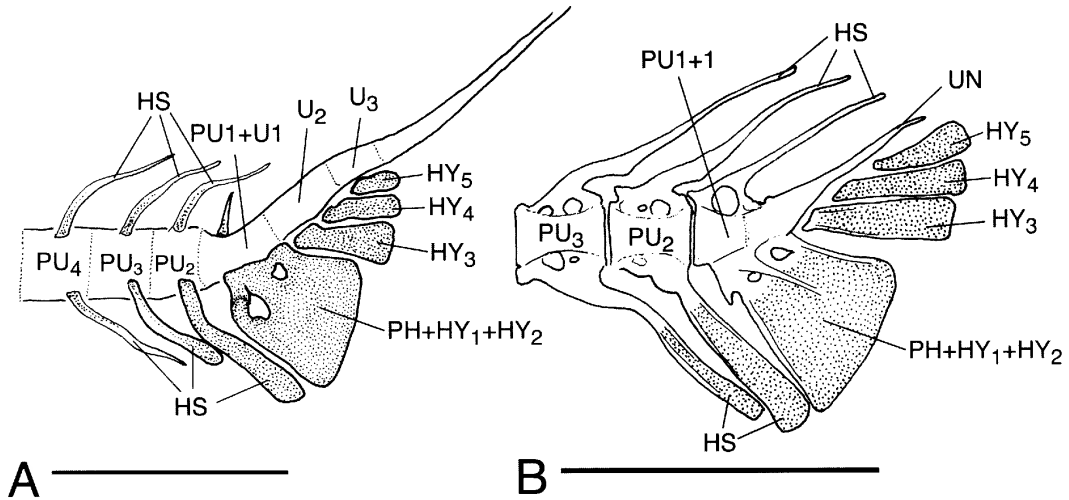


Fig. 7. Development of the caudal skeleton of *Trichogenes longipinnis* (Trichomycteridae; MZUSP 80933). **A.** at 9.1 mm SL, **B.** at 18.2 mm SL. Stippling represents cartilage, open areas represent membrane (A) or bone (B). Scale bars = 0.5 mm (A) and 1 mm (B).

ined. The fate of U_2 material may not be uniform among various catfish taxa.

Also, we found only little evidence of fusion between PU_1 and U_1 . The region corresponding to the two centra before the onset of ossification is always continuous in all juveniles examined. On the other hand, a larger juvenile of *Trichogenes* (fig. 7B) shows a tenous line of suture at the expected limit between PU_1 and U_1 which was not evident before ossification (fig. 7A). Perhaps fusion of the precursors of the two centra occurs very early in development, yet beginning of ossification still reveals a vestige of the primitive separation between them. In adults, fusion is again complete.

THE SECOND URAL CENTRUM IN SILURIFORM FAMILIES

We were able to examine several taxa not available to other authors and to verify that U_2 forms a full vertebral joint anteriorly in several additional catfish taxa not previously recorded. Appendix 1 summarizes our results, with a list of the material examined and an indication of the degree of development of the second ural centrum for Siluriforms (types 1, 2, or 3; see above). Below we provide a discussion on each of the catfish families known to have at least one instance of a well-developed U_2 .

AKYSIDAE

A previously unreported fully developed U_2 forming an intervertebral joint is present and very conspicuous in all akysids examined, and is the primitive condition for the family (fig. 3). In all cases, the second ural centrum is very well developed, and almost the same size as the anterior half of the second preural vertebra. Also, the centrum and associated upper hypural plate are positioned nearly along the longitudinal axis of the vertebral column.

AMBLYCIPITIDAE

Lundberg and Baskin (1969) reported some variation in U_2 development in this family, with *Liobagrus* showing a well-developed condition and *Amblyceps* lacking it. Our observations confirm theirs. In *Liobagrus reini*, three of the four specimens examined show a very conspicuous full development of U_2 (fig. 8), while a fourth specimen shows a rather reduced condition. In *Amblyceps*, the centrum is poorly developed. We did not confirm the observations by Chen (1994: 111) that the U_2 is fused to the compound centrum in *Amblyceps*. In the specimens we examined, the two are clearly separate, and the U_2 is reduced. However, there seems to be some variation in this fusion

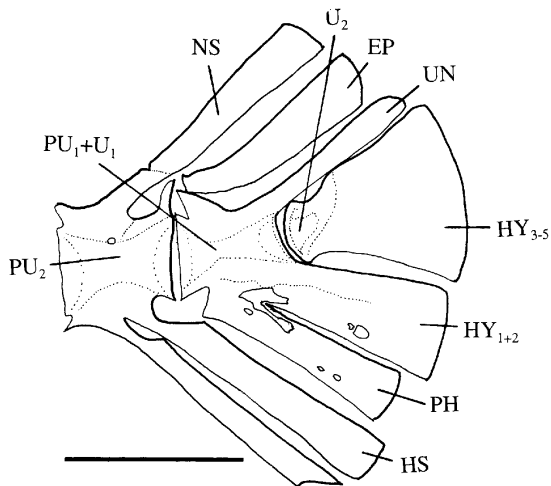


Fig. 8. Caudal skeleton of *Liobagrus anguillicaudatus* (Amblycipitidae; AMNH 11069, disarticulated adult specimen). Scale bar = 1 mm.

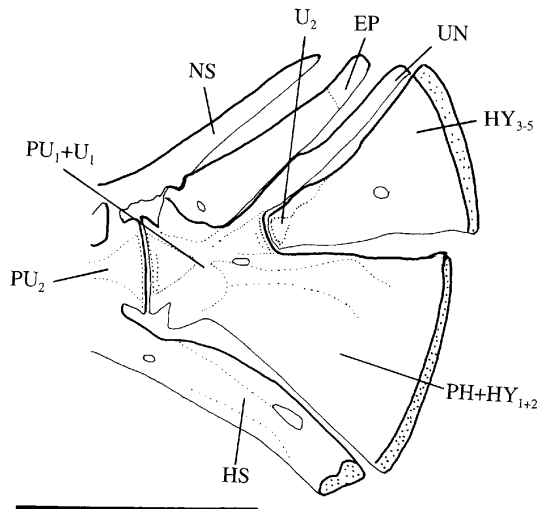


Fig. 9. Caudal skeleton of *Leptoglanis brevis* (Amphiliidae, UMMZ 199990, 29 mm SL). Scale bar = 1 mm.

among amblycipitids, since Lundberg and Baskin (1969: 17) reported that 3 out of 29 specimens examined of *Liobagrus anguillicaudatus* showed fusion between U_2 and $PU_1 + U_1$. In *Xiurenbagrus*, sister group to all other amblycipitids (Chen, 1994; Chen and Lundberg, 1995), U_2 is reported as well developed and forming a full intervertebral joint with the compound centrum (Chen, 1994: 111; Chen and Lundberg, 1995: 790). The presence of a well-developed U_2 in *Xiurenbagrus* and *Liobagrus* indicates that this is the plesiomorphic condition for amblycipitids, and that the reduced state in *Amblyceps* is a reversal.

