

Taxonomy and Phylogeny of Clariidae—An Overview

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Clariidae, commonly named air-breathing or walking catfishes, are a group of catfishes naturally occurring in Africa, Asia Minor, the Indian subcontinent and South-east Asia. Some species (e.g. the African *Clarias gariepinus*, the Asian *C. batrachus*) are of great economic importance as food fish and have been introduced, generally without thorough consideration, for aquacultural purposes in other parts of the world, where they might represent a considerable threat to the biodiversity of local species. *Clarias gariepinus* escaped from fish culture stations in Brazil and has now been found in natural waters in South America (Alves et al, 1999); more than 60% of all known catfishes occur in this subcontinent (Teugels, 1996) and many of them undoubtedly have a much better aquacultural potential than *C. gariepinus*.

The bulk of clariid literature deals only with the few economically important species. However, clariids are a highly diversified and speciose group and presently include 14 genera, of which only *Clarias* is common

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to Africa and Asia. One of the characters uniting all clariids is undoubtedly the unique suprabranchial organ, discussed below (Fig. 16.1). In this paper we present an overview of the taxonomy of clariid genera; the state of the art of clariid phylogeny is also discussed.



Fig. 16.1 The suprabranchial organ in a specimen of *Clarias gariepinus* from Kenya. Upper side of head (left side of figure) and body removed. The organ is formed by extensions of the second and fourth epibranchials (photo, D. Adriaens).

TAXONOMY OF CLARIIDAE

Clarias Scopoli, 1777

The first officially described clariids were the African *Clarias anguillaris* (Linnaeus, 1758) and the Asian *Clarias batrachus* (Linnaeus, 1758). Both species were originally assigned to the genus *Silurus*. Gronovius (1763) was the first to propose the generic name *Clarias*, but his publication was rejected for zoological nomenclature and the authorship of the generic name was attributed to Scopoli (1777) (see Teugels, 1986a). Teugels and Roberts (1987) considered *C. anguillaris* the type species of the genus by subsequent designation. Several synonyms have been published for *Clarias* (for details see Teugels, 1986a). Anatomical features for the genus, already used in the description of the earliest known species, are fusiform body, flattened head and long dorsal and anal fins.

A. African *Clarias* species

The first overall revision was undertaken by David (1935) and David (in David and Poll, 1937) who mentioned 63 nominal African *Clarias* species, arranged in three subgenera: *Clarias* (*Clarias*), *Clarias* (*Clarioides*) and *Clarias* (*Allabenchelys*). At present, 120 nominal *Clarias* species have been described from Africa and the Near East. Teugels (1982, 1986a) in a classical systematic revision, recognised 32 of them as valid species and arranged them in six subgenera. Some of the latter are easily diagnosable on unique characters; this already suggested that genus *Clarias* is probably not monophyletic. This hypothesis is confirmed by genetic data (see below). The subgenera recognised by Teugels (1982, 1986a) are briefly discussed below (Fig. 16.2):

Clarias (*Dimotopteroides*) Fowler, 1930. Species of this subgenus are diagnosed by a long head, completely covered with bone, and the presence of a small, but clearly defined, adipose fin, supported by 10 to 12 elongated neural spines. Two valid species were originally included: *C. ngamensis* Castelnau, 1861 (Fig. 16.2A) and *C. lamottei* Daget et Planquette, 1967. However, the validity of the latter species can be questioned as it probably is a natural hybrid between a *Clarias* and a *Heterobranchus* species (see Legendre et al., 1992; Teugels, 2003).

Clarias (*Clarias*) Scopoli, 1777. Species of the nominate subgenus have about the same head length as the former but lack the adipose fin, although a few extended neural spines can be discerned between the dorsal and the caudal fin. Two valid species were included: the type species *C. anguillaris* (Fig. 16.2B) and *C. gariepinus* (Burchell, 1822).

Clarias (*Platycephaloides*) Teugels, 1982. The head length in species of this subgenus is shorter than in the two subgenera mentioned above; the head is broad and flattened and the eyes laterally positioned. *Clarias platycephalus* Boulenger, 1902 (Fig. 16.2C), *C. jaensis* Boulenger, 1909, *C. stappersii* Boulenger, 1915 and *C. maclareni* Trewavas, 1962 are the valid species assigned to this subgenus.

Clarias (*Clarioides*) David (in David and Poll, 1937). The pectoral spine in species of this subgenus is strongly serrated on both sides (serrated only on the outer side in the above-mentioned subgenera). The neuromasts on the flanks are irregularly placed (regular in all other subgenera). Seven valid species are included: *Clarias macromystax* Günther, 1864, *C. angolensis* Steindachner, 1866, *C. gabonensis* Günther,

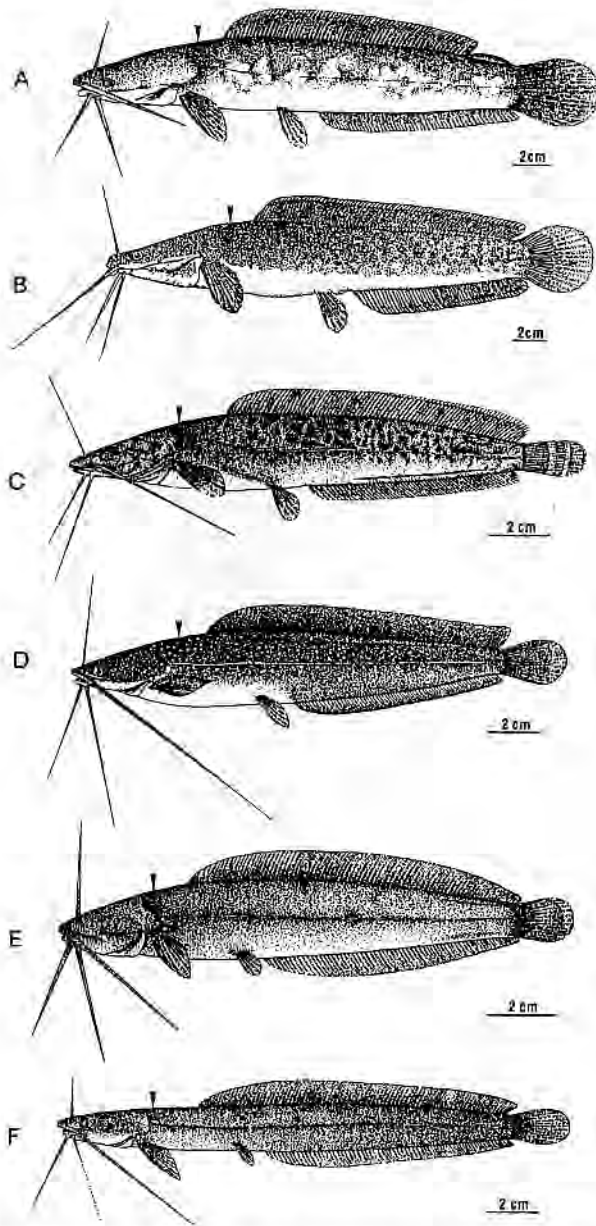


Fig. 16.2 Representative species of the six subgenera in *Clarias* recognised by Teugels (1982; 1986a). Arrows indicate posterior end of head, **A.** *Clarias* (*Dinotopteroides*): *C. ngamensis*. **B.** *Clarias* (*Clarias*): *C. anguillaris*. **C.** *Clarias* (*Platycephaloides*): *C. platycephalus*. **D.** *Clarias* (*Claroides*): *C. buthupogon*. **E.** *Clarias* (*Angullociarias*): *C. theodora*. **F.** *Clarias* (*Brevicephaloides*): *C. laeviceps* (after Teugels, 1986a).

1867, *C. buthupogon* Sauvage, 1879 (Fig. 16.2D), *C. buettikoferi* Steindachner, 1895, *C. albopunctatus* Nichols et La Monte, 1953 and *C. agboyiensis* Sydenham, 1980.

Clarias (*Anguilloclarias*) Teugels, 1982. Species of this subgenus are diagnosed by a markedly elongated body, with very long dorsal and anal fins. Their pectoral spine is serrated on both sides, although not that strongly marked as in species of *C. (Clarioides)*. The subgenus includes nine valid species: *Clarias salae* Hubrecht, 1881, *C. submarginatus* Peters, 1882, *C. theodorae* Weber, 1897 (Fig. 16.2E), *C. pachynema* Boulenger, 1903, *C. alluaudi* Boulenger, 1906, *C. werneri* Boulenger, 1906, *C. ebriensis* Pellegrin, 1920, *C. cavernicola* Trewavas, 1936 and *C. nigromarginatus* Poll, 1967.

Clarias (*Brevicephaloides*) Teugels, 1982. Species of this subgenus are diagnosed by a markedly elongated body, short and broad head, postorbital margin entirely or partially covered with bone and the pectoral spine serrated only on its outer side. Eight valid species are listed: *Clarias laeviceps* Gill, 1862 (Fig. 16.2F), *C. dumerilii* Steindachner, 1866, *C. camerunensis* Lönnberg, 1895 (Fig. 16.3C), *C. liocephalus* Boulenger, 1898, *C. longior* Boulenger, 1907, *C. dhonti* (Boulenger, 1919), *C. engelseni* (Johnson, 1926) and *C. hilli* Fowler, 1936.

All the species originally described in genus *Allabenchelys* Boulenger, 1902 and transferred to subgenus *Clarias* (*Allabenchelys*) by David (1935), were transferred to genus *Clariallabes* by Teugels (1986a) (see below).

B. Asian *Clarias* species

Thirty-two nominal *Clarias* species have presently been described from the Indian subcontinent and South-east Asia. Preliminary results from a systematic revision recognised only 8 valid species (Teugels et al., 2001), but it is likely that ongoing research will reveal the presence of additional new species. No subgenera have been recognised but species complexes can be discerned: the first includes those species with a short distance between the occipital process and the dorsal fin origin (and consequently a small number of predorsal vertebrae) and includes three valid species: *Clarias meladerma* Bleeker, 1846, *C. macrocephalus* Günther, 1864 and *C. intermedius* Teugels, Sudarto et Pouyaud, 2001. In the second species complex, the distance between the occipital process and the dorsal fin origin (and consequently a higher number of predorsal vertebrae) is long. This complex includes the remaining five valid species: *C. batrachus*

(Linnaeus, 1758), *C. punctatus* Valenciennes, 1840, *C. nieuhoftii* Valenciennes, 1840, *C. leiacanthus* Bleeker, 1851 and *C. teijsmanni* Bleeker, 1857. All Asian *Clarias* species show the regular pattern for neuromasts displacement on the flanks.

No detailed morphological and osteological comparison has been so far made between the African and Asian *Clarias* species. This is the subject of ongoing research by one of us (GGT). Presently available data indicate that important differences exist between the two groups. Genetic evidence supports this (see below).

***Heterobranchus* Geoffroy-Saint-Hilaire, 1809**

Teugels et al. (1990) diagnosed this genus on the presence of a large adipose fin supported by 21-27 extended neural spines. The external morphology of *Heterobranchus* species is similar to that of *Clarias* (*Clarias*) and *C. (Dinotopteroides)* species). The most important difference is the presence of a large adipose fin. Eleven nominal species have been described in this genus and Teugels et al. (1990) recognised four of them as valid: *Heterobranchus bidorsalis* Geoffroy-Saint-Hilaire, 1809 (type species), *H. longifilis* Valenciennes, 1840 (Fig. 16.3A), *H. isopterus* Bleeker, 1863 and *H. boulengeri* Pellegrin, 1922. The genus is endemic to Africa. Its monophyletic nature was recently confirmed by genetic evidence (Agnès and Teugels, 2001).

***Gymnallabes* Günther, 1867**

Species of this anguilliform clariid genus have dorsal and anal fins confluent with the caudal fin. Pectoral fins are present while the pelvic fins may be present or absent. The head is very short and its lateral sides are not protected by bone but filled with the greatly enlarged external jaw muscles. The genus is endemic to Africa. Four nominal species are known; three of them are presently considered valid (Teugels, 1986b) but their taxonomic status is poorly known and a systematic revision is the subject of ongoing research (Devaere et al., submitted): *Gymnallabes typus* Günther, 1867 (type species) (Fig. 16.3F), *G. alvarezi* Roman, 1970 and *G. nops* Roberts et Stewart, 1976.

