

Comparative Study on the Cranial Morphology of *Gymnallabes typus* (Siluriformes: Clariidae) and Their Less Anguilliform Relatives, *Clariallabes melas* and *Clarias gariepinus*

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ABSTRACT We compare the cranial morphology of four fish species with an increasing anguilliformism in the following order: *Clarias gariepinus*, *Clariallabes melas*, *Gymnallabes typus*, and *Channallabes apus*. The main anatomical-morphological disparities are the stepwise reduction of the skull roof along with the relative enlargement of the external jaw muscles, which occurred in each of them. *Gymnallabes typus* and *C. apus* lack a bony protection to cover the jaw muscles. The neurocranial bones of *C. gariepinus*, however, form a closed, broad roof, whereas the width of the neurocranium in *C. melas* is intermediate. Several features of the clariid heads, such as the size of the mouth and the bands of small teeth, may be regarded as adaptations for manipulating large food particles, which are even more pronounced in anguilliform clariids. The jaw musculature of *G. typus* is hypertrophied and attached on a higher coronoid process of the lower jaw, causing a larger adductive force. The hyomandibula interdigitates more strongly with the neurocranium and its dentition with longer teeth is posteriorly extended, closer to the lower jaw articulation. The anguilliform clariids also have their cranial muscles modified to enable a wider gape. The adductor mandibulae and the levator operculi extend more posteriorly, and the anterior attachment site of the protractor hyoidei dorsalis shifts toward the sagittal plane of the head. A phylogenetic analysis of the Clariidae, which is in progress, could check the validity of Boulenger's hypothesis that predecessors of the primitive fishes, such as *Heterobranchus* and most *Clarias*, would have evolved into progressively anguilliform clariids. *J. Morphol.* 240:169–194, 1999. © 1999 Wiley-Liss, Inc.

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The external morphology of the Clariidae, or air-breathing catfishes that live in freshwater, is characterized by an elongated body with long dorsal and anal fins. An adipose fin, supported by elongated neural spines, is present in *Heterobranchus*, *Dinotopterus*, and two *Clarias* species (Teugels, '83). The head of clariids is flattened dorso-ventrally and has small eyes and four pairs of barbels surrounding the terminal mouth. Clariids have a suprabranchial organ formed by arborescent structures originating from the second and fourth epibranchials (Moussa, '56; Greenwood, '61; Munshi, '61; Vandewalle and Chardon, '91). These organs enable them to utilize atmospheric

air. These fishes have their greatest diversity in Africa, but they also occur in Syria, southern Turkey, and Southeast Asia (Teugels, '96). Anguilliform clariids such as *Gymnallabes*, *Dolichallabes*, and *Channallabes*, however, have a more restricted distribution and only occur in Central- and West Africa.

Some African clariids can be ordered in an orthogenetic series with an increasing eel-like form: *Heterobranchus longifilis*, *Dinotopterus cunningtoni*, *Clarias poensis*,

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Clariallabes melas, *Clariallabes variabilis*, *Gymnallabes typus*, *Channallabes apus* (Boulenger, '07; Pellegrin, '27). *Heterobranchus* is positioned at the beginning of this series. Its fusiform body is provided with a well-developed adipose fin and unpaired and paired fins (Teugels et al., '90). A closed roof of thick bones makes up the neurocranium (Gregory, '33: Fig. 77A; Teugels et al., '90). *Channallabes apus*, at the other end of the series, is the most extremely anguilliform species. Its dorsal and anal fins are relatively much larger and are confluent with the caudal fin, whereas the adipose fin and the paired fins are absent. The neurocranium is narrow and the lateral cranial bones are strongly reduced (Boulenger, '07, '11; David, '35; Poll, '42a, '77).

After Boulenger ('07) and Pellegrin ('27), many other authors became inspired by this regressive evolution among the clariids, as they called it (David, '35; Poll, '41, '42a, '77; Greenwood, '56, '61; Lambert, '60). David ('35) has described this regressive trend in detail in the first comprehensive anatomical and systematic study on clariids. She considered the eel-like clariids as more developed, specialized catfishes. According to Poll ('77), the anguilliform body would have evolved many times independently.

Boulenger's orthogenetic series ('07) is partly represented here by examining four different species: *Clarias gariepinus*, *Clariallabes melas*, *Gymnallabes typus*, and *Channallabes apus*. The genus *Clarias* covers the greatest number of species, i.e., 32, of which *C. gariepinus* has an almost Pan-African distribution (Teugels, '82; Skelton and Teugels, '92). *Clariallabes* numbers 15 species, of which *C. melas* is distributed in the Congo system (Teugels, '86a). *Clariallabes* tends to be associated with swift water and coarse rocky substrates where it can hide (Winemiller and Kelso-Winemiller, '96). This genus has not been studied thoroughly and the precise separation between this genus and *Clarias* is, therefore, open to argument. The formerly defined subgenus *Clarias* (*Allabenchelys*) (David, '35), which recently has been classified under the genus *Clariallabes*, consists of intermediate forms ranging between *Clariallabes* and *Clarias* (Teugels, '86b). The genus *Gymnallabes* is currently known to consist of three species: *G. typus* (Günther, 1867), *G. alvarezii* (Roman, '70), and *G. nops* (Roberts and Stewart, '76). The area of distribution of *G. typus* is