AMPHILIIDAE

A well-developed U_2 was previously unreported in amphiliids. We found the structure forming an anterior intervertebral joint in *Leptoglanis brevis* (fig. 9) and *Zaireichthys zonatus*. Similar yet slightly less well-developed conditions are seen in the very similar *L. rotundiceps* and in *L. camerunensis*. All other amphiliids examined, including *L. xenognathus*, lack a well-developed second ural centrum.

ASPREIDINIDAE

Most aspredinids examined have a well-developed U_2 (fig. 10). In some, such as *Ag-*

mus (fig. 10A), the limit between U_2 and the compound centrum is partly covered by additional ossification, but still clearly visible. In representatives of the tribe Hoplomyzontini examined here (*Ernstichthys* and *Hoplomyzontin*), the whole portion posterior to the compound centrum is heavily covered by thick superficial ossification, and a separate U_2 is not evident. Considering that all other aspredinid representatives have a well-developed U_2 , and further that hoplomyzontins are not basal in the family (Friel, 1994), it seems that the absence of an evident U_2 in that tribe is secondary, and that the primitive condition for the family Aspredinidae is to have a well-developed second ural centrum. It is likely that the condition in hoplomyzontins is a result simply of additional ossifications in the caudal skeleton, and that the normal aspredinid condition is present but obscured in members of that tribe. Intermediate conditions such as that in *Agmus* demonstrate that such a configuration is likely. The condition in the basal undescribed genus which is the sister group to all other aspredinids (referred to as "*Pseudobunocephalus*" by Friel, 1994) seems to be similar to that in hoplomyzontins (cf. Friel, 1994: fig. 27). The condition of U_2 in such cases should be examined in juvenile specimens, before the onset of superficial ossification on the caudal skeleton. Lundberg

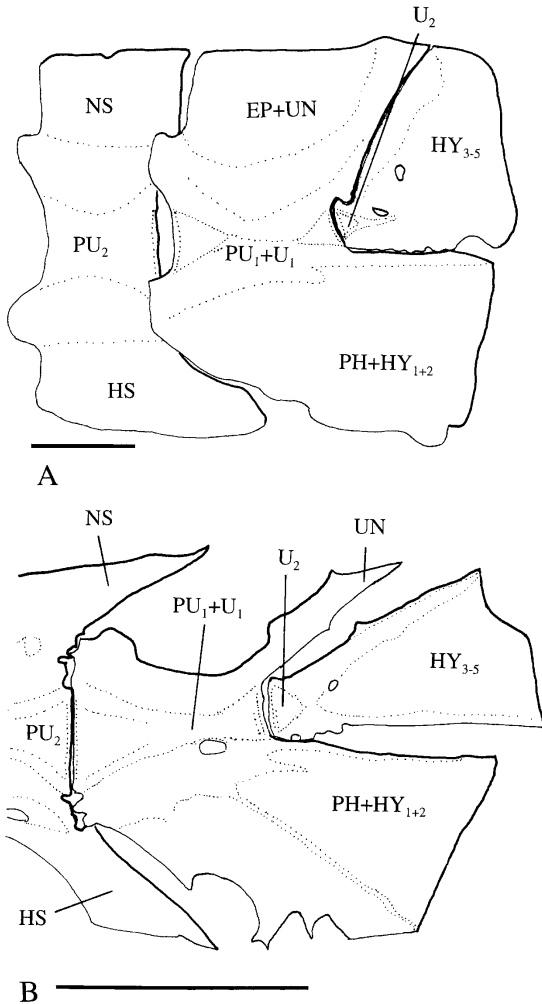


Fig. 10. Caudal skeletons in Aspredinidae: **A.** *Agmus* sp. (AMNH uncat., disarticulated adult specimen), **B.** *Platystacus cotylephorus* (USNM 87834, approx. 100 mm SL). Scale bar = 1 mm.

and Baskin (1969: 17) reported that U_2 is developed in all aspredinids except one species of *Bunocephalus*, which they referred to as *Bunocephalus* sp. That specimen is actually a representative of *Scoloplax* (Scoloplacidae), which was yet undescribed in 1969 (cf. Bailey and Baskin, 1976: 2).

AUCHENIPTERIDAE

A type 3 U_2 was reported in *Entomocorus* by Ferraris (1988: 58), and considered autapomorphic for the genus. Among auchenipterids examined for this study, we also found

a similar situation in the specimens examined of *Asterophysus*. The two genera are separated by a number of nodes in the current tree of auchenipterid relationships (Ferraris, 1988; cf. de Pinna, 1998), and the two occurrences of the derived condition must be optimized as convergent. Schultze and Aratia (1989: fig. 10A) also illustrated a seemingly functional U_2 in a juvenile specimen identified as *Centromochlus* sp. Since the condition has not been seen in adult specimens of the genus examined here, we presume the centrum regresses with growth in that taxon.

CETOPSIDAE

This family comprises two subfamilies, Cetopsinae and Helogeninae (de Pinna and Vari, 1995), previously considered as separate families. The presence of a well-developed U_2 in helogenines was reported by Lundberg and Baskin (1969: 17, fig. 7a). The phrasing of their description led Vari and Ortega (1986: 5) to consider that Lundberg and Baskin reported a totally autogenous U_2 for *Helogenes marmoratus*, that is, separate from both the compound centrum and from the upper hypural plate. Vari and Ortega, after examining the caudal skeleton of over 100 specimens of all species of *Helogenes*, concluded that the specimen illustrated and described by Lundberg and Baskin was abnormal, and that *Helogenes* has a U_2 fused to the upper hypural plate, as observed in aspredinids, amblycipitids, and mochokids. Vari and Ortega, however, did not examine the specimen studied by Lundberg and Baskin (AMNH 13332; their fig. 7a cites AMNH 3332, which we consider to be a misprint). We examined that same specimen and confirm that its U_2 is fused to the base of the upper hypural plate formed by fused hypurals 3 and 4, as described and illustrated by Vari and Ortega (1986: 5, fig. 1), rather than totally autogenous. In our view, the confusion stems from an ambiguous interpretation of the following passage in Lundberg and Baskin (1969: 17): "In all [groups that have a separate U_2 autocentrum] except *Helogenes* the U_2 autocentrum is fused to a single compound upper hypural element." It seems that Lundberg and Baskin meant that in *Heloge-*