***Channallabes* Günther, 1873**

Channallabes apus (Günther, 1873) (Fig. 16.3G), endemic to Africa, is the only species in this genus. It has an even more anguilliform body than

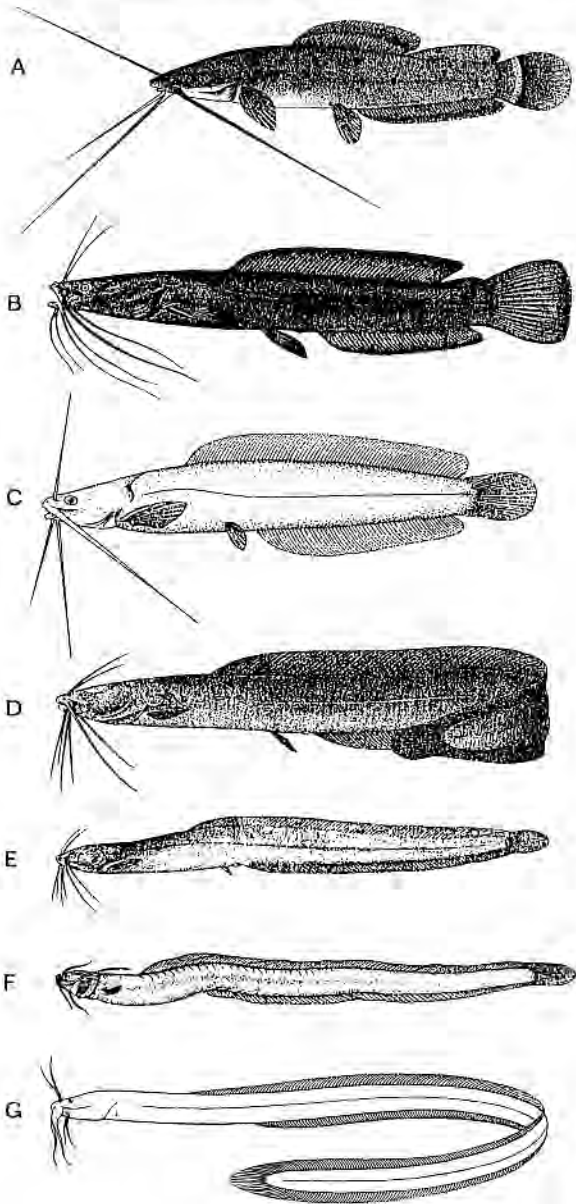


Fig. 16.3 The orthogenetic series in Clariidae as discussed by Pellegrin (1927). **A.** *Heterobranchus longifilis* (after Teugels et al., 1990). **B.** *Dinotopterus cunningtoni* (after Boulenger, 1911). **C.** *Clarias camerunensis* (after Teugels, 1986a; mentioned as *C. poensis* Boulenger, 1908 by Pellegrin, 1927). **D.** *Clariallabes melas* (after Boulenger, 1911). **E.** *Clariallabes variabilis* (after Pellegrin, 1928). **F.** *Gymnallabes typus* (after Teugels, 1992). **G.** *Channallabes apus* (after Boulenger, 1911).

Gymnallabes species; pectoral and pelvic fins show a true intraspecific and even intrapopulational variation in absence/presence (Adriaens et al., 2002). The α -level taxonomy of the genus is presently under revision (Devaere et al., in preparation).

***Clariallabes* Boulenger, 1900**

This genus is considered in the literature as intermediate between *Clarias* and *Gymnallabes*, both in elongation of the body and ossification of the head (Cabuy et al., 1999). Paired fins are present but the pelvic fins may sometimes be rudimentary or absent. The systematic position of this genus is problematic, mainly due to the lack of a thorough phylogenetic study. The species level taxonomy is also confused and a revision is presently underway by Musschoot, Adriaens and Teugels. The genus is endemic to Africa. Sixteen valid species are presently known (Teugels, 1986b; Taverne and De Vos, 1998): *Clariallabes melas* (Boulenger, 1887) (type species) (Fig. 16.3D), *C. longicauda* (Boulenger, 1902), *C. laticeps* (Steindachner, 1911), *C. manyangae* (Boulenger, 1919), *C. brevibarbis* Pellegrin, 1913, *C. variabilis* Pellegrin, 1926 (Fig. 16.3E), *C. attemsi* (Holly, 1927), *C. longibarbis* (David and Poll, 1937), *C. pietschmanni* (Güntert, 1938), *C. simeonsi* Poll, 1941, *C. uelensis* (Poll, 1941), *C. petricola* Greenwood, 1956, *C. centralis* (Poll and Lambert, 1958), *C. platyprosopos* Jubb, 1965, *C. heterocephalus* Poll, 1967 and *C. mutsindoziensis* Taverne and De Vos, 1998.

***Dinotopterus* Boulenger, 1906**

The genus is endemic to Lake Tanganyika (East Africa). *Dinotopterus cunningtoni* Boulenger, 1906 (Fig. 16.3B) is the only species known. It is recognised by the presence of a small adipose fin, supported by 9 to 12 elongated neural spines. The head is long and incompletely ossified laterally. It somewhat resembles *Clarias* (*Dinotopteroideus*) (cf. *supra*) and *Bathyclarias* (cf. *infra*) in external morphology.

***Uegitglanis* Gianferrari, 1923**

Uegitglanis zammaranoi Gianferrari, 1923 is the only species in this genus. It is known only from caves in Somalia (East Africa) and shows the typical features of cave-dwelling fish: degenerated eyes and lack of pigmentation. The lateral head bones are reduced and replaced by external jaw muscles. Chardon (1968) created the family Uegitglanididae for this genus (see below).

***Encheloclarias* Herre and Myers, 1937**

This genus was originally described for the Asian *Heterobranchus tapeinopterus* Bleeker, 1852 because of the presence of a large adipose fin. Contrary to *Heterobranchus*, the adipose fin is not supported by extended neural spines. Several other differences occur (Ng and Lim, 1993): smaller overall size, proportionally smaller head, junction of dorsal, caudal and anal fins. At present six species are included in this genus, which is endemic to South-east Asia: *Encheloclarias tapeinopterus* (type species) (Fig. 16.4A), *E. baculum* Ng et Lim, 1993, *E. prolatus* Ng et Lim, 1993, *E. kelioides* Ng et Lim, 1993, *E. curtisoma* Ng et Lim, 1993 and *E. velatus* Ng et Tan, 2000.

***Dolichallabes* Poll, 1942**

Dolichallabes microphthalmus Poll, 1942 is the only species in this genus. It is known only from the Congo Basin (Central Africa) and is diagnosed by an extremely elongated body, greatly reduced eyes and lateral sides of the head not covered with bone and filled with external jaw muscles.

***Tanganyikallabes* Poll, 1943**

This monotypic genus is endemic to deeper waters in Lake Tanganyika (East Africa). *Tanganyikallabes mortiauxi* Poll, 1943 has the lateral sides of the head not covered with bone; the suprabranchial organ is greatly reduced. It resembles *Clarias* in other external morphological characters.

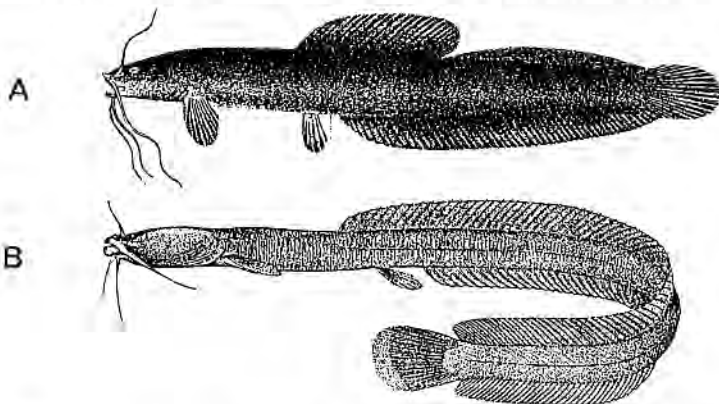


Fig. 16.4 Some representatives of elongated clariid genera. **A.** *Encheloclarias tapeinopterus* (after Bleeker, 1858). **B.** *Platyclarias machadoi* (after Poll, 1977).

***Horaglanis* Menon, 1950**

This remarkable monotypic genus was described for *Horaglanis krishnai* Menon, 1950 found in a well in southern India. The species is blind and devoid of pigmentation. It is a most unusual clariid in having few dorsal and anal fin rays. The pectorals are extremely small (without spine) while the pelvic fins are normally developed. The suprabranchial organ is also reduced.

***Xenoclarias* Greenwood, 1958**

This genus was described for *Clarias eupogon* Norman, 1928 known from deeper waters in Lake Victoria (East Africa), merely because of the macroscopically visual absence of the suprabranchial organ. In other external characters it resembles *Clarias*. The validity of this genus can be questioned (see below).

***Bathyclarias* Jackson, 1959**

Jackson (1959) described this genus for some species from Lake Malawi (East Africa), previously assigned to *Clarias*, but differing in numerous morphological and osteological characters, such as the longer, incompletely ossified head, presence of 5 to 8 extended neural spines supporting a small, hardly visible adipose fin and reduced suprabranchial organ. Several new species were added later, all endemic to Lake Malawi. Agnèse and Teugels (2001a) showed that this species flock descends from *Clarias gariepinus*. Greenwood (1961) synonymised *Bathyclarias* with *Dinotopterus*, but Anseume and Teugels (1999) provided morphological and osteological evidence to rehabilitate the genus. The genus presently embraces 12 species: *Bathyclarias nyasensis* (Worthington, 1933), *B. longibarbis* (Worthington, 1933) (type species), *B. foveolatus* (Jackson, 1955), *B. loweae* Jackson, 1959, *B. ilesi* Jackson, 1959, *B. rotundifrons* Jackson, 1959, *B. euryodon* Jackson, 1959, *B. filicibarbis* Jackson, 1959, *B. worthingtoni* Jackson, 1959, *B. gigas* Jackson, 1959, *B. jacksoni* (Greenwood, 1961) and *B. atribranchus* (Greenwood, 1961). The validity of some of these species can be questioned; a revision is currently underway by G. Banda and G.G. Teugels.

***Platyallabes* Poll, 1977**

Poll (1977) described this genus for *Gymnallabes tihoni* Poll, 1944, known only from the Pool Malebo in Congo (Central Africa). It resembles the

other anguilliform genera but differs in absence of the suprabranchial organ, well-developed paired fins, sides of the head not ossified but filled with well-developed external jaw muscles and confluent dorsal, caudal and anal fins.

***Platyclarías* Poll, 1977**

This is another monospecific genus, including only *Platyclarías machadoi* Poll, 1977 (Fig. 16.4B), known from the Cuango river in Angola (West-Central Africa). The body is anguilliform. The lateral head bones are greatly reduced, paired fins well developed, and the dorsal, caudal and anal fins not confluent

PHYLOGENY OF CLARIIDAE

Several authors have published works concerning clariid phylogeny. These studies can be divided into two groups: (1) those based on the orthogenetic approach and (2) those using the cladistic approach. The most important contributions are briefly discussed below, followed by a synthesis of our present knowledge.

Historic Account

Boulenger (1908: 1062) noted that "the clariids (Clariinae, [sic]) are of special interest from an evolutionary point of view, the series *Clarias* – *Allabenchelys* – *Clariallabes* – *Gymnallabes* – *Channallabes* forming what may be termed an orthogenetic series leading from a more typical catfish to one that is truly eel-like, with almost every link in the chain connecting the two extremes". In his paper on the disappearance of paired fins in clariids (Clariinae, [sic]), Pellegrin (1927: 209) noted that this group is of special interest because "the African freshwaters present even today an unusually complete series of all stages of this curious differentiation". He presented an orthogenetic evolution starting from *Heterobranchus* and ending with *Channallabes* (Fig. 16.3) based mainly on disappearance of the paired fins and anguilliform body shape. According to Pellegrin (op. cit.), these transformations are explained by rapid, evolutionary mutations.

David (1935), adding other characters such as head skeleton, structure of the suspensorium, etc., confirmed the evolutionary trend proposed by Boulenger (1908) and Pellegrin (1927). However, she recognised three groups within the family: (1) *Heterobranchus*, *Dinotopterus*

and her subgenus *Clarias* (*Heterobranchoides*), subsequently changed to *Clarias* (*Clarias*) (see David in David and Poll, 1937) and including the species presently arranged under *Clarias* (*Clarias*) and *C.* (*Dinotopteroïdes*) by Teugels (1986a); (2) her other two subgenera in *Clarias*, *C.* (*Clarias*), subsequently changed to *Clarias* (*Clarioïdes*) (see David in David and Poll, 1937) and *C.* (*Allabenchelys*) including most of the species presently arranged in the other subgenera of *Clarias* and the species originally described in genus *Allabenchelys* but transferred to *Clariallabes* by Teugels (1986a); and (3) *Clariallabes*, *Channallabes* and *Gymnallabes*. According to David (1935), each of the three groups was subjected to an identical orthogenesis. The three groups descended from a common ancestor or derived one out of the other.