situated between Nigeria and Cameroon (Teugels, '86a), which in part corresponds with the Lower Guinean ichthyofaunal province recognized by Roberts ('75). The precise habitat of *G. typus* is not well known, but river and lake banks (Matthes, '64) as well as marshes (Poll, '42a; Gosse, '63; Teugels et al., '92) are places where it can be found. *Gymnallabes nops* is caught in fast-running rivers (Roberts and Stewart, '76). *Channallabes apus*, the only representative of its genus, is distributed in the Congo system (Teugels, '86a). They have been caught in the river silt or under vegetation in nearly dried marshes by fishermen searching for worms (Poll, '59).

Anguilliform clariids occupy an apparently different habitat and would be adapted to a burrowing way of life (Nelson, '94). Their anatomy has hardly been studied at all to the present, and no attempt has been made to give a detailed description. Their external morphology is very similar, but the cranial skeleton is an important determination factor to distinguish them from each other. This is clearly shown in the present study when two out of the seven specimens, which had originally been determined as *Gymnallabes typus*, revealed different osteological characters. In addition, an intraspecific variation is noted in the remaining five specimens. It is to be expected, therefore, that in the future, more or less species may be classified under the genus *Gymnallabes*.

This report mainly addresses the skeleton and cranial muscles because differences relating to them are more pervasive. A basic comparative osteology and cranial myology between *Gymnallabes typus* and *Clarias gariepinus* is given. Both species are at the opposite ends of the series, i.e., anguilliform vs. fusiform, respectively. *Gymnallabes typus* is used as a starting point in the description. *Clarias gariepinus* is taken instead of *Clarias poensis* (= *C. camerunensis* [Teugels, '86a]) of the series of Boulenger because much more information on it is available. Intermediate forms on the basis of the external morphology between *G. typus* and *C. gariepinus* can be easily found among the Clariidae. *Clariallabes melas* is used here as such an example; *Channallabes apus* is dealt with only in the Discussion.

The aim of the present work is: (1) to give the main functional-morphological disparities between the anguilliform *Gymnallabes typus*, the fusiform *Clarias gariepinus*, and

the intermediate *Clariallabes melas*, and (2) to comment on the functional implications of the larger jaw muscles of anguilliform clariids. This study is also meant to encourage similar additional observations on Clariidae or of other animal groups to unravel possible convergences.

MATERIALS AND METHODS

The material examined in the present study belongs to the Department of Ichthyology, Koninklijk Museum voor Midden-Afrika (KMMA) Tervuren, Belgium, and the University of Ghent. The research on *Clarias gariiepinus* (Burchell 1822), *Clariallabes melas* (Boulenger 1887), *Gymnallabes typus* (Günther 1867), and *Channallabes apus* (Günther 1873) was carried out on a total of 18 alcohol-preserved specimens. Only specimens of which the most complete data were gathered are listed in Table 1, i.e., *Clariallabes melas*: (KMMA 38495–508) 114–186 mm TL, Kunangu; *G. typus*: (KMMA 92–083-P-0035–0036) 217 mm TL, (KMMA 91–067–0135–0136) 238 mm TL, (KMMA RG84–16-P-1–2) 167 mm TL, Nigeria; *C. apus*: (KMMA 90–29-P-151–163) 273–274 mm TL; Zaire. All other specimens in Table 1 are commercially bred. A dry cranial skeleton of an adult *C. gariiepinus* (194 mm cranium length) was compared with the juveniles of *C. gariiepinus*. Live specimens of *G. typus* and *C. gariiepinus* (commercially obtained) were also observed in a 90 L aquarium. Specimens were sexed by examination of gonads, whereby no differences were noted in the urogenital papilla. All measurements of fresh and alcohol specimens are expressed in millimeters. These consist of the total length (TL), preanal length, body depth at anus, and cranium length. The distance measured

on the cranium, hereafter named “cranium length,” is taken from the rostral tip of the premaxilla to the rostral side of the fourth parapophysis instead of the caudal end of the supraoccipital process (see Discussion). The body depth at anus, expressed as % TL, indicates the degree of anguilliformism of the specimen. Stomach analyses were carried out on all specimens except those that were commercially reared (all *C. gariiepinus*) or kept in captivity (two of the seven *G. typus*). Where not mentioned in the text, relative lengths are expressed in relation to body length. The material was cleared and stained for bone following Taylor and Van Dyke ('85). Vertebral counts exclude those of the Weberian apparatus and the compound caudal centrum. Although the Weberian centrum consists of the fusion of the first five vertebrae (Rademaker et al., '89), the numbering of the remaining vertebrae in this study starts from 1. The last abdominal vertebra is interpreted here as the one located above the anus.