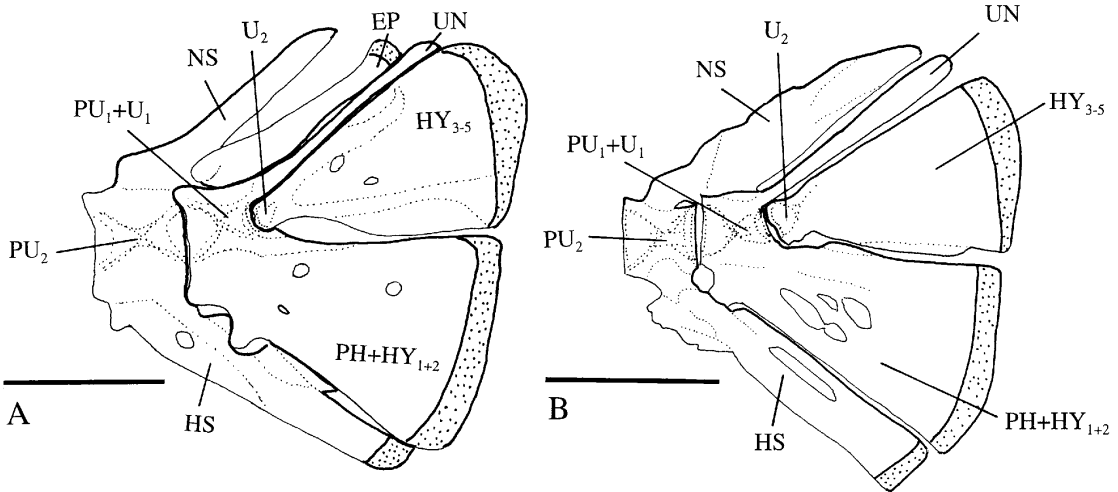


Fig. 11. Caudal skeletons in Erethistidae: **A.** *Conta conta* (UMMZ 208632, 43 mm SL), **B.** *Erethistes pusillus* (UMMZ 208697, 39 mm SL). Scale bar = 1 mm.

nes the U_2 is fused only to the base of the compound hypural 3 + 4 (hypural 5 is free in the genus), rather than to a single upper hypural plate formed by the fusion of hypurals 3, 4, and 5, as in all other taxa with a well-developed U_2 .

ERETHISTIDAE

Previously unreported for the members of this family, a well-developed condition of U_2 is present in all erethistids examined (fig. 11). In *Conta* (fig. 11A), the centrum is re-

duced in overall size, but still forms a full joint anteriorly with $PU_1 + U_1$.

MOCHOKIDAE

A well-developed U_2 centrum was found in some, but not all, species of *Chiloglanis* by Lundberg and Baskin (1969). We have confirmed that variation in our sample. The four specimens examined of *C. polypogon* (fig. 12) all have a full U_2 , while it is poorly developed in all three of *C. disneyi*. In all other mochokids examined, there is extensive secondary ossification that fuses the upper hypural plate with $PU_1 + U_1$ and obscures the condition of the U_2 . Examination of growth series is needed to investigate the actual condition of the structure in other mochokids.

PIMELODIDAE

Among pimelodids examined, a well-developed U_2 was observed only in *Pseudopimelodus raninus* (fig. 13) but not in the other species available. It has not been observed in *P. roosevelti* and *P. villosus* examined by Lundberg and Baskin (1969). Because a full U_2 is also absent in *Microglanis*, the closest relative of *Pseudopimelodus* (Lundberg et al., 1991), we conclude that the U_2 seen in *P. raninus* is autapomorphic for the species, or synapomorphic for a very restricted subclade of pseudopimelodines.

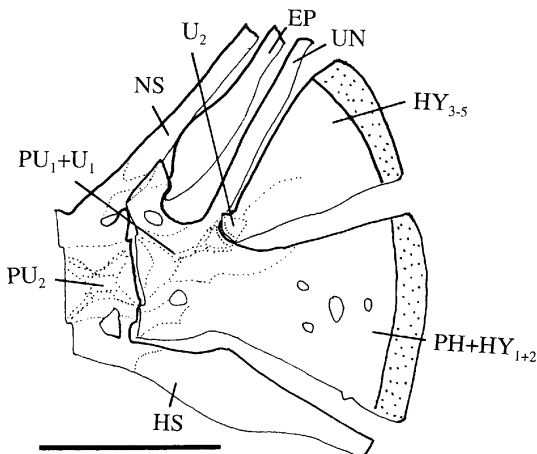


Fig. 12. Caudal skeleton of *Chiloglanis polypogon* (Mochokidae; USNM 304264, 29 mm SL). Scale bar = 1 mm.

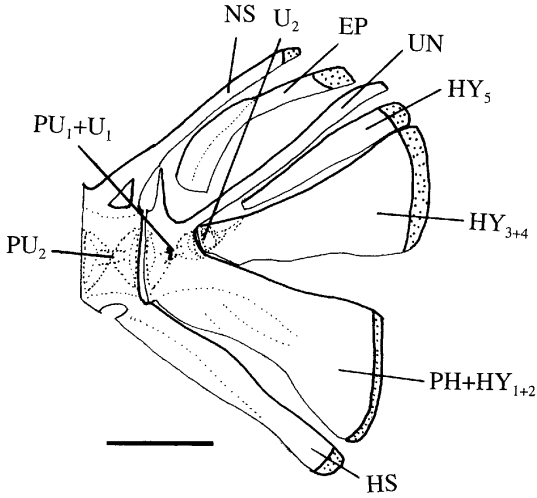


Fig. 13. Caudal skeleton of *Pseudopimelodus raninus* (AMNH 55370, disarticulated late juvenile specimen). Scale bar = 1 mm.

SISORIDAE

A full intervertebral joint of U_2 has not been previously reported in Sisoridae, although we found the condition in most taxa of the family examined (fig. 14). In *Glyptothorax*, some species have the fully developed U_2 , such as *G. major*, while in others, the centrum is somewhat reduced yet clearly forming a full anterior joint with the compound centrum. In *Bagarius*, the U_2 is not developed and corresponds to type 1, the primitive state for catfishes. This is the only such case in Sisoridae. The condition of U_2 in *Sisor* is currently unobservable, because the specimens examined have extensive additional ossification over the compound centrum and proximal portion of hypurals, obscuring the actual condition of underlying structures. Considering the currently accepted hypothesis of sisorid interrelationships (de Pinna, 1996), we regard a well-developed U_2 forming a full intervertebral joint with the compound centrum to be the primitive condition for the family, with some species of *Glyptothorax* having a somewhat reduced condition and *Bagarius* having a secondarily reduced U_2 .

PHYLOGENETIC IMPLICATIONS OF THE PRESENCE OF A WELL-DEVELOPED U_2

The presence of a type 3 second ural centrum in the cases discussed above can be mapped onto phylogenetic schemes currently accepted for various siluriform clades. It also provides additional evidence for some unsettled or controversial questions on the relationships of different subgroups of catfishes, at widely divergent levels of generality.

The most important phylogenetic implications of the second ural centrum are in the superfamily Sisoroidea, specifically the inclusion of the neotropical Aspredinidae therein, the only non-Asiatic taxon in the group. The first time aspredinids were aligned with Asiatic taxa was in Ferraris (1989), who proposed the family as the sister group to Akysidae. Chen (1994) placed aspredinids as the sister group to asiatic sisoroids (Sisoridae—including Erethistidae—Amblycipitidae, and Akysidae). Friel (1994), on the other hand, suggested that aspredinids were more closely related to doradoids (comprising the neotropical families Doradidae and Auchenipteridae—including Centromochlidae and Ageneiosidae—plus the African Mochokidae) than to any other siluriforms. De Pinna (1996) hypothesized that aspredinids were related to sisoroids, as the sister group to Erethistidae (members of which were formerly included in Sisoridae). The evidence for the monophyly of the suborder so far includes three relatively homoplasy-free synapomorphies (de Pinna, 1996): (1) the compressed and vertically expanded posterior center of ossification of the palatine; (2) the articular region of the lateral ethmoid laterally produced, with the articular facet for the palatine at the tip; and (3) the presence of a humero-vertebral ligament (connecting the humeral process—or the soft tissue in the humeral region—to the anterior portion of the vertebral column). Other potential characters exist, but these depend on more extensive ad hoc hypotheses of reversal within sisoroids and convergence in other catfish groups (for these, see de Pinna, 1996). All families included in Sisoroidea by de Pinna (1996) can be hypothesized as primitively having a fully formed U_2 . The few excep-

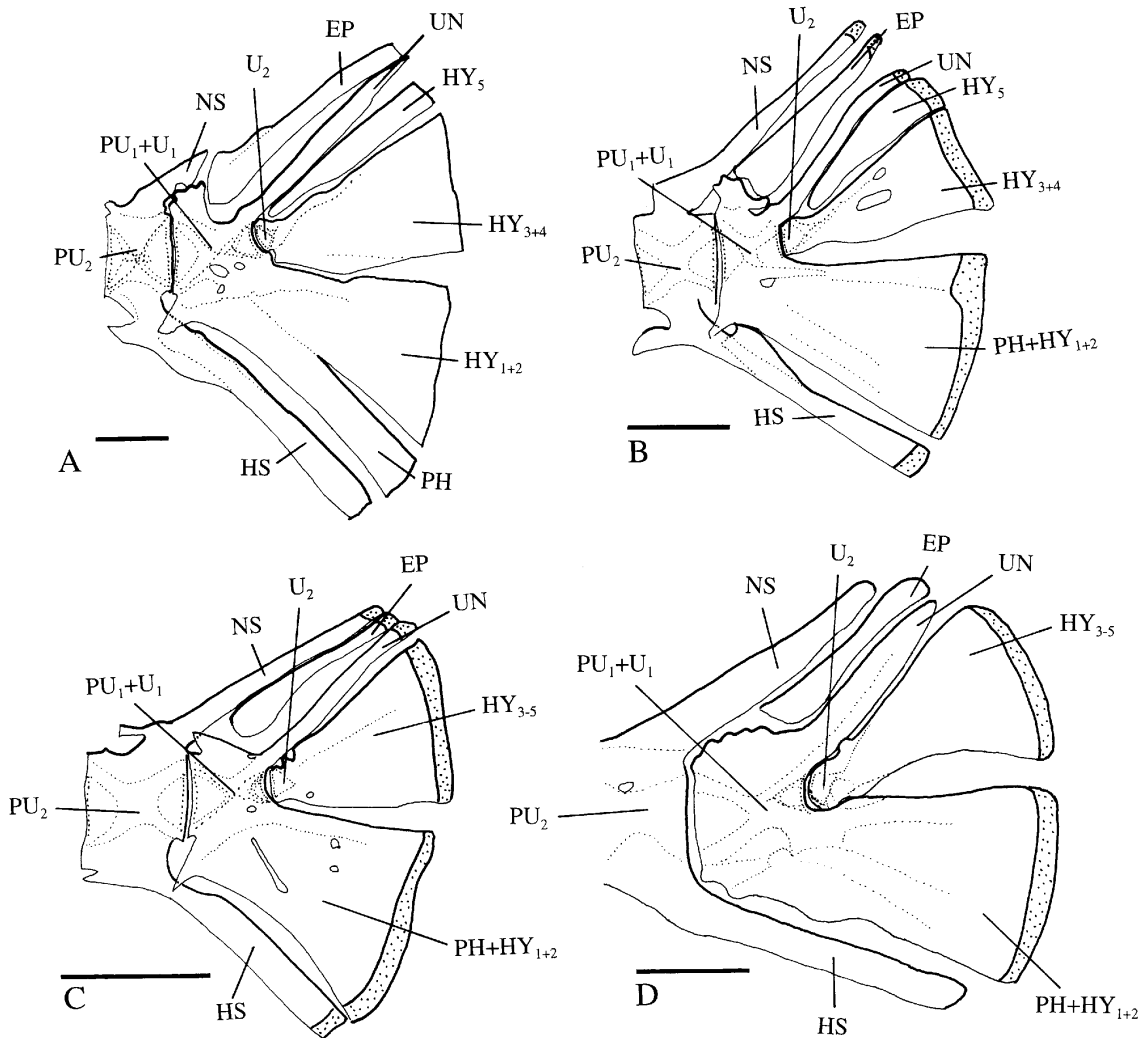


Fig. 14. Caudal skeletons in Sisoridae: **A.** *Gagata gagata* (AMNH 8358, disarticulated specimen), **B.** *Glyptothorax sinensis* (AMNH 10265, 51.9 mm SL), **C.** *Nangra nangra* (CMK 6369, 39 mm SL), **D.** *Pseudexostoma yunnanensis* (NRM 25124, 82 mm SL). Scale bar = 1 mm.

tions therein are parsimoniously interpreted as secondary reversals, based on congruence with other character data. The presence of a well-developed, type 3 U_2 can be interpreted as additional support for the monophyly of Sisoroidea, including the neotropical Aspredinidae.

The presence of a type 3 U_2 in helogenines is the most well documented in the literature (cf. Lundberg and Baskin, 1969; Vari and Ortega, 1986). It seems to constitute an autapomorphy for the subfamily. It has been demonstrated (de Pinna, 1993; de Pinna and

Vari, 1995) that former Cetopsidae and Helogenidae constitute a monophyletic group, now recognized as an expanded Cetopsidae (comprising monophyletic subfamilies Cetopsinae and Helogeninae). Cetopsines do not show a well-developed U_2 , as confirmed by our own observations and those of other authors. There is some indication that the phylogenetic position of cetopsids may be close to the base of the siluriform cladogram (Mo, 1991, in part; de Pinna, 1993; de Pinna and Vari, 1995), perhaps as the sister group to all other non-diplomystid catfishes. If that

is so, the immediate outgroups to helogenines are, in sequence, cetopsines, a clade containing most other catfishes, and diplomystids. This indicates that the condition of U_2 in helogenines can only be parsimoniously optimized as a transition at the base of the subfamily, and is therefore autapomorphic for it. A well-developed U_2 should be included among the diagnostic features of the subfamily Helogeninae.

Among Amphiliidae, the type 3 U_2 is present in *Zaireichthys zonatus* and a subgroup of *Leptoglanis* that includes forms similar in general aspect to *Zaireichthys* (*L. rotundiceps* and *L. brevis*). Therefore, it may be a synapomorphy indicating that those species are more closely related to *Z. zonatus* than to remaining species of *Leptoglanis* and that the latter genus may not be monophyletic. The type species of *Leptoglanis*, *L. xenognathus*, has the plesiomorphic type 1 U_2 . Considering that amphiliids (including *Leptoglanis*) are a monophyletic group (de Pinna, 1993), the type 3 U_2 that occurs in some members of the family is convergent with that in other catfishes.