In 1942, Poll clearly stated that the orthogenetic series as described by Boulenger (1908) and Pellegrin (1927) is not a natural one; *Heterobranchus* and *Dinotopterus* should not be considered as the ancestors of *Clarias*. According to Poll (1942) *Clarias* includes two lineages: (1) small-size species with a completely ossified cranium and belonging to subgenus *Clarioïdes* and (2) large-size species, that definitely do not include the ancestor of the *Clarioïdes* group. The *Clarioïdes* group gives rise to the *Allabenchelys* group and the *Clariallabes* group. *Dolichallabes*, *Gymnallabes* and *Channallabes*, still according to Poll (1942), independently derived from the *Clarioïdes* group. A schematic illustration of clariid phylogeny as described by Poll (1942) is given in Figure 16.5.

In a new synopsis for clariid genera, Poll (1977) considers the tendency towards an anguilliform body an evolutionary trend linked to an evolutive regression of several structures such as paired fins, skull, air-breathing organ or caudal skeleton. In each of the eel-like genera this regression reaches a different degree in each of the characters involved, resulting in an overlap that allows no statement on the relationships between species and consequently their generic placement. Still according to Poll (1977), regression is expressed by a real convergent evolution that is typical of polyphyletic orthogenesis; the end-products (species) of the different polyphyletic radiations differ in one or another character, demonstrating their independent origin. Convergent evolution should be considered adaptative radiation, often related to burrowing behaviour.

Although Poll was strongly opposed to the cladistic approach (see Poll and Gosse, 1982), due simply to ignorance as this method had just recently been introduced in ichthyological research, his ideas (see above) clearly tend towards this approach.

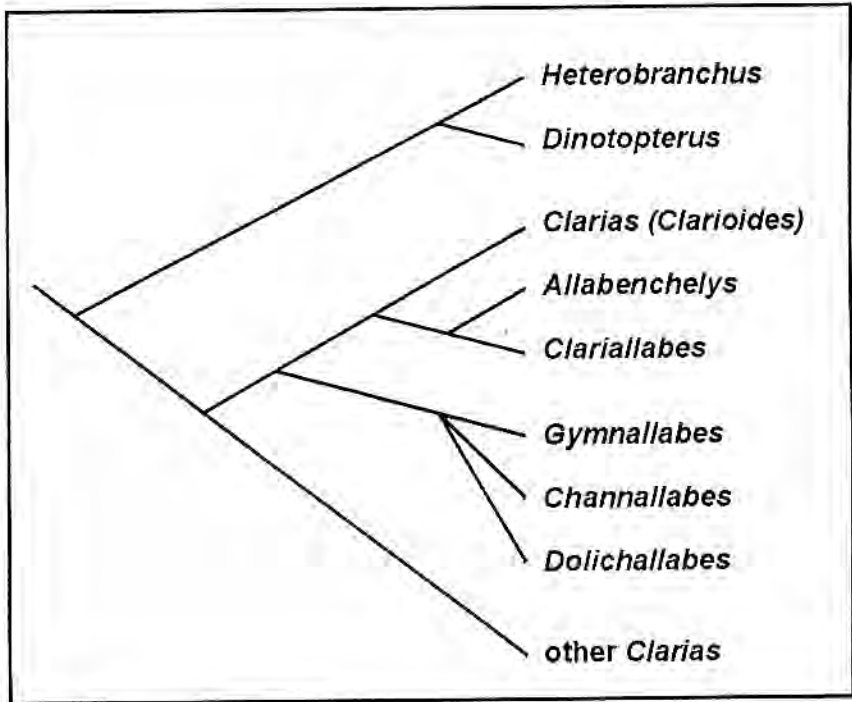


Fig. 16.5 Schematic illustration of clariid phylogeny as suggested by Poll (1942).

The first attempt to apply cladistics in clariid phylogeny was made by Teugels et al. (1990) in their systematic revision of genus *Heterobranchus*. The presence of a larger number (21 to 27) of extended neural spines entering and supporting the adipose fin and its increased length and depth, with correlated shortening of the dorsal fin, were considered the synapomorphies of the genus.

Graham (1997) presents a tentative cladistic arrangement for clariid genera and subgenera "derived from the genus *Clarias*" [sic] based only on the air-breathing organ. Data on the organ are largely taken from Greenwood (1961). Five genera (*Bathyclarias*, *Uegitglanis*, *Platyclarias*, *Platyallabes*, *Encheloclaris*) are not included and the subgeneric division of *Clarias* is that given by David (1935). Figure 16.6 illustrates the tentative cladogram given by Graham (1997).

About ten years ago, a multidisciplinary approach including both the classic morphological and the more recent genetic methods was introduced in the study of clariid relationships. Teugels et al. (1992)

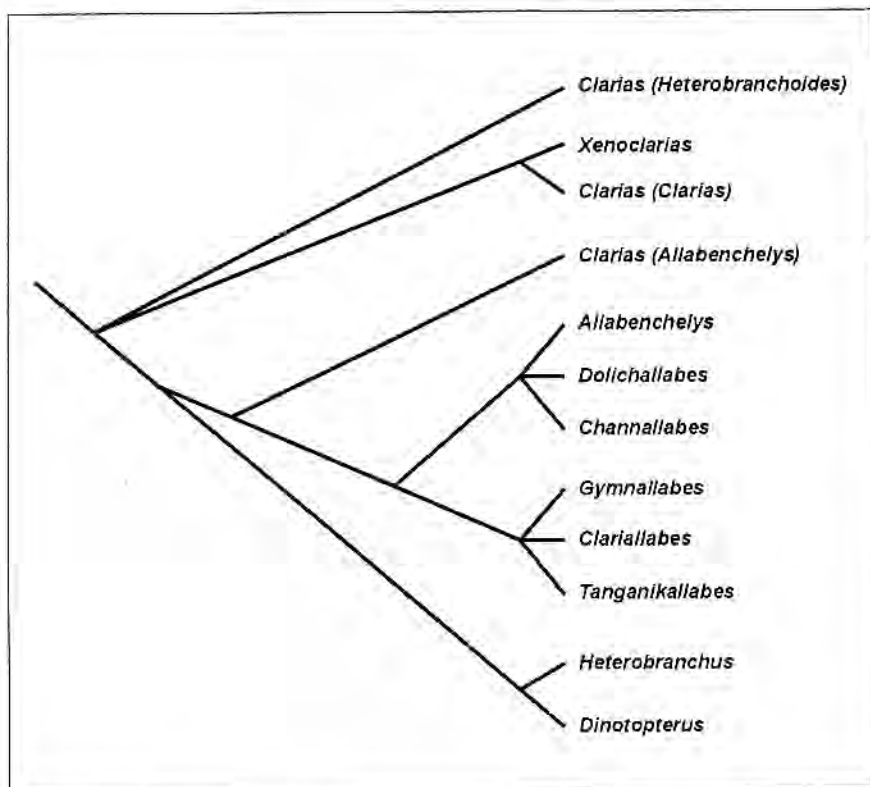


Fig. 16.6 Tentative hypothesis of phylogenetic relationships of Clariidae, based on air-breathing organ development as given by Graham (1997).

indicated, using allozymes, that *Clarias gariepinus* and *C. anguillaris*, both belonging to *Clarias (Clarias)*, were more closely related to *Heterobranchus longifilis* than to *Clarias ebriensis* belonging to *Clarias (Anguilloclarias)* and therefore suggesting that *Clarias* apparently is not a monophyletic genus. Similar results were obtained by Rognon et al. (1998), also using allozymes: the two *Clarias (Clarias)* species are more closely related to *Heterobranchus longifilis* than to *Clarias albopunctatus*, arranged in *Clarias (Clarioides)*. Agnèse and Teugels (2001b), studying the cytochrome b gene in the mitochondrial DNA of the four known *Heterobranchus* species, four *Clarias* species (*C. gariepinus*, *C. anguillaris*, *C. buettikoferi* and *C. ebriensis*) and *Channallabes apus*, clearly demonstrated the monophyly of genus *Heterobranchus* and the paraphyly of *Clarias*. Interestingly, still according to Agnèse and Teugels (2001b), *Channallabes apus* is genetically closely

related to *Clarias buettikoferi*, a *Clarias* (*Clarioides*) species; this result tends to confirm the observations made by Poll (1942).

Finally, Agnès and Teugels (2001a) studying sequences of part of cytochrome b, showed that the *Bathyclarias* species flock endemic to Lake Malawi (E. Africa) descends from *Clarias gariepinus*. In their analysis, *Clarias* (*Dinotopteroideis*) and *Heterobranchus* species seem to be closely related to this group, while species from other *Clarias* subgenera were distantly set, indicating once again the paraphyletic nature of *Clarias*.

Present State of the Art

The synapomorphy uniting all Clariidae is undoubtedly the unique morphology of the suprabranchial organ (Fig. 16.1). It is formed by extensions of the epibranchials of the second and fourth gill arches; they are situated in the suprabranchial chambers, above and behind the branchial cavity. For a detailed description of this respiratory organ in clariids, we refer to Greenwood (1961) and Graham (1997); the latter also provides a review on related literature.

In many clariid genera, the suprabranchial organ is reduced and even macroscopically absent. We consider this a secondary loss, definitely related to ecophenotypic variation. Three examples of strategies are given to illustrate this: (1) clariids living in deep waters (e.g. *Xenoclarias* in Lake Victoria, E. Africa; some *Bathyclarias* species living in Lake Malawi, E. Africa) do not need air-breathing—that would implicate an important energetic loss—and have increased their branchial respiration capacity by larger Gills. (2) burrowing clariids (e.g. most anguilliform genera, including *Gymnallabes*, *Channallabes*) spend most of their life submerged in the muddy bottom (Adriaens et al., 2002); they generally have a greatly reduced suprabranchial organ and cavity. This, in our opinion, is related to spatial constraints as a result of miniaturisation of the skull. The latter is presumably related to the elongation of the body (Devaere et al., 2001). (3) Cave-dwelling clariids also display a reduced suprabranchial organ (e.g. *Clarias cavernicola*). In *Uegitglanis* it is supposedly absent (macroscopically). The reduced air-breathing abilities in these fishes might well be compensated by an increase in vascularisation of the dorsal fin (Tortonese, 1952).

Chardon (1968) considered the (supposed macroscopical) absence of the suprabranchial organ as one of the characters justifying creation of Uegitglanididae for the genus *Uegitglanis*. We are presently unable to

confirm Chardon's (1968) view but doubt the synapomorphic nature of his characters. Based on the configuration of the Weberian apparatus, similar to that found in Bagridae (see David, 1936), *Uegitglanis* could be considered a primitive clariid.

The origin and structure of the air-breathing organ in Heteropneustidae, differ considerably from that found in Clariidae (for details see Graham, 1997). Heteropneustidae may probably be considered the sister-group of Clariidae; further comparative research on the ontogeny of the air-breathing organ in both is necessary to confirm this.

Both morphological and genetical researches tend to confirm the existence in Clariidae of a separate lineage formed by the species of *Heterobranchus*, *Dinotopterus*, *Clarias* (*Dinotopteroide*s), *Clarias* (*Clarias*) and *Bathyclarias*. The monophyletic nature of this lineage is supported by several synapomorphies. All species included have elongated neural spines in the caudal part of the body (Fig. 16.7). In those genera and species showing a clearly marked adipose fin, the elongated neural spines enter and support the fin. In those lacking a notable adipose fin, the last neural spines are still elongated, reaching the dorsal part of the body. All the species included in this lineage also display a very long, heavily ossified head. The branchial apparatus is well developed with long gill arches provided with numerous slender Gill rakers.

Zoogeographically, this lineage is typical for African savannah areas: *Heterobranchus* species and the *Clarias* (*Clarias*) species are widespread in tropical African savannah and absent in forested areas (Teugels, 1986a; Teugels et al., 1990); *C. (Dinotopteroide*s) has a more limited distribution and is only known from Lake Malawi, the Upper Congo, the Middle and Upper Zambezi, the Okavango, Lake Ngami, the Chobe, the Cunene and the Quanza (Southern Africa)—all situated in savannah areas (Teugels, 1986a); *Dinotopterus* is endemic to Lake Tanganyika and *Bathyclarias* is endemic to Lake Malawi; both Lakes are situated in savannah areas. The oldest clariid fossils known, dating from the Miocene, belong to this lineage (see Greenwood, 1968; Van Neer, 1989). However, this does not mean that this lineage should be considered as the most primitive (see below); probably due to unfavourable environmental conditions, no clariid fossil records have been preserved from forested areas.

Within this lineage, the *Heterobranchus* species form a monophyletic group (cf. *supra*; Agnèse and Teugels, 2001b). *Dinotopterus* should probably be considered its sister-group; synapomorphies uniting them include the

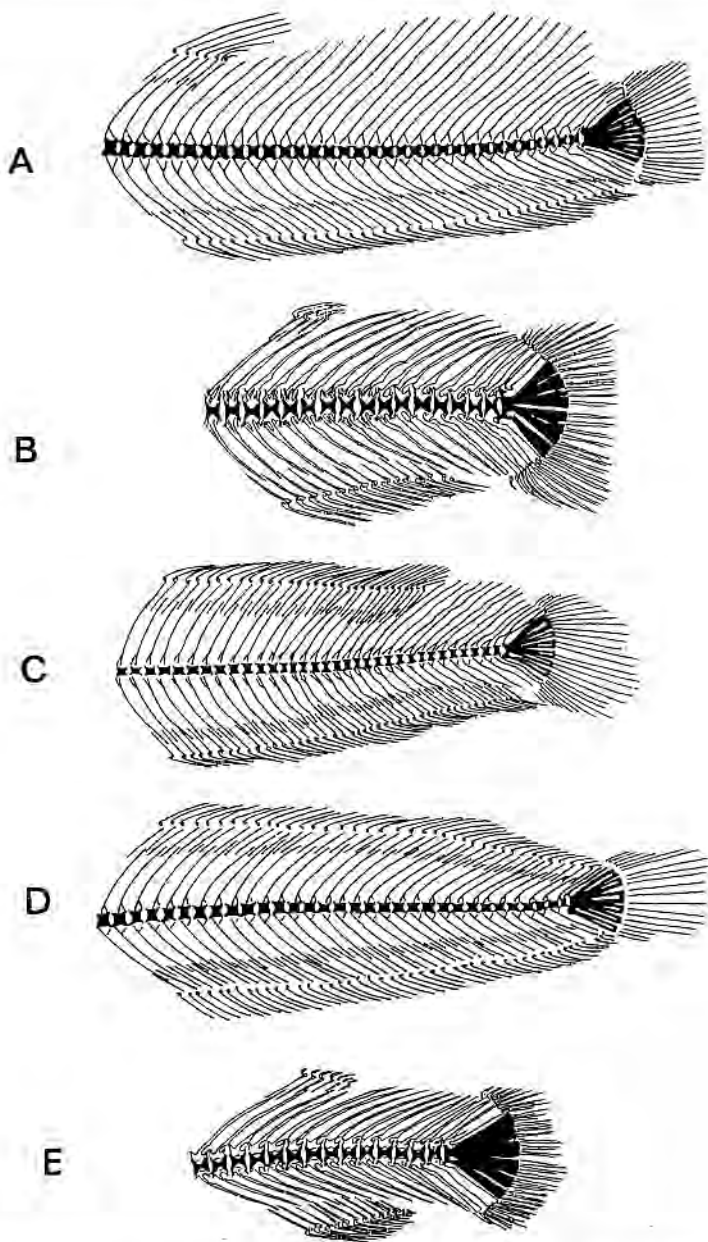


Fig. 16.7 Elongated neural spines in clariids. **A.** *Heterobranchus longifilis*. **B.** *Dinotopterus cunningtoni*. **C.** *Clarias ngamensis*. **D.** *C. gariepinus*. **E.** *Bathyclarias loweae*. Modified from Teugels (1983) and Anseaume and Teugels (1999).

clearly marked adipose fin and the degree of extension of the elongated neural spines. More research is necessary to confirm this.

Clarias (*Clarias*) and *Bathyclarias* also seem to form a monophyletic group (cf. *supra*; Agnèse and Teugels, 2001a). The *Bathyclarias* species flock descended from *C. gariepinus* and the *Bathyclarias* species display numerous derived characters that very likely developed as adaptations to the particular lacustrine conditions in Lake Malawi (Greenwood, 1961; Anseaume and Teugels, 1999). Based on molecular data, *Clarias* (*Dinotopteroides*) appears as the sister-group of *Clarias* (*Clarias*) and *Bathyclarias* (Agnèse and Teugels, 2001a); additional morphological research is necessary to support this.

Genetical evidence tends to support the existence of another separate lineage, considered the sister-group of all other clariids. It includes the Asian *Clarias* (Agnèse and Teugels, 2001b). A synapomorphy uniting the Asian *Clarias* species could well be the clearly marked neuromasts on the body, seen as big white spots showing a regular pattern on the flanks, but more research is necessary to prove this. Interestingly, the typical rounded occipital process seems restricted to the Asian *Clarias* and could represent the plesiomorph condition. Based on zoogeographical evidence, *Encheloclarias* and *Horaglanis* probably descended independently from Asian *Clarias*.

Except for the two lineages discussed above, the relationships of the remaining clariids are at present largely unsolved. However, preliminary morphological and genetical evidence tend to confirm, at least in part, the ideas of Poll (1942). According to this author, *Clarias* (*Clarioides*) species [= *C. (Clarioides)*, *C. (Anguilloclarias)* and in part *C. (Platycephaloides)* *sensu* Teugels, 1986a] are ancestral forms for *Clarias* (*Allabenchelyls*) [= *C. (Brevicephaloides)* and *Clariallabes sensu* Teugels, 1986a], *Clariallabes* and the complex formed by *Gymnallabes*, *Dolichallabes* and *Channallabes*. Cytochrome b sequences of the mitochondrial DNA clearly indicated that *C. (Clarioides)* *sensu* Teugels (1986a) and *C. (Anguilloclarias)* are monophyletic taxa (Agnèse and Teugels, pers. obs.). Interestingly, the former appeared as the sister-group of *Channallabes* and the latter as the sister-group of *Gymnallabes*. Both subgenera differ from all other African *Clarias* by the clearly marked serrations on both the anterior and the posterior side of the pectoral spine (only anterior side in the others); further, *C. (Clarioides)* species are distinguished by the unique pattern of the neuromasts on their flanks (cf. *supra*). The pectoral spine, strongly serrated on its outer and inner side, is a condition also present in some

Asian *Clarias* species. As the Asian *Clarias* are considered the sister-group of all other clariids (see above), we could hypothesise that based on this character, *C. (Clarioides)* and *C. (Anguilloclarias)* are most closely related to the Asian *Clarias*. The phylogenetic significance of this feature, however, is not known and more research is necessary to confirm this.

Based on the position of *Channallabes* and *Gymnallabes* in the preliminary tree obtained from the genetic study (Agnès and Teugels, pers. obs.), we have tentatively tried to complete the cladogram with the remaining genera. *Tanganikallabes* and *Platyallabes* share with *Gymnallabes* a narrow skull roof and tubular fourth infraorbitals. These features are also present to some extent in *Dolichallabes*, but other characters suggest that this genus is more closely related to *Channallabes*. Finally, *Platyallabes* and *Gymnallabes* are in this group diagnosed by the confluency of dorsal, caudal and anal fins, as a result of the high degree of anguilliformity; *Platyallabes* is distinguished by the short distance between the occipital process and the dorsal fin origin. *Channallabes* shares with *Dolichallabes* the highly increased number of dorsal and anal fin rays in relation to number of vertebrae and a similar pattern of hyomandibular interdigitations with the neurocranium.

The position of the remaining subgenera of *Clarias* and of *Platyclarias* and *Clariallabes* is presently not known.

A tentative cladogram summarising the present state of clariid phylogeny as explained above, is given in Figure 16.8. *Bagrus docmak* (Bagridae) was used as the outgroup (data based on Diogo et al., 1999 and Mo, 1991; see text to Figure 16.8 for further details). The data were not subjected to phylogenetic numerical analysis, due to the insufficient number of characters and taxa examined so far.

Nomenclatorial Implications

It is clear from the above that should this tentative phylogeny eventually be confirmed, important nomenclatorial changes would have to be made. The genus *Clarias* is paraphyletic. *Clarias (Dinotopterooides)* and *Clarias (Clarias)* would have to be raised to the generic level and established as separate genera. This is the subject of ongoing research.

All other species presently arranged in *Clarias* would probably have to be placed in other genera. The Asian *Clarias* species would probably have to be placed in a separate genus. This probably also goes for the African species of *Clarias (Platycephaloides)*, *C. (Brevicephaloides)*, *C. (Clarioides)*

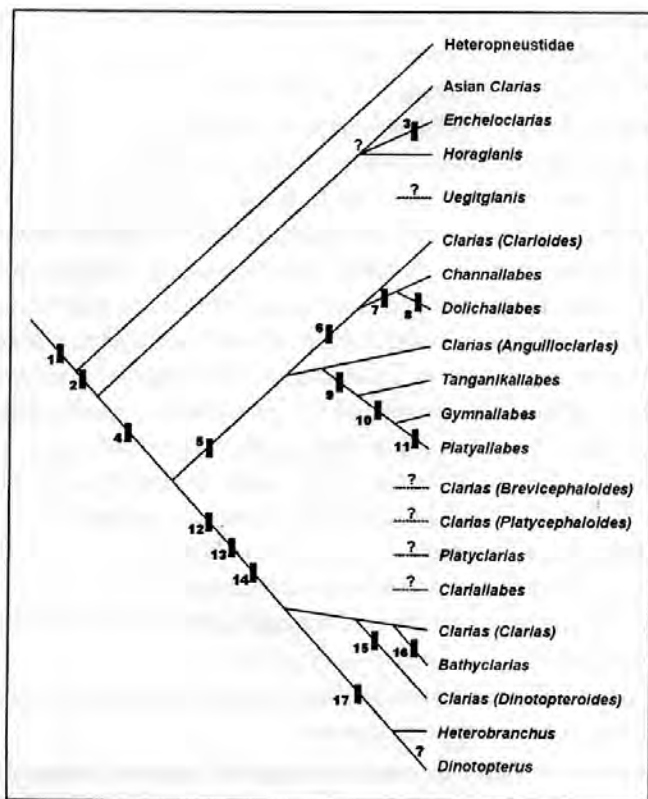


Fig. 16.8 Tentative cladogram illustrating the present state of knowledge of clariid phylogeny. Black boxes indicate derived character sites: 1. Epibranchial, accessory breathing apparatus present; swim bladder almost completely enclosed by enlarged parapophyses of vertebrae 4 and 5; antorbital not enclosing the forked rostral tip of the infraorbital canal; antorbital lacking a marked rostral process; posterior fontanel in adults completely enclosed by the parieto-supraoccipital bone; extrascapulars absent; posttemporo-supracleithral bone immovably sutured to pterotic bone; ectopterygoid absent; parurohyal deeply notched posteriorly, bearing three marked but slender processes of almost equal length; anal fin substantially elongated; dorsal fin lacking a spine; nuchal plates absent. 2. Arborescent suprabranchial organ present on epibranchials 2 and 4; long dorsal fin. 3. Adipose fin present (not supported by elongated neural spines). 4. Neuromasts indistinctly arranged in regular pattern; occipital process pointed. 5. Pectoral spine strongly serrated on both sides. 6. Neuromasts placed in an irregular pattern. 7. Body extremely elongated and anguilliform; increased number of dorsal and anal fin rays (in relation to number of vertebrae); unpaired fins confluent; hyomandibula with one pre- and two post-articulation processes that are well developed (a second small pre-articulation one present in *Channallabes*). 8. Infraorbital bones absent, except the fourth one. 9. Narrow skull roof with a tubular fourth infraorbital. 10. Body anguilliform, unpaired fins confluent (as in 7; convergence; based on genetic data). 11. Dorsal fin anteriorly placed. 12. Last caudal neural spines elongated. 13. Very long, heavily ossified head. 14. Gill rakers long and slender. 15. Well-developed vomerine toothplate. 16. Greatly extended hypo- and ceratobranchials. 17. Numerous extended neural spines supporting the clearly marked adipose fin.

and *C. (Anguilloclarias)*. The validity of the former two subgenera, remains to be tested, however.

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