

Intraspecific variation in the postcranial skeleton morphology in African clariids: a case study of extreme phenotypic plasticity

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Taxonomic relationships within the Clariidae, especially within the anguilliform species, are currently ambiguous due to the lack of a reliable structure of valid generic and specific characteristics. Based on the information available, it is difficult to properly diagnose the different elongated genera and species; this is due in part to a high degree of variability of certain traits generally considered to be important taxonomically. For example, the caudal skeleton is often considered to be an important diagnostic trait. However, the degree of phenotypic plasticity has not hitherto been adequately assessed. This paper deals with interspecific variation of the caudal skeleton of *Clarias gariepinus*, *Platyallabes tihoni*, *Platyclarias machadoi*, *Gymnallabes typus*, *Channallabes apus* and *Dolichallabes microphthalmus*. The caudal skeleton of *C. apus* is studied, using specimens from three regions in Gabon. Hypural fusions and haemal and neural spines show most variation. The observed morphological variation appears to be geographically independent, in contrast to other morphological features such as vertebrae. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 437–446.

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INTRODUCTION

The Clariidae (Teleostei: Siluriformes) is a family of catfishes distributed throughout northern and central Africa and extending to south-east Asia. In Africa there are 12 genera (74 species) and in Asia three genera (18 species), two of which are endemic (Teugels, 1996). The family shows a trend toward increasing anguilliformity as reported by Boulenger (1908) and Pellegrin (1927). Although this tendency is present in other families of teleosts, amphibians, reptiles and mammals, the extensiveness of the transformation from fusiform to anguilliform in Clariidae is distinctive (Lande, 1978; Withers, 1981). Its most notable characteristic is the elongation of the postcranial skeleton, although a whole set of other morphological

transformations has been observed: disappearance of adipose fin; continuous dorsal, caudal and anal fins; reduction of pectoral and pelvic fins (limblessness); reduction of skull bones; reduction of eyes; and hypertrophy of the adductor-mandibulae muscle complex (Pellegrin, 1927; Poll, 1977; Cabuy *et al.*, 1999; Devaere *et al.*, 2001; Adriaens *et al.*, 2004).

Currently, the taxonomy of some genera and species within the Clariidae, especially those which are anguilliform, is confusing. In order to study the functional implications of these adaptations, a reliable structure of generic and specific characteristics is required. Based on the identification key produced by Poll (1977), it is difficult to discern between the different elongated genera and species because the degree of phenotypic plasticity has not been considered adequately, largely due to the limited numbers of specimens used to describe the species.

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Features of the caudal skeleton are considered by many authors to be important diagnostic traits and are used for interpreting systematic and phylogenetic relationships within Teleostei (Arratia, 1983, 1997, 1999; Schultze & Arratia, 1988;). However, intraspecific variation in different parts of the caudal skeleton has rarely been investigated, and conclusions are often based on a handful of specimens. Morphological variation in the postcranial and caudal skeletons within species of elongated clariids, however, appears to be frequent and substantial. The objective of this paper is to focus on the caudal skeletal morphology of different representatives of the Clariidae in order to: (1) describe interspecific morphological variation and (2) describe intraspecific variation of the caudal skeleton in *Channallabes apus*, one of the most abundant anguilliform species.

MATERIAL AND METHODS

For the study of interspecific variation, specimens preserved in alcohol were used, obtained from the Africa Museum (MRAC), Tervuren, Belgium. This study focused on six clariid species (ranked in order of increasing anguilliformity): *Clarias gariepinus* (Burchell, 1822) (04-12-98n3, 1 specimen), *Platyclarias machadoi* Poll, 1977 (MRAC 78-6-P-1348-364, 1 specimen), *Platyallabes tihoni* (Poll, 1944) (MRAC 73-68-P-144, 1 specimen), *Channallabes apus* (Günther, 1873) (unregistered samples from Gabon, 37 specimens), *Gymnallabes typus* Günther, 1867 (KMMA-75-84-P-683-693, 1 specimen) and *Dolichallabes microphthalmus* Poll, 1942 (MRAC 78808-810, 1 specimen). Additional data on the caudal skeleton of *Platyclarias machadoi*, *Platyallabes tihoni* and *Gymnallabes typus* were obtained from Poll (1977).

In order to study intraspecific variation, 37 specimens of *Channallabes apus* were used, which were collected in 1999 and 2000 in three different regions in Gabon (West-Central Africa). Twenty-four specimens originated from the Woleu River system in northern Gabon (Oyem), while seven were from eastern Gabon (Liboumba River Makokou, which is part of the Ivindo Basin, Ogowe System). A southern population was represented by six specimens collected in two different river systems: the Djoué River (Congo Basin), and the Ogowe Basin.

All specimens were cleared and stained following Hanken & Wassersug (1981), modified as follows: during maceration, trypsin is replaced by 1–4% KOH. In order to allow a detailed osteological study of the caudal skeleton morphology, the bulk of the body musculature was removed. Nomenclature of skeletal elements follows that of Gosline (1965), Monod (1968) and Lundberg & Baskin (1969).

RESULTS

INTERSPECIFIC VARIATION

The caudal skeleton of *Clarias gariepinus* shows no fusions between the different hypurals (Fig. 1). All hypurals, the parhypural and the urostyl are separate structures. However, these elements, except the upper hypurals, are fused at their bases both with each other and with the compound centrum. The two halves of the neural arch of the compound centrum do not fuse dorsally. The epural is supported by both these halves. The dorsal lobe, which supports 14 caudal fin-rays, is formed by hypurals 3, 4 & 5, the urostyl and the epural. The neural spine of the third preural centrum, which is elongated and plate-like, is, in contrast to the other species, added to the dorsal lobe of the caudal fin. The ventral lobe, supporting 12 caudal fin-rays, is not exclusively formed by the parhypural and hypurals 1 & 2 – the haemal spines of the second and third preural centrum are also involved. This contrasts with other clariid species (see below).

The caudal skeleton of two specimens of *Platyclarias machadoi* shows some intraspecific variation. In the first specimen, hypurals 4 & 5 and 3 & 4 are fused, whereas the second specimen shows no hypural fusions (Fig. 2A, B). Other features are similar in the two specimens. Incomplete neural and haemal arches of the compound centrum are present. The epural is

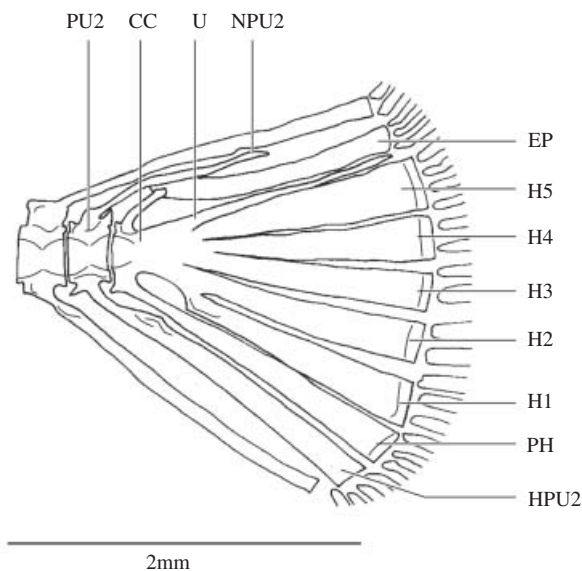


Figure 1. The caudal skeleton of *Clarias gariepinus* shows no hypural fusions. *Abbreviations:* H: hypural; PH: parhypural; EP: epural; CC: compound centrum; U: urostyl; PU: preural centrum; HPU: haemal spine of the preural centrum; NPU: neural spine of the preural centrum.