The cranial muscles have been studied only by means of dissection on a 167 and 239 mm TL *Gymnallabes typus*, a 186 mm TL *Clariallabes melas*, and a 166 mm TL *Clarias gariiepinus*. Stated differences between the three species and interpretations about the function of the muscles are based on these dissections. The cranial muscles of *Carias apus* could not be examined due to the poor state of preservation. We have adopted the osteological and myological terms used by Adriaens and Verraes ('96, '97a,b,c, '98) and Adriaens et al. ('97). They provided a thorough account of the ontogeny of the cranial osteology and myology of *C. gariiepinus* and can be consulted for those aspects of the cranium, which are not mentioned here.

TABLE 1. Morphometric (in mm) and meristic characters of four clariid species

	<i>Clarias gariiepinus</i>		<i>Clariallabes melas</i>		<i>Gymnallabes typus</i>					<i>Channallabes apus</i>		
	m	m	m	m	f	m	m	m	m	m	m	f
Sex												
Total length	173	166	117	114	186	217	238	167	214	226	273	274
Preanal length	75	74	41	41	64	65	68	48	58	65	69	63
Body depth at anus	21.4	22	13.4	11.9	20.9	14.2	15	10.5	12	11.5	13.8	13.8
Cranium length	38.0	35.6	18.5	17.6	28.6	23.3	23.7	19.6	23.8	23.0	20.2	19.8
Dorsal fin rays	74	69	96	97	103	102	99	105	109	99	154	155
Anal fin rays	59	58	82	82	86	87	86	87	94	84	51 + 56 ¹	133
Caudal fin rays	29	24	21	21	21	16	18	18	18	19	15	15
Pectoral fin rays	8/8	deformed	8/9	7/8	8/8	7/7	7/7	7/7	7/7	7/7	0	0
Pelvic fin rays	6/5	5/5	6/6	6/6	0/6	6/6	6/6	6/6	6/6	6/6	0	0
Vertebrae	59	59	65	69	71	78	76	76	80	78	108	108
Ribs	12/12	12/12	10/11	11/11	10/11	10/9	9/9	9/9	10/9	8/8	18/18	18/18
Branchiostegal rays	9/9	9/9	9/8	9/9	8/9	10/9	11/11	9/9	9/9	10/11	8/8	8/9

¹One of the two examined *C. apus* exhibited two separate ventral median fins.

Drawings were made with a camera lucida attached to a stereomicroscope. Areas filled with open circles on the drawings represent cartilage.

RESULTS

External morphology

Gymnallabes typus is an agile, brown-colored, eel-like fish of which the most striking feature is its wide gape and long, power-

ful tail. The hypertrophied jaw muscles, which characterize its peculiar head (Fig. 1A,C), are not covered by skull bones as in *Clarias gariepinus*. The terminal, broad mouth is surrounded by large fleshy upper and lower lips, which are fused with each other by a skin fold at the mouth corners. The size of the head, in relation to body length, equals approximately half the size of the head of *C. gariepinus* and increases

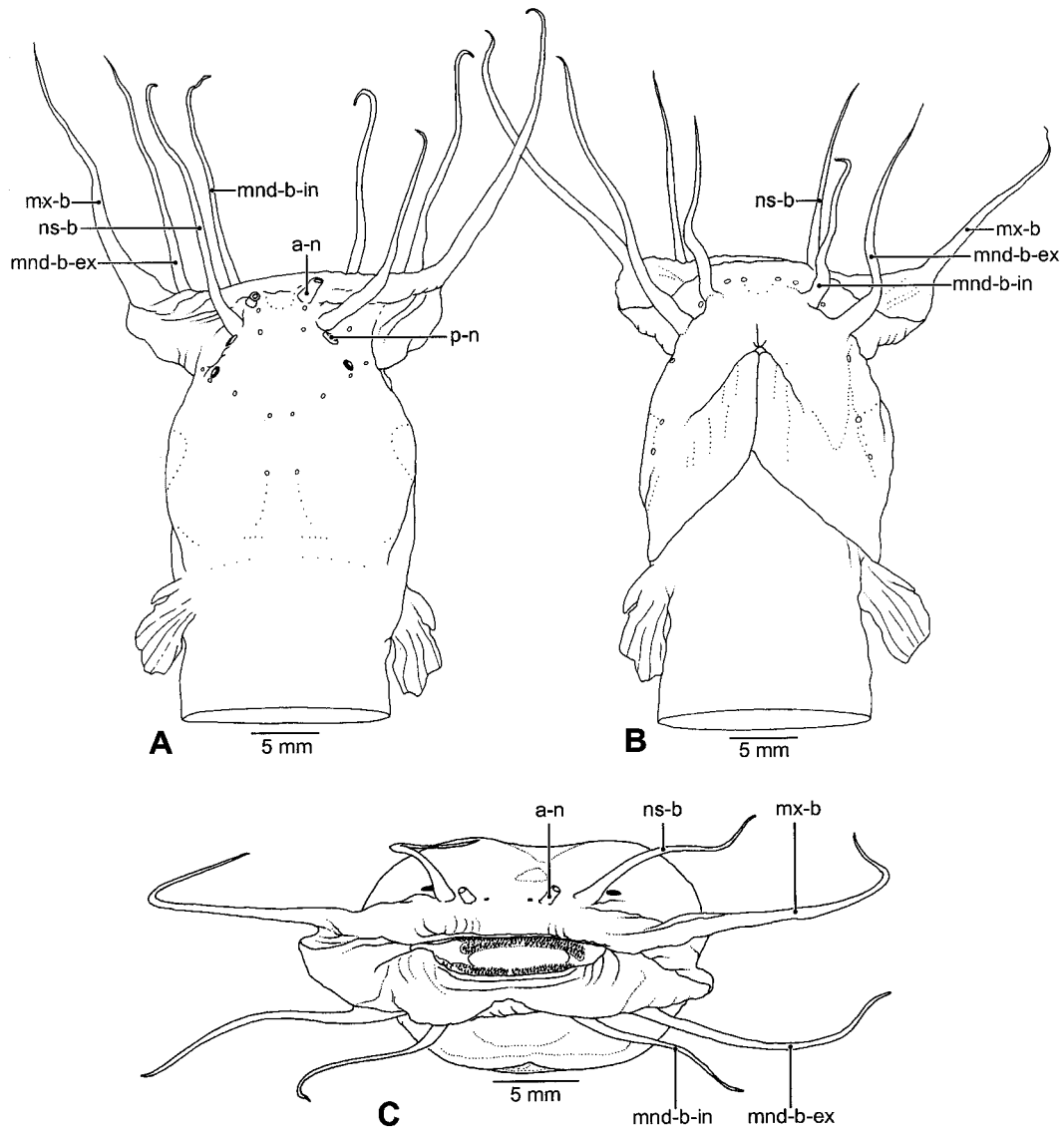


Fig. 1. External morphology of the head of *Gymnallabes typus*. **A**: dorsal; **B**: ventral view of the head (167 mm TL); **C**: rostral view (217 mm TL). a-n, anterior

nostril; mnd-b-ex, external mandibular barbel; mnd-b-in, internal mandibular barbel; mx-b, maxillary barbel; ns-b, nasal barbel; p-n, posterior nostril.

gradually from *G. typus* to *C. gariepinus* (Fig. 2A–C). The eyes are small and positioned dorsally when the mouth is closed. They become gradually larger and more laterally positioned in the series from *G. typus* to *C. gariepinus*.

The body of *Gymnallabes typus* is exceedingly elongate, ovoid behind the head, and laterally compressed caudally. The body depth at the anus is very small. The degree of anguilliformism varies between 5.1% and 6.5%. The other two species in the series become gradually less elongated. The degree of anguilliformism of *Clariallabes melas* is ~11%, whereas that of *Clarias gariepinus* is 13%. The dorsal and anal fins of *G. typus* are confluent with the caudal fin. The dorsal fin starts approximately at a distance from the supraoccipital process, which equals the cranial length. The beginning of the anal fin is located at approximately three times the length of the skull starting from the tip of the head. The median fins of *C. gariepinus* are separated from the caudal fin, but less in *C. melas*. They start gradually more posteriorly in the series. The pectoral and pelvic fins are present (except in one *C. melas* of which the right pelvic fin is missing). The pectoral fins are positioned at the posterior ventrolateral side of the head in the three

species. They have the same length in relation to the skull size, but are slightly broader in *C. gariepinus*. The pelvic fins are abdominal in position, ventrally located, and slightly anterior to the anal fin.

Cranial skeleton

The overall skull of *Gymnallabes typus* is relatively less broad, compared with the other species. Also, the neurocranium of *G. typus* (Fig. 3A) is narrow, whereas that of *Clarias gariepinus* (Fig. 3C) is much broader. The relative size of the neurocranial bones of *Clariallabes melas* (Fig. 3B) is in between those of the other two species, except for some rostral bones (mesethmoid, nasal, ant-orbital), which are nearly identical with those of *G. typus*. The relative size of the skull increases: *G. typus* has approximately an average cranial length of 11% TL, *C. melas* 16% TL, and *C. gariepinus* 22% TL. Histological observations revealed that some cranial bones of *G. typus* are substantially less spongy than those in *C. gariepinus*.

The tubulous nasal bone of *Gymnallabes typus* and *Clariallabes melas*, the anterior-most bone with a supraorbital canal of the lateral line system covering the nasal sac longitudinally, is much more reduced compared with that of *Clarias gariepinus*. The

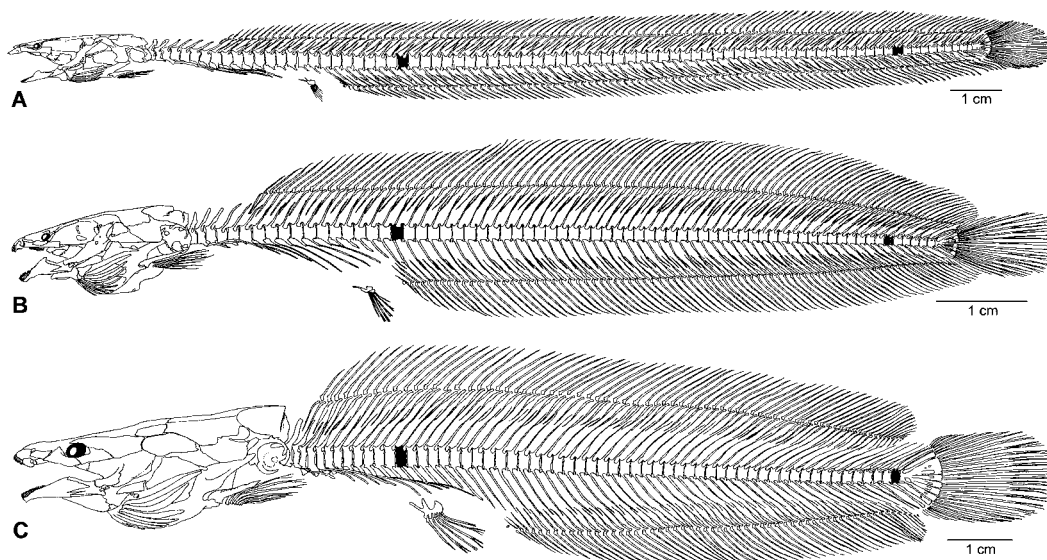


Fig. 2. Lateral view of the skeletons of **A:** *Gymnallabes typus* (214 mm TL); **B:** *Clariallabes melas* (114 mm TL); **C:** *Clarias gariepinus* (173 mm TL). The body sizes are scaled to equal each other in length. The length

between the left and right marked vertebrae, equaling an arbitrary number of 47 vertebrae, is approximately the same for the three species, illustrating that the individual vertebrae do not lengthen in this region.

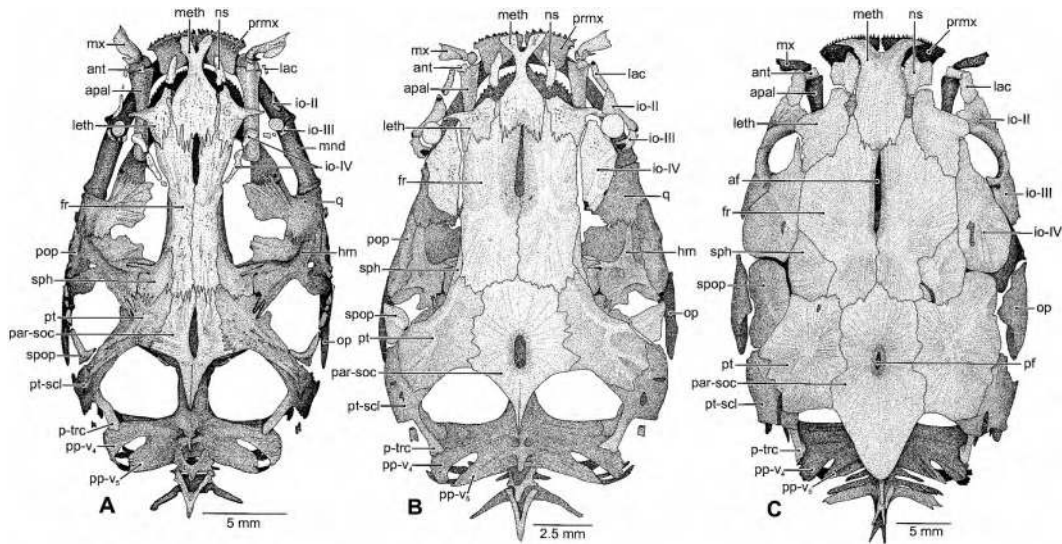


Fig. 3. Dorsal view of the skull of **A:** *Gymnallabes typus* (214 mm TL); **B:** *Clariallabes melas* (114 mm TL); **C:** *Clarias gariepinus* (173 mm TL). The skull of *C. gariepinus* is asymmetrical because the right suprapercle is absent. The vacated territory is taken over by the neighboring bones: the fourth infraorbital, the sphenotic and mainly the pterotic. The distance between the tip of the premaxilla and the caudal side of the braincase (exoccipital) is scaled to the same length. af, anterior fontanel; ant, antorbital; apal, autopalatine; fr, frontal;

hm, hyomandibula; io-II, infraorbital II; io-III, infraorbital III; io-IV, infraorbital IV; lac, lacrimal; leth, lateral ethmoid; meth, mesethmoid; mnd, mandible; mx, maxilla; ns, nasal; op, opercle; par-soc, parieto-supraoccipital; pf, posterior fontanel; pop, preopercle; pp-v₄, parapophysis of vertebra 4; pp-v₅, parapophysis of vertebra 5; prmx, premaxilla; pt, pterotic; p-trc, transscapular process; pt-scl, posttemporo-supracleithrum; q, quadrate; sph, sphenotic; spop, suprapercle.

nasal bone is connected to the surrounding bones (mesethmoid and lateral ethmoid) with connective tissue, which allows a dorsoventral expansion of the nasal cavity.

The mesethmoid of *Gymnallabes typus* and *Clariallabes melas* is narrower behind the two rostral wings compared with that of *Clarias gariepinus*. Because the lateral ethmoid of *G. typus* does not make any contact with the second infraorbital bone, as is found in the other two species, the articulation ridge is absent. The lateral ethmoid of *G. typus* does not make any contact with the fourth infraorbital bone either and is narrower posteriorly to its lateral process.

The antorbital is a very small bone that surrounds the base of the nasal barbel anteriorly with its posteriorly concave shape. It is situated above the rostral tip of the autopalatine, close to the articulation with the maxilla. The infraorbital canal of *Gymnallabes typus* does not run through the antorbital bone as in *Clariallabes melas* and *Clarias gariepinus*.

The infraorbitals of *Gymnallabes typus* are strongly reduced, but are still identifi-

able as the four separate bones observed in *Clarias gariepinus*. The fourth infraorbital of *G. typus* is the largest and is situated posterolaterally of the lateral ethmoid and anterolaterally of the frontal from which it is separated by connective tissue. This bone partly covers the jaw muscle anteriorly. It is sometimes broken in two parts, either on one or on both sides of the cranium. Characteristic for the other infraorbitals of *G. typus* is that they consist of only a neurodermal component, i.e., the part surrounding the sensory canal (Adriaens et al., '97). In addition, they lie far from each other with tiny fragmented bones bridging the gaps between them. The second infraorbital bone lacks a medial ridge to support the eye and does not articulate with the lateral ethmoid, as in the other two species.

The dermal frontals are the largest bones of the skull roof in all three species. The frontals of *Gymnallabes typus* and *Clariallabes melas* reach at their full length nearly the same width, whereas those of *Clarias gariepinus* are broader in the middle. The relative width of the frontals gradually wid-

ens in the series from *G. typus* to *C. gariepinus*. At midline of the skull, the contralateral frontals abut each other whereas they are separated in the front by the anterior fontanel for approximately one-third (*G. typus*) or one-half (*C. gariepinus*) of their entire length. As in most catfishes, this fontanel reaches the mesethmoid. The anastomosis between the supraorbital and the infraorbital canals shifts posteriorly from *G. typus* to *C. gariepinus*. In *G. typus* and *C. melas*, the infraorbital canal branches off from the supraorbital in the frontal bone. In *C. gariepinus*, this bifurcation takes place in the sphenotic bone (Adriaens et al., '97: Fig. 4A).

The sphenotic of *Gymnallabes typus* and *Clariallabes melas* differs substantially from that of *Clarias gariepinus*. The sphenotic of the former species partly forms the sidewall of the neurocranium, whereas that of *C. gariepinus* lines the skull roof dorsally. The sphenotic of *G. typus* interdigitates rostrally with the frontal, to which it abuts laterally, and caudally with the pterotic. In *C. gariepinus*, this bone also makes contact with the fourth infraorbital and the supra-

preopercle laterally (see left side of the aberrant skull in Fig. 3C). Anterolaterally of the sphenotic in *G. typus* and *C. melas*, two long processes descend to interdigitate with the hyomandibula (Fig. 3A,B). Posterolaterally, a cartilaginous ridge articulates with the hyomandibula. The sphenotic of *C. gariepinus* has only one process, which is situated on the ventral side (Adriaens and Verraes, '98: Fig. 21E). The sphenotic of *G. typus* and *C. melas* carries the otic canal that runs from mediorostral to mediocaudal, whereas the sphenotic of *C. gariepinus* carries the anastomosis between the supra- and infraorbital canals.

Similarly, the pterotic of *Gymnallabes typus* curves down, partly forming a dorsal attachment site for the jaw muscle. This bone is nearly horizontal in *Clarias gariepinus*, whereas that of *Clariallabes melas* is intermediate in form. Anterolaterally, pterotic processes interdigitate with the posterodorsal side of the hyomandibula of *G. typus* (Fig. 3A). The number of processes decreases from *G. typus* (3), *C. melas* (2), to *C. gariepinus* (0). The pterotic becomes gradually broader in the series from *G. ty-*

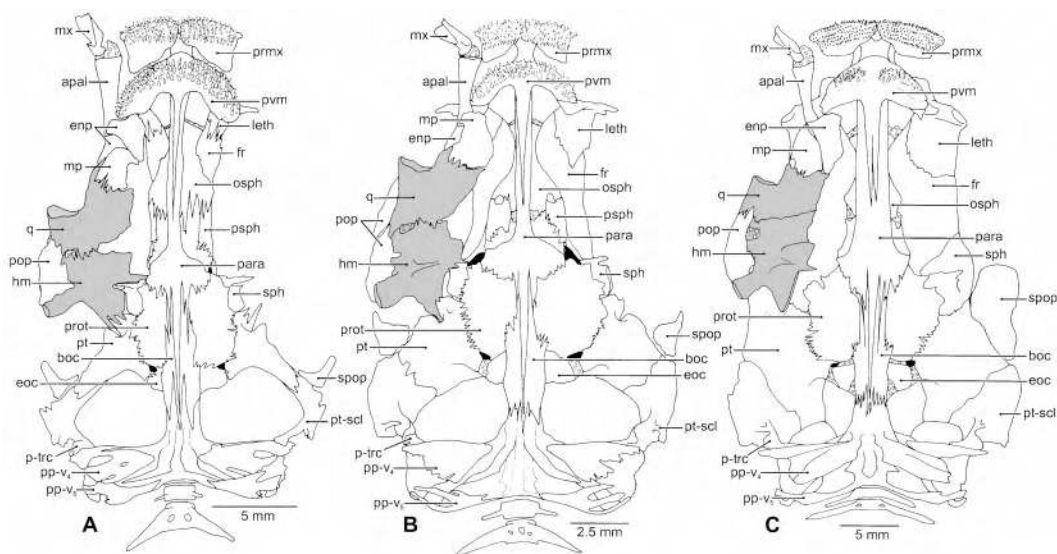


Fig. 4. Ventral view of the neurocranium of **A**: *Gymnallabes typus* (217 mm TL); **B**: *Clariallabes melas* (117 mm TL). The entopterygoid of *C. melas* is half the size of the bone in the other two specimens. **C**: *Clarias gariepinus* (173 mm TL). The prevomer tooth plates are fused with each other in adult *C. gariepinus*. apal, autopalatine; boc, basioccipital; enp, entopterygoid; eoc, exoccipital; fr, frontal; hm, hyomandibula; leth, lateral ethmoid;

mp, metapterygoid; mx, maxilla; osph, orbitosphenoid; para, parasphenoid; pop, preopercle; pp-v₄, parapophysis of vertebra 4; pp-v₅, parapophysis of vertebra 5; p-mx, premaxilla; prot, prootic; psph, pterosphenoid; p-trc, transscapular process; pt, pterotic; pt-scl, posttemporo-supracleithrum; pvm, prevomer; q, quadrate; sph, sphenotic; spop, suprapreopercle.

pus to *C. gariepinus*. Posterolaterally, connective tissue links the pterotic of *G. typus* to the much more reduced suprapreopercle. On the pterotic of *G. typus*, a medial ridge is present for the attachment of the jaw muscle.

The parieto-supraoccipital is situated medioposteriorly of the skull roof and is characterized by a pointed, posteriorly directed process. In some specimens of *Clariallabes melas* and *Gymnallabes typus*, this bone is divided caudal to the posterior fontanel. In one *G. typus*, the parieto-supraoccipital even consists of two symmetrical bones (Fig. 3A). The caudal part of this bone gradually lengthens in the series from *G. typus* to *C. gariepinus*. In dorsal view, the supraoccipital process of *G. typus* almost reaches the fourth vertebra. The parieto-supraoccipital of *C. gariepinus* (Fig. 3C) is larger posteriorly and the supraoccipital process covers the sixth vertebra.

The posttemporo-supracleithrum, which makes contact with the pterotic medially, is the posteriormost dermal, canal bone. The posttemporo-supracleithrum of *Gymnallabes typus* is more reduced compared with that of *Clariallabes melas* and *Clarias gariepinus*. Its transscapular process makes only contact with the rostral side of the fourth parapophysis.

The suspensorium of *Gymnallabes typus* and Siluriformes in general consists of six bones: hyomandibula, preopercle, quadrate, metapterygoid, entopterygoid, and autopalatine (Fink and Fink, '96). The latter, however, develops separately from the pterygoquadrate in Siluriformes (Arratia, '92; Adriaens and Verraes, '97b). The hyomandibula of the three species differs mainly in the number of dorsal processes that interdigitate with the neurocranium. The neurocranial-hyomandibula articulation in *G. typus* and *C. melas* is situated at the level of the posterolateral part of the sphenotic and the anterolateral part of the pterotic (Figs. 3A,B; 4A,B). In *Clarias gariepinus*, the hyomandibula articulates with the ventral side of these bones (Fig. 4C). Because of the reductions of the sphenotic and pterotic in *G. typus*, the dorsal articulation of the hyomandibula is situated more medially and the height of this bone is slightly increased. Dorsally, the hyomandibula of *G. typus* (Fig. 5A,B) can be subdivided in three zones: two to three anterodorsal processes articulating with the sphenotic; a cartilaginous ridge also articulating with the sphenotic; and three pos-

terodorsal processes articulating with the pterotic. The first anterodorsal process is always the largest, the second is smaller, and there may be a smaller third one. The posterodorsal processes grow larger toward the back. The hyomandibula of *C. gariepinus* (Fig. 5C) has only one anterodorsal process. The cartilaginous articulatory ridge of *G. typus* runs parallel with the midline of the skull, but is obliquely oriented in *C. gariepinus* and *C. melas* (Fig. 4A-C). The hyomandibula shifts gradually anteriorly in the series from *G. typus* to *C. gariepinus*. The caudoventrally directed opercular process of *G. typus*, which articulates with the opercle, is situated more posteriorly. The morphology of the quadrate shows no gradual trend in the three species, as the quadrate of *C. melas* is larger than in the others. Its articulatory facet for the lower jaw is situated most anteriorly. This facet is inclined in *C. gariepinus* and *C. melas*, but not in *G. typus*.

The pterygoid bones of the three species differ substantially. In general, the morphology of these bones in the examined specimens is similar to those illustrated in Figure 4, except for the specimen of *Gymnallabes typus* (Fig. 4A) where the right entopterygoid was probably broken during ontogeny, as both parts together make up the entopterygoid in the other specimens. The metapterygoid is defined here as the pterygoid bone, which interdigitates with the quadrate posteriorly. The anterior rim of the metapterygoid of *G. typus* (Fig. 4A) is perpendicular with the long axis of the suspensorium, in contrast with *Clarias gariepinus*, which has an inclined facet (Fig. 4C). The medial ridge of the metapterygoid of *G. typus* is concave and is not used for the attachment of the adductor arcus palatini muscle, as is the case in the other two species. The metapterygoid of *Clariallabes melas* (Fig. 4B) is remarkable in that it almost reaches the lateral wing of the prevomer, thereby leaving less space for the entopterygoid. The metapterygoid of *C. gariepinus* is situated laterad of the entopterygoid, unlike in the other two species. The entopterygoid of *G. typus* is posteriorly separated from the quadrate by the metapterygoid, except laterally. The entopterygoid of *C. gariepinus* is laterally separated from the quadrate, but contacts with it posteriorly. In *C. gariepinus* and *G. typus*, this bone is relatively large, whereas it is small and narrow in *C. melas*.

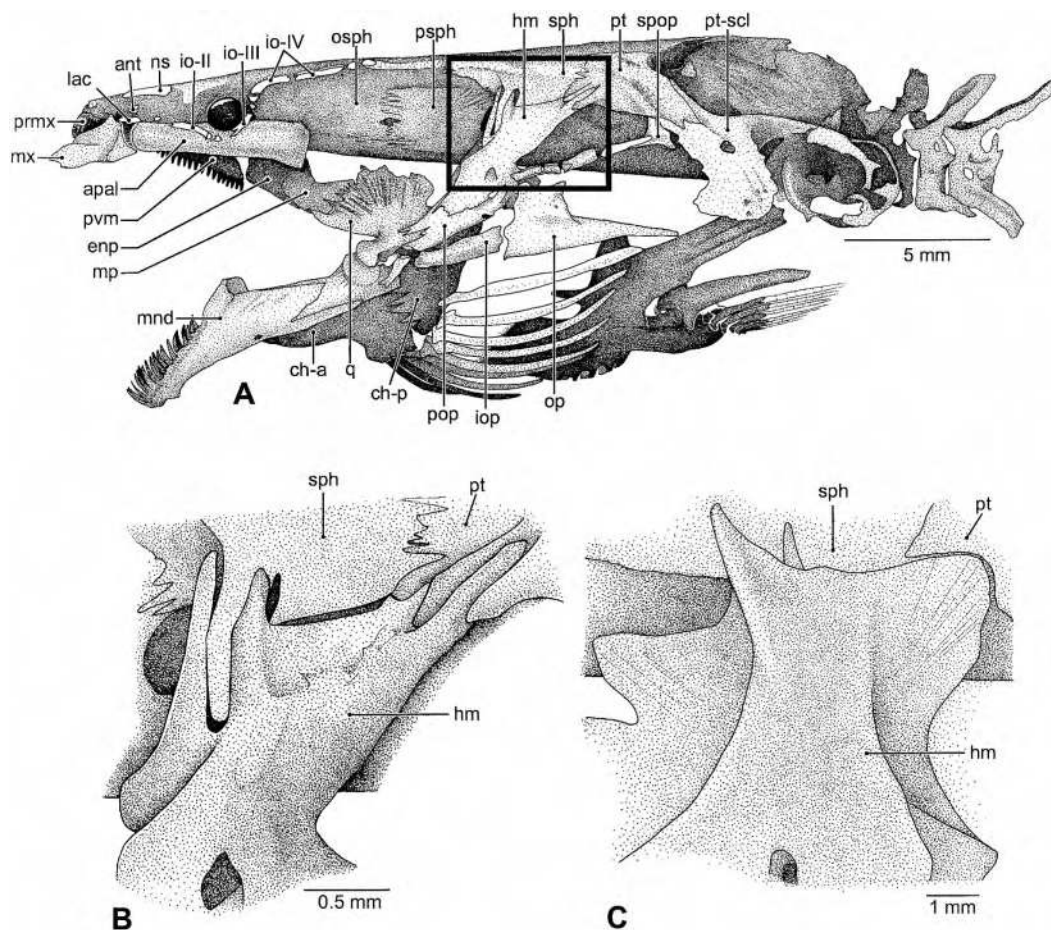


Fig. 5. **A:** Left lateral view of the skull of *Gymnallabes typus* (214 mm TL). **B:** Detail of the upper part of the hyomandibula of *G. typus*. **C:** *Clarias gariepinus*. ant, antorbital; apal, autopalatine; ch-a, anterior ceratohyal; ch-p, posterior ceratohyal; enp, entopterygoid; hm, hyomandibula; io-II, infraorbital II; io-III, infraorbital

III; io-IV, infraorbital IV; iop, interopercle; lac, lacrimal; mnd, mandible; mp, metapterygoid; mx, maxilla; ns, nasal; op, opercle; osph, orbitosphenoid; pop, preopercle; psph, pterosphenoid; prmx, premaxilla; pt, pterotic; pt-scl, posttemporo-supