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Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei): an overview

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Abstract

An overview is given of our present knowledge on taxonomy, phylogeny and biogeography of catfishes or Siluroidei, one of the worlds economically important groups of fresh and brackish water fishes. In an introductory chapter, the taxonomic position of catfishes in the ichthyological classification is discussed; their external morphology is briefly described and synapomorphies showing their monophyly are listed. In the following chapter, catfish systematics are presented. Thirty three families with 416 genera and 2,584 species are presently recognized, but these numbers are continuously changing; it is therefore obvious that the systematics of many taxa are still rather poorly known. For each family, data (if any) supporting their monophyly are given together with a short description of their external morphology. The valid genera are listed, with for each genus, the number of presently recognized species with a reference (if any) to a recent revisionary study. Contributions to the phylogenetic study of catfishes are scarce, and dealing only with a few families and with a limited number of taxa within the families. As a results only few data on catfish phylogeny are presently known. Therefore, also our knowledge on historical biogeography of catfishes is seriously limited, until more date become available on interfamilial and intergeneric relationships.

Keywords: Siluroidei, taxonomy, phylogeny, biogeography.

Taxinomie, phylogénie et biogéographie des poissons-chats (Ostariophysi, Siluroidei).

Résumé

Un aperçu général de notre connaissance sur la taxinomie, la phylogénie et la biogéographie des poissons-chats ou Siluroidei, un des groupes de poissons d'intérêt économique dans le monde est présenté. En premier lieu, la position taxinomique des poissons-chats dans la classification ichtyologique est présentée ; leur morphologie externe est brièvement décrite et les synapomorphies indiquant leur monophylie sont données. Ensuite leur systématique est présentée. Trente-trois familles, comprenant 416 genres et 2 584 espèces, sont actuellement reconnues, mais ces nombres changent continuellement, ce qui démontre que la systématique de plusieurs taxons est toujours peu connue. Pour chaque famille, des données (si elles existent) démontrant leur monophylie sont présentées, suivies d'une courte description de la morphologie externe. Les genres valides sont donnés, avec pour chaque genre le nombre d'espèces actuellement connues et une référence (si elle existe) d'une révision récente. Les contributions à l'étude de la phylogénie des poissons-chats sont rares. Celles qui existent ne traitent que d'un nombre limité de familles, comprenant un nombre restreint de taxons. Par conséquent, la phylogénie des Siluroidei est très peu connue. L'histoire biogéographique des poissons-chats souffre de ce manque de données et ne pourra être connue que lorsqu'il y aura plus de données sur les relations interfamilliales et intergénériques.

Mots-clés : Siluroidei, taxinomie, phylogénie, biogéographie.

INTRODUCTION

Catfishes are one of the economically important groups of fresh and brackish water fishes in the world: in many countries, they form a significant part of inland fisheries; several species have been introduced in fishculture; numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade.

Catfishes have a wide geographical distribution and are found in North, Central and South America, Africa, Eurasia, South-East Asia, Japan and Australasia. Except for two families (Ariidae and Plotosidae) with essentially marine species, catfishes are in general primary freshwater fishes.

I first briefly discuss the taxonomic position of catfishes in ichthyological classification. Secondly, derived characters of catfishes are given together with some general data on their external morphology. Then, all recent families are briefly documented and their genera are listed together with an indication of the most recent data on valid species number. Finally a state of the art on the phylogeny of the catfishes is discussed and a summary of our present, limited, knowledge on their zoogeography is given.

Taxonomic position of catfishes in ichthyological classification

Fink and Fink (1981) on the basis of a cladistic study considered the order Siluriformes as a monophyletic group formed by two suborders: the Siluroidei, commonly known as catfishes, and the Gymnotoidei, known as electric eels and knifefishes (previously considered as characiform derivations). In their model of phylogenetic relationships (*fig.* 1), which has subsequently been supported by other authors (*e.g.* Arratia, 1992), Siluroidei form one of the five major lineages of the Ostariophysi, a superorder of "euteleost" fishes that contains about 64% of the freshwater fishes of the world (Nelson, 1994).

In Ostariophysi, the Siluriformes are the sistergroup to the Characiformes, with which they form the Characiphysi, that together with the Cypriniformes forms the Otophysi. The Otophysi together with the Gonorynchiformes comprises the superorder Ostariophysi (*fig.* 1).

One of the most important characters common for Ostariophysi is the notable modification of the anterior four or five vertebrae (primitive in Gonorynchiformes where the first three vertebrae are specialized and associated with one or more cephalic ribs) into the so-called Weberian apparatus, a connection of alternating ligaments and small bones (Weberian ossicles) between the gas bladder and the otic capsule (*fig.* 2). A detailed description of the Weberian apparatus for different catfish families is given by Chardon (1968). It has an important role in sound perception and its development in

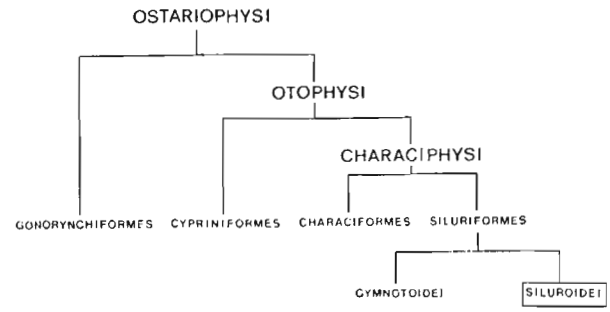

Figure 1. – Hypothesis of phylogenetic relationships of Ostariophysi according to Fink and Fink (1981).

Ostariophysi is undoubtedly related to their almost exclusive occurrence in freshwaters, where often limited visibility reduces visual perception.

Grande (1987) recommended that a new name (not specified) should be given to the group containing his Siluriformes plus Gymnotiformes, rather than including Gymnotoidei plus Siluroidei in Siluriformes. Still, according to Grande (*l.c.*) this group would have an infra series rank, leaving Siluriformes and Gymnotiformes with their more conventional usage, *i.e.* Siluriformes referring to catfishes. Although I agree with Grande (1987), I follow here the nomenclature as introduced by Fink and Fink (1981).

In the present study, only the catfishes (Siluroidei *sensu* Fink and Fink, 1981) will be discussed in detail. The other suborder of Siluriformes, Gymnotoidei, with six families (Sternopygidae; Rhamphichthyidae; Hypopomidae; Apteronotidae; Gymnotidae and Electrophoridae) including some 60 species, has no importance in aquaculture at present.

External morphology of catfishes

A great variation exists in the external morphology of catfishes and it is difficult to give a standard definition of their external appearance. In general the body is naked although in some families (*e.g.* Callichthyidae; Loricariidae) it is covered with bony plates. Up to four pairs of circumoral barbels may be present: one nasal pair, one (or two) maxillary pair(s) and two mandibular or mental pairs; in many families one or more pairs are missing. The barbels are provided with numerous taste-buds and are used in detecting food. The mouth is in general non-protractile. The eyes are usually small. The dorsal and pectoral fins are often provided with a leading spine or a leading soft ray. An adipose fin is often present and in some families it has a spine. The pelvic fin is medially placed and has an abdominal position. Important variations are also noted in size, ranging from a few millimeters (*e.g.* some Scoloplacidae) and a few centimeters (*e.g.* some Helogenidae) up to several meters (*e.g.* some Ictaluridae and some Pimelodidae).

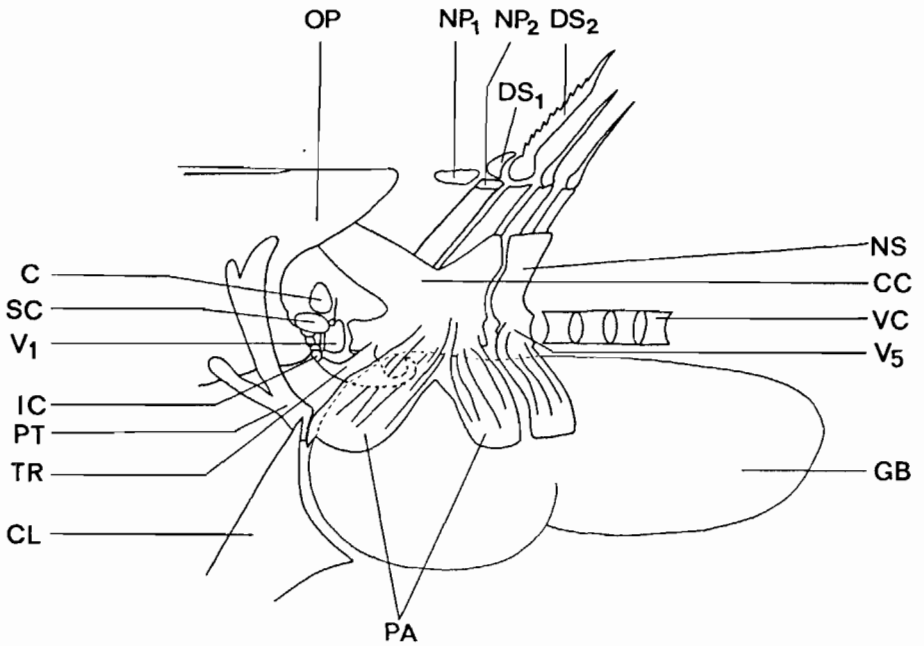

Figure 2. – Schematic illustration of a lateral view of the Weberian apparatus and its connecting structures in primitive catfishes (modified after Chardon, 1968). **C** Claustrum; **CC** Complex centrum; **CL** Cleithrum; **DS** Dorsal spine; **GB** Gas bladder; **IC** Intercalare; **NS** Neural spine; **NP** Nuchal plate; **OP** Supraoccipital process; **PT** Posttemporal; **PA** Modified parapophysis; **Sc** Scaphium; **TR** Tripus; **VC** Vertebral column; V_1 First vertebra; V_5 Fifth vertebral centrum.

Monophyly of catfishes

A phylogenetic analysis by Fink and Fink (1981) led to the recognition of catfishes (Siluroidei) as a monophyletic assemblage on the basis of numerous synapomorphies. Only a few are listed here: there are no separate ossifications of the parietals; the subopercle is absent; the neural arches of the third and fourth vertebrae are fused together and to the complex centrum; the centra of the second, third and fourth vertebrae (or more in primitive catfishes) form the complex Weberian vertebra; the parapophysis of the second centrum is present; the transverse process of the fourth vertebra is expanded in a horizontal plane and the ovoid anterior face articulates with the suspensorium of the pectoral fin; the os suspensorium has no posteromedial process; the supracleithrum, the ossified Baudelot's ligament and perhaps also the posttemporal form a single ossified element; dorsal and pectoral spines are present and can be locked into an erect position due to modifications in dorsal and pectoral fin structures unique to catfishes; the body is naked.

Arratia (1992), on the basis of a study of the suspensorium of primitive catfishes, confirmed the phylogenetic relationships as described by Fink and Fink (1981) and added several other synapomorphies for Siluroidei: the posterior part of the palatoquadrate is fused with the hyoid arch; the palatoquadrate is separated into a pars autopalatina and a pars pterygoquadrate; the pterygoquadrate is fused with the hyo-symplectic cartilage; the articulation between the autopalatine and vomer is placed at the midlength of the autopalatine; the articulation between the autopalatine and the lateral ethmoid is placed near the midlength of the autopalatine (in primitive catfishes); two large articular facets on the maxilla articulate with the anterior cartilage of the autopalatine (in primitive catfishes); a small entopterygoid is present; the metapterygoid is the main support of the eye; the metapterygoid is anterodorsal to the quadrate and forms part of the ventrolateral border of the suspensorium; the posterior margin of the metapterygoid is sutured and synchondrally articulates with the hyomandibula and the quadrate (in primitive catfishes); the quadrate and the hyomandibula are sutured with the preopercle; a symplectic is absent; the proximal part of the interhyal does not articulate with the dorsal part of the hyoid arch and a ligament joins the posterior ceratohyal and the hyomandibular; the retroarticular is fused to the articular; a well-developed coronoid process of the Meckelian cartilage is present.

CATFISH SYSTEMATICS

Nelson (1984) listed 31 families containing about 400 genera and 2,211 species of catfishes. However, the systematics of many taxa are still rather poorly known at the taxonomic levels. New species, new genera and even new families are still being described and various phylogenies of family intra- and interrelationships have been proposed. Nelson

(1994) reported 34 families with about 412 genera and about 2,405 species. The present account, based on most recent literature data, recognises 33 families with 416 genera and 2,584 species.

For each family, data (if any) supporting their monophyly are given, followed by a short description of their external morphology. The valid genera are listed, with for each genus, the number of presently recognized species. When a recent revisionary study of the genus is available, a reference is given.

Family DIPLOMYSTIDAE (*fig. 3a*)

This family is generally considered morphologically and phylogenetically the most primitive in the suborder Siluroidei. Arratia (1987, 1992) listed ten autapomorphies characterizing this family; one of them is the presence of more than one row of functional teeth along most of the ventral margin of the maxilla. In all other recent Siluroidei, the maxilla is edentate, and has no role in feeding; it is reduced and merely serves as a supporting bone for the maxillary barbel. Interestingly in diplomystid catfishes only the maxillary barbels are present while the skin of the whole body is covered with large papillae and buds. The dorsal fin has a strong spine. A relatively long adipose fin is present. The pectoral fin is provided with a strong spine.

Two genera are known: *Diplomystes* Duméril with three valid species and the monospecific *Olivaichthys* Arratia.

Diplomystids are benthic freshwater catfishes restricted to rivers and lakes in southern South America. Although previously widely distributed in central and southern Chile, and from San Juan to Patagonia in Argentina, they are at present becoming rare due to their intolerance to environmental changes (Arratia, 1983, 1987). They had some economic importance as food fish (maximum length about 30 cm) but are not used in aquaculture.

Family ICTALURIDAE (*fig. 3b*)

Grande and Lundberg (1988) and Lundberg (1992) considered modern ictalurid catfises (often referred to as Ameiuridae) to be a monophyletic group based mainly on the position of jaw muscles on the skull roof and on the presence of a subpterotic process on the supracleithrum.

Ictalurids have a moderately elongated body. Four pairs of barbels are present. The vomer is edentulous. Strong dorsal (except in *Prietella*) and pectoral spines are present; the latter has a poison gland at its base in some species of *Noturus*. An adipose fin is present.

Seven living genera are recognized: *Ictalurus* Rafinesque (9 species – Lundberg, 1982), *Ameiurus Rafinesque* (7 species – Lundberg, 1992), *Noturus* Rafinesque (25 species – Grady and Legrande, 1992), *Pylodictis* Rafinesque (1 species), *Trogloglanis* Eigenmann (1 species), *Satan* Hubbs (1 species) and *Prietella* Carranza (1 species). The species of the latter three genera are blind and cavernicolous.

Ictalurid catfishes are present in North and Central American freshwaters from southern Canada to Guatemala and Mexico. In view of their economic importance in aquaculture some of the larger species of *Ictalurus* (maximum length of about 1.5 m) have been introduced in temperate zones in South America, Europe and Australia. Several *Noturus* species are presently considered as endangered (Shute *et al.*, 1991; Wenke *et al.*, 1992).

Family BAGRIDAE (*fig. 3c*)

Mo (1991) recently rediagnosed bagrid catfishes on the basis of six synapomorphies including the presence of a unique, well-developed muscle, *retractor posttemporalis*, stretching between the cranium and the posttemporal; a long, ventrally turned Müllerian process; the presence of a prominent posterior process of the posttemporal; a thickened dorsomedian limb of the posttemporal, bearing a prominent posterior surface on which a thick layer of the epaxial muscle attaches; a large, crescentic vomerine head; and a well-developed posttemporal fossa with a posterolateral opening.

Morphologically bagrid catfishes are recognized by a moderately elongated body which is compressed posteriorly. They have four pairs of barbels (2 pairs in *Rita*), a strong dorsal spine, an adipose fin and strong pectoral spines.

As a result of the phylogenetic study of Mo (1991) the Bagridae presently contains only two subfamilies, Bagrinae and Ritinae. The subfamily Bagrinae is diagnosed by a slender ventral extension of the Müllerian process, the possession of a prominent posterior process of the pelvic girdle and by a "distinct" gap between anal and genital pores (Mo, 1991). It has 13 genera: *Bagrus* Bosc (10 species); *Aorichthys* Wu (2 species); *Mystus* Scopoli (with *Heterobagrus* Bleeker as its junior synonym and including 23 species); *Hemibagrus* Bleeker (15 species); *Neotropius* Kulkarni (previously placed in Schilbeidae and including 4 species); *Olyra* McClelland (type genus of Olyridae, synonymised with Bagridae by Mo, 1991 and including 4 species); *Pseudobagrus* Bleeker (with *Coreobagrus* Mori as its junior synonym and including 29 species); *Pelteobagrus* Bleeker (13 species); *Bagrichthys* Bleeker (4 species); *Bagroides* Bleeker (1 species); *Leiocassis* Bleeker (8 species): *Pseudomystus* Jayaram (13 species) and *Batasio* Blyth (with *Chandramara* Jayaram as its junior synonym and including 4 species). The subfamily Ritinae is defined by 7 or 8 ventral fin rays, the absence of a mesocoracoid loop, the presence of the *retractor tentaculi* muscle, the last two dorsal fin rays articulating with the last radial and the dorsal fin with only five proximal radials (Mo, 1991). It has 2 genera: *Rita* Bleeker (4 species) and *Nanobagrus* Mo which is monospecific. Data on species numbers

are from Mo (1991) but are doubted by De Pinna and Ferraris (1992).

All other genera previously assigned to the Bagridae have been placed in two new families Claroteidae and Austroglanididae except for *Horabagrus* which is transferred to the Schilbeidae (Mo, 1991). Mo's study (1991), in particular his analysis of siluroid phylogeny, has seriously been critised (*cf. infra*). I do, however, consider his rearrangement of the bagrids as a valuable contribution which is, moreover, supported zoogeographically: in an area cladogram, the only African element (*Bagrus*) appears as the derived sister group of all the others.

Bagrids are freshwater catfishes. As a result of the complete rearrangement of the family by Mo (1991) only one bagrid genus, *Bagrus* occurs in Africa, where it is endemic. All other bagrid genera are found in Central and South-East Asia.

Some bagrids attain an edible size (*e.g. Bagrus* with maximum length of 720 mm). They are important food fishes; others (*e.g. Mystus*) have been introduced in aquaculture in South-East Asia.

Family CLAROTEIDAE (*fig. 3d, e, f*)

Mo (1991) diagnosed this new family on 8 derived features including the presence of a prominent anterolateral laminar sheath of the palatine. All the genera included were previously placed in the Bagridae.

An important variation exists in the external morphology of genera and species of Claroteidae. The body is moderateley elongated. There are usually four pairs of barbels (three in *Auchenoglanis*). The dorsal fin is provided with a strong spine. The adipose fin is present. The pectoral fin has a strong leading spine. An intraspecific variation is found in many *Chrysichthys* species where the head in mature specimens becomes broadly enlarged, particularly in males (Risch, 1992*a*).

Following Mo (1991), this family contains 13 genera all endemic to Africa and assigned to two subfamilies. The first is that of the Claroteinae. Mo (1991) diagnosed it by seven derived features including the presence of an accessory toothplate on the palate. The subfamily includes the following genera: *Clarotes* Kner (with its junior synonyms *Gnathobagrus* Nichols and Griscom and *Pardiglanis* Poll, Lanza and Sassi and including 4 species – Mo, 1991), *Chrysichthys* Bleeker (18 species – Mo, 1991; Risch, 1988; 1992*b*); *Gephyroglanis* Boulenger (7 species – Mo, 1991; Risch, 1992b), *Bathybagrus* Bailey and Stewart (6 species – Mo, 1991), *Lophiobagrus* Poll (4 species – Mo, 1991), *Phyllonemus* (3 species – Mo, 1991) and *Amarginops* Nichols and Griscom (with its junior synonym *Rheoglanis* Poll and including 17 species – Mo, 1991).

The second subfamily is that of the Auchenoglanidinae. Fifteen derived features were given by Mo (1991) to diagnose this subfamily, including the position of the anterior nostrils on the anteroventral side of the upper lip, the rounded caudal fin; the distinct body coloration and the position of the mandibulary barbels at the outer margin of the lower jaw bones. It includes *Auchenoglanis* Günther (2 species – Teugels *et al.*, 1991), *Parauchenoglanis* (19 species – Teugels *et al.*, 1991), *Anaspidoglanis* Teugels *et al.* (3 species – Teugels *et al.*, 1991), *Platyglanis* Daget (2 species – Mo, 1991), *Notoglanidium* Günther (1 species) and *Liauchenoglanis* Boulenger (2 species – Mo, 1991).

Claroteid catfishes are confined to freshwater fishes although some species are also found in estuaries and lagoons. Some species attain an edible size and are important food fish. *Chrysichthys nigrodigitatus* has been introduced in aquaculture in West Africa.

Family AUSTROGLANIDIDAE (*fig. 3g*)

Mo (1991) recently described this family for the African genus *Austroglanis* Skelton *et al.* (1984) previously placed in the Bagridae. The family is closely related to the Bagridae and the Claroteidae. The monophyly of this family is based on ten synapomorphies including the presence of a thin laminar flange along the posterior margin of the maxillary and the presence of an elevated coronoid process on the strongly developed mandibular (Mo, 1991).

Morphologically, the family is recognized amongst others by the presence of three pairs of simple barbels, the nasal pair being absent. Strong dorsal and pectoral spines are present. The adipose fin is relatively small and has a posterior position. Some rheophilic adaptations are noted on the body.

Austroglanididae are freshwater catfishes known only from the Orange and Olifants river systems in southern Africa. One genus, *Austroglanis* Skelton, Risch and De Vos (3 species) is assigned to this family. The maximum length reported is about 250 mm. All the austroglanidids are threatened (Skelton, 1990).

Family CRANOGLANIDIDAE (*fig. 3h*)

No derived features have been reported for this family so far and its phylogenetic status therefore is not clear. Many characters are shared in common with Bagridae and Pangasiidae.

Externally cranoglanidid catfishes are characterised by the large eyes in a somewhat inferior position, by four pairs of barbels, strong dorsal and pectoral spine, a high number of anal fin rays (35-41) and a small posteriorly placed adipose fin.

The family has one genus, *Cranoglanis* Peters which is monospecific and only known from freshwaters in the Yunnan province in China. The maximum total length reported is 295 mm (Jayaram, 1955).

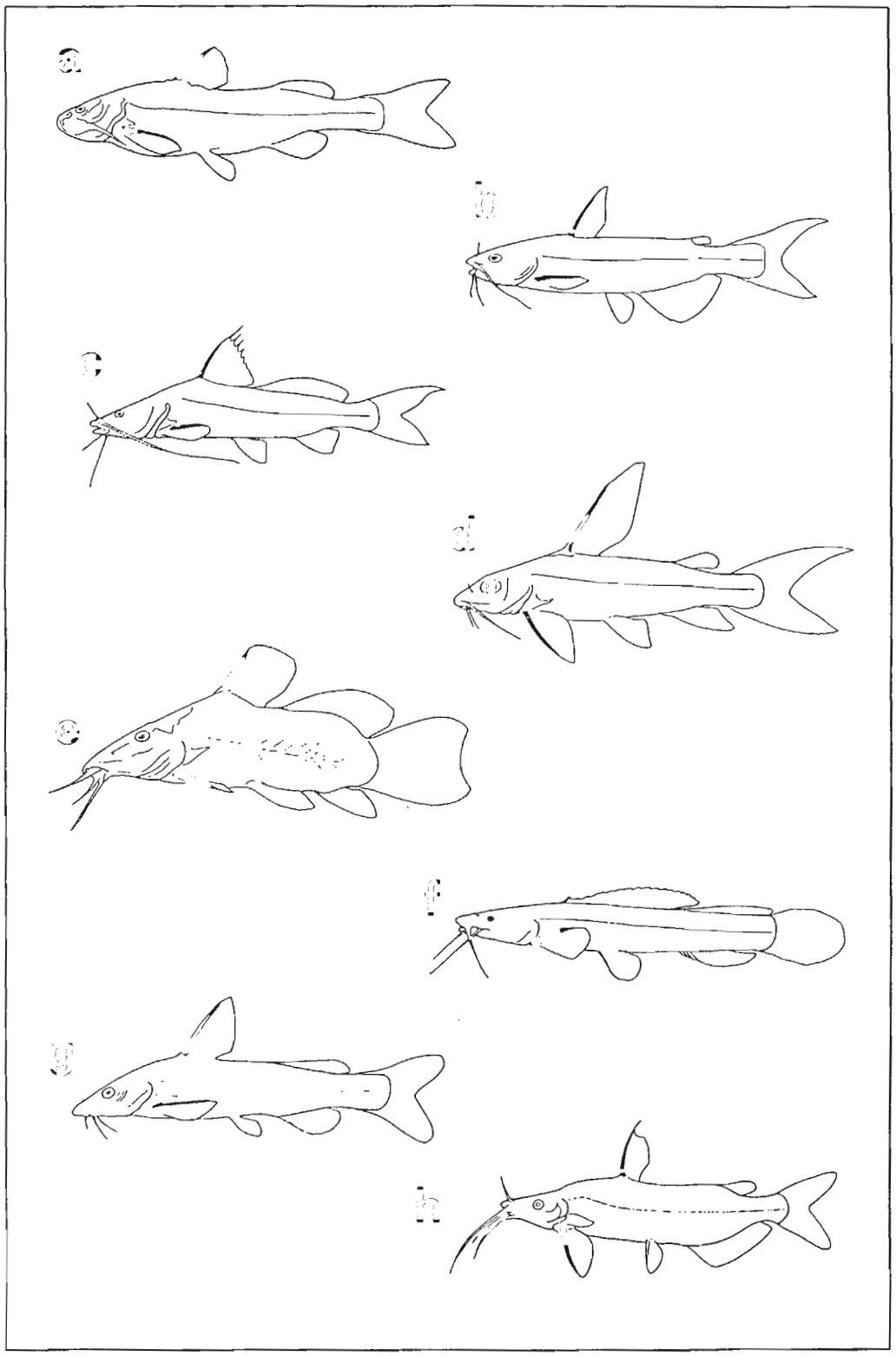

Figure 3. – Outline drawings of representatives of catfish families. a. *Diplomystes chilensis* (Diplomystidae); b. *Ictalurus punctatus* (Ictaluridae); c. *Bagrus docmak* (Bagridae); d. *Chrysichthys nigrodigitatus* (Claroteidae); e. *Auchenoglanis occidentalis* (Claroteidae); f. *Notoglanidium thomasi* (Claroteidae); g. *Austroglanis sclateri* (Austroglanididae); h. *Cranoglanis sinensis* (Cranoglanididae).

Family SILURIDAE (*fig.* 4*a, b*)

Bornbusch (1991) published on the monophyly of the Siluridae: the family is diagnosed on five synapomorphies, including the reduced autopalatine; the contact of lateral ethmoid and sphenotic by narrow extensions, lateral to the frontal; the ossified transscapular ligament, anteroposteriorly compressed; the absence of, the distal radials of the dorsal fin pterygiophores; and the posterodorsally shifted articulations of the anal fin rays with their pterygiophores.

Howes and Fumihito (1991) added three other synapomorphies involving frontal sensory canals, the hyomandibular crest and the *extensor tentaculi* muscle.

The external morphology of this family is rather distinct from that found in other catfishes: the head and the body are compressed; the nasal barbels are always absent; one, and in some genera two pairs of mandibular barbels are present; the dorsal spine is flexible and in some genera the dorsal fin is absent; the pectoral spines are usually weak; the anal fin is very long with numerous rays (41-112); an adipose fin is absent.

Nine extant genera of Siluridae are known: *Belodontichthys* Bleeker (1 species), *Ceratoglanis* Myers (1 species), *Hemisilurus* Bleeker (3 species – Bornbusch and Lundberg, 1989), *Hito* Herre (1 species), *Kryptopterus* Bleeker (15 species), *Ompok* Lacépède (14 species), *Silurichthys* Bleeker (4 species), *Silurus* Linnaeus (18 species), *Wallago* Bleeker (3 species – Roberts, 1982*a*).

Siluridae are Eurasian freshwater catfishes. Only the genus *Silurus* occurs in Europe; all other genera are confined to Central and South-East Asia. *Silurus glanis* is the most studied species in the family. It is an important food fish. Its maximum total length reported is more than 5 m but its average size is about 1.5 m.

Family SCHILBEIDAE (*fig.* 4*c*)

Most authors agree that this family is a non-monophyletic assemblage. Mo (1991) suggests the existence of three major groups, one representing the real schilbeids, another phylogenetically distinct and closer to Clariidae and Heteropneustidae and a third closer to Bagridae or Pangasiidae. A detailed phylogenetic study is absolutely necessary.

Morphologically schilbeid catfishes are recognized by a laterally compressed body; two to four pairs of barbels on the snout; a short dorsal fin is present or absent; when present, it is provided with a strong spine; an adipose fin is present or absent. The anal fin is very long, with numerous fin rays. The pectoral fin has a strong spine.

Schilbeids are pelagic catfishes found in freshwaters of Africa and southern Asia. In Africa, De Vos (1995) recognized five genera with 34 species: *Schilbe* Oken (22 species), *Parailia* Boulenger (5 species), *Siluranodon* Bleeker (1 species), *Irvinea* Trewavas (2 species) and *Pareutropius* Regan (4 species).

In southern Asia, especially in the Indian subcontinent, eight genera are presently known: *Ailia* Gray (1 species), *Ailiichthys* Day (1 species), *Clupisoma* Swainson (5 species), *Eutropiichthys* Bleeker (3 species), *Horabagrus* Jayaram (1 species – transferred to Schilbeidae by Mo, 1991), *Platytropius* Hora (1 species), *Proeutropiichthys* Hora (1 species), *Pseudeutropius* Bleeker (4 species). The genus *Neotropius* Kulkarni formerly assigned to the Schilbeidae was transferred to the Bagridae by Mo (1991).

Some schilbeids are important food fishes (*e.g. Schilbe* with a maximum total length of 590 mm in some species).

Family PANGASIIDAE (*fig.* 4*d*)

A phylogenetic study of this family is lacking but most authors consider it as closely related to Schilbeidae.

Morphologically, pangasiid catfishes are recognized by a laterally compressed body, the presence of two pairs of barbels (maxillary and one pair of mandibular), the invariable presence of an adipose fin, the relatively long anal fin and the short dorsal fin with one or two spines. An elastic spring apparatus (*cf.* Malapteruridae) is present.

In a recent systematic revision Roberts and Vidthayanon (1991) recognized only two genera with 21 species: *Pangasius* Valenciennes (19 species) and *Helicophagus* Bleeker (2 species).

Pangasiids are pelagic catfishes generally occurring in freshwaters in southern Asia from Pakistan to Indonesia. One *Pangasius* species is found in brackish tidal waters and two occur even in the sea (Roberts and Vidthayanon, 1991). Some *Pangasius* species attain important sizes up to 3 m standard length. Some are of great economic importance in fisheries and fishculture.

Family AMBLYCIPITIDAE (*fig.* 4*e*)

Mo (1991) hypothetically considered the Amblycipitidae as a monophyletic group on the basis of a uniquely derived feature, namely the presence of a laminar process on the dorsal surface of the fourth parapophysis. The phylogenetic position of the family, however, is not known.

Morphologically this family is characterized by a small-sized, robust body, a depressed head, four pairs of barbels, short dorsal and pectoral spines which are smooth and covered with thick skin and the presence of an adipose fin which is more or less confluent with the caudal fin.

Amblycipitids are freshwater catfishes known from southern Asia, from India to southern Japan. Two genera are known, *Amblyceps* Blyth (2 species) and *Liobagrus* Hilgendorf (11 species). They are not used in aquaculture.

Family AKYSIDAE (*fig. 4f*)

This family forms a monophyletic lineage on the basis of a number of derived features such as the distinct dorsal spine, showing a deep lateral groove. As these characters are also present in the recently described Parakysidae (Roberts, 1989), Mo (1991) synonymised the latter with the Akysidae.

Morphologically akysid catfishes are recognized by the presence of four pairs of barbels, strong dorsal and pectoral spines, a long adipose fin (absent or represented by a ridge in *Parakysis*). The head, body and fins are covered with unculiferous plaques, with some of those situated on the body greatly enlarged and arranged in longitudinal rows.

These small-sized (up to 10 cm) stream catfishes are arranged in four genera, known from freshwaters in southern Asia: *Acrochordonichthys* Bleeker (exact number of species unknown – 4 species recognized as valid by Weber and de Beaufort, 1913), *Akysis* Bleeker (10 species), *Breitensteinia* Steindachner (1 species) and *Parakysis* Herre (2 species – Roberts, 1989).

Family SISORIDAE (*fig. 4g*)

The monophyly of this family has not yet been demonstrated and the genera and species are in urgent need of revision.

Morphologically sisorid catfishes are recognized by the more or less thickened leathery skin with unculiferous tubercles or plaques (see Roberts, 1982*b*); four pairs of barbels are present; the dorsal fin is small and a spine is sometimes present; the adipose fin is present and in one genus, *Sisor*, consists of a spine. In some genera, in particular those inhabiting fast flowing mountain streams, the mouth is developed into a sucker and the belly has special adhesive modifications.

These bottom-dwelling catfishes, with adults ranging in size from 20 mm to 2 m, are mainly known from freshwaters in particular mountain rapids but also large rivers in southern and eastern Asia. One genus, *Glyptothorax*, is also known from the Tigris-Euphrates basin in Turkey, Syria, Iraq and Iran and from the Black Sea drainage of Turkey (Coad and Delmastro, 1985). 20 genera with 97 species are presently recognized: *Bagarius* Bleeker (3 species – Roberts, 1983), *Conta* Hora (2 species), *Erethistes* Müller and Troschel (2 species), *Erethistoides* Hora (1 species), *Euchiloglanis* Regan (8 species – with *Coraglanis* Hora and Silas as its junior synonym), *Exostoma* Blyth (5 species), *Gagata* Bleeker (5 species), *Glaridoglanis* Norman (1 species), *Glyptosternon* McClelland (7 species), *Glyptothorax* Blyth (with *Laguvia* Hora as its junior synonym – 42 species in need of revision), *Hara* Blyth (4 species), *Myersglanis* Hora and Silas (1 species), *Nangra* Day (4 species), *Oreoglanis* Smith (2 species), *Pareuchiloglanis* Pellegrin (4 species), *Pseudecheneis* Blyth (2 species), *Pseudexostoma* Chu (1 species), *Pseudolaguvia* Misra (1 species), *Sisor* Hamilton (1 species) and *Sundagagata* Boeseman (1 species).

Data on the introduction of Sisoridae in aquaculture could not be found.

Family AMPHILIIDAE (*fig. 4h, i*)

The monophyletic condition of this family has not yet been demonstrated.

In their external morphology, amphiliid catfishes are somewhat similar to some genera of Akysidae and Sisoridae. They have three pairs of barbels, the nasal pair is absent; spines in the dorsal and pectoral fins are absent (except in some *Leptoglanis*, *Trachyglanis* and *Zaireichthys*); an adipose fin is present (in *Trachyglanis* it is preceded by a spine). In some rheophilic genera pectoral and pelvic fins are greatly enlarged. Some genera also have series of imbricate bony scutes on the body.

Amphiliids are small freshwater catfishes (maximal total length 195 mm but usually much smaller) endemic to tropical Africa. Nine genera are known (Bailey and Stewart, 1984; Skelton and Teugels, 1986): *Amphilius* Günther (22 species), *Andersonia* Boulenger (1 species), *Belonoglanis* Boulenger (2 species), *Doumea* Sauvage (5 species), *Leptoglanis* Boulenger (9 species), *Paramphilius* Pellegrin (4 species), *Phractura* (12 species) and *Trachyglanis* Boulenger (4 species) and *Zaireichthys* Roberts (1 species). Amphiliidae are of no interest to aquaculture.

Family CLARIIDAE (*fig. 5a, b, c*)

The monophyletic nature of this family has not yet been demonstrated. A phylogenetic analysis is one of my projects.

The external morphology of clariid catfishes is characterized by an elongated body with long dorsal (always without a spine) and anal fins; an adipose fin, supported by elongated neural spines (Teugels, 1983) is present in some genera (*e.g. Heterobranchus*). The pectoral fin has a strong spine. They have four pairs of barbels. In the extremely elongated genera (*e.g. Gymnallabes*) the paired fins are reduced or absent and the dorsal and anal fins are confluent with the caudal fin.

Clariids have a suprabranchial organ (reduced or virtually absent in some genera), formed by arborescent structures originating from the second and fourth epibranchials, that enable them to utilize atmospheric air. Members of some genera are therefore able to leave the water and to walk on land for several hundred meters using their pectoral spines and making sinuous movements with their body.

This freshwater family is present in Africa extending to Syria and southern Turkey and South-East Asia. Fourteen genera are presently recognized of which only *Clarias* is in common to both continents. Teugels

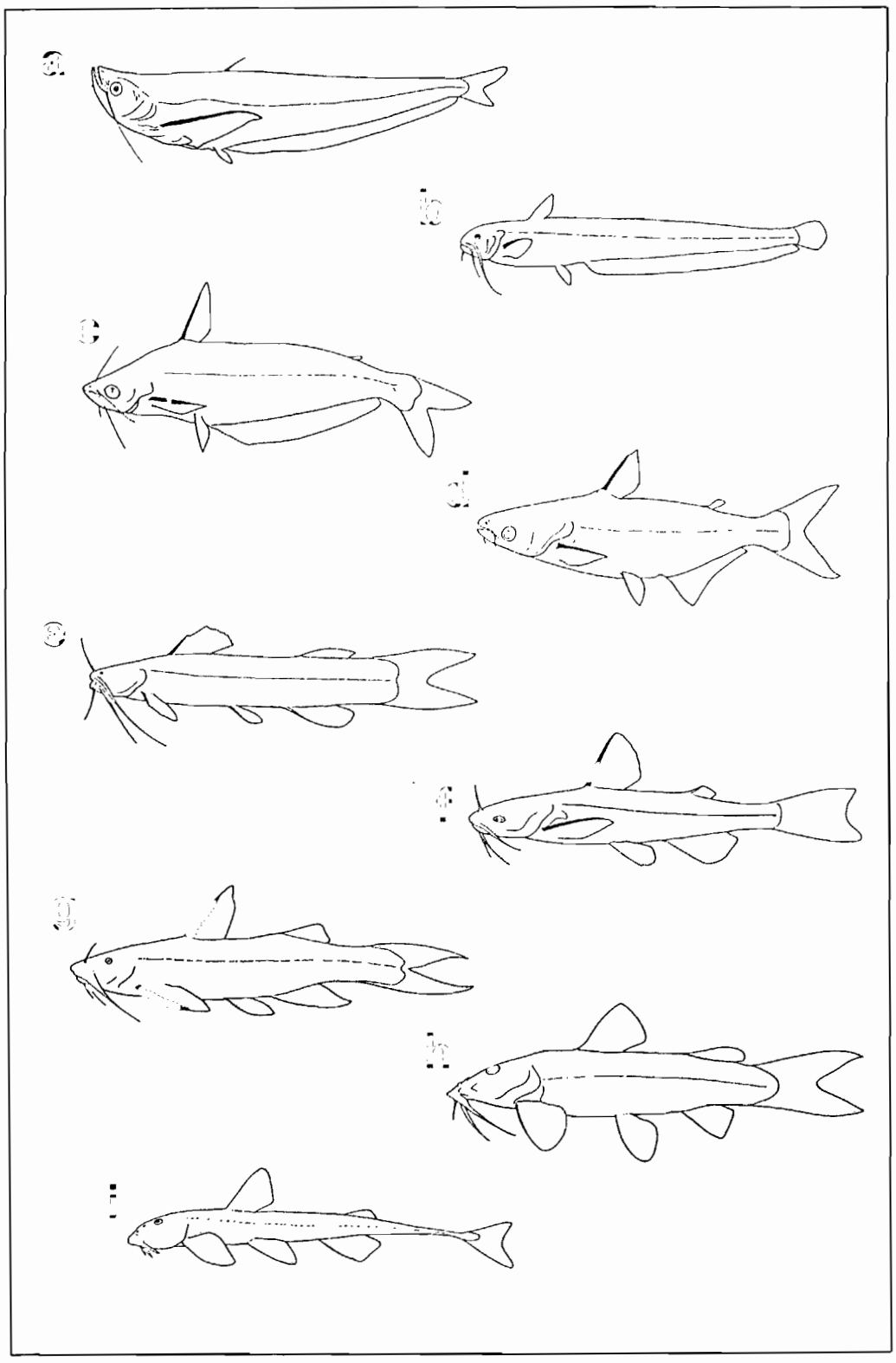

Figure 4. – Outline drawings of representatives of catfish families. a. *Belodontichthys dinema* (Siluridae); b. *Silurus glanis* (Siluridae); c. *Schilbe mandibularis* (Schilbeidae); d. *Pangasius gigas* (Pangasiidae); e. *Amblyceps mangois* (Amblycipitidae); f. *Akysis leucorynchus* (Akysidae); g. *Glyptosternon mainanensis* (Sisoridae); h. *Amphilius kakrimensis* (Amphiliidae); i. *Phractura clauseni* (Amphiliidae).

(1986*a*) listed 12 African genera with 74 species: *Channallabes* Günther (1 species), *Clariallabes* Boulenger (15 species), *Clarias* Scopoli (32 species, including a cave dwelling species – Teugels, 1986*b*), *Dinotopterus* Boulenger (with *Bathyclarias* Jackson as its junior synonym – 13 species), *Dolichallabes* Poll (1 species), *Gymnallabes* Günther (3 species), *Heterobranchus* Geoffroy Saint-Hilaire (4 species – Teugels *et al.*, 1990), *Platyallabes* Poll (1 species), *Platyclarias* Poll (1 species), *Tanganikallabes* Poll (1 species), *Uegitglanis* Gianferrari (1 cave dwelling species) and *Xenoclarias* Greenwood (1 species). The Asian clariid genera are: *Clarias* Scopoli (about 12 species – Teugels, in preparation), *Encheloclarias* Herre and Myers (5 species – Ng and Lim, 1993) and *Horaglanis* Menon (1 species).

The Asian *Clarias batrachus* and *C. macrocephalus* and the African *C. gariepinus* are the most studied species in this family and are of great importance in fisheries and fishculture. Recently the African *Heterobranchus longifilis* has successfully been introduced in aquaculture; under identical conditions its growth rate doubles that of *C. gariepinus* (Legendre *et al.*, 1992).

Family HETEROPNEUSTIDAE (*fig.* 5*d*)

Heteropneustid catfishes appear closely related to clariids in their morphology; the monophyly of this family has not yet been demonstrated.

This family, often referred to as Saccobranchidae, is recognized by an elongated body, four pairs of barbels, a short spineless dorsal fin, a very long anal fin which may be confluent with the caudal fin and a pectoral spine connected with a venomous gland. An air sac is present behind the gills. It serves as a lung enabling the fish to practice aerial respiration.

This family is found in freshwaters in southern Asia from Pakistan to Thailand. One genus *Heteropneustes* Müller including two species is known. The average total length is about 200 mm, although larger specimens (300 mm) have been reported. *Heteropneustes fossilis* has been introduced in aquaculture in India.

Family CHACIDAE (*fig.* 5*e*)

Several characters are unique for the Chacidae, including the branched anterior ray of the pelvic fin; the palatine with a lateral flexure posteriorly; the two obliquely orientated arms of the palatine joined together along their lateral surfaces with a bony lamina ventrally; the paired orbitosphenoid not meeting along the ventral midline; the mesethmoid with two large anterolaterally expanded cornua; the first three basibranchial elements greatly reduced in size; and the premaxilla with a posteromedially directed process (Brown and Ferraris, 1988). The affinities of Chacidae within the catfishes are poorly known.

Externally chacid catfishes are characterized by a long, broad and flattened head, a posteriorly compressed body, three pairs of barbels (a minute nasal barbel may be present), numerous cutaneous flaps or cirri on head and body, a small dorsal fin preceded by a spine and a pectoral fin also provided with a spine. Their vernacular name is angler catfish because of their luring or angling behaviour: the maxillary barbels are moved in such a way that they suggest the contortions of a small worm to attract small fishes.

Roberts (1982*c*) revised this South and South-East Asian (from the Ganges in India to Borneo) freshwater catfish family and recognized a single genus *Chaca* Gray with two species. Brown and Ferraris (1988) described a third species. Roberts (1982*c*) reported a maximum standard length of 238 mm.

Family MALAPTERURIDAE (*fig.* 5*f*)

Of all currently recognized families of Siluroidei, only the species of the Malapteruridae possess an electric organ. Howes (1985) in a study on the phylogenetic relationships of this family, concluded that despite its obvious specializations including the electrogenic organ, it is basically a plesiomorphic group and its relationships lie with some taxa belonging to the Old-World Siluridae.

Morphologically malapterurid catfishes are characterized by a more or less elongated cylindrical body; there are three pairs of barbels (nasal pair absent); the dorsal fin is lacking but an adipose fin is present; the pectoral fin is spineless. The electric organ, of muscular origin (see Howes, 1985) produces violent electric discharges (up to 450 Volts). Malapterurids possess an elastic spring apparatus, consisting of the anterior ramus of the fourth parapophysis with the expanded tip attached to the swimbladder. The sudden relaxation of the muscles, extending from the apparatus to the cranium, causes the parapophyses to vibrate the swimbladder; these vibrations produce a loud sound (Howes, 1985; Curran, 1989).

The electric catfishes are endemic to freshwaters in tropical Africa. One genus, *Malapterurus* Lacépède, and three species are presently recognized. The maximum total length is about 1.5 m (Daget and Durand, 1981).

Family ARIIDAE (*fig.* 5*g*)

According to Mo (1991) Ariidae (excluding the Madagascar genus *Ancharius* transferred to Mochokidae) is considered a monophyletic taxon on the basis of two uniquely derived features: a greatly enlarged utricular otolith occupying a space formed by the prootic, pterotic and exoccipital bones and an extensive superficial ossification on the ventral side of the complex centrum.

Morphologically, ariid catfishes are recognized by a robust body which is posteriorly compressed. There

are three pairs of barbels, the nasal pair being absent. Dorsal and pectoral fins with a strong spine. An adipose fin is present. The caudal fin is forked. In some species the latter is connected with a venomous gland. An elastic spring apparatus (*cf.* above) is present. Almost all species produce relatively small numbers of large eggs that are carried through hatching in the male's mouth.

Most ariids are marine catfishes; some, however, are confined to freshwaters. Ariidae are found worldwide in tropical and subtropical regions. In some areas, particularly in the Far East, they form an important part of commercial catches. Some taxa are used in aquaculture.

The systematics of genera and species of Ariidae are poorly known and in need of revision. The following genera are presently recognized. *Ariopsis* Gill (1 species), *Arius* Valenciennes (121 species), *Bagre* Linnaeus (5 species), *Batrachocephalus* Bleeker (1 species), *Doiichthys* Weber (1 species), *Galeichthys* Valenciennes (1 species), *Genidens* Castelnau (1 species), *Hemipimelodus* Bleeker (12 species), *Ketengus* Bleeker (1 species), *Nedystoma* Ogilby (1 species), *Netuma* Bleeker (1 species), *Osteogeneiosus* Bleeker (1 species), *Paradiplomystes* Bleeker (1 species), *Tetranesodon* Weber (1 species).

Family PLOTOSIDAE (*fig.* 5*h*)

No data on the monophyletic condition and the phylogeny of this family have been published.

Plotosid catfishes are morphologically characterized by an elongated body with a pointed tail. Four pairs of barbels are present. There are two dorsal fins; the anterior has a strong spine, the posterior is very long and confluent with the caudal. The latter is also confluent with the anal fin. The pectoral fins have a spine. Some marine species possess an arborescent organ between the anus and the anal fin; it is highly vascularized and probably has a salt-secreting function.

Plotosids are found in the western Pacific and the Indian Ocean from the east coast of Africa to Australia. About half of the species are confined to freshwater and occur in Australia and New Guinea.

Nine genera with 32 species are presently recognized: *Anodontoglanis* Rendahl (1 species), *Cnidoglanis* Günther (3 species), *Euristhmus* Ogilby (2 species), *Neosilurus* Steindachner (3 species), *Oloplotosus* Weber (3 species), *Paraplotosus* Bleeker (1 species), *Plotosus* Lacépède (5 species), *Porochilus* Weber (3 species), *Tandanus* Mitchell (11 species).

Family MOCHOKIDAE (*fig.* 6*a, b*)

According to Mo (1991) the Mochokidae appears to be a monophyletic group on the basis of a reduced epioccipital and a distinct modification of the jaw teeth.

The external morphology of Mochokidae consists in a robust body, slightly compressed posteriorly. There are three pairs of barbels (the nasal pair absent). In some genera (*e.g. Synodontis*) the mandibulary barbels (and sometimes also the maxillary ones) are branched. In *Chiloglanis* upper and lower lips are expanded and united to form a sucker. The dorsal fin has a strong spine and is followed by an adipose fin, which in one genus (*Mochokus*) is rayed. The caudal fin is generally forked (except in *Microsynodontis*). The leading pectoral ray is also spiny. An elastic spring apparatus is present.

The Mochokidae is a freshwater catfish family, endemic to Africa. Gosse (1986) recognized 10 genera and Mo (1991) added another one; at present they include 177 species: *Acanthocleithron* Nichols and Griscom (1 species), *Ancharius* Steindachner (transferred from Ariidae by Mo, 1991 and including 2 species), *Atopochilus* Sauvage (7 species), *Brachysynodontis* Bleeker (1 species), *Chiloglanis* Peters (38 species), *Euchilichthys* Boulenger (5 species), *Hemisynodontis* Bleeker (1 species), *Microsynodontis* Boulenger (3 species), *Mochokiella* Howes (1 species), *Mochokus* de Joannis (2 species), *Synodontis* Cuvier (116 species).

The maximum total length reported is 800 mm in a species of *Synodontis*. Generally, however, mochokids are much smaller. Reports on their introduction in aquaculture could not be found. They are, however, increasingly popular aquarium fishes.

Family DORADIDAE (*fig.* 6*c*)

No derived features have so far been reported to demonstrate the monophyly of this family. Curran (1989) considered this family as the sister group to the Auchenipteridae.

The external morphology of the Doradidae consists of a thick-set body, generally covered laterally with a row or series of bony plates which may bear strong, spiny scutes. There are three pairs of barbels, the nasal pair being absent. The dorsal and pectoral fins have a strong spine. The adipose fin is usually present. As in Malapteruridae, Doradidae possess an elastic spring apparatus which due to relaxation of related muscles causes vibrations in the swimbladder; in some species these vibrations produce a loud sound (Curran, 1989).

Doradids are freshwater catfishes endemic to South America and live mainly in rivers and lagoons. The taxonomy of this family is poorly known, both on the generic and the specific level, and is in urgent need of revision. At present, 37 genera, including 94 species are recognized:

Acanthodoras Bleeker (3 species), *Agamyxis* Cope (2 species), *Amblydoras* Bleeker (1 species), *Anadoras* Eigenmann (4 species), *Anduzedoras* Fernández-Yépez (3 species), *Apuredoras* Fernández-Yépez (1 species), *Astrodoras* Bleeker (1 species), *Autanadoras* Fernández-Yépez (1 species), *Centrochir*

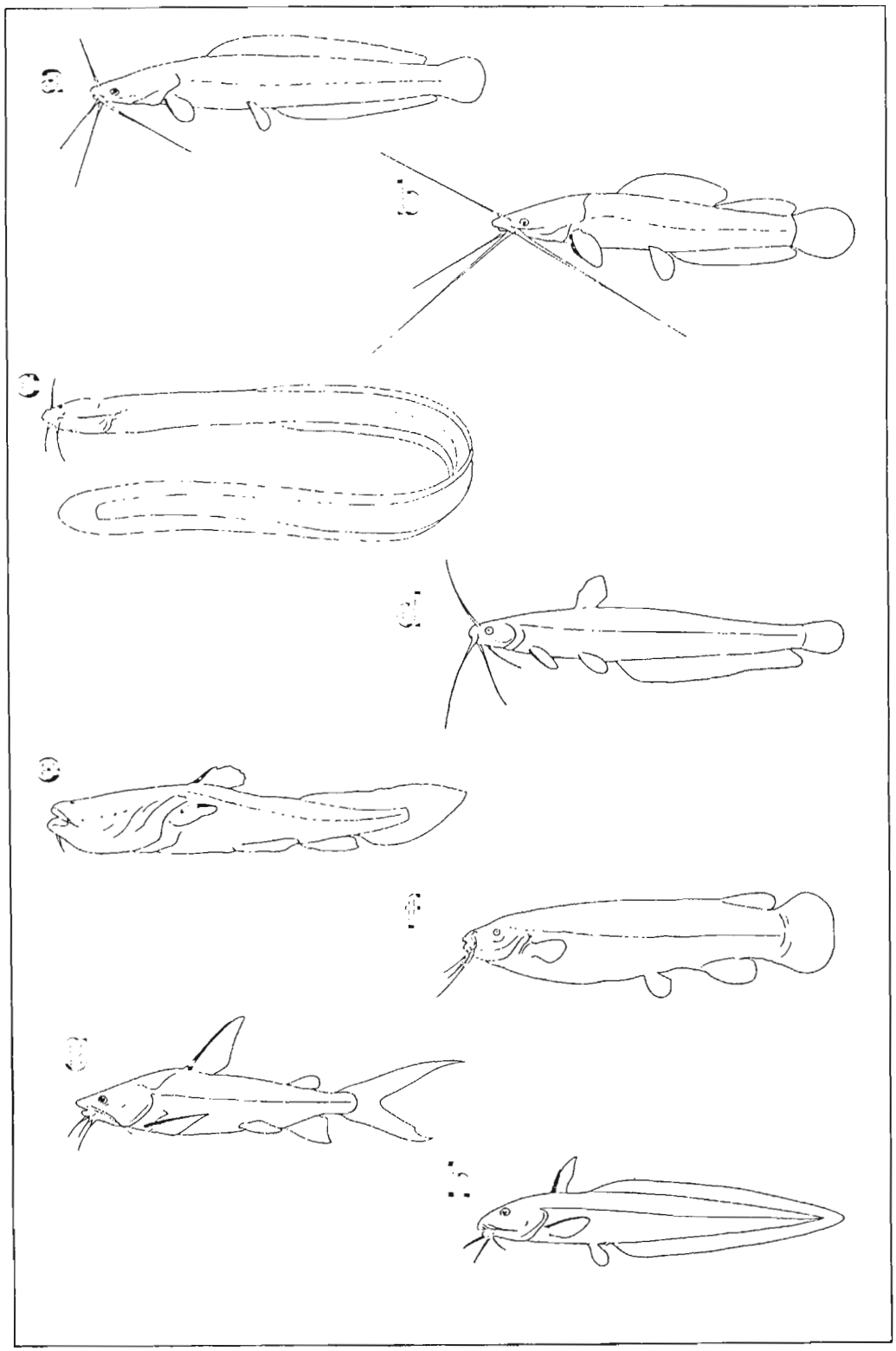

Figure 5. – Outline drawings of representatives of catfish families. a. *Clarias gariepinus* (Clariidae); b. *Heterobranchus longifilis* (Clariidae); c. *Channallabes apus* (Clariidae); d. *Heteropneustes fossilis* (Heteropneustidae); e. *Chaca bankanensis* (Chacidae); f. *Malapterurus electricus* (Malapteruridae); g. *Arius gigas* (Ariidae); h. *Plotosus ukunga* (Plotosidae).

Agassiz (1 species), *Centrodoras* Eigenmann (1 species), *Deltadoras* Fernández-Yépez (1 species), *Doraops* Schultz (1 species), *Doras* Lacépède (5 species), *Franciscodoras* Eigenmann (1 species), *Hemidoras* Bleeker (11 species), *Hildadoras* Fernández-Yépez (2 species), *Hoplodoras* Eigenmann (2 species), *Hypodoras* Eigenmann (1 species), *Kalyptodoras* Higuchi, Britski and Garavello (1 species), *Leptodoras* Boulenger (4 species), *Lithodoras* Bleeker (1 species), *Megalodoras* Eigenmann (4 species), *Nemadoras* Eigenmann (2 species), *Opsodoras* Eigenmann (11 species), *Orinocodoras* Myers (1 species), *Oxydoras* Kner (3 species), *Physopyxis* Cope (1 species), *Platydoras* Bleeker (4 species), *Pseudodoras* Bleeker (3 species), *Pterodoras* Bleeker (3 species), *Rhinodoras* Bleeker (2 species), *Rhynchodoras* Klausewitz and Rössel (2 species), *Sachsdoras* Fernández-Yépez (1 species), *Scorpiodoras* Eigenmann (1 species), *Trachydoras* Eigenmann (4 species), *Wertheimeria* Steindachner (1 species; transferred from Auchenipteridae – De Pinna, pers. comm.), *Zathorax* Cope (3 species).

Important size differences are noted between the genera. *Megalodoras* has a maximum total length of 1 meter. They have no importance to aquaculture but are valued for the tropical aquarium trade.

Family AUCHENIPTERIDAE (*fig.* 6*d*)

Curran (1989) diagnosed this family as a monophyletic group on the basis of three derived features: 1) a post-epioccipital process that reaches the nuchal plates or vertebral column; 2) a genital papilla formed with modified rays of the anal fin; 3) a unique groove that holds the maxillary barbel under the eye. The same author considers Auchenipteridae as the sister group to Doradidae.

Morphologically, auchenipterids are recognized by an elongated body, compressed laterally. The flanks are naked. There are three pairs of barbels (the nasal pair is absent) except in one species with only the maxillary pair present (*Entomocorus benjamini*). The dorsal fin is small and its enlarged ray is spiny. A small adipose fin is present or absent. The anal fin is very long in some genera (*e.g. Epapterus*). The pectoral fin is provided with a strong spine. An elastic spring apparatus is present.

Auchenipterid catfishes are confined to freshwaters in South America and Panama. Curran (1989) mentioned 21 genera; one of them, *Wertheimeria* has been transferred to Doradidae (De Pinna, pers. comm). At present 61 species are recognized as valid: *Asterophysus* Kner (1 species), *Auchenipterichthys* Bleeker (2 species), *Auchenipterus* Valenciennes (1 species), *Centromochlus* Kner (2 species), *Entomocorus* Eigenmann (2 species), *Epapterus* Cope (3 species – Vari *et al.*, 1984), *Gelanoglanis* Böhlke (1 species), *Glanidium* Lütken (5 species), *Liosomadoras* Fowler (1 species), *Parauchenipterus* Bleeker (11 species), *Pseudauchenipterus* Bleeker (4 species), *Pseudepapterus* Steindachner (2 species), *Pseudotatia* Mees (1 species), *Tatia* Miranda-Ribeiro (15 species – Mees, 1974; 1988*a*), *Taunayia* Miranda-Ribeiro (1 species), *Tocantinsia* Mees (1 species – Mees, 1984), *Trachelyichthys* Mees (2 species), *Trachelyopterichthys* Bleeker (2 species – Ferraris and Fernandez, 1987), *Trachelyopterus* Valenciennes (2 species), *Trachycorystes* Bleeker (2 species).

Auchenipterids are small sized catfishes of no interest for aquaculture.

Family PIMELODIDAE (*fig.* 6*e, f*)

The family Pimelodidae, one of the largest freshwater families, containing numerous genera and species, is most likely not a monophyletic lineage (Lundberg and McDade, 1986). A phylogenetic analysis of this group is still lacking.

The external morphology of Pimelodidae shows a high degree of diversity. The body is naked and somewhat elongated. There are three pairs of barbels, the nasal pair being absent. In some genera the maxillary barbels are longer than the body. A dorsal spine is sometimes absent. The adipose fin is always present. A pectoral spine may be present.

Pimelodids are freshwater catfishes found in South America, Central America, southern Mexico and the Caribbean Islands. The systematic status of many genera and species is in urgent need of revision. Three subfamilies are presently recognised with about 53 genera and 323 species.

Following Lundberg *et al.* (1991*a*), the Rhamdiinae is diagnosed by the following synapomorphies: the posterior limb of the fourth transverse process is laterally expanded above the swimbladder and is notched once to several times; the neural spines of the Weberian complex centrum are joined by a straight-edged, horizontal or sometimes sloping bony lamina; the process for insertion of the levator operculi muscle on the posterodorsal corner of the hyomandibula is greatly expanded; the quadrate has a free dorsal margin and a bifid shape, its posterior and anterior limbs articulate separately with the hyomandibula and the metapterygoid; an anteriorly recurved process is present drawn out from the ventrolateral corner of the mesethmoid.

The following genera are assigned to this subfamily: *Brachyglanis* Eigenmann (5 species), *Brachyrhamdia* Myers (1 species – Lundberg and McDade, 1986), *Caecorhamdella* Borodin (1 species), *Cetopsorhamdia* Eigenmann and Fisher (9 species), *Gladioglanis* Ferraris and Mago-Leccia (2 species – Lundberg *et al.*, 1991*a*), *Goeldiella* Eigenmann and Norris (1 species), *Heptapterus* Bleeker (with *Acentronichthys* Eigenmann and Eigenmann, *Phreatobius* Goeldi and possibly *Chasmocranus* Eigenmann, *Phenacorhamdia* Dahl, *Medemichthys* Dahl and *Imparales* Schultz as its junior synonyms and including 30 species –

Buckup, 1988), *Horiomyzon* Stewart (1 species – Stewart, 1986*b*), *Imparfinis* Eigenmann and Norris (17 species – Mees and Cala, 1989), *Myoglanis* Eigenmann (4 species), *Nannorhamdia* Regan (6 species), *Nemuroglanis* Eigenmann and Eigenmann (2 species – Ferraris, 1988), *Pariolius* Cope, *Pimelodella* Eigenmann and Eigenmann (64 species), *Rhamdella* Eigenmann and Eigenmann (12 species), *Rhamdia* Bleeker (with *Caecorhamdia* Norman as its junior synonym and including 63 species), *Rhamdiopsis* Haseman (1 species) and *Typhlobagrus* Miranda-Ribeiro (1 species).

The second subfamily, Pseudopimelodinae, is diagnosed by Lundberg *et al.* (1991*a*) by the following synapomorphies: the lateral ethmoid is lacking a spike-like wing of membrane bone projecting beyond the palatine condyle; the metapterygoid is foreshortened; the endopterygoid and ectopterygoid are broad, distinctively shaped and moveably linked between the neurocranium from near the lateral ethmoid – orbitosphenoid suture and the palatine; the third to seventh proximal radials of the dorsal fin are broad and the adjacent radials are in full contact for their entire lengths; and the dorsal hypohyal bones are absent. The following genera are assigned to this subfamily: *Lophiosilurus* Steindachner (1 species), *Microglanis* Eigenmann (9 species), *Pseudopimelodus* Bleeker (7 species) and *Zungaro* Bleeker (with its junior synonym *Paulicia* von Ihering and including 1 species; Lundberg *et al.*, 1991*a*; Silfvergrip, 1992). Possibly *Zungaropsis* Steindachner (1 species) has to be included in this subfamily (Lundberg *et al.*, 1991*a*).

The third subfamily, Pimelodinae, is diagnosed on three synapomorphic characters by Lundberg *et al.* (1991*b*): the dendritic arrangement of the lateral line tubes in the skin of snout, cheek and nape; the uniquely shaped, much elongated articulation surface on lateral ethmoid for the palatine; and the deep sutural joint between the fifth and the sixth vertebral centra. The following genera are assigned to this subfamily: *Aguarunichthys* Stewart (3 species – Stewart, 1986*a*; Zuanon *et al.*, 1993), *Bagropsis* Lütken (1 species), *Bergiaria* Eigenmann and Norris (2 species), *Brachyplatystoma* Bleeker (7 species), *Calophysus* Müller and Troschel (1 species), *Cheirocerus* Eigenmann (3 species – Stewart and Pavlik, 1985), *Conorhynchus* Bleeker (2 species), *Duopalatinus* Eigenmann and Eigenmann (4 species), *Exallodontus* Lundberg, Mago-Leccia and Nass (1 species), *Goslinia* Myers (1 species), *Hemisorubim* Bleeker (1 species), *Iheringichthys* Eigenmann and Norris (2 species), *Leiarius* Müller and Troschel (2 species), *Luciopimelodus* Eigenmann and Eigenmann (1 species), *Megalonema* Eigenmann (5 species), *Merodontotus* Britski (1 species), *Parapimelodus* La Monte (2 species – Lucena *et al.*, 1992), *Perrunichthys* Schultz (1 species), *Phractocephalus* Agassiz (1 species), *Pimelodina* Steindachner (1 species – Stewart, 1986*a*), *Pimelodus* Lacépède (21 species), *Pinirampus* Bleeker (1 species), *Piramutana* Bleeker (1 species), *Platynematichthys* Bleeker (3 species), *Platysilurus* Haseman (1 species), *Platystomatichthys* Bleeker (2 species), *Pseudoplatystoma* Bleeker (4 species), *Sorubim* Cuvier (3 species), *Sorubimichthys* Bleeker (with *Pteroglanis* Eigenmann and Pearson as its junior synonym and including 2 species – Lundberg *et al.*, 1989) and *Steindachneridion* Eigenmann and Eigenmann (4 species).

Many pimelodid catfishes have an important position in commercial freshwater fisheries. Some *Brachyplatystoma* species grow to over 2 m long; *Zungaro zungaro* attains an edible size of over 1 m. Some species of *Lophiosilurus, Pseudoplatystoma, Rhamdia, Sorubim* and *Steindachneridion* are studied for aquaculture purposes.

Family AGENEIOSIDAE (*fig.* 6*g*)

Data on the phylogeny of this family are scarce and contradictory. Curran (1989) considered the family as forming a monophyletic group together with Malapteruridae, Pangasiidae, Ariidae, Mochokidae, Doradidae and Auchenipteridae based on, a modified Müllerian process, which, in association with the protractor muscle causes vibrations in the swimbladder and produces sound. Mo (1991) however, considered the presence of the elastic spring apparatus as homoplastic.

Ageneiosid catfishes are recognized by an elongated naked body. There is only one small (sometimes rudimentary) pair of maxillary barbels (occasionally a small pair of mandibular barbels). The dorsal fin is anteriorly placed; its enlarged ray is flexible. A small adipose fin is present. The anal fin is relatively long. The pectoral fin has a spine.

This family of pelagic freshwater catfishes occurs only in South America. Three genera including 28 species are presently recognized: *Ageneiosus* Lacépède (24 species), *Tetranematichthys* Bleeker (1 species) and *Tympanopleura* Eigenmann (3 species). They have no importance in aquaculture but are used as food fishes by local fishermen.

Family HELOGENIDAE (*fig.* 6*h*)

Mo (1991) considered this family as the second most primitive group of all Recent catfishes, characterized by six derived features including two completely separate orbitosphenoids and the presence of a separate cranial element between pterotic and supraoccipital.

Externally helogenid catfishes are recognized by an elongated naked body, posteriorly compressed. Three pairs of barbels are present; the nasal pair is absent. The dorsal fin origin is somewhat intermediate between the snout and the caudal fin base. The dorsal spine is flexible. The adipose fin in present or absent, but when present it is small to minute. The anal fin is long with numerous fin rays. The pectoral fin is spineless.

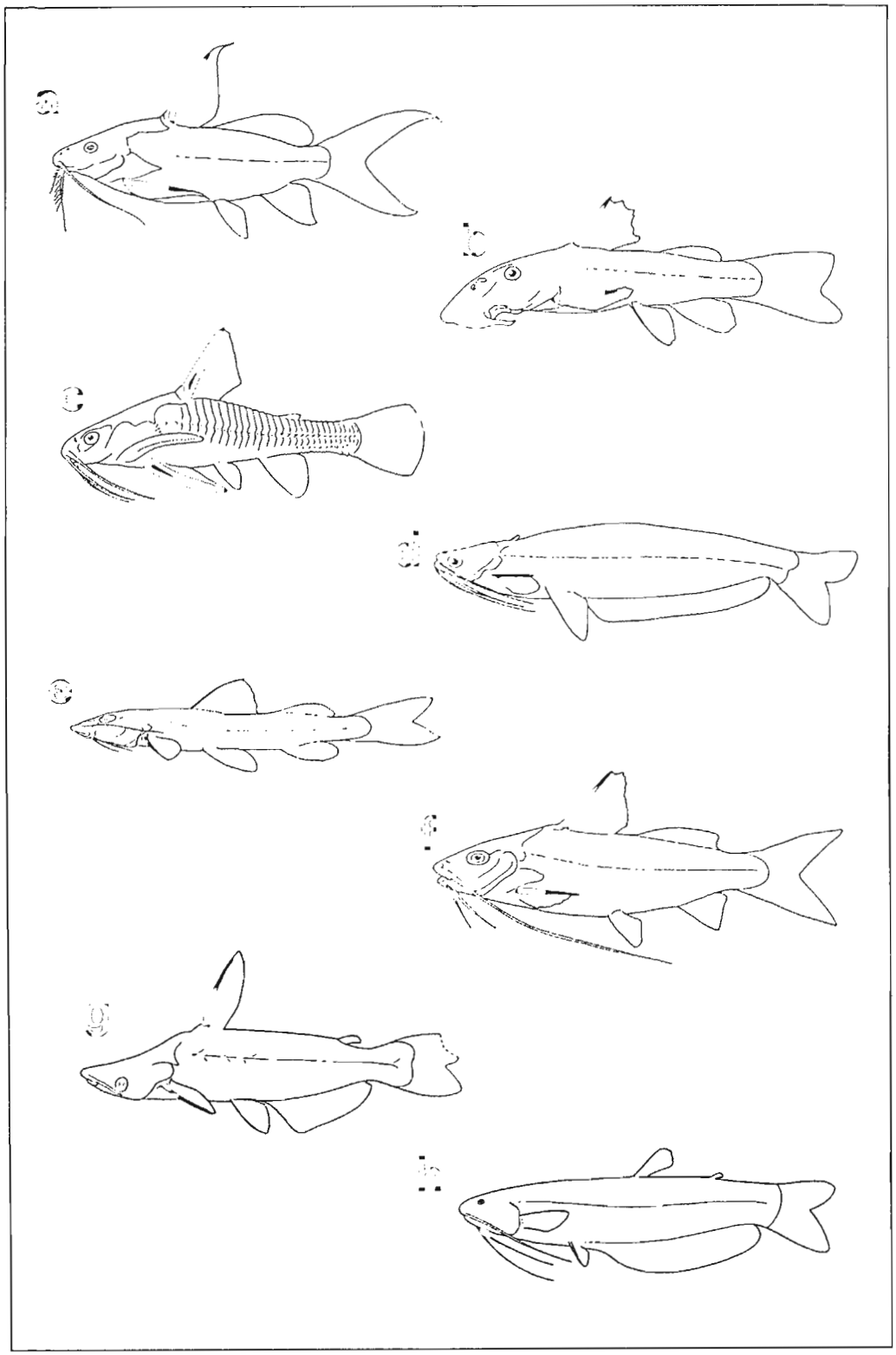

Figure 6. – Outline drawings of representatives of catfish families. a. *Synodontis schall* (Mochokidae); b. *Chiloglanis normani* (Mochokidae); c. *Doras pectinifrons* (Doradidae); d. *Epapterus blohmi* (Auchenipteridae); e. *Imparfinis pristos* (Pimelodidae); f. *Pimelodus clarias* (Pimelodidae); g. *Ageneiosus madeirensis* (Ageneiosidae); h. *Helogenes marmoratus* (Helogenidae).

This family is confined to freshwaters of tropical South America. Vari and Ortega (1986) recognized one genus *Helogenes* Günther with four species. Helogenids are small sized fishes (73 mm largest total length) of no importance in aquaculture.

Family CETOPSIDAE (*fig. 7a*)

Mo (1991) doubted the monophyly of this family, but lacking detailed anatomical descriptions, he was unable to distinguish phylogenetically distinct groups. However, he considered this group as the third basal taxon (after Diplomystidae and Helogenidae) of Siluroidei.

Cetopsid catfishes are recognized by an oval shaped elongated body, lacking bony plates. There are three pairs of barbels, the nasal pair is absent. The dorsal fin, anteriorly placed, has no spine and is preceded by a buckler. In many species, the first dorsal and pectoral fin rays of males are produced into long filaments. An adipose fin is absent. The anal fin is relatively long. In some genera the swimbladder is reduced and encapsulated.

Cetopsids are mostly pelagic and occur in freshwaters in South America. Four genera are known with 14 species: *Cetopsis* Agassiz (2 species), *Cetopsogiton* Eigenmann (1 species), *Hemicetopsis* Bleeker (1 species) and *Pseudocetopsis* Bleeker (10 species – Ferraris and Brown, 1991).

They attain lengths of 250 mm and have no importance for aquaculture because of their predatory behaviour.

Family HYPOPHTHALMIDAE (*fig. 7b*)

Howes (1983) considered the Hypophthalmidae as a monophyletic group because of the unique arrangement of eye and jaw musculature, the reduction of ethmoidal ossification, the complex mandibular barbel supporting elements, the elongated gill- and hyoid arch elements and the typical vertebral and swimbladder elements. Following, the same author, this family is the sister group of Pimelodidae. Lundberg *et al.* (1991*b*) considered *Hypophthalmus* as a pimelodid genus, of indeterminate position within the Pimelodinae.

Externally, hypophthalmid catfishes have an elongated body. There are three pairs of barbels, the nasal pair is absent. The eyes are located on the lower side of the head. The dorsal fin origin is somewhat closer to the snout than to the caudal fin base; it has a leading spine. A small adipose fin is present. The anal fin is very long with numerous rays. The pectoral fin has a leading spine. The swimbladder is reduced and encapsulated.

This family of pelagic catfishes is found in freshwaters in a large part of South America. One genus, *Hypophthalmus* Cuvier, and four species, are presently recognized. *Hypophthalmus* species are common commercial food fish, with a maximum length of about 500 mm.

Family ASPREDINIDAE (*fig. 7c, d*)

The monophyletic nature of this family, sometimes referred to as Bunocephalidae, has not yet been demonstrated.

In aspredinid catfishes the head and the anterior part of the body are broad, while the posterior part of the body and the tail are compressed and slender. The body is usually provided with knobs and sometimes series of small plates are present along the lateral line and the base of dorsal and anal fins. There are three pairs of barbels, the nasal pair is missing. Additionally some species have numerous small barbels on the chin and the anterior part of the body. The dorsal fin is small and often spineless. The adipose fin is absent. The leading pectoral ray is spiny.

Myers (1960) divided this South-American family in two subfamilies: 1) the Aspredininae known from the lowland, muddy coast of Guiana and Amazonia where it occurs in the sea, in brackish water and in the estuaries and tidal portions of the rivers; and 2) the Bunocephalinae that is strictly freshwater, occurring throughout tropical South America, east of the Andes and in the isolated basins of the Rio Magdalena and Lake Maracaibo. Aspredininae contains two genera with 4 species (Mees, 1987): *Aspredinichthys* Bleeker (2 species) and *Aspredo* Scopoli (2 species). Bunocephalinae contains eight genera with 28 species (Mees, 1988*b*; Ferraris, 1991): *Amaralia* Fowler (1 species), *Bunocephalus* Kner (1 species), *Dysichthys* Cope (14 species – Mees, 1989), *Dupouyichthys* Schultz (1 species – Stewart, 1985), *Ernstichthys* Fernández-Yépez (3 species – Stewart, 1985), *Hoplomyzon* Myers (3 species – Stewart, 1985; Taphorn and Marrero, 1990), *Petacara* Böhlke (1 species), *Xiliphius* Eigenmann (4 species).

Most aspredinid catfishes are small-sized catfishes. Some, however, (*e.g. Aspredo*) can attain an edible size (over 400 mm) and are common market fish.

Family TRICHOMYCTERIDAE (*fig. 7e, f*)

De Pinna (1992), referring to an unpublished Ph.D. thesis of Baskin (1973), states that a fairly large number of unequivocal synapomorphies indicate that this family (exclusive of *Nematogenys*) is a monophyletic group. In the same paper, De Pinna (*l.c.*) lists the following unambiguous synapomorphies: the body of the interopercle is extremely reduced antero-posteriorly; the presence of a large ventral or postero-ventral expansion on the interopercle, with odontodes along its distal margin; the ventral half of the opercle narrows strongly towards its ventral tip and the whole ventral region is compact and irregularly rounded in cross-section; the opercular-interopercular articulation is unique as the two bones are freely movable relative to one another; the rictal barbels

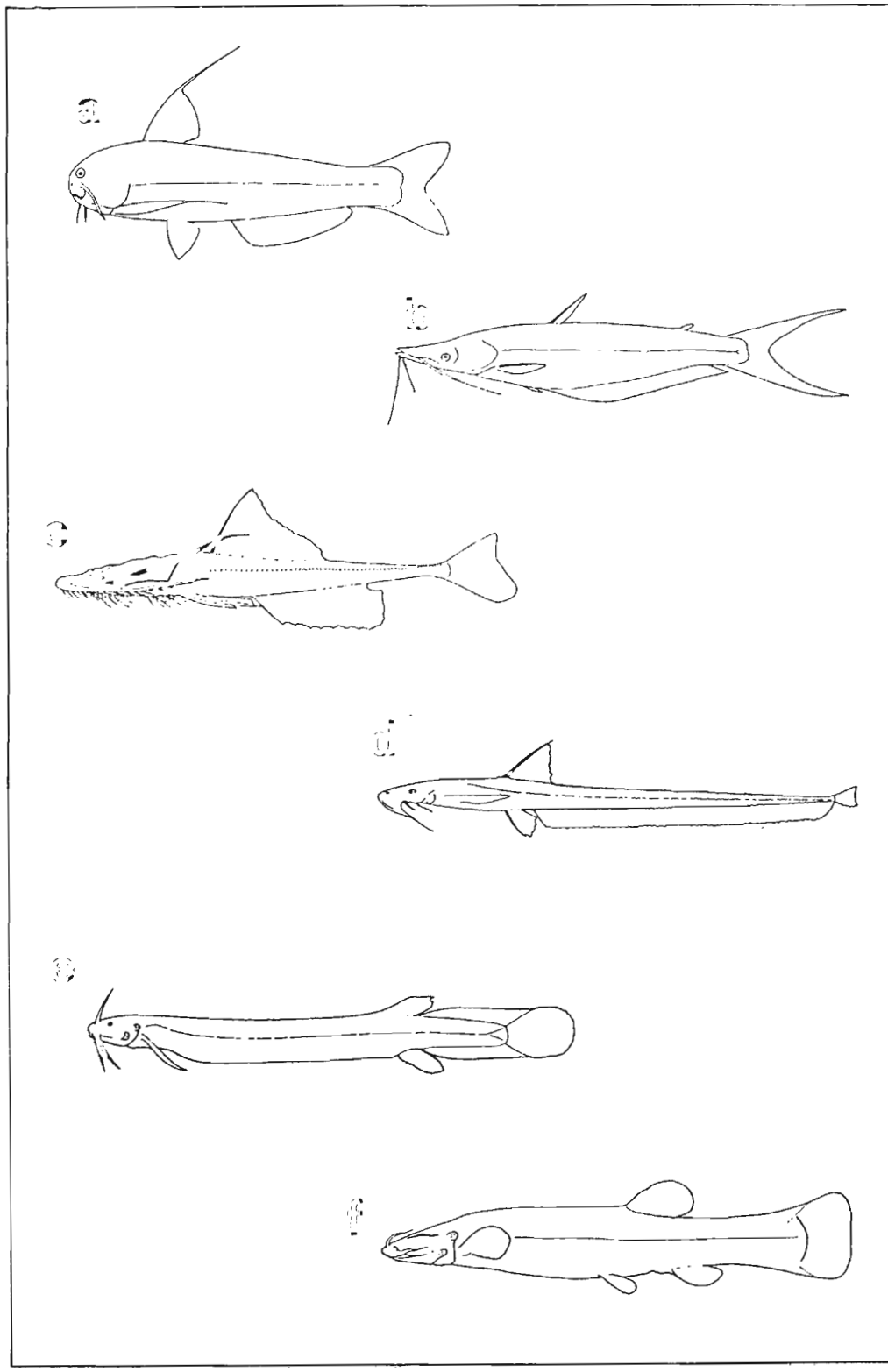

Figure 7. – Outline drawings of representatives of catfish families. a. *Pseudocetopsis gobroides* (Cetopsidae); b. *Hypophthalmus edentatus* (Hypophthalmidae); c. *Ernestichthys intonsus* (Aspredinidae); d. *Aspredo aspredo* (Aspredinidae); e. *Listrura nematopteryx* (Trichomycteridae); f. *Trichomycterus castroi* (Trichomycteridae).

are inserted immediatly ventral to the origin of the mandibular barbels.

Trichomycterid catfishes have an elongated naked body. There are usually two pairs of maxillary barbels; the nasal barbels are also present but the mandibular pairs may be absent. The dorsal fin has a posterior position (not in *Nematogenys*); it is spineless. An adipose fin is generally absent. The pectoral fins are usually spineless (present in *Nematogenys*). The swimbladder is reduced and encapsulated.

Trichomycterids are freshwater catfishes known from Costa Rica, Panama and South America including southern Patagonia. Some are parasitic (*e.g. Vandellia*), living on blood within the gill cavities of other fish; others pierce the skin of fish or other animals and feed on their blood. Some feed on mucus and scales of other fish. Winemiller (1989) postulated that *Ochmacanthus alternus* developed an obligate mucus feeding on the slime layer of larger teleost fishes. Most trichomycterids, however, are free living.

Trichomycterids form a large group containing 40 genera with about 154 species. Nine subfamilies are recognized:

1) Copionodontinae with 2 genera forming a monophyletic lineage on the basis of five synapomorphies including the posteriorly directed lateral process of the lateral ethmoid; the maxilla articulating with the lower jaw; the outer row of premaxillary and dentary teeth strongly expanded distally and spatulate in shape; the premaxilla with a lateral process on the posterior margin, articulating with the maxilla; and the scaphium with a hypertrophied ventral process, articulating with the complex centrum (De Pinna, 1992). *Copionodon* De Pinna (2 species – De Pinna, 1992), *Glaphyropoma* De Pinna (1 species – De Pinna, 1992);

2) Glanapteryginae with 4 genera considered as forming a monophyletic lineage on the basis of five synapomorphies: three or less pectoral fin rays, 5+6 or less principal caudal rays, fusion between all elements of the caudal skeleton, reduction of the latero-sensory canal system on the head and the reduction or absence of pelvic fin and girdle (De Pinna, 1989*a*): *Glanapteryx* Myers (1 species – De Pinna, 1989*a*), *Listrura* De Pinna (2 species – De Pinna, 1988), *Pygidianops* Myers (1 species), *Typhlobelus* Myers (2 species);

3) Nematogenyinae with one genus *Nematogenys* Girard and one species;

4) Sarcoglanidinae with 5 genera considered as forming a monophyletic lineage by De Pinna and Starnes (1990), and confirmed by Costa and Bockmann (1994) on the basis of three derived features: a premaxilla with a long lateral process (different from the conditions in Diplomystidae), a separate anterior ossification of the palatine and a quadrate with a large dorsal process directed backwards. *Microcambeva* Costa and Bockmann (1 species), *Malacoglanis* Myers and Weitzman (1 species), *Sarcoglanis* Myers and Weitzman (1 species); *Stauroglanis* De Pinna (1 species – De Pinna, 1989*b*), *Stenolicmus* De Pinna and Starnes (1 species – De Pinna and Starnes, 1990);

5) Stegophilinae, a subfamily of parasitic catfishes with 13 genera are considered a monophyletic lineage by Baskin (1973; after De Pinna and Britski, 1991) on the basis of six characters: the mouth opening in a wide crescent-shaped disc; the median premaxilla; the closed fontanel; the pterotic-supracleithral shelf; the well-developed hyomandibular plate and the scapulo-coracoid ring. Only the first and last characters are recognized as synapomorphic for this subfamily by De Pinna and Britski (1991). *Acanthopoma* Lütken (2 species), *Apomatoceros* Eigenmann (1 species), *Haemomaster* Myers (1 species), *Henonemus* Eigenmann and Ward (7 species), *Homodiaetus* Eigenmann and Ward (3 species), *Megalocentor* De Pinna and Britski (1 species – De Pinna and Britski, 1991), *Ochmacanthus* Eigenmann (5 species), *Parastegophilus* Miranda-Ribeiro (1 species), *Pareiodon* Kner (1 species), *Pleurophysus* Miranda-Ribeiro (1 species), *Pseudostegophilus* Eigenmann and Eigenmann (3 species), *Schultzichthys* Dahl (1 species), *Stegophilus* Reinhardt (1 species);

6) Trichomycterinae with 6 genera which according to De Pinna (1989*b*) and Arratia (1990) form the only non-monophyletic lineage in Trichomycteridae: *Bullockia* Arratia, Chang, Menu-Marque and Rojas (1 species), *Eremophilus* Humboldt (2 species), *Hatcheria* Eigenmann (1 species), *Ituglanis* Costa and Bockman (9 species), *Rhizosomichthys* Miles (1 species), *Scleronema* Eigenmann (3 species), *Trichomycterus* Valenciennes (about 70 species in need of revision – Arratia, 1990);

7) Trichogeninae with one genus *Trichogenes* Britski and Ortega (1 species);

8) Tridentinae with 4 genera: *Miuroglanis* Eigenmann and Eigenmann (1 species), *Tridens* Eigenmann and Eigenmann (1 species), *Tridensimilis* Schultz (2 species), *Tridentopsis* Myers (3 species);

9) Vandelliinae, a subfamily of parasitic catfishes with 4 genera and considered a monophyletic group by Schmidt (1993; after Baskin, 1973) on 11 synapomorphies including the toothed vomer, situated in the middle of the upper jaw; the claw-like teeth encased in skin pocket on the distal end of the premaxillae; the dentaries which are widely separated medially; the distinct postero-lateral finger-like process on the pterotic; the absence of the fifth ceratobranchial and of pharyngeal teeth; the absence of second or third hypobranchials; the unossified fourth pharyngobranchial; the toothless upper pharyngeal tooth plate; the absence of a mesocoracoid; and their parasitism on vertebrate blood. *Paracanthopoma* Giltay (1 species – Schmidt, 1993), *Paravandellia* Miranda-Ribeiro (5 species), *Plectrochilus* Miranda-Ribeiro (3 species), *Vandellia* Valenciennes (6 species).

Trichomycterids are small to minute catfishes with no interest for aquaculture. Many of the

trichomycterids living in the high Andean region are, already since the Incas'Empire used as food fish; an important food fish in the Bolivian and Peruvian Altiplane is *Trichomycterus rivulatus*; before it became an endangered species, *Nematogenys inermis* was sold as a delicatessen in Chile (Arratia, *in litt.*).

Family CALLICHTHYIDAE (*fig.* 8*a*)

There is at present no reported evidence to consider this family as a monophyletic taxon.

The external morphology characterizing Callichthyidae consists of a relatively short body covered with two rows of bony plates. There are up to two pairs of rictal barbels and one pair of mental barbels; fleshy flaps may also be present. The snout is blunt and the mouth inferior. The dorsal fin has a strong spine. The adipose fin is also provided with a leading spine. The pectoral fin has a strong spine. The swimbladder is encapsulated in bone. Certain callichthyid catfishes can practice aerial respiration and are able to move on land.

Callichthyids are freshwater catfishes known from forest streams in a large part of South America and from Panama and Trinidad.

Seven genera with about 144 species are presently known: *Aspidoras* von Ihering (14 species), *Brochis* Nijssen and Isbrücker (3 species – Nijssen and Isbrücker, 1983), *Callichthys* Scopoli (1 species), *Cataphractops* Fowler (1 species), *Corydoras* Lacépède (±119 species – Nijssen and Isbrücker, 1986), *Dianema* Cope (2 species) and *Hoplosternum* Gill (4 species).

Callichthyids are of little importance in aquaculture. *Hoplosternum*, a common market fish, has recently been introduced in experimental fishculture in French Guiana. In some areas, Callichthyidae are, despite their small size, used as food fishes. They are of great importance in the aquarium trade.

Family LORICARIIDAE (*fig.* 8*b, c*)

Schaefer (1987) offered ten synapomorphies in support of loricariid monophyly. They are summarized as follows: (1) Dorsal margin of the metapterygoid contacting the lateral ethmoid; (2) Presence, at least primitively, of a metapterygoid channel; (3) Presence of a canal plate formed by incorporation of the ventral branch of the propercular latero-sensory canal with a dermal cheek plate; (4) Gill rakers modified as rows of fine, comb-shaped epithelial structures on the oral surface of the gill basket, including the accessory flange of the first ceratobranchial (when present) and the lower pharyngeal jaws; (5) Presence, at least primitively, of an accessory flange on the first ceratobranchial supporting the first row of modified gill rakers; (6) Anterior margin of the anterohyal expanded; (7) Pterotic fused with supracleithrum and expanded posteriorly; (8) Presence, at least primitively, of flattened expanded transverse processes on at least the third anal fin pterygiophore, and frequently subsequent posterior pterygiophores as well; (9) Expanded rib on the sixth vertebral centrum; (10) Body totally or partially encased by three or more rows of overlapping dermal plates bearing integumentary teeth.

Schaefer (1990) listed five additional synapomorphies: the cusp shape of the teeth is asymmetrically bifid; two separate ligaments are present between the mesethmoid and the premaxilla; presence of a ligament between the anteroventral margin of the opercle and a posterior process of the anguloarticular; presence of subdivision of the medial adductor; and the presence of a subdivion of the *extensor tentaculi* muscle.

Loricariid catfishes are recognized by an elongated body compressed ventrally and generally covered with bony plates. The mouth is ventrally placed and is often modified into a sucking disc. A pair of maxillary barbels (sometimes extremely reduced) is present, connecting upper and lower lip. Nasal and mandibulary barbels are absent. The dorsal fin and the paired fins have a flexible spine. An adipose fin is, when present, provided with a spine. Numerous odontodes are present on the snout and on the fin spines.

Loricariids are freshwater catfishes from Central and South America. They mainly live in rocky or stony places, often in streams which become torrential seasonally. Some genera (*e.g. Ancistrus*) have been reported from brackish water.

Loricariidae is the largest of the catfish families. Schaefer and Stewart (1993) compared its tremendous evolutionary radiation with that of the well-known species flocks of cichlid fishes in the African rift lakes. Remarkably both these cichlids and the Loricariidae display a low trophic status, have a low fecundity, intensive parental care and no spawning migrations. A bibliographical search revealed that at present some 651 species are recognized as valid. Isbrücker (1992*b*) listed 88 valid genera. They are arranged in five subfamilies:

1) Ancistrinae: *Acanthicus* Agassiz (2 species), *Baryancistrus* Rapp Py-Daniel (1 species), *Chaetostoma* von Tschudi (41 species), *Cordylancistrus* Isbrücker (1 species), *Dolichancistrus* Isbrücker (3 species), *Exastilithoxus* Isbrücker and Nijssen (2 species), *Glyptoperichthys* Weber (6 species – Weber, 1992), *Hemiancistrus* Bleeker (14 species), *Hopliancistrus* Isbrücker and Nijssen (1 species), *Hypancistrus* Isbrücker and Nijssen (1 species), *Lasiancistrus* Regan (24 species), *Leporacanthicus* Isbrücker and Nijssen (4 species), *Leptoancistrus* Meek and Hildebrand (2 species), *Lipopterichthys* Norman (1 species), *Lithoxancistrus* Isbrücker, Nijssen and Cala (1 species), *Lithoxus* Eigenmann (6 species), *Megalancistrus* Isbrücker (3 species), *Neblinichthys* Ferraris, Isbrücker and Nijssen (1 species), *Oligancistrus* Rapp Py-Daniel (1 species), *Panaque* Eigenmann and Eigenmann (9 species

– Schaefer and Stewart, 1993; Schaefer, *in litt.*), *Parancistrus* Bleeker (1 species – Rapp Py-Daniel, 1989), *Peckoltia* Miranda-Ribeiro (19 species), *Pseudacanthicus* Bleeker (5 species), *Scobinancistrus* Isbrücker and Nijssen (1 species).

2) Hypoptopomatinae: Schaefer (1991) diagnosed this subfamily by several derived characters of which the modifications of the pectoral fin skeleton are the most notable ones. The following genera are included: *Acestridium* Haseman (1 species), *Eurycheilichthys* Reis and Schaefer (1 species – Reis and Schaefer, 1992; 1993), *Hypoptopoma* Günther (12 species), *Microlepidogaster* Eigenmann and Eigenmann (8 species), *Otocinclus* Cope (20 species), *Otothyris* Myers (1 species), *Oxyropsis* Eigenmann and Eigenmann, *Parotocinclus* Eigenmann and Eigenmann (18 species – Schaefer and Provenzano, 1993), *Pseudotocinclus* Nichols (1 species), *Pseudotothyris* Britski and Garavello (2 species), *Schizolecis* Britski and Garavello (1 species).

3) Hypostominae: *Aphanotorulus* Isbrücker and Nijssen (1 species), *Cochliodon* Heckel (6 species), *Corymbophanes* Eigenmann (2 species), *Delturus* Eigenmann and Eigenmann (3 species), *Hemipsilichthys* Eigenmann and Eigenmann (6 species), *Hypostomus* Lacépède (116 species), *Isorineloricaria* Isbrücker (2 species), *Kronichthys* Miranda-Ribeiro (2 species), *Liposarcus* Günther (4 species – Weber, 1992), *Pareiorhaphis* Miranda-Ribeiro (2 species), *Pareiorhina* Gosline (1 species), *Pogonopoma* Regan (1 species), *Pogonopomoides* Gosline (1 species), *Pseudancistrus* Bleeker (6 species), *Pseudorinelepis* Bleeker (3 species), *Pterygoplichthys* Gill (3 species – Weber, 1992), *Rhinelepis* Agassiz (3 species), *Spectracanthicus* Nijssen and Isbrücker (1 species), *Upsilodus* Miranda-Ribeiro (1 species).

4) Loricariinae: *Ancistrus* Kner (49 species), *Apistoloricaria* Isbrücker and Nijssen (1 species), *Aposturisoma* Isbrücker, Britski, Nijssen and Ortega (1 species), *Brochiloricaria* Isbrücker and Nijssen (2 species), *Crossoloricaria* Isbrücker (4 species), *Cteniloricaria* Isbrücker and Nijssen (3 species), *Dasyloricaria* Isbrücker and Nijssen (5 species), *Dekeyseria* Rapp Py-Daniel (5 species), *Dentectus* Martin Salazar, Isbrücker and Nijssen (1 species), *Farlowella* Eigenmann and Eigenmann (37 species), *Furcodontichthys* Rapp Py-Daniel (1 species), *Harttia* Steindachner (10 species), *Harttiella* Boeseman (1 species), *Hemiodontichthys* Bleeker (1 species), *Ixinandria* Isbrücker and Nijssen (2 species), *Lamontichthys* Miranda-Ribeiro (2 species), *Limatulichthys* Isbrücker and Nijssen (1 species), *Loricaria* Linnaeus (10 species), *Loricariichthys* Bleeker (16 species), *Metaloricaria* Isbrücker (1 species), *Paraloricaria* Isbrücker (3 species), *Planiloricaria* Isbrücker (1 species), *Pseudohemiodon* Bleeker (7 species), *Pseudoloricaria* Bleeker (1 species), *Pterosturisoma* Isbrücker and Nijssen (1 species), *Pyxiloricaria* Isbrücker and Nijssen (1 species), *Reganella* Eigenmann (1 species), *Rhadinoloricaria* Isbrücker and Nijssen (1 species), *Ricola* Isbrücker and Nijssen (1 species), *Rineloricaria* Bleeker (44 species), *Spatuloricaria* Schultz (11 species), *Sturisoma* Swainson (15 species), *Sturisomatichthys* Isbrücker and Nijssen (4 species).

5) Neoplecostominae: *Neoplecostomus* Eigenmann and Eigenmann (6 species – Langeani, 1990).

Loricariid catfishes are very important aquarium trade subjects.

Family ASTROBLEPIDAE (*fig. 8d*)

This family is often considered as part of the Loricariidae. Schaefer (1990) offered three derived features in support of its monophyletic character: the premaxillae bear expanded dorsolateral and anterolateral processes; the presence of a ligament between the posterior portion of the palatine and the lateral ethmoid; and the presence of a thick, broad ligament between the opercle and the expanded interhyal bone.

Astroblepid catfishes have an elongated body, which is not covered by bony scutes. The mouth is inferior, forming a sucker disc. Two pairs of barbels are present: a maxillary and a nasal pair. The dorsal fin has a strong spine. An adipose fin may be present. When present it is generally long and often provided with a spine.

Astroblepids are freshwater catfishes known from mountainous regions in Panama and western South America up to Peru. Two genera are considered as valid, *Astroblepus* Humboldt (about 40 species) and *Lithogenes* Eigenmann (1 species). They are small-sized (maximal length reported 300 mm). Some are used in fisheculture in Colombia (Arratia *in litt.*).

Family SCOLOPLACIDAE (*fig. 8e*)

Initially considered as a subfamily of Loricariidae, Isbrücker (1980) raised this group to the family level. Schaefer (1990) fully resolved scoloplacid relationships and offered four uniquely derived, unreversed character-state changes: the swimbladder fenestra is large and not occluded by the compound pterotic; there are no separate exoccipital bones; there is no separate vomer; and the presence of a large, shield shaped plate located in the skin above the dorsal surface of the lateral ethmoids and mesethmoid.

Scoloplacids are small-sized catfishes with a somewhat compact body, covered with two bilateral series of odontode-bearing plates. The maxillary barbels are well developed. Mandibular barbels are present or absent. Mental barbels are present on the midline. The dorsal fin is provided with a spine. An adipose fin is absent. The pectoral fin has a strong spine.

Scoloplacid catfishes are confined to freshwaters in South America (Brazil, Peru and Bolivia). One genus *Scoloplax* Bailey and Baskin and three species

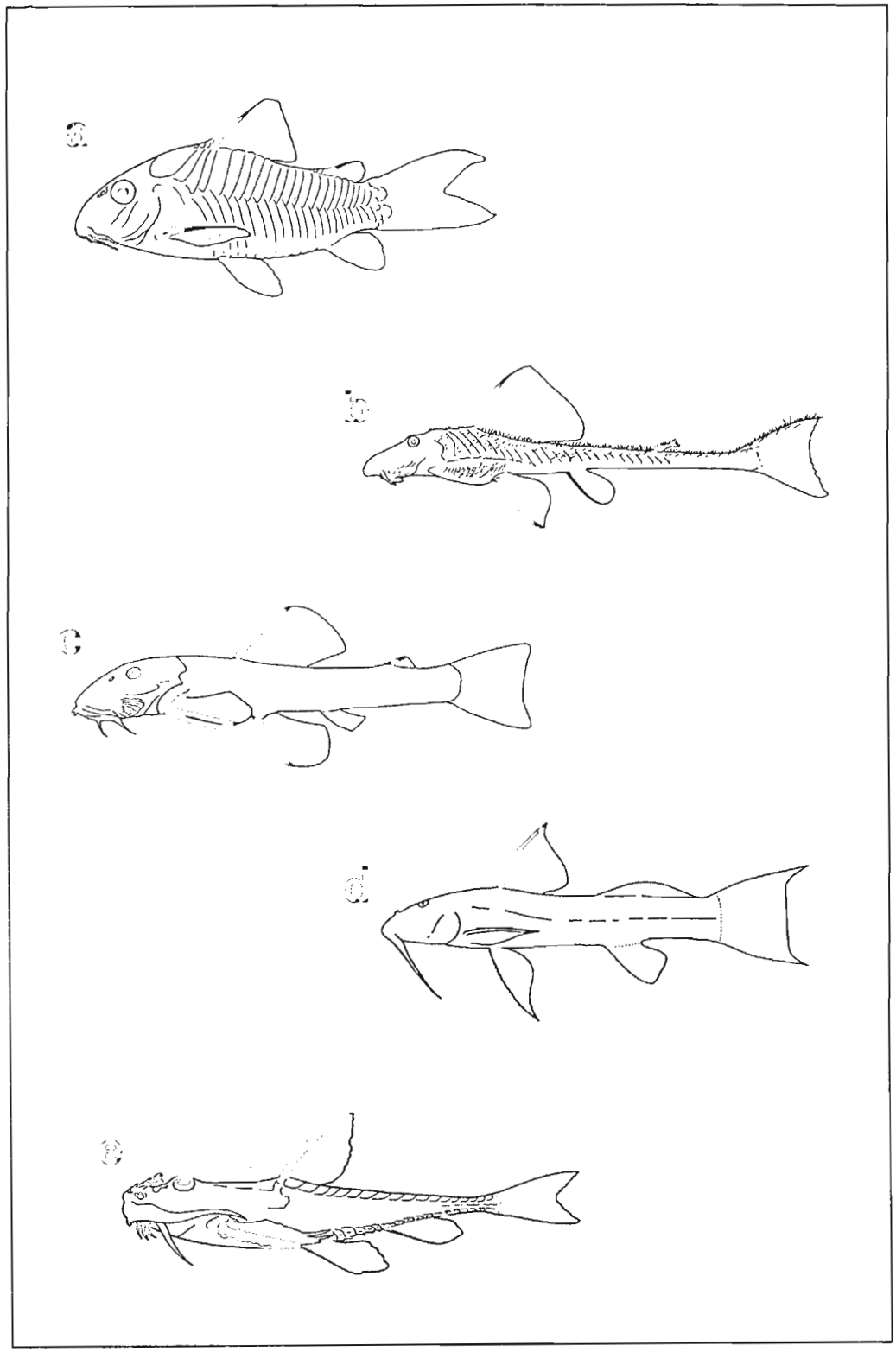

Figure 8. – Outline drawings of representatives of catfish families. a. *Corydoras aeneus* (Callichthyidae); b. *Isorineloricaria festae* (Loricariidae); c. *Exastilithoxus fimbriatus* (Loricariidae); d. *Astroblepus grivalvii* (Astroblepidae); e. *Scoloplax dicra* (Scoloplacidae).

(Schaefer *et al.*, 1989) are known. The largest individual reported measured 19.94 mm standard length (Schaefer *et al., l.c.*).

Their small size and secretive habits precludes any aquacultural use.

PHYLOGENY

Several authors have discussed the intrarelationships of catfishes. A basic outline was made by Regan (1911) who discussed 23 families and their relationships. An important contribution was made by Chardon (1968) who recognised seven major taxa, which he regarded as suborders: Diplomystoidei, including the Diplomystidae; Siluroidei with three superfamilies all including one family, Helogeneidae, Siluridae and Amblycipitidae; Malapteruroidei, including the Malapteruridae; Bagroidei, with nine superfamiles, Bagroidae (Bagridae, Pimelodidae, Ictaluridae, Ariidae, Olyridae), Plotosoidae (Plotosidae), Schilbeoidae (Schilbeidae), Pangasioidae (Pangasiidae), Chacoidae (Chacidae), Doradoidae (Mochokidae, Auchenipteridae, Doradidae, Ageneiosidae), Sisoroidae (Amphiliidae, Sisoridae), Akysoidae (Akysidae), Clarioidae (Uegitglanididae, Clariidae, Heteropneustidae); Cetopsoidei including the Cetopsidae; Hypophthalmoidei including the Hypophthalmidae and Loricarioidei with three superfamilies, Aspredinoidae (Aspredinidae), Trichomycteroidae (Trichomycteridae) and Loricarioidae (Astroblepidae, Loricariidae and Callichthyidae).

More recently, and using a cladistic approach, Grande (1987) divided the Siluriformes (Siluroidei *sensu* Fink and Fink, 1981) in two major lineages (*fig.* 9): Diplomystoidei *sensu* Chardon, 1968, containing a single family (Diplomystidae for synapomorphies see above) and the Siluroidei containing all other catfish families. The synapomorphies for the latter, as given by Grande (*l.c.*) are: 17 or fewer principal caudal rays; an extension of lamellar bone over the ventral surface of the fifth vertebral centrum and the fifth vertebral centrum joined closely to the complex centrum. The Siluroidei are subdivided by Grande (1987) in two superfamilies: † Hypsidoroidea, a fossil taxon and the Siluroidea. The synapomorphies for the latter lineage are: the loss of the maxillary teeth; the loss or reduction of the distal expansion of the maxilla; the loss of the elongate mesial process of the maxilla; the reduction of the autopalatine and the development of long sutural contacts between the ceratohyal and the epihyal.

Arratia (1992) on a phylogenetic analyses of 75 morphological characters confirms that Diplomystidae are the sistergroup of † Hypsidoridae + Siluroidea.

The only cladistic approach to the study of interfamilial relationships is that given by Mo (1991). His results, however, are doubted by Arratia (1992) who mentioned that the most recent study showed

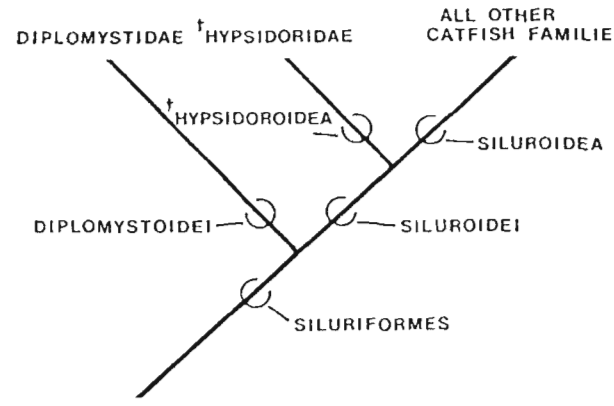

Figure 9. – Hypothesis of siluriform relationships (Siluroidei *sensu* Fink and Fink, 1981) according to Grande (1987).

a polytomy among catfishes above Diplomystidae. I agree with Arratia because, as indicated in the systematic account of the families, contributions to phylogeny are scarce, dealing only with a few families and with a limited number of taxa within the families. De Pinna and Ferraris (1992) reviewed Mo's study. Their comments on his proposed phylogeny of Siluroidei clearly indicate that it suffers from serious limitations. As stated by these authors, the most pervasive problem of Mo's siluroid analysis is (once again) the mostly unchecked monophyly of terminal taxa, *in casu* the nominal catfish families. His excessive *a priori* reliance on the naturalness of nominal families is unjustified.

BIOGEOGRAPHY

As mentioned above, catfishes have a wide distribution and are represented in all continents. Figure 10 illustrates the proportional distribution of freshwater catfishes (excluding Plotosidae and Ariidae) in the world: some 64% of all species known are confined to Central and South America; about 19% of the catfish species occur in Africa; about 15% is found in Eurasia and South-East Asia while about 2% of the species are present in North America.

On the basis of the current concept of continental drift, the origin of catfishes can probably be situated before the splitting of Gondwanaland in the late Mesozoic when Africa and India broke away, followed by East Antarctica and Australia, New Zealand and then West Antarctica and South America.

Lowe-McConnell (1987) stated that South American catfishes developed by spectacular adaptive radiations initiated during South America's long isolation during the Tertiary, when this continent was separated from North America.

The poor occurrence of catfish species (and freshwater fish species in general) in Europe and North America is certainly related to Pleistocene glaciation

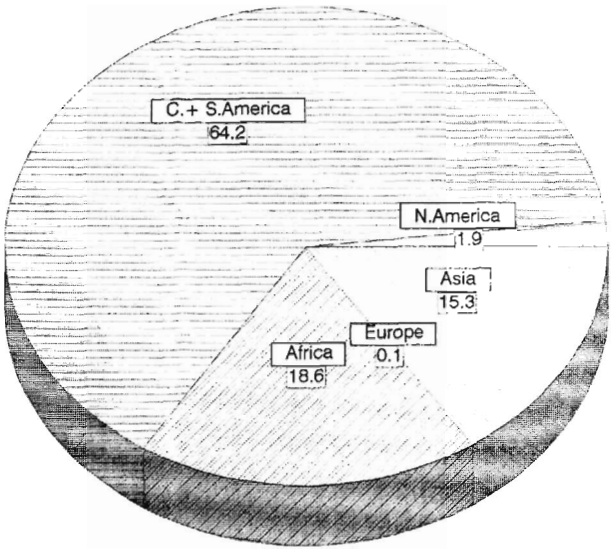

Figure 10. – Proportional continental representation of catfish species (excluding Ariidae and Plotosidae).

that caused extinction (Briggs, 1970). According to Roberts (1972) all or almost all presently known Western European freshwater fish species (*e.g. Silurus glanis*) derived from stocks that populated the area in post glacial times.

Apart from these general data, it is presently impossible to make a reliable statement on biogeography of catfishes. To determine historical biogeography, a thorough knowledge of the phylogeny of the group is absolutely necessary which as mentioned above is not applicable to catfishes at present. Until more data on the interrelationships of catfish families become available, the reconstruction of distributional patterns will be merely guesswork.

A continental review of biogeographical studies of catfish taxa based on a phylogenetic approach revealed only few data. According to Bornbusch and Lundberg (1988) allopatric distributions of *Hemisilurus* species (forming a monophyletic silurid genus) indicate a post-Pleistocene vicariance between drainages of mainland South East Asia and the Indonesian islands. Sympatry among *Hemisilurus* species and *Ceratoglanis*, the sister group to *Hemisilurus*, indicates post-speciation dispersal between Sunda drainages during lowered Pleistocene sea levels.

So far, phylogenetic studies have progressed most for South American families. As a result, a few attempts of phylogenetic biogeography were made for some loricariid taxa (*e.g.* Hypoptopomatinae, see Schaefer, 1991; *Panaque*, see Schaefer and Stewart, 1993; *Parotocinclus*, see Schaefer and Provenzano, 1993); the poor knowledge of alpha-level taxonomy of these taxa, the poor representation of specimens in Museum collections and the patchy knowledge of fish distribution, however, does not allow for tests of biogeographic hypotheses to be made at present. As mentioned for the families, until more data become available on intergeneric relationships, knowledge of historical biogeography of these groups will be seriously limited.

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