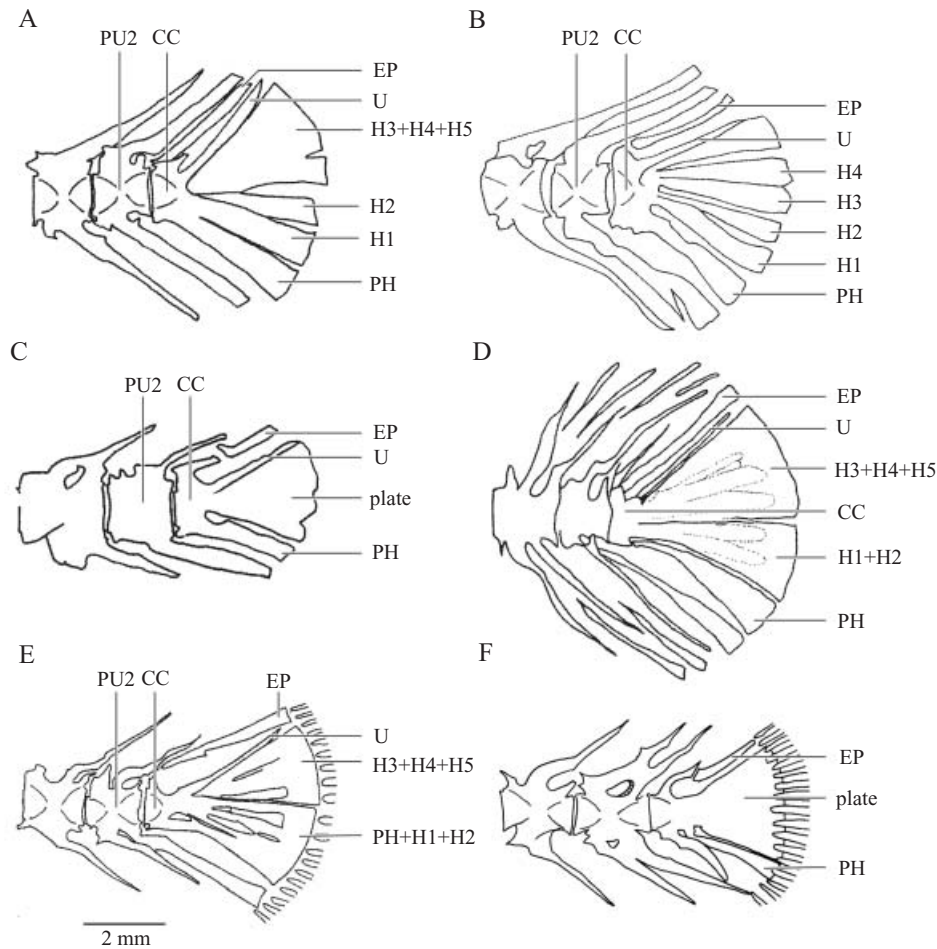


Figure 2. Caudal skeletons. A, *Platyclarias machadoi*. B, *Platyclarias machadoi*. C, *Platyallabes tihoni*. D, *Gymnallabes typus*. E, *Gymnallabes typus*. F, *Dolichallabes microphthalmus*. B, C, D modified after Poll (1977). Abbreviations per Fig. 1.

proximally supported by both halves of the neural arch. The plate-like neural and haemal spines of the second preural centrum are elongated.

The caudal skeleton of *Platyallabes tihoni* consists of a caudal plate formed by fused hypurals and urostyle and of the parhypural and the plate-like haemal spine of the second preural centrum, which flank the caudal plate (Fig. 2C) (Poll, 1977). An incomplete neural arch of the compound centrum is present and supports the epural. The second preural centrum has an elongated haemal spine and a short neural spine.

The caudal skeleton of *Gymnallabes typus* is divided into ventral and dorsal lobes. In one specimen, the dorsal lobe is formed by a distinct urostyle and fused hypurals 3, 4 & 5 (Fig. 2D). The ventral lobe consists of a separate parhypural and fused hypurals 1 & 2. Anterior to the epural, a neural spine of the neural arch of the compound centrum is present. The second preural centrum has double haemal arches and spines, while

the third preural centrum has double neural and haemal arches and spines. A second specimen has a ventral lobe that, in contrast to the other specimen, is formed by the fusion of the parhypural and hypurals 1 & 2 (Fig. 2E). Only the second preural centrum has double haemal arches and spines.

The caudal skeleton of *Dolichallabes microphthalmus* consists of an independent parhypural and a caudal plate, formed by fusion of all hypurals and the urostyle (Fig. 2F). The neural arch of the compound centrum is open distally. Both halves of the neural arch, which are relatively long, articulate with the epural. Ventral to the compound centrum, two haemal arches and spines can be observed. The parhypural supports caudal fin rays. The other haemal spine is shorter and does not support caudal fin rays. The second preural centrum has two neural and haemal arches and spines, which have partially fused.

INTRASPECIFIC VARIATION

The caudal skeleton of *Channallabes apus* displays a high degree of intraspecific variation in the pattern of hypural fusions. The unfused configuration (five separate hypurals and a separate parhypural) is found in 45% of the specimens of *C. apus* examined (Fig. 3A). However, 63% of these have at least two hypurals that are partially fused at their bases. In 25% and 19% of the individuals examined, only the bases of hypurals 1 & 2 or 3 & 4, respectively, are fused. In 19%, partial fusions of these hypurals can be observed (Fig. 3B). An overview of all the different patterns of hypural fusion observed is given in Table 1. Apparently, fusions between hypurals 3 & 4 (30%) and 1 & 2 (27%), with or without additional fusions, occur most frequently (Fig. 3C, D). Fusions of hypurals 3, 4 & 5, forming a

Table 1. Summary of the observed patterns of hypural fusion in *Channallabes apus*. Abbreviations: H: hypural; PH: parhypural

No. specimens and percentage	Pattern of hypural fusion
17 (45%)	PH; H1; H2; H3; H4; H5
1 (3%)	(PH + H1 + H2); (H3 + H4 + H5)
4 (11%)	PH; (H1 + H2); H3; H4; H5
3 (8%)	PH; (H1 + H2); (H3 + H4); H5
3 (8%)	PH; (H1 + H2); (H3 + H4 + H5)
7 (19%)	PH; H1; H2; (H3 + H4); H5
1 (3%)	(PH + H1); H2; (H3 + H4); H5
1 (3%)	(PH + H1 + H2 + H3 + H4 + H5)

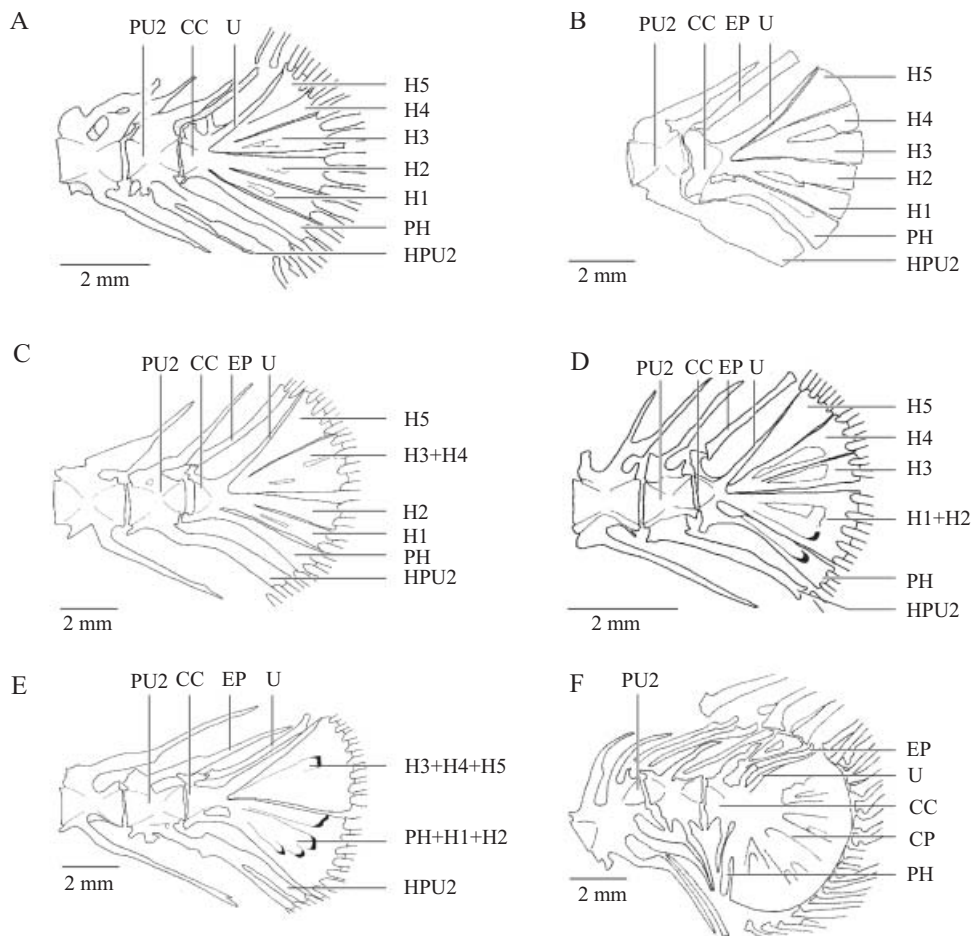


Figure 3. Morphological variation in the caudal skeleton of *Channallabes apus*. A, unfused configuration: five separate H and a separate PH, no EP is present; both left and right neural arches of PU2 bear a neural spine. B, partial fusions of H1 & H2 and H3 & H4, the EP is supported by the right half of the neural arch of CC. C, H3 & H4 are fused, the EP is fused with the neural spine of PU2. D, H1 & H2 are fused, the neural spine of PU3 is branched. E, PH and H1 & H2 are fused, forming a ventral plate; H3, H4 & H5 are fused forming a dorsal plate. F, PH and H1–5 are fused forming one caudal plate. Abbreviations per Fig. 1.

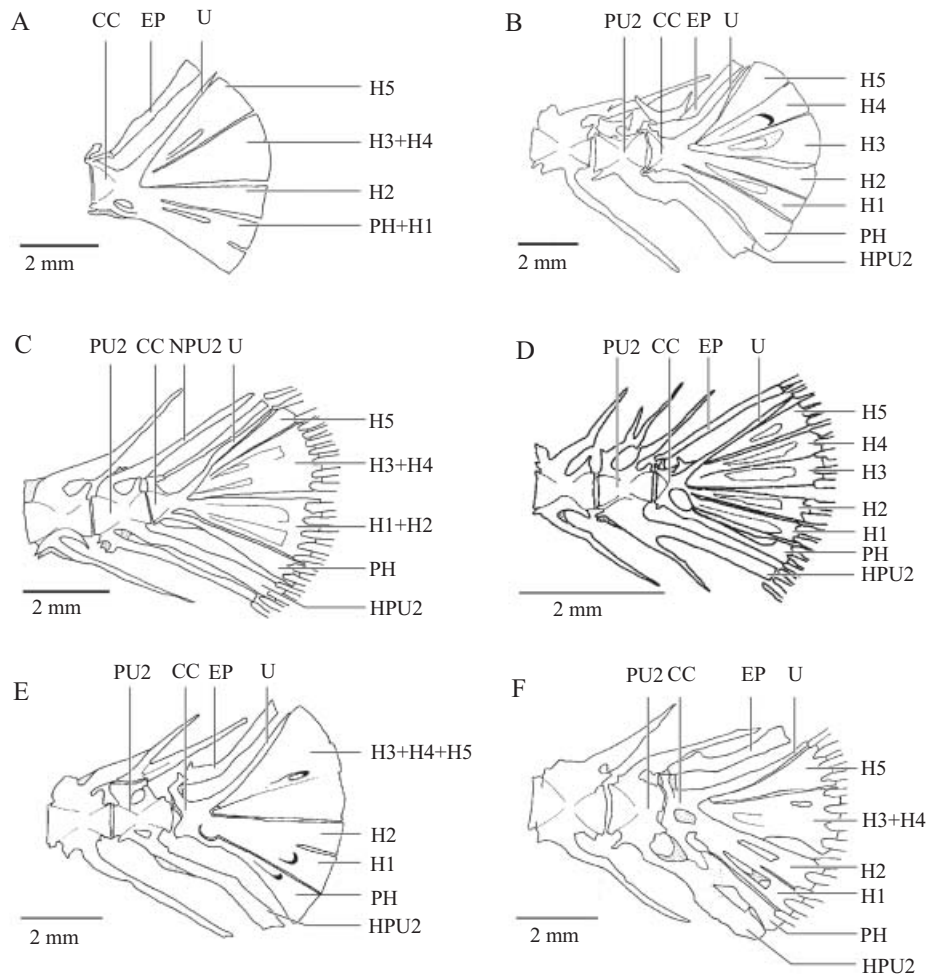


Figure 4. Morphological variation in the caudal skeleton of *Channallabes apus*. A, unfused configuration: H1–5 are separated and a separate PH, no EP is present; both left and right neural arches of PU2 bear a neural spine. B, partial fusions of H1 & H2 and H3 & H4, the EP is supported by the right half of the neural arch of the CC. C, H3 & H4 are fused, the EP is fused with the neural spine of the PU2. D, H1 & H2 are fused, the neural spine of the PU3 is branched. E, the PH and H1 & H2 are fused, forming a ventral plate; H3, H4 & H5 are fused forming a dorsal plate. F, the PH and H1–5 are fused forming one caudal plate. Abbreviations per Fig. 1.

dorsal plate, are present in 8% of the specimens, while the presence of a dorsal (H3 + H4 + H5) and a ventral plate (PH + H1 + H2), was observed in 3% (Fig. 3E). A complete fusion, forming one plate (PH + H1–5), was observed in only 3% (Fig. 3F), as was fusion of the parhypural with the first hypural (Fig. 4A).

The frequency of the different patterns of hypural fusion of the different populations has been examined. Half of the southern and northern populations, and 29% of the eastern population have caudal skeletons lacking hypural fusions. Hypurals 1 & 2 are fused in, respectively, 17%, 21% and 57% of the southern, northern and eastern populations; the equivalent percentages for fusion of hypurals 3 & 4 are 17%, 33% and 29%. Half of the northern population and 14% of the eastern population show fusions of hypurals 3, 4 & 5,

forming a dorsal plate. Fourteen percent of the eastern population has two plates, a dorsal and a ventral one. Fusion of all hypurals and the parhypural is observed once (eastern population). No specimens of the southern population have dorsal or ventral caudal plates. A correlation between the pattern of hypural fusion and geographical distribution appears to be nonexistent. However, in the eastern population, 75% of specimens show hypural fusions in the ventral lobe. This number is substantially lower in the two other populations (i.e. 20% in the southern, 0.4% in the northern population).

Unfused neural arches of the compound centrum appears to be a shared feature of the Clariidae. In *C. apus* two halves of the neural arch can be distinguished. The epural is supported by either or both bases. The caudal skeleton of 6% of the examined spec-

imens of *C. apus* lacks an epural (Fig. 3A). In this case, the neural spine of the second preural centrum functions as an epural. The epural is present in 95% of the specimens, of which 59% have an epural supported by both halves of the neural arch. On the other hand, in 38% the epural is supported by only one of the neural halves: 18% by the right half (Fig. 3B) and 21% by the left (Fig. 4A). Two specimens possess an atypically elongated and broad epural: in one it is fused to the neural spine of the second preural centrum (Fig. 3C), while in the other it consists of two parts (Fig. 4B). Probably, the morphology of the latter is the result of healing after a trauma.

The morphology of the parhypural shows little variation. In some cases a double haemal arch and spine appear to precede the parhypural (Fig. 4C).

There are many specimens with aberrant neural or haemal spines on the first preural centrum. In *C. apus*, the neural spines of the second preural centrum have a characteristic spine-like morphology and show little variation in shape. In 8% of the specimens such a neural spine is lacking (Fig. 4B), while in 6% the second preural centrum has two neural arches and spines (Fig. 4D). In 11% the neural spines of the second preural centrum are supported by the right half only of the neural arch (Fig. 4E). In 5% both left and right neural arches of the second preural centrum bear a separate neural spine (Fig. 3A). Only one specimen has a neural spine that is fused to the third preural centrum (Fig. 4E).

The haemal spines of the second preural centrum articulate with caudal fin-rays. These usually elongated and broad spines show some variation in their morphology. In 6% of the specimens, two spines are present (Fig. 4C), while in 11% the spines are branched (Fig. 4D). The spine of only one specimen is fused with the parhypural (Fig. 4F).

The neural and haemal spines of the third preural centrum show little variation. None of the examined third preural centra have double neural spines or spines that are elongated and support caudal fin-rays. In 8% of the specimens the neural spines are branched (Fig. 3D), while in one the spine is fused to that of the second preural centrum (Fig. 4E).

DISCUSSION

Two types of diural caudal skeleton are observed in teleosts (de Pinna, 1996). In most of the higher Teleostei it is stegural, while in Ostarioclupeomorpha it is pleurostylar (Gosline, 1971). The stegural urocentrum is formed by the fusion of the first and second ural vertebrae as well as the first preural centrum and supports the parhypural and the first and second hypurals (Arratia, 1997). The stegural urostyl is formed by the fusion of the remaining ural vertebrae

and supports the third up to the sixth hypurals. The pleurostylar urocentrum is formed by fusion of the first preural centrum and the first and second ural vertebrae, and supports the parhypural and the first and second hypurals. The pleurostylar urostyl, however, is formed by the fusion of the first and second uroneurals and supports the remaining hypurals (Fink & Fink, 1981; Arratia, 1983).

The caudal skeleton of Siluriformes consists of a series of characters, explained below.

The compound centrum is generally formed by the fusion of the first preural centrum and one or two ural centra (Arratia, 2002; Monod, 1968; Gosline, 1997). A second ural centrum, which in most cases is fused to the base of hypurals 3 & 4, is present (Lundberg & Baskin, 1969). The caudal skeleton of Siluriformes consists of a maximum of six hypurals, which is considered to be the most primitive pattern. The hypurals and parhypural are located ventral to the urostyl (Rojo, 1991). Two lobes can be distinguished: a dorsal lobe, of a maximum of four, independent hypurals, and a ventral lobe, which consists of the first and second hypurals and the parhypural (Eastman, 1980). A small, incomplete and commonly dorsally positioned neural arch of the compound centrum is present. Usually one of the halves of the neural arch supports the epural (Monod, 1968). In some specimens, both halves of the neural arch are fused to the epural, which has also been observed in different species by Arratia (1983) and Schultze & Arratia (1988). The epural can vary phenotypically and may be elongated, rounded, oval or absent (Arratia, 1983). The posterior part of the compound centrum is fused to the uroneural element, the urostyl. The haemal arch of the parhypural bears a small processus or hypurapophysis (Nursall, 1963). A second hypurapophysis may be present on the first or the second hypural (Lundberg & Baskin, 1969; Arratia, 2002).

Different fusion patterns of hypurals can be observed. Within the Siluriformes, as in other teleosts, a trend towards loss and fusion of hypurals has been noted (Arratia, 2002; Lundberg & Baskin, 1969; Poll, 1977; Teugels & Adriaens, 2002). Thus, the observed variation in *C. apus* may be an evolutionary transition towards fused hypurals.

The features described in the following section are generally applicable to the caudal skeletons of all Clariidae, although a great amount of variation between the different species can be observed. In Clariidae, five hypurals are present. The dorsal lobe consists of hypurals 3, 4 & 5. The ventral lobe consists of hypurals 1 & 2 and the parhypural. The second ural centrum (U_2), which precedes the urostyl, is fused to the bases of hypurals 3 & 4. In some species neural and/or haemal spines of the second and/or third preural vertebrae are elongated to support caudal fin rays.

The haemal arch of the parhypural lacks hypurapophyses, a feature in which the Clariidae differ from the closely related Heteropneustidae (Lundberg & Baskin, 1969) (Fig. 5). Secondary hypurapophyses are absent as well. An elongated, bony epural, articulating with the bases of one or two procurvent caudal lepidotrichia is present (Lundberg & Baskin, 1969; Arratia, 1983).

According to Boulenger (1908) and Pellegrin (1927), the following clariid species form an orthogenetic series, starting with a more fusiform species and ending with an extremely elongated species: *Clarias gariepinus*, *Platyallabes tihoni*, *Platyclarias machadoi*, *Gymnallabes typus*, *Channallabes apus* and *Dolichallabes micropthalmus*. However, later studies revealed the polyphyletic nature of these genera (Teugels & Adriaens, 2002). In Figure 6 the average degree of anguilliformity and the minimum and maximum values (ratio of the standard length and the abdominal depth) for each species used in this study are shown. Obviously, the series based on the degree of anguilliformity does not correspond with the orthogenetic series of Boulenger. This confirms the polyphyletic statement of Teugels & Adriaens (2002).

As mentioned by Lundberg & Baskin (1969), caudal skeletons with a trend towards loss and fusion of hypurals are considered to be more advanced. Among the different species examined, different patterns of fusion occur. One could expect that with an increasing degree of anguilliformity, the degree of hypural fusion would increase as well, as this is frequently the case in other anguilliform species (see below) (Fig. 7) (Smith & Castle, 1972; Gago, 1998). Nevertheless, no such relationship appears to exist in clariids.

The caudal skeleton of *C. apus* reveals a high degree of intraspecific variation in hypural fusions. Analysing

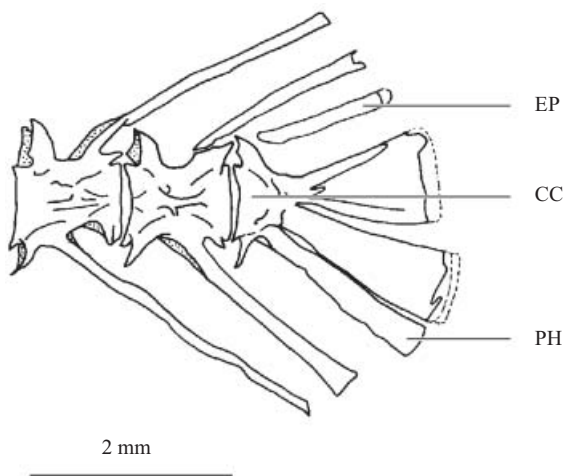


Figure 5. The caudal skeleton of *Heteropneustes fossilis*. Abbreviations per Fig. 1.

the patterns of fusions within the three different geographical regions, a similar morphological variation is observed, which means that the observed variation is randomly distributed among the specimens and populations. Another aspect of this research (N. De Schepper, D. Adriaens, S. Devaere, G.G. Teugels, unpubl. data) deals with variation in the shape of vertebrae. Vertebral structures also show morphological variation between the different specimens. A geometric-morphometric analysis of the vertebral morphology reveals distinct groups: the northern population can be distinguished from the eastern and southern ones.

Therefore, two hypotheses can be posited. First, if all specimens from the three populations from Gabon belong to *C. apus* and thus are one species, the observed variation is intraspecific. Second, if the eastern and southern populations belong to another species, it could turn out to be interspecific. Current research on the taxonomical status of these populations is in progress. Based on the results reported in this paper, the variation appears to be intraspecific.

The morphological variation can be the result of different factors. The relationship between the gender of the specimens and the morphology of the caudal skeleton could not be studied because the majority of the specimens examined were males. However, the presence of considerable variation in the caudal skeleton of males may indicate that there is no relationship between variation and gender. According to Arratia (1983) intraspecific variation in Trichomycteridae occurs independently of age. Even though the current study does not deal with the ontogeny of the caudal skeleton, a relationship between standard length and hypural fusion appears to be absent in these clariids, which confirms the observations in trichomycterids.

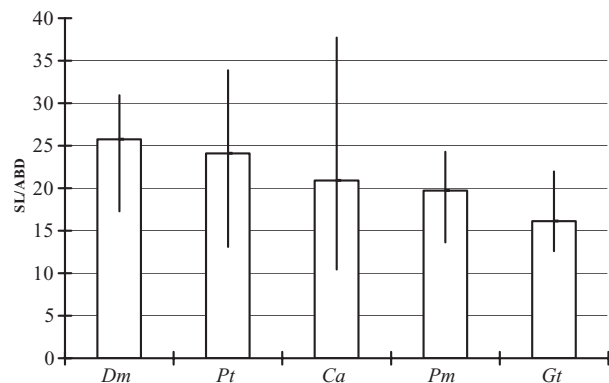


Figure 6. A graphic representation of the degree of anguilliformity (SL/ABD). The average, maximum and minimum of the ratio is shown for each species. Abbreviations: SL: standard length; ABD: abdominal body depth; Dm: *D. micropthalmus*; Pt: *P. tihoni*; Ca: *C. apus*; Pm: *P. machadoi*; Gt: *G. typus*.

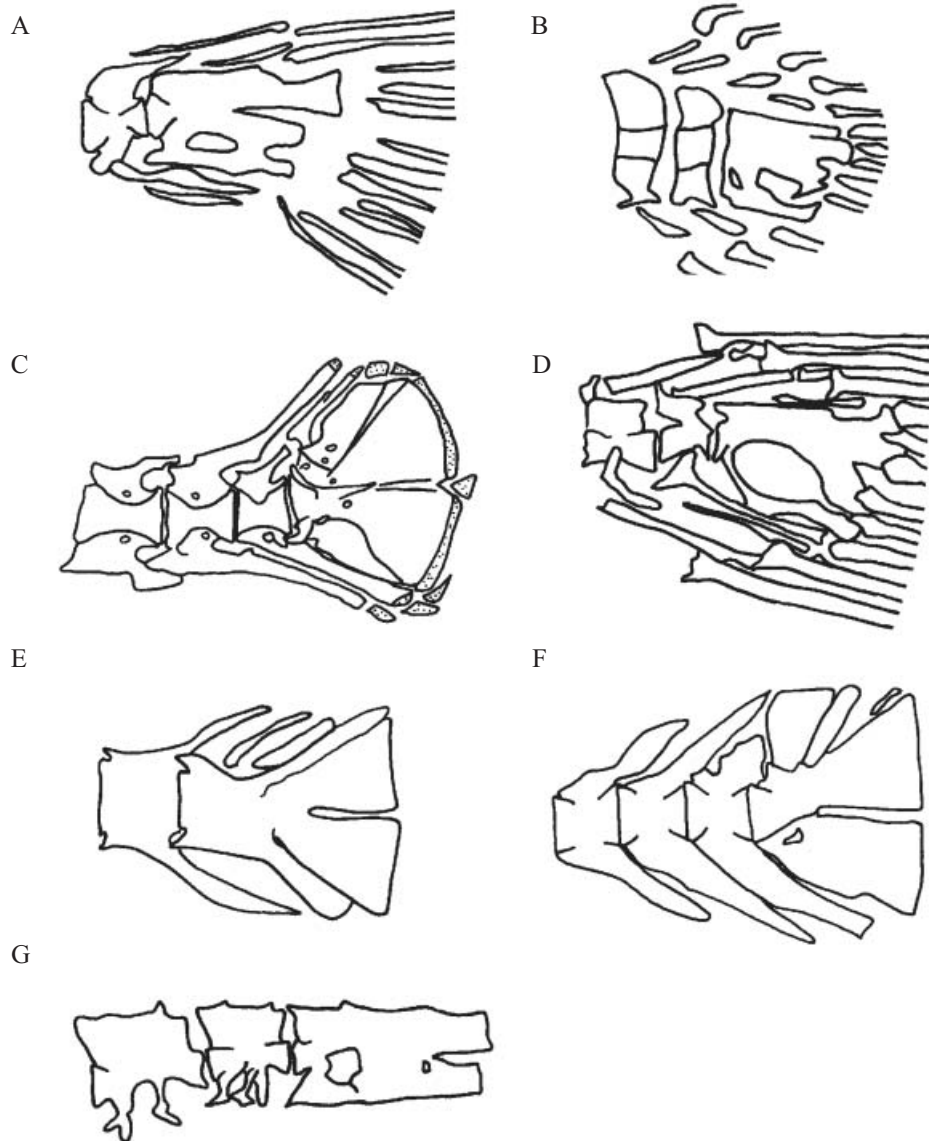


Figure 7. Lateral view of the caudal skeleton. A, *Anguilla rostrata* (Anguillidae). B, *Moringua edwardsi* (Moringuidae). C, *Assurger anzac* (Trichiuridae). D, *Neoconger vermiformis* (Moringuidae). E, *Hypoptychus dybowski* (Hypoptychidae). F, *Tripteron atriceps* (Tripterygiidae). G, *Pythonichthys* sp. (Heterenchelyidae). A, B, D, G modified after Smith & Castle (1972); C modified after Gago (1998); E, F modified after Gosline (1963).

According to Gosline (1997) fusion of hypurals occurs in both slow and fast swimmers. Therefore, it does not seem possible to generalize the functional significance of the caudal skeleton in clariids. All species studied have an elongated, rod-like epural, which articulates distally with caudal fin-rays and is supported at the base by the neural arch of the compound centrum. The unpaired fins of more eel-like clariids tend to be confluent. Therefore, the presence of an epural can be considered a functional advantage to support fin-rays at the transition from the dorsal to

the caudal fin. Some representatives of the Siluriformes (Trichomycteridae) show intraspecific variation in the shape of the epural (Arratia, 1983). All studied clariids, as well as representatives of the Heteropneustidae (Fig. 5) appear to have a similar (elongated and rod-like) epural.

Shape and size of the neural arch of the compound centrum of the Clariidae is highly variable. One common feature can be observed: the neural arch of the compound centrum is dorsally open and supports the epural. Furthermore, both halves of the neural arch

may be of equal size or one half can be reduced. This character thus has little systematic value.

The presence of two neural and/or haemal spines on the second preural centrum has been observed in several clariid species (*Dolichallabes microphthalmus*, *Gymnallabes typus*, *Channallabes apus*). Chanet & Wagemans (1997) note that this feature has been found in Pleuronectinae, Gadidae, Samaridae, Soleidae, Bothidae, Rhombosoleinae, Cynoglossidae and Scopthalmidae. A developmental study of the turbot (*Scophthalmus maximus*) reveals that the multiple occurrences of these neural and haemal spines are the result of the fusion of the second and the third preural centrum. It is possible that in clariids the same developmental pattern occurs. However, this hypothesis has to be confirmed by ontogenetic studies on the caudal skeleton of Clariidae. Fujita (1992) described the ontogeny of the caudal skeleton of *Clarias batrachus*, although deformities and/or variation were not included.

According to Lundberg & Baskin (1969) all species with weak or undeveloped hypurapophyses tend toward an anguilliform type of locomotion. As mentioned above, Clariidae do not have hypurapophyses. Due to the fact that all species used in this study have a pronounced anguilliform body, strict anguilliform locomotion can be expected. Even though *Clarias gariepinus* does not have a strictly anguilliform body shape, the applied type of locomotion is presumably a combination of both anguilliform and subcarangiform types of locomotion. The results of this study thus confirm the statement proposed by Lundberg & Baskin (1969).

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