Remaining occurrences of a Type 3 U_2 seem to be synapomorphic for very small clades. In mochokids, it is likely a synapomorphy for a subgroup of *Chiloglanis*. Similarly, the occurrence in *Pseudopimelodus* is either autapomorphic for *P. raninus* or synapomorphic for a subset of the genus. In Auchenipteridae, type 3 U_2 occurs in two taxa which are not close relatives (see above), and which must be hypothesized as results of separate events.

Lundberg and Baskin (1969) estimated that a fully developed U_2 developed independently four times within siluriforms: in Helogenidae, Aspredinidae, Amblycipitidae, and Mochokidae. Considering the new descriptive data within an updated phylogenetic context, it seems that the conditions in Amblycipitidae and Aspredinidae are homologous. On the other hand, other occurrences imply additional cases of convergence, such as in some amphiliids, some pseudopimelodines, and twice in auchenipterids. A total of six events can thus be hypothesized: (1) Helogeninae (Cetopsidae); (2) *Pseudopimelodus raninus* (Pimelodidae); (3) Sisoroidea (Amblycipitidae, Akysidae, Sisoridae, Aspredi-

nidae, and Erethistidae); (4) *Zaireichthys* and some *Leptoglanis* (Amphiliidae); (5) *Entomocorus* (Auchenipteridae); and (6) *Asterophysus* (Auchenipteridae).

ACKNOWLEDGMENTS

The authors thank Marcelo Britto, Lance Grande, and an anonymous reviewer for comments on the manuscript. Carl Ferraris kindly donated juvenile specimens of *Gagata melanopterus* for examination and discussed with us various topics treated herein. For access to collections and loans of specimens, we thank Melanie Stiassny, Scott Schaefer, Barbara Brown, Radford Arrindell, and Norma Feinberg (AMNH), John Lundberg, Bill Saul, and Mark Sabaj (ANSP), Gordon Howes and Darrell Siebert (BMNH), Bill Eschmeyer and David Catania (CAS), Maurice Kottelat (CMK and formerly ZSM), Barry Chernoff and Mary-Anne Rogers (FMNH), Roberto Reis (MCP), Karsten Hartel (MCZ), Guy Duhamel and Patrice Pruvost (MNHN), the late Guy Teugels (MRAC), Sven Kullander and Erik Åhländer (NRM), Paul Skelton and Roger Bills (RUSI), Bill Fink and Doug Nelson (UMMZ), and Richard Vari and Susan Jewett (USNM). Research funding to MP is provided by CNPq (#301082, Brazilian Federal Government), FAPESP (#99/09781-6, São Paulo State Government), NSF (DEB9903533), and National University of Singapore (Visiting Scientist Fellowship). Financial support for HN came from a Short-Term Visitor Grant from the Smithsonian Institution and from Research Grant RP 960314 to Peter K. L. Ng (National University of Singapore).

REFERENCES

- Arratia, G. 1983. The caudal skeleton of ostariophysan fishes (Teleostei): intraspecific variation in Trichomycteridae (Siluriformes). *Journal of Morphology* 177: 213–229.
- Arratia, G. 1987. Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications. *Bonner Zoologische Monographien* 24: 1–123.
- Arratia, G. 1997a. Basal teleosts and teleostean phylogeny. *Palaeo Ichthyologica* 7: 5–168.
- Arratia, G. 1997b. The monophyly of Teleostei and stem-group teleosts. *Consensus and dis-*

- agreements. In G. Arratia and H.-P. Schultze (editors), *Mesozoic fishes 2—systematics and fossil record*: 265–334. München: Friedrich Pfeil.
- Arratia, G., and H.-P. Schultze. 1992. Reevaluation of the caudal skeleton of certain actinopterygian fishes: III. Salmonidae. Homologization of caudal skeletal structures. *Journal of Morphology* 214: 187–249.
- Bailey, R.M., and J.N. Baskin. 1976. *Scoloplax dicra*, a new armored catfish from the Bolivian Amazon. *Occasional Papers of the Museum of Zoology University of Michigan* 674: 1–14.
- Chen, X.-P. 1994. Phylogenetic studies of the amblycipitid catfishes (Teleostei, Siluriformes) with species accounts. Ph.D. diss., Duke University, Durham, NC.
- Chen, X.-P., and J.G. Lundberg. 1995. *Xiurenbagrus*, a new genus of amblycipitid catfishes (Teleostei: Siluriformes), and phylogenetic relationships among the genera of Amblycipitidae. *Copeia* 1995: 780–800.
- de Pinna, M.C.C. 1993. Higher-level phylogeny of Siluriformes, with a new classification of the order. Ph.D. diss., City University of New York, NY.
- de Pinna, M.C.C. 1996. A phylogenetic analysis of the Asian catfish families Sisoridae, Akysidae and Amblycipitidae, with a hypothesis on the relationships of the neotropical Aspredinidae (Teleostei, Ostariophysi). *Fieldiana Zoology* 84: 1–83.
- de Pinna, M.C.C. 1998. Phylogenetic Relationships of Neotropical Siluriformes (Teleostei: Ostariophysi): Historical Overview and Synthesis of Hypotheses. In L. Malabarba, R. Reis, R.P. Vari, C. Lucena, and M. Lucena (editors), *Phylogeny and classification of neotropical fishes*: 123–142. Porto Alegre: Edipucrs.
- de Pinna, M.C.C., and R.P. Vari. 1995. Monophyly and phylogenetic diagnosis of the family Cetopsidae, with synonymization of the Helogenidae (Teleostei: Siluriformes). *Smithsonian Contributions to Zoology* 571: 1–26.
- Ferraris, C.J. 1988. The Auchenipteridae: putative monophyly and systematics, with a classification of the neotropical doradoid catfishes (Ostariophysi, Siluriformes). Ph.D. diss., City University of New York, NY.
- Ferraris, C.J. 1989. On the interrelationships between the Aspredinidae and the Akysidae (Ostariophysi, Siluriformes). Abstracts of the 1989 Meeting of the American Society of Ichthyologists and Herpetologists, San Francisco State University: 86.
- Fink, S., and W. Fink. 1996. Interrelationships of the ostariophysan fishes (Teleostei). In M. Stiassny, L. Parenti, and D. Johnson (editors), *Interrelationships of fishes*: 209–249. New York: Academic Press.
- Friel, J.P. 1994. A phylogenetic study of the neotropical banjo catfishes (Teleostei: Siluriformes: Aspredinidae). Ph.D. diss., Duke University, Durham, NC.
- Fujita, K. 1992. Ontogeny of the caudal skeleton in the clariid catfish *Clarias batrachus*. *Japanese Journal of Ichthyology* 38: 430–432.
- Fujita, K. 1994. Development of caudal skeleton in the cichlid fish *Tilapia sparrmanii*. *Journal of the Tokyo University of Fisheries* 81: 47–55.
- Grande, L. 1987. Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. *Journal of Vertebrate Paleontology* 7: 24–54.
- Grande, L. 1994. Repeating patterns in nature, predictability, and “impact” in science. In L. Grande and O. Rieppel (editors), *Interpreting the hierarchy of nature—from systematic patterns to evolutionary process theories*: 61–84. San Diego: Academic Press.
- Grande, L., and M.C.C. de Pinna. 1998. Description of a second species of the catfish *Hypsidoris* and a reevaluation of the genus and the family Hypsidoridae. *Journal of Vertebrate Paleontology* 18: 451–474.
- Hilton, E.J. 2002. Osteology of the extant North American fishes of the genus *Hiodon* Lesueur, 1818 (Teleostei: Osteoglossomorpha: Hiodontiformes). *Fieldiana Zoology* 100: 1–142.
- Ichyanagi, T., and K. Fujita. 1995. Development of the caudal skeleton in the cobitid fish *Misgurnus anguillicaudatus*. *Journal of the Tokyo University of Fisheries* 82: 99–102.
- Johnson, G.D., and C. Patterson. 1996. Relationships of lower euteleostean fishes. In M.L.J. Stiassny, L.R. Parenti, and G.D. Johnson (editors), *Interrelationships of fishes*: 251–332. San Diego: Academic Press.
- Lundberg, J.G., and J.N. Baskin. 1969. The caudal skeleton of the catfishes. Order Siluriformes. *American Museum Novitates* 2398: 1–49.
- Lundberg, J.G., A.H. Bornbusch, and F. Mago-Leccia. 1991. *Gladioglanis conquistador* n. sp. from Ecuador, with diagnoses of the subfamilies Rhamdiinae Bleeker and Pseudopimelodinae n. subf. (Siluriformes: Pimelodidae). *Copeia* 1991: 190–209.
- Mo, T. 1991. Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei) with a hypothesis of siluroid phylogeny. *Theses Zoologicae* 17; vii + 216 pp. Koenigstein: Koeltz Scientific Books.
- Monod, T. 1968. Le complexe urophore des poissons téléostéens. *Mémoires de l’Institut Fondamental d’Afrique Noire* 81: 1–705.
- Nybelin, O. 1971. On the caudal skeleton in

- Elops*, with remarks on other teleostean fishes. Acta Regiae Societatis Scientiarum et Litterarum Gothoburgensis Zoologica 7: 1–52.
- Patterson, C., and D.E. Rosen. 1977. Review of ichthyodectiform and other mesozoic teleost fishes and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158: 81–172.
- Poyato-Ariza, F.J. 1996. A revision of the ostarionophysan fish family Chanidae, with special reference to the Mesozoic forms. Palaeo Ichthyologica 6: 5–52.
- Rosen, D.E., and C. Patterson. 1969. The structure and relationships of the paracanthopterygian fishes. Bulletin of the American Museum of Natural History 141: 375–474.
- Schultze, H.-P., and G. Arratia. 1988. Reevaluation of the caudal skeleton of some actinopterygian fishes: II. *Hiodon*, *Elops*, and *Albula*. Journal of Morphology 195: 257–303.
- Schultze, H.-P., and G. Arratia. 1989. The composition of the caudal skeleton of teleosts (Actinopterygii: Osteichthyes). Zoological Journal of the Linnean Society 97: 189–231.
- Taylor, W.R., and G. van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9: 107–119.
- Vari, R.P., and H. Ortega. 1986. The catfishes of the neotropical family Helogenidae (Ostariophysi: Siluroidei). Smithsonian Contributions to Zoology 442: 1–20.

APPENDIX 1

MATERIAL EXAMINED AND, FOR SULURIFORMES, CONDITION OF SECOND URAL CENTRUM

Types 1, 2, and 3 of U₂ are explained in text. The number in parentheses following each catalog number is the number of specimens examined, not the total number of specimens. See text (Material and Methods) for institutional abbreviations.

Species	Catalog no.	U ₂ centrum type
SILURIFORMES		
Akysidae		
<i>Acrochordonichthys guttatus</i>	MZUSP 42468 (1)	3
<i>Akysis ephippifer</i>	CMK 4296 (1)	3
<i>Akysis heterurus</i>	MZUSP uncat. (4)	3
<i>Akysis leucorhynchus</i>	USNM 109636 (1)	3
<i>Akysis recavus</i>	MZUSP uncat. (1)	3
<i>Akysis similis</i>	UMMZ 214907 (4)	3
<i>Akysis varius</i>	USNM 232930 (1)	3
<i>Akysis</i> sp.	BMNH 1980.10.10:188 (1)	3
<i>Breitensteinia insignis</i>	AMNH 58378 (1)	3
<i>Parakysis grandis</i>	CMK 7915 (2)	3
Amblycipitidae		
<i>Amblyceps mangois</i>	UMMZ 208906 (1)	2
	ANSP 59316 (1)	2
<i>Liobagrus anguillicaudatus</i>	AMNH 11069 (2)	3
<i>Liobagrus reini</i>	AMNH 26744 (1)	3
	USNM 89370 (4)	2 or 3 ^a
Amphiliidae		
<i>Amphilius atesunensis</i>	USNM 296969 (1)	1
<i>Amphilius jacksoni</i>	UMMZ 199987 (2)	1
<i>Amphilius platyichir</i>	AMNH 71925 (1)	2
<i>Andersonia pellegrini</i>	MNH 1959.316 (1)	1
<i>Doumea thysi</i>	USNM 303564 (2)	1
<i>Leptoglanis brevis</i>	UMMZ 199990 (5)	3
<i>Leptoglanis camerunensis</i>	MNH 1988.1152 (1)	2
<i>Leptoglanis rotundiceps</i>	UMMZ 20020 (2)	3
<i>Leptoglanis xenognathus</i>	MRAC 118490-501(1)	1
<i>Paramphilius firestonei</i>	USNM 118812 (1)	1
<i>Paramphilius trichomycteroides</i>	MNH 1982-1206 (2)	1
<i>Phractura scaphirhynchura</i>	AMNH 6622 (2)	1
<i>Trachyglanis</i> sp.	AMNH 58446 (1)	1
<i>Zaireichthys zonatus</i>	CAS-SU 64127 (1)	3
Anchariidae		
<i>Ancharius fuscus</i>	AMNH 93702 (1)	1
Ariidae		
<i>Arius africanus</i>	AMNH 88024 (1)	1
<i>Arius solidus</i>	AMNH 58711 (1)	1
<i>Bagre bagre</i>	AMNH 20718 (2)	1
<i>Genidens genidens</i>	AMNH 20725 (3)	3, 1 ^b
Aspredinidae		
<i>Agmus</i> sp.	AMNH uncat. (2)	3
<i>Amaralia hypsiura</i>	AMNH uncat. (1)	3
<i>Aspredinichthys filamentosus</i>	USNM 207452 (2)	3
<i>Aspredo aspredo</i>	USNM 226072 (1)	3
<i>Bunocephalus coracoideus</i>	AMNH21815 (1)	3

^atype 2 in one specimen, type 3 in the others.

^btype 3 in one specimen, type 1 in the others.

APPENDIX 1
(Continued)

Species	Catalog no.	U ₂ centrum type
SILURIFORMES (continued)		
Aspredinidae (continued)		
<i>Ernstichthys</i> sp.	MZUSP 37814 (1)	— ^c
<i>Hoplomyzon sexpapilostoma</i>	AMNH 97232 (1)	— ^c
<i>Platystacus cotylephorus</i>	USNM 87834 (1)	3
<i>Xyliphius melanopterus</i>	DUVC-31-79 (1)	3
Astroblepidae		
<i>Astroblepus chotae</i>	USNM 167875 (1)	1
<i>Astroblepus</i> sp.	AMNH 20873 (1)	1
Auchenipteridae		
<i>Ageneiosus marmoratus</i>	AMNH uncat. (1)	1
<i>Asterophysus batrachus</i>	ANSP 158294 (1)	3
<i>Auchenipterichthys thoracatus</i>	MZUSP 36934 (1)	2
<i>Centromochlus existimatus</i>	MZUSP 48868 (2)	1
<i>Entomocorus gameroi</i>	AMNH 55404 (4)	1
<i>Tetranematchthys quadrifilis</i>	MZUSP 37517 (1)	1
<i>Trachelyichthys decaradiatus</i>	MZUSP 6830 (1)	2
<i>Tatia</i> sp.	MZUSP 37599 (1)	1
Austroglanidae		
<i>Austroglanis gilli</i>	MZUSP 65822 (1)	2
<i>Austroglanis barnardi</i>	MZUSP 62630 (1)	2
<i>Austroglanis sclateri</i>	MZUSP 63075 (1)	1
Bagridae		
<i>Hemibagrus macropterus</i>	AMNH 11103 (1)	1
<i>Horabagrus brachysoma</i>	CAS 141072 (1)	1
<i>Pseudomystus siamensis</i>	CAS 53212 (1)	1
<i>Rita chrysea</i>	USNM 114948 (1)	1
Callichthyidae		
<i>Corydoras aeneus</i>	AMNH 21772 (1)	1
Cetopsidae		
<i>Helogenes marmoratus</i>	AMNH 13332 (1)	3
	AMNH 91372 (1)	3
<i>Pseudocetopsis</i> sp.	USNM 302348 (1)	1
	USNM 257763 (1)	1
Chacidae		
<i>Chaca chaca</i>	AMNH 58393 (1)	1
Clariidae		
<i>Channallabes apus</i>	AMNH 6613 (1)	1
<i>Clarias vandenhoutei</i>	AMNH 32778 (2)	1
<i>Heterobranchus isopterus</i>	AMNH 32759 (1)	1
<i>Horaglanis krishnai</i>	BMNH 1981.11.20:1 (1)	1
Claroteidae		
<i>Auchenoglanis ballayi</i>	CAS 15449 (1)	1
<i>Bathybagrus tetranema</i>	UMMZ 196086 (1)	1
<i>Chrysiichthys ornatus</i>	AMNH 6700 (1)	1
<i>Lophiobagrus cyclurus</i>	MRAC 131157-184 (1)	1
<i>Parauchenoglanis guttatus</i>	MRAC 179230-233 (1)	1
<i>Phyllonemus filinemus</i>	MRAC 90257 (1)	1
<i>Platyglanis depierrei</i>	MNHN 1978-760 (1)	1
<i>Rheoglanis dendrophorus</i>	BMNH 1976.5.21:26 (1)	1

^cUnknown, obscured by secondary ossification.

APPENDIX 1
 (Continued)

Species	Catalog no.	U ₂ centrum type
SILURIFORMES (continued)		
Cranoglanididae		
<i>Cranoglanis boudierius</i>	USNM 94590 (1)	1
Diplomystidae		
<i>Diplomystes</i> sp.	AMNH 55318 (1)	1
<i>Diplomystes mesembrinus</i>	MZUSP 62595 (1)	1
Doradidae		
<i>Anduzedoras macrostoma</i>	AMNH 74491 (2)	1
<i>Leptodoras linnelli</i>	AMNH uncat. (3)	1
<i>Trachydoras paraguayensis</i>	AMNH uncat. (1)	1
<i>Wertheimeria maculata</i>	MCZ 91317 (1)	— ^c
Erethistidae		
<i>Conta conta</i>	UMMZ 208632 (2)	3
<i>Erethistes pusillus</i>	UMMZ 208697 (2)	3
<i>Erethistoides montana</i>	UMMZ 208745 (1)	3
<i>Hara hara</i>	UMMZ 208748 (3)	3
<i>Hara jerdoni</i>	AMNH 58394 (4)	3
<i>Laguvia ribeiroi</i>	UMMZ 208955 (5)	3
<i>Laguvia shawi</i>	UMMZ 208633 (1)	3
<i>Pseudolaguvia tuberculatus</i>	UMMZ 209010 (1)	3
Ictaluridae		
<i>Ictalurus meridionalis</i>	AMNH 25357 (2)	1
<i>Noturus gyrinus</i>	AMNH 22744 (1)	1
Loricariidae		
<i>Farlowella</i> sp.	AMNH uncat. (1)	1
<i>Neoplecostomus</i> sp.	MZUSP uncat. (1)	1
Malapteruridae		
<i>Malapterurus electricus</i>	AMNH uncat. (2)	1
Mochokidae		
<i>Brachysynodontis batensoda</i>	MNH 1959-525 (1)	1
<i>Chiloglanis disneyi</i>	USNM 303505 (3)	1
<i>Chiloglanis polypogon</i>	USNM 304264 (4)	3
<i>Euchilichthys dybowskii</i>	AMNH 6690 (1)	1
<i>Hemisynodontis membranaceus</i>	UMMZ 313407 (1)	1
<i>Microsynodontis christyi</i>	ZSM 22895 (1)	1
<i>Microsynodontis batesii</i>	AMNH 11741 (1)	1
<i>Mochokiella paynei</i>	AMNH 58398 (1)	1
<i>Mochokus niloticus</i>	USNM 229657 (1); AMNH 55703 (1)	1 1
<i>Synodontis clarias</i>	USNM 229746 (2)	1
<i>Synodontis nigriventris</i>	AMNH 55333 (8)	1
<i>Synodontis notatus</i>	AMNH 6254 (1)	1
Nematogenyidae		
<i>Nematogenys inermis</i>	CAS 12692 (1)	1
Pangasiidae		
<i>Helicophagus waandersii</i>	UMMZ 186797 (1)	2
<i>Pangasius nasutus</i>	AMNH 57267 (3)	1
<i>Pangasius pangasius</i>	UMMZ 208434 (2)	1

^cUnknown, obscured by secondary ossification.

APPENDIX 1
(Continued)

Species	Catalog no.	U ₂ centrum type
SILURIFORMES (continued)		
Pimelodidae		
<i>Brachyglanis</i> sp.	AMNH 91028 (1)	1
<i>Brachyrhamdia imitator</i>	AMNH 58322 (1)	1
<i>Callophysus macropterus</i>	AMNH uncat. (1)	1
<i>Duopalatinus</i> sp.	ANSP 139007 (1)	1
<i>Hypophthalmus edentatus</i>	AMNH 55369 (3)	1
<i>Luciopimelodus pati</i>	BMNH 1878.5.16:25 (1)	1
<i>Pimelodus altipinnis</i>	AMNH 33818 (1)	1
<i>Pseudopimelodus raninus</i>	AMNH 55370 (2)	3
<i>Pseudopimelodus</i> sp.	AMNH 40127 (3)	1
<i>Rhamdiopsis</i> sp.	MZUSP 35841 (1)	1
<i>Sorubim lima</i>	AMNH 55150 (1)	1
Plotosidae		
<i>Plotosus papuensis</i>	USNM 217106 (1)	1
<i>Porochilus rendahli</i>	AMNH 36827 (3)	1
Schilbeidae		
<i>Ailia coilia</i>	UMMZ 208442 (3)	1
<i>Clupisoma garua</i>	UMMZ 208355 (2)	1
<i>Eutropiellus buffei</i>	BMNH 1975.6.16:2 (1)	1
<i>Neotropius khavalchor</i>	BMNH 1992.2.11:8 (1)	1
<i>Schilbe mystus</i>	AMNH 6521 (1)	1
<i>Silonia silondia</i>	UMMZ 208460 (1)	1
Scoloplacidae		
<i>Scoloplax empousa</i>	MZUSP 37489 (2)	1
Siluridae		
<i>Kryptopterus</i> sp.	AMNH uncat. (2)	1
<i>Silurus glanis</i>	AMNH 18758 (1)	1
Sisoridae		
<i>Bagarius bagarius</i>	UMMZ186793 (1)	1
<i>Bagarius yarrelli</i>	AMNH 58363 (2)	1
<i>Euchiloglanis kishinouyei</i>	USNM 120365 (1)	3
<i>Exostoma labiatum</i>	NRM 25105 (1)	3
" <i>Exostoma</i> " sp.	USNM 13083 (1)	3
<i>Gagata cenia</i>	AMNH 58392 (1)	3
<i>Gagata gasawuyuh</i>	AMNH 8358 (1)	3
<i>Gangra viridescens</i>	UMMZ 208725 (1)	3
<i>Glyptothorax major</i>	AMNH 58410 (2)	3
<i>Glyptothorax pectinopterus</i>	BMNH 15.445 (2)	3
<i>Glyptothorax platypogon</i>	USNM 87431 (1)	2
<i>Glyptothorax sinensis</i>	AMNH 10265 (3)	2
<i>Glyptothorax trilineatus</i>	UMMZ 186849 (1)	2
<i>Glyptothorax</i> sp.	USNM 288474 (1)	2
<i>Nangra nangra</i>	CMK 6369 (1)	3
<i>Oreoglanis siamensis</i>	USNM 118430 (1)	1
	CMK 4351 (1)	1
<i>Pseudecheneis sulcatus</i>	FMNH 99630 (1); BMNH 1985.9.16:50 (1)	3 2
<i>Pseudexostoma yunnanensis</i>	NRM 25124 (1)	3
<i>Sisor rhabdophorus</i>	BMNH 1970.6.25:2 (1)	— ^c

^cUnknown, obscured by secondary ossification.

APPENDIX 1
(Continued)

Species	Catalog no.	U ₂ centrum type
SILURIFORMES (continued)		
Trichomycteridae		
<i>Pareiodon</i> sp.	MZUSP 23522 (3)	1
<i>Trichomycterus nigricans</i>	MCP 10649 (1)	1
<i>Trichogenes longipinnis</i>	MZUSP uncat. (3)	1
CHARACIFORMES		
Hepsetidae		
<i>Hepsetus odoe</i>	USNM 231553 (1)	—
CYPRINIFORMES		
Cyprinidae		
<i>Opsariichthys bidens</i>	AMNH 10955 (1)	—
<i>Nocomis leptocephalus</i>	MZUSP 45979 (1)	—
<i>Pimephales notatus</i>	MZUSP 45956 (1)	—
GONORYNCHIFORMES		
Chanidae		
<i>Chanos chanos</i>	MZUSP 62470 (1)	—
Kneriidae		
<i>Kneria auriculata</i>	MZUSP 63121 (1)	—
CLUPEOMORPHA		
Denticipitidae		
<i>Denticeps clupeoides</i>	MZUSP 62480 (1)	—
<i>Pellona harroweri</i>	MZUSP 11238 (1)	—
PROTACANTHOPTERYGII		
Salmonidae		
<i>Salmo salar</i>	MZUSP 28531 (1)	—
Argentinidae		
<i>Argentina striata</i>	MZUSP 17914 (1)	—
Galaxiidae		
<i>Galaxias maculatus</i>	MZUSP 16600 (1)	—
<i>Galaxias auratus</i>	USNM 344895 (1)	—
Osmeridae		
<i>Osmerus mordax</i>	AMNH 32663 (1)	—
	AMNH 110489 (2)	—
ESOCIFORMES		
Esocidae		
<i>Esox masquinongy</i>	MZUSP 28038 (1)	—
Umbridae		
<i>Dallia pectoralis</i>	MZUSP 38284 (1)	—
<i>Umbrina limi</i>	USNM 034033 (1)	—
ELOPOMORPHA		
Albulidae		
<i>Albula vulpes</i>	MZUSP 10625 (1)	—
<i>Elops</i> sp.	MZUSP 60346 (1)	—

APPENDIX 1
(Continued)

Species	Catalog no.	U ₂ centrum type
OSTEOGLOSSOMORPHA		
Hiodontidae		
<i>Hiodon tergisus</i>	MZUSP 28540 (1)	—
Osteoglossidae		
<i>Osteoglossum</i> sp.	MZUSP 17686 (1)	—
Arapaimidae		
<i>Arapaima gigas</i>	MZUSP 26083 (1)	—
STOMIIFORMES		
Chauliodontidae		
<i>Chauliodus sloani</i>	MZUSP uncat. (1)	—
Gonostomatidae		
<i>Maurolicus muelleri</i>	MZUSP 18361 (1)	—
AULOPIIFORMES		
Chlorophthalmidae		
<i>Chlorophthalmus agassizi</i>	MZUSP 10648 (1)	—
Paralepididae		
<i>Lestidium atlanticum</i>	MZUSP 60327 (1)	—
Synodontidae		
<i>Saurida caribbaea</i>	MZUSP 18359 (1)	—
MYCTOPHIFORMES		
Myctophidae		
<i>Diaphus dumerili</i>	MZUSP 35852 (1)	—
<i>Hygophum hygomii</i>	MZUSP uncat. (1)	—
PARACANTHOPTERYGII		
Aphredoderidae		
<i>Aphredoderus sayanus</i>	MZUSP 55046 (2)	—
Batrachoididae		
<i>Thalassophryne punctata</i>	MZUSP 47262 (1)	—
Gadidae		
<i>Urophycis mystaceus</i>	MZUSP 40220 (1)	—
Merlucciidae		
<i>Merluccius</i> sp.	MZUSP 60347 (1)	—