Monophyly of the catfish family Siluridae (Teleostei: Siluriformes), with a critique of previous hypotheses of the family's relationships

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Received October 1989, accepted for publication June 1990

Monophyly of the Eurasian catfish family Siluridae is established according to five synapomorphies unique to the family: (1) palatine reduced to a small nodule; (2) lateral ethmoid and sphenotic contact by narrow extensions lateral to the frontal; (3) ossified transscapular ligament anteroposteriorly compressed; (4) distal radials of dorsal-fin pterygiophores absent; (5) articulations of anal-fin rays with pterygiophores posterodorsally shifted. Previous hypotheses of silurid non-monophyly or a close relationship of the Siluridae to the Malapteruridae, Plotosidae or Amblycipitidae are shown to be poorly supported by available evidence. Silurids share with other subgroups of the Siluroidea character states that are derived within the Siluroidea; these are described in an appendix. Additional character state evidence is needed before a hypothesis of sister-group relationship between the Siluridae and another siluroid subgroup can be proposed.

KEY WORDS:—Siluridae — phylogenetic analysis — catfishes — Eurasia.

CONTENTS

INTRODUCTION

The Eurasian catfish family Siluridae comprises 101 extant and four extinct species (Bornbusch, 1988; Kobayakawa, 1989). Of the 12 other siluriform families that occur in Eurasian freshwaters, only the Sisoridae and Bagridae show a Eurasian diversity that is comparable to that of silurids. The widely accepted diagnosis of the Siluridae was established by Regan (1911), who recognized two diagnostic characters: "palatine short and broad" and "lateral...
ethmoid ... with a slender posterior extension which meets a similar forward
extension of the sphenotic, so that the frontal has no free edge" (Regan, 1911:
560). Regan included in the Siluridae the Eurasian genus Silurus Linnaeus, 1758
and Asiatic relatives in the nominal genera Parasilurus Bleeker, 1862, Silurichthys
Bleeker, 1858, Wallago Bleeker, 1851, Belodontichthys Bleeker, 1858, Ompok
Lacèpède, 1803 (= Callichrous Hamilton, 1822), Kryptopterus Bleeker, 1858, and
Hemisilurus Bleeker, 1858.

Previous classifications by Bleeker (1863), Günther (1864) and Gill (1872) also
placed these genera together in higher taxa, but added other externally similar
catfishes. Bleeker (1863: 113–116), whose classification was the most detailed of
those mentioned, included silurids and schilbeids in his “Siluriformes”, but
divided it into subgroups that reflected some separation of silurids and schilbeids:

“Subfamilia Siluriformes”
“Stirps 1. Schilbeini” – Clupisoma, Schilbe
“Stirps 2. Silurini” – Silurus, Wallago, Parasilurus, Belodontichthys,
Silurichthys, Silurodes, Callichrous, Siluranodon
“Stirps 3. Kryptopterini” – Kryptopterus, Pterocryptis, Kryptopterichthys
“Stirps 4. Phalacronotini” – Micronema, Phalacronotus, Hemisilurus

Günther (1864) placed silurids in a more heterogeneous group, the “Silurina”,
that also included without further subdivision heteropneustids, schilbeids and
pangasiids. Gill (1872) placed Günther’s “Silurina” into the “Siluridae” and
without subdivision added a large number of other catfishes, such as bagrids,
pimelodids, ictalurids, ariids and mochokids.

Regan’s (1911) classification thus restricted the Siluridae to those genera
sharing certain diagnostic osteological features in addition to external similarities
upon which previous classifications were based. Since his classification, several
nominal genera have been added to the Siluridae without alteration of Regan’s
(1911) diagnosis: Hito Herre, 1924, Penesilurus Herre, 1924 (= Hito), Herklostella
Herre, 1933 (= Pterocryptis Peters, 1862), Ceratoglanis Myers, 1938, Wallagonia
Myers, 1938 (= Wallago) and Pliosilurus Weiler, 1956 from the Pliocene of
Europe (see Bornbusch, 1988 for discussion of generic synonyms).

Although Regan (1911) did not formally propose a suprafamilial classification
of catfishes, he listed the Siluridae adjacent to the Indo-Pacific Plotosidae
because of their similar elongate anal fins and increased pelvic-fin ray counts.
Regan’s placement of both families near the beginning of his list suggests that he
considered silurids and plotosids to be relatively primitive catfishes. Tilak (1963)
maintained that the Siluridae are more primitive than the Plotosidae, and that
the two families are “closely related” according to similarities in the
neurocranium and Weberian apparatus. Chardon (1968) grouped the Siluridae
with the Asian Amblycipitidae and South American Helogenidae into the
primitive suborder Siluroidei defined primarily by features of the Weberian
apparatus and adjacent elements of the pectoral girdle. Howes (1985) proposed
that the Siluridae are not monophyletic. Although he did not clearly describe
synapomorphies of the hypothesized lineages, Howes (1985) suggested that
Wallago and Silurus are sister-taxa and more closely related to the African
Malapteruridae (electric catfishes) than to other silurids. The remaining silurids
were suggested, without character state evidence, to be closely related to

†Denotes an extinct taxon.
unspecified taxa within the Afro-Asian Schilbeidae. Howes’ hypothesis challenges conventional notions of silurid monophyly and carries significant implications for the evolutionary history of Old World siluriforms.

A phylogenetic analysis of the Siluridae has led to a re-evaluation of the family’s status and relationships to other siluriforms. Here evidence is presented in support of monophyly of the Siluridae. Hypotheses of relationships of the Siluridae to other siluriforms proposed by Tilak (1963), Chardon (1968) and Howes (1985) are reviewed; this analysis suggests that these hypotheses are not well supported by available information. Silurids share with other subgroups of the Siluroidea (sensu Grande, 1987) character states that are derived within the Siluroidea. However, in the absence of a more resolved hypothesis of silurid relationships, it is unclear whether each of these character states is uniquely derived for a lineage inclusive of the Siluridae, or has been independently derived in several lineages including the Siluridae. Studies of siluriform inter-relationships have increased in recent years and additional character state information may support a choice between alternative hypotheses. The Appendix describes silurid character states that are derived within the Siluroidea and occur in other siluroids, and are thus potentially informative of higher siluroid relationships.

MATERIAL AND METHODS

Methods of phylogenetic analysis were used (Hennig, 1966). The phylogenetic status of the Siluridae was inferred from the distributions of derived character states. Evolutionary polarities of character states were inferred according to the outgroup comparison method. The outgroup framework was as follows: (1) monophyly of the Siluriformes (sensu Greenwood et al., 1966) is well corroborated (Fink & Fink, 1981); (2) the Diplomystidae are the sister-group to a group comprised of all other catfishes, i.e. the Siluroidei (sensu Grande, 1987); (3) within the Siluroidei, the †Hypsidoridae are the sister-group to remaining catfishes, i.e. the Siluroidea (sensu Grande, 1987), including the Siluridae. The outgroup relationships for inferring the polarities of character states within the Siluroidea can be summarized as: [(Diplomystidae(†Hypsidoridae(Siluroidea)))] (Grande, 1987). No further assumptions were made about basal relationships of subgroups within the Siluroidea. However, although diagnoses for few of the 34 extant siluroid families have been established that are explicitly phylogenetic, it is clear from studies by current workers and Regan (1911) that the monophyly of many siluroid subgroups can be well corroborated and this information is also taken into account in the character state analysis (Baskin, 1972; Howes, 1983b; Lundberg, 1982; Lundberg & McDade, 1986; Schaefer, 1987; Stewart, 1985, 1986).

Character state polarities within the Siluroidea (i.e. extant non-diplomystid siluriforms) were inferred by following the “doublet rule” of the outgroup method (Maddison, Donoghue & Maddison, 1984) with the Diplomystidae and †Hypsidoridae as outgroups to the Siluroidea. Extension of the character state analysis to other otophysans, following the hypothesis of otophyan relationships proposed by Fink & Fink (1981), was necessary if the two outgroups gave ambiguous or conflicting information. A character state present in the Siluridae and absent in all other subgroups of the Siluroidea, the Diplomystidae and
†Hypsidioridae was inferred to be phylogenetically derived and indicative of silurid monophyly. Character states shared by silurids and other taxa of the Siluroidea, and lacking in diplomystids and †hypsidiorsids, were also inferred to be derived within the Siluroidea. These character states may be: (1) additional synapomorphies of the Siluridae that have been independently derived in other siluroid lineages and their presence in silurids is thus homoplasious, or (2) synapomorphies of a larger lineage that includes the Siluridae and their presence in silurids is thus plesiomorphic.

Representative taxa from the following siluriform families were examined in this study: Ageneiosidae, Amblycipitidae, Amphiliidae, Ariidae, Aspredinidae, Astroblepidae, Auchenipteridae, Bagridae, Callichthyidae, Cetopsidae, Chacidae, Claridae, Cranoglanididae, Diplomystidae, Doradidae, Helogenidae, Heteropnuestidae, Hypophthalmidae, Ictaluridae, Loricariidae, Malapteruridae, Mochokidae, Olyridae, Pangasiidae, Pimelodidae, Plotosidae, Schilbeidae, Siluridae (including representatives of all 18 genera recognized by Bornbusch, 1988), Sisoridae and Trichomycteridae. Representatives of the Gymnotiformes, Cypriniformes and Characiformes were also examined. A complete detailed list of material examined for this study is included in Bornbusch (1988) or can be obtained from the author. Cleared and stained specimens were prepared according to Potthoff (1984). Independent examination of non-silurid catfishes was supplemented by reference to previous studies of siluriform anatomy. These included: Arratia (1987), Baskin (1972), Bridge & Haddon (1893), Brown & Ferraris (1988), Chardon (1968), Fink & Fink (1981), Grande (1987), Howes (1983a, b), Lundberg (1970, 1982), Lundberg & Baskin (1969), Lundberg & McDade (1986). Institutional abbreviations follow Leviton et al. (1985).

RESULTS

This study identified five character states that were inferred to be synapomorphies of the Siluridae. These character states constitute a phylogenetic diagnosis of the Siluridae, as follows: (1) palatine nodular with no posterior extension; (2) frontal laterally occluded by slender extensions of the lateral ethmoid and sphenotic; (3) ossified transscapular ligament compressed into a thin blade; (4) distal radials of dorsal-fin pterygiophores absent; and (5) anal-fin ray articulations with pterygiophores shifted posterodorsally such that each ray articulates directly with the proximal radial of the next posterior pterygiophore.

Palatine

In siluroids the palatine is primitively a rod-like bone that extends posteriorly to articulate with the lateral ethmoid. Often the palatine extends posterior to the lateral ethmoid articulation and the lateral ethmoid antorbital process (Fig. 1A, B). In silurids the palatine is uniquely reduced to a nodular element that lies entirely anterior to the antorbital process and lacks a well-developed articulation with the lateral ethmoid; the palatine simply abuts the ethmoid cartilage bordering the anterolateral edge of the lateral ethmoid (Fig. 1C).
Howes (1985: 59) interpreted an “anteriorly placed, truncated palatine” as derived for a group comprising the Malapteruridae and Siluridae. Although the malapterurid palatine is somewhat shortened relative to that in some other catfishes, it is a rod-like element, has a well-developed articulation with the lateral ethmoid, and extends slightly beyond this articulation to the lateral ethmoid antorbital process, as is primitive for siluroids (Fig. 1B). The Siluridae and Malapteruridae exhibit non-homologous conditions of the palatine that offer no evidence of a close relationship between the two families.

Regan (1911) and Gosline (1975) noted the unusual nature of the palatine in silurids. Gosline (1975: 9) added that the palatine-maxillary mechanism of barbel movement in silurids is “one of the most specialized of all catfishes”. Although the palatine is specialized, movements of the palatine and maxilla during barbel protraction in silurids are as described for most catfishes by Alexander (1965). The silurid *extensor tentaculi* (sensu Winterbottom, 1974) is well developed, originates on the posterolateral face of the orbitosphenoid and is subdivided into dorsal and ventral parts that insert on the posterior face of the palatine. A subdivided *extensor tentaculi* is lacking in diplomystids, but is common in other catfishes (e.g. ictalurids, loricariids, hypophthalmids: Alexander, 1965; Howes, 1983a, b; Lundberg, 1970). The silurid *extensor tentaculi* is unusual as it is longer and more longitudinally oriented than in other siluroids, a probable correlate of the shortened palatine. The silurid *retractor tentaculi* (sensu Winterbottom, 1974) is well developed as a separate subdivision of the *A₃* division of the *adductor mandibulae* that acts to retract the maxillary barbel. A separate *retractor tentaculi* is not unique to silurids and is considered to have been independently derived several times among siluriforms, including within the Ictaluridae (Lundberg, 1982).

**Lateral ethmoid, sphenotic and frontal**

Most siluriforms, including diplomystids and thyspidorids, exhibit the condition whereby the lateral ethmoid and sphenotic do not contact each other.
and the frontal has a free lateral edge above the orbit (Fig. 2A; Arratia, 1987: fig. 22; Grande, 1987: fig. 3B). According to comparisons with non-siluriform otophysans, this is considered to be the plesiomorphic condition in catfishes. In silurids the lateral ethmoid extends posteriorly and the sphenotic anteriorly along the lateral margin of the frontal to narrowly contact each other; the frontal thus lacks a free edge (Fig. 2E).

Occlusion of the frontal is not unique to silurids, and is also encountered in the auchenipterid *Trachycorystes*, the pimelodid *Phractocephalus*, clariids and heteropneustids. The silurid condition differs from those in these groups, as follows. In clariids and heteropneustids the frontal is occluded by a plate-like expansion of the posteriormost (fourth) infraorbital which is probably synapomorphic for the two families (Fig. 2D). In *Trachycorystes* the lateral ethmoid lacks any extension and the frontal is bordered laterally only by a
broad, anterior expansion of the sphenotic (Fig. 2B). In *Phractocephalus* both the lateral ethmoid and sphenotic extend lateral to the frontal, but by extensions broader than those in silurids (Fig. 2C; Lundberg *et al.*, 1988). Additionally, *Phractocephalus* and *Trachycorystes* have synapomorphies with, respectively, other pimelodids and auchenipterids that lack a lateral ethmoid-sphenotic contact (Curran, 1989; Lundberg, personal communication). These observations indicate that occlusion of the frontal has evolved independently in several siluroid subgroups and the condition encountered in silurids is unique and synapomorphic for the group.

Howes (1985) suggested that elongation of the sphenotic is a synapomorphy of the Malapteruridae and the silurid genera *Silurus, Wallago* and *Kryptopterus*, but did not note the presence of this condition in other silurids. The sphenotic, relative to the frontal in malapterurids, though, is not elongated over the primitive siluriform condition, and the malapterurid frontal has a free lateral edge (cf. Fig. 2A, F). The malapterurid sphenotic is anteriorly narrowed and turned laterally in association with a modification of the frontal; both modifications are not present in other siluriforms (Fig. 2F). It is likely that the derived conditions of the sphenotic in silurids and malapterurids are independent and are not evidence of silurid non-monophyly (because all silurids share the same condition of an elongate sphenotic) or of a sister relationship between the two families.

**Supracleithrum**

In catfishes the transscapular ligament (also referred to as Baudelot’s ligament or the lower or mesial limb of the supracleithrum) is primitively ossified for its entire length as part of the supracleithrum. It is robust, thick and tightly attached, if not sutured, to the basioccipital (Fig. 3A; Grande, 1987: fig. 5). Silurids show a derived condition in which the ossified portion of the transscapular ligament is reduced and anteroposteriorly compressed into a thin blade (Fig. 3B, C). It is connected ligamentously to the basioccipital, and in many subgroups there is a clear gap separating the two bones. Reduction of the mesial limb of the supracleithrum and its ligamentous connection to the basioccipital are not unique to silurids, but its compression into a blade-like element has not been observed in other examined siluriforms, including diplomystids and Hypsidoridae.

**Dorsal- and anal-fin supports**

In otophysans the dorsal- and anal-fin pterygiophores primitively consist of three elements: proximal, middle and distal radials. In siluriforms and gymnotiforms, middle radial ossifications are absent from both dorsal- and anal-fin pterygiophores (Fink & Fink, 1981). In all silurids the dorsal-fin pterygiophores are further reduced by the absence of distal radials (Fig. 4). The dorsal-fin rays in silurids are thus supported by a single series of elements, the proximal radials (following Fink & Fink, 1981). This condition has not been found in other siluriforms and is interpreted as a synapomorphy of the Siluridae.

In most otophysans the anal-fin rays articulate with corresponding pterygiophores such that each ray articulates with its distal radial and is offset
posterior to the long axis of its proximal radial and anterior to that of the next proximal radial (Fig. 5A). In silurids the anal-fin rays are shifted posterodorsally such that each ray articulates directly with a proximal radial, presumably that of the next pterygiophore, and the long axes of both are aligned with each other (Fig. 5B). This shift also reduces the articulation of each ray with its own distal radial. Although a similar condition occurs in gymnotiforms (Fink & Fink, 1981: fig. 22), the shapes of the elements are different and a direct anal-fin ray–proximal radial articulation has most likely evolved independently in the two groups. In no other siluriform has a similar shift of the anal-fin ray articulation been observed.

**DISCUSSION**

The Siluridae, as established by Regan (1911) with little subsequent change in composition, are clearly a monophyletic lineage of Old World catfishes. This
Figure 4. Dorsal-fin ray bases and fin supports in right lateral view (anterior toward right), *Wallago leerii*, USNM 227965. Heavy stippling indicates cartilaginous areas. Scale bar: 1 mm. Abbreviations: dr1, first dorsal-fin ray; prl-5, proximal radials.

Figure 5. Anal-fin rays and fin supports in left lateral view (anterior toward left), photographed from cleared and double-stained specimens. A, *Ictalurus punctatus*, DU F-930. B, *Ompok bimaculatus*, USNM uncat. Scale bars: A, B, 1 mm. Abbreviations: ar, anal-fin ray; dr, distal radial; pr, proximal radial.
hypothesis is supported by the distributions of the five character states described in the preceding section. Two of these character states—those of the palatine and frontal—were incorporated by Regan (1911) in his osteological description of the Siluridae.

In the published literature, only Howes (1985) has challenged the monophyly of the Siluridae. Howes (1985) hypothesized that the Malapteruridae and the silurid genera *Silurus* and *Wallago* constitute a monophyletic lineage, and that the remaining silurid genera are related in an unspecified way to schilbeid catfishes. Howes (1985: 64) stated “indications are that the Siluridae and Schilbeidae, as currently defined are paraphyletic”. Howes (1985: 64) further stated that “in the literature, the only character that distinguishes the Siluridae and the Schilbeidae is the presence, in the latter, of nasal barbels”. This statement overlooks two important facts: (1) as indicated above, Regan (1911) clearly proposed two distinguishing features of the Siluridae, and (2) nasal barbels are lacking in the schilbeid genus *Laides*.

The character state evidence for Howes’ hypothesis of silurid paraphyly was poorly enumerated, and from the summary of eleven character state distributions given by Howes (1985: 64–65) it is difficult to identify unambiguous synapomorphies of the lineages hypothesized by Howes (1985). However, the character state evidence given in Howes (1985) can be criticized on the following grounds: most important, with respect to all of the character states cited by Howes (1985), silurids are more similar to each other than to other siluriforms. Additionally, for some features Howes did not note character state differences that indicate independent derivations in silurids and malapterurids (e.g. modifications of the sphenotic, and *epaxialis* invasion of the skull roof—see Appendix), or incorrectly described character state distributions (e.g. extension of the dorsal oblique portion of the *hypaxialis*—see Appendix). Howes (1985) thus offers no evidence that effectively refutes silurid monophyly.

The Siluridae also possess a number of character states that are shared with other subgroups of the Siluroidea and are derived within the Siluridae. Some of these character states are described in the Appendix. No known set of congruent character state distributions constitutes strong evidence of a sister-group relationship between the Siluridae and another siluroid subgroup. Hypotheses of higher relationships between the Siluridae and other siluriforms have been proposed by Tilak (1963) and Chardon (1968). Phylogenetic analysis indicates that these hypotheses are poorly supported. Tilak (1963: 437) suggested that although the Siluridae are more primitive than the Plotosidae, the two groups are closely related according to similarities in the Weberian apparatus. It is difficult to criticize Tilak’s hypothesis since he did not specify those character states to which he was referring. No shared derived character states of the Weberian apparatus have been found that would suggest a close relationship between silurids and plotosids. Tilak’s assertion that the Siluridae are more “primitive” than the Plotosidae is based on his inference that the following silurid character states are primitive (Tilak, 1963: 437): “rudimentary supraoccipital spine”, “practically no excavation of the occipital region of the skull” and “ectethmoids [= lateral ethmoids] are united to the sphenotics laterally”. From arguments given in the preceding section and the Appendix, the first and third character states are derived among siluroids, but it is unclear what Tilak meant by “excavation of the occipital region of the skull”.

Plotosids and silurids each show different modifications of the posterior skull roof that are associated with invasion of the *epaxialis* (see Appendix). Because the extent of *epaxialis* invasion is greater in silurids, it might be inferred that silurids share a more derived state than plotosids.

Derived character states that are shared by silurids and plotosids include: invasion of the *epaxialis* of the skull roof, absence of a *levator arcus palatini* crest on the hyomandibular, posterior cardinal vein grooves asymmetric, ossified transscapular ligament reduced, adipose dorsal fin absent, and anal fin elongate. None of these character states is unique to silurids and plotosids and all but *epaxialis* invasion are often present in other siluroids (see Appendix). Together, these character states do not constitute convincing evidence of a sister-group relationship between silurids and plotosids.

Chardon (1968) grouped the Siluridae, Helogenidae and Amblycipitidae into the relatively primitive suborder Siluroidei, defined primarily by features of the Weberian apparatus and associated elements. Chardon's classification is not explicitly phylogenetic and is based on the definition of "structural levels" in siluroid evolution. Chardon's definition of the Siluroidei is reviewed by listing the character states (Chardon, 1968; 221, 225) with the polarity of each within the Siluroidea indicated in parentheses.

1. Maxilla reduced and lacking teeth (primitive; Grande, 1987).
2. Utricular otolith [lapillus] largest otolith. (This is true of all siluriforms, except diplomystids in which either the lagenar or saccular otolith [astericus or sagitta, respectively] is largest—Arratia, 1987; Frost, 1925. Predominance of the lapillus is primitive within the Siluroidea.)
3. Separation of fifth and complex vertebrae obvious. (This is true of *Helogenes* and *Amblycephes*; in silurids the fifth and complex vertebrae are tightly attached by a posterior extension of the superficial ossification, but not fused as stated by Chardon. The silurid condition is primitive among siluroids—Grande, 1987.)
4. Neural complex [= supraneural of Fink & Fink, 1981] absent. (A neural complex is present in cypriniforms, non-siluriform characiphysans, and diplomystids—Fink & Fink, 1981. By outgroup comparisons with these taxa, its absence may be derived within the Siluroidea. This condition, though, is widespread among siluroids and its level of synapomorphy remains unclear.)
5. Third neural spine articulates with supraoccipital process. (Although this condition does not occur in diplomystids, it is present in †hypsiderions and many siluroids, and is probably the primitive condition within the Siluroidea.)
6. Sinus impar separated from "elongate medulla" by ventral processes of exoccipital. (By Chardon's own account this is true of all catfishes except those he placed in his Loricarioidei; it is unclear whether his distinction between an "elongate medulla" in his Siluroidei and the spinal column in other catfishes is accurate.)
7. Posttemporal [= supracleithrum] loosely attached to cranium. (Derived within the Siluroidea—see Appendix.)
9. Hyomandibular articulates with either pterotic and sphenotic [silurids, *Helogenes*] or sphenotic alone [*Amblycephes*]. (The former condition is present in most siluroids and considered primitive within the Siluroidei.)
(10) Extrascapular [= posttemporal sensu Lundberg, 1975] absent. (An extrascapular is present in diplomystids and †hypsiderids, and may be considered the primitive condition within the Siluroidea—Lundberg, 1975: 70. Absence of an extrascapular may be derived for the Siluroidea, but because this condition is widespread among siluroids its level of synapomorphy remains unclear.)

(11) Rudimentary rib sometimes present on fifth vertebra. (This condition occurs in at least some diplomystids and †hypsiderids, and is probably primitive for the Siluroidea—Arratia, 1987; Grande, 1987.)

Of the three derived character states identified by Chardon as shared by silurids, helogenids and amblycipitids (nos 4, 7, 10 above), none are unique to these taxa. Two of these character states—absence of a neural complex and an extrascapular—are widespread among siluroids and, in the absence of additional supporting evidence, it would be premature to identify either character state as synapomorphic for the Siluridae, Helogenidae and Amblycipitidae. Chardon’s Siluroidei is thus not well supported as a monophyletic group. The Siluridae and Helogenidae, though, share several derived character states not listed by Chardon (1968), none of which are unique to the two families; these include: reduction of the supraoccipital process, absence of a levator arcus palatini crest on the hyomandibular, anterodorsal extension of the dorsal oblique division of the hypaxialis muscle, anterior process of the pectoral-fin spine reduced, and dorsal fin reduced and posteriorly shifted (see Appendix).

I have shown that Howes’ (1985) hypothesis of non-monophyly of the Siluridae is not tenable. Howes’ study raises the question of whether the Siluridae, as a monophyletic group, are more closely related to the Malapteruridae than to other catfishes. I have identified only two derived character states that are shared by these two families—anterior extension of the epaxialis onto the skull roof and reduction of the dorsal fin. Different and apparently non-homologous skull roof modifications in the Siluridae and Malapteruridae indicate that epaxialis invasion of the skull roof has occurred independently in these two groups (see Appendix). Reduction of the dorsal fin is present in other siluroids, the relationships of which are unclear (see Appendix). It is necessary to conclude that there is insufficient evidence at present to support a hypothesis of close relationship between the Siluridae and Malapteruridae.

Howes (1985) also suggested a close relationship between some silurids and schilbeids. There is, however, insufficient evidence at present to propose a close relationship between the Siluridae and members of the Schilbeidae, although silurids share with the schilbeid genus Schilbe several derived character states, none of which are unique to the two groups; these include conditions of the third infraorbital, epaxialis muscle and skull roof; hypaxialis muscle and posterior cardinal vein grooves (see Appendix).

SUMMARY

Phylogenetic analysis offers strong evidence of silurid monophyly. A review of previous hypotheses of higher relationships between the Siluridae and other siluriforms shows that all are poorly supported and there is no known set of character state distributions supporting an alternative hypothesis.
ACKNOWLEDGEMENTS


Some of this research was done during a tour of institutions in the People’s Republic of China and Thailand. I thank the governments and peoples of these countries for permission to make collections and conduct research. I especially thank Chen Xin-Yu, Li Si-Zhong, Chen Yi-Yu, Jin Xin-Bo, Wu Han-Ling, Chen Xiang-Lin, Liu Chen-Han, Pan Jiong-Hua, Chu Xin-Luo, Cui Gui-Hua, Yang Jun-Xin, S. Monkolprasit, J. Karnasuta and P. Wongrat for their kind hospitality and permission to study materials under their care. L. Knapp of the Smithsonian Oceanographic Sorting Center provided valuable logistical help for handling collections made in the People’s Republic of China and Thailand.

This research was supported by National Science Foundation grant BSR 86-12233, the Graduate School of Duke University, the Stephen H. Tyng Foundation of Williams College, a Raney Award from the American Society of Ichthyologists and Herpetologists, and an Ernst Mayr Grant from the Museum of Comparative Zoology, Harvard University.

REFERENCES

APPENDIX

This Appendix describes silurid character states that are derived within the Siluroidea, but are more general in distribution than character states that are here inferred as synapomorphic for the Siluridae. These characters states are referred to in the Discussion and are potentially informative of higher siluroid relationships; each may be an additional silurid synapomorphy or a synapomorphy of a larger lineage inclusive of the Siluridae.
Infraorbitals. In most siluriforms the infraorbitals are reduced to tubular ossicles with few, if any, non-canal-bearing portions; this is the plesiomorphic condition in catfishes (Arratia, 1987: figs 4, 13, 22; Fink & Fink, 1981; Grande, 1987: figs 3B, 7). Most silurids possess a modified third infraorbital whereby the anterior end of this bone is laminar and from the posterior tip there extends posterovertrally a non-canal-bearing process, the extent and shape of which varies among silurid subgroups. Among other silurids I have observed a similar modification only in the schilbeid genus Schilbe and, developed to a lesser extent, some pangasids. In some silurids the fourth infraorbital also bears a prominent process; this is synapomorphic for several silurid subgroups (Bornbusch, 1988).

Hyomandibular. In most siluriforms, including diplomystids and thyspiderids, the anterodorsal portion of the lateral face of the hyomandibular bears a prominent horizontal crest for attachment of the levator arcus palatini (Arratia, 1987: fig 6B; Grande, 1987: fig 10A; Grande & Lundberg, 1988; Lundberg, 1982; Schaefer, 1987). This condition is the primitive state for the Siluroidea. In silurids a levator arcus palatini crest is absent, although the levator arcus palatini is well developed. The anteriormost fibres of the levator arcus palatini attach tendinously to the dorsal portion of the vertical crest on the hyomandibular that also serves as the site of attachment for the A2 division of the adductor mandibulare. Most of the levator arcus palatini has a subvertical attachment to the hyomandibular posterior to the A2 crest. Absence of a levator arcus palatini crest is most probably a derived condition within the Siluroidea; among examined siluroids, this condition also occurs in helogenids, hypopthalmids, some pimelodids (see also Lundberg & McDade, 1986a), ageneiosids, doradids and plotosids.

Supraoccipital process. A median supraoccipital process is present in otophyans. The silurid supraoccipital process is typically composed of a vertical lamina that articulates with the bifid third neural spine and a dorsal horizontal lamina that may be forked posteriorly to articulate with the supraneural. The supraoccipital process in silurids lacks a horizontal lamina and extends little beyond its articulation with the third neural spine. Although in diplomystids the supraoccipital process is also short (but longer than in silurids) and lacks a horizontal lamina (Arratia, 1987: figs 23, 22), thyspiderids exhibit the condition just described. Reduction of the supraoccipital process is probably a derived feature and is often associated with a posterior shift of the dorsal fin and/or absence of the dorsal-fin spines in catfishes. This combination of features occurs in silurids, trichomycterids (Baskin, 1972), helogenids, heteropneustids and clarids.

Epaxialis musculature. Extension of the epaxialis onto the skull roof is encountered in several siluriform subgroups, including diplomystids, cetopsids, some ictalurids, some plotosids, malapterurids (contrary to Howes, 1985: 61), silurids and the schilbeid genera Schilbe and Siluranodon. Although found in diplomystids, epaxialis invasion is derived among catfishes, because it does not occur in gymnophosphids and is uncommon in characiforms and cypriniforms. Absence of epaxialis extension is thus parsimoniously inferred to be primitive for siluriforms. Modifications of the dermal elements of the skull roof associated with epaxialis invasion, malapterurids and cetopsids the anterior extent of the epaxialis has evolved independently in different catfish lineages. Cranial depressions similar to those encountered in silurids, Schilbe and Siluranodon are not present in other siluriforms. In diplomystids, ictalurids with epaxialis invasion, malapterurids and cetopsids the anterior extent of the epaxialis is marked by sharp transverse crests extending from the supraoccipital process along the posterior margin of the skull roof (Arratia, 1987; Grande & Lundberg, 1988: fig 19C; Lundberg, 1970). This crest also marks the posterior extent of the jaw muscles that extend onto the skull roof in these catfishes. Similar crests are not present in silurids, Schilbe or Siluranodon. In plotosids slight extension of the epaxialis is indicated by shallow excavations of the posterior margin of the supraneural (Tilak, 1963: fig 3).

Hypaxialis musculature. In siluriforms, the hypaxialis divides anteriorly into the dorsal oblique and ventral oblique muscles (respectively obliquus superioris and obliquus inferioris of Winterbottom, 1974). Primitively, the superficial fibres of the dorsal oblique muscle attach to the fourth transverse process or overlying connective tissue, and the lateral line nerve is exposed. Silurids exhibit a derived condition whereby superficial fibres of the dorsal oblique muscle extend dorsally over the lateral line nerve as a distinct segment or series of small bundles lateral to the epaxialis (Howes, 1985: fig 2); these fibres intermesh dorsally with the underlying epaxialis. It should be noted that Howes (1985) incorrectly suggested that this condition is synapomorphic for the Siluridae, Malapteruridae and Schilbeidae. Among schilbeids dorsal extension of the dorsal oblique occurs only in Schilbe. A similar condition is also possessed by clarids, heteropneustids and helogenids. Malapterurids possess a different and phylogenetically independent modification of the dorsal oblique: it is directed antovertrally to insert on the coronoids (Howes, 1985: fig 3).

Weberian apparatus. In siluriforms, the posterior cardinal vein grooves along the complex centrum are symmetrical: the plesiomorphic condition. In silurids they are asymmetrical—the right groove is larger than the left groove; in some silurid subgroups the left groove is absent (Bornbusch, 1988). The distribution of asymmetrical cardinal grooves in catfishes is unknown, although Bridge & Haddon (1893) stated that this condition is almost always present in the group. Among catfishes examined by myself and J. Lundberg, symmetrical cardinal grooves are present in Diplomyctes (in the specimen available to us—DU F-913—the left posterior cardinal vein is visible along the complex centrum; Arratia (1987) makes no mention of asymmetrical cardinal groove development in diplomystids), some pimelodids (e.g. Brachyramdia, Pimelodella, Rhadamia), Malapterurus, Olyra, some schilbeids and the arid Aristida. Among non-silurid catfishes examined, asymmetrical cardinal grooves are encountered in Pangasius, Schilbe, ictalurids, the bagrids Mystus and Pseudolognathus, the plotosid Tandanus, Cranoglanis, and pimelodids of the “Pimelodini” (e.g. Pimelodus, Sorubim, Brachyplatystoma; Lundberg, personal communication).
Pectoral girdle. In its basic architecture, the supracleithrum of silurids is like that of most catfishes. Two divergences from the primitive condition, however, are associated with a loose attachment of the supracleithrum to the neurocranium: (1) compression of the ossified transscapular ligament is interpreted as synapomorphic for the Siluridae (see Results); (2) the relationship of the upper limb of the supracleithrum to the dorsal neurocranium. Regan (1911) stated that the upper limb of the supracleithrum is “wedged” between the pterotic and epioptic (= epioptic) in silurids. This condition is present in many siluriforms, including diplomystids and thypsidorids, in which the upper limb of the supracleithrum is tightly wedged in a vertical groove that is often deep and bounded by the pterotic, epioptic and, when present, posttemporal (Arratia, 1987: fig. 22; Howes, 1985: fig. 10; Lundberg & McDade, 1986). In silurids, contrary to Regan’s observation, the upper limb of the supracleithrum lies in what, at most, is a shallow groove and is horizontally aligned over the epioptic and sometimes the pterotic; it is loosely attached to the neurocranium by ligaments. No groove comparable to that described for other catfishes is present in silurids. Among catfishes examined, a similar condition is present in Helogenes, Amblyceps and the schilbeid Physasilo. Although the supracleithrum of silurids is loosely attached to the neurocranium, it is tightly attached to the anterior ramus of the fourth transverse process in all subgroups except Belodontichthys (Bornbusch, 1988).

Pectoral-fin spines. In many siluriforms, including diplomystids and thypsidorids, the pectoral-fin spine base bears an anterior process (sensu Hubbs & Hibbard, 1951; Grande, 1987: fig. 5B). This process lies between the dorsal and ventral processes, being separated from the latter by a deep notch, i.e. the anteroventral emargination of Hubbs & Hibbard (1951: plate 1). Because the anterior process is well developed in diplomystids and thypsidorids, this condition is plesiomorphic within the Siluroidei. In silurids, although the pectoral-fin spine is usually pungent and in some taxa heavy and robust, the anterior process is reduced or absent. Reduction of this process is a derived character state. In other siluriforms, this character state is often, but not always, associated with reduction of the pectoral-fin spines (e.g. helogenids, some schilbeids, trichomycterids).

Dorsal fin and dorsal-fin supports. In diplomystids, thypsidorids, and many other siluriforms the dorsal fin includes two well-ossified dorsal-fin spines (first spine sometimes referred to as “spinelet” and second as “defensive spine”). This condition is plesiomorphic within the Siluriformes. In silurids no element homologous to the fourth and fifth neural spines are closely apposed, bracing each other as supports of the dorsal fin (Arratia, 1987). In diplomystids, thypsidorid, and many other siluriforms the dorsal fin is shifted posteriorly. (In Helogenes, Amblyceps and the schilbeid Physasilo. Although the supracleithrum of silurids is loosely attached to the neurocranium, it is tightly attached to the anterior ramus of the fourth transverse process in all subgroups except Belodontichthys (Bornbusch, 1988).

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In most siluriforms with well-developed dorsal fins, the first dorsal proximal radial extends anteroventrally to insert on the bifid fourth neural spine. This is apparently true for thypsidorids, but not always so for diplomystids in which the ventral tip of the first dorsal proximal radial is variably positioned in a large space between the divergent halves of neural spines 4–7 (personal observation; Arratia, 1987). In silurids the dorsal fin is shifted posteriorly. (In Hemisilurus, Ceratognathus and some Kryptoporus the dorsal fin is absent, but the first, and sometimes second, pterygiophores are present.) The ventral tip of the first dorsal proximal radial lies between the divergent halves of neural spines 7, 8, or 9, or in the space between neural spines 7 and 8. By comparison with diplomystids and thypsidorids, the posterior position of the dorsal fin in silurids is inferred to be derived. The dorsal fin is posteriorly located in other catfishes, many of which also lack well-developed dorsal-fin spines and expanded anterior dorsal-fin supports (e.g. clarids, heteropneustids, helogenids, olyrids, trichomycterids, cetopsids and some pimelodids also lack well-ossified dorsal-fin spines and have reduced dorsal-fin pterygiophores).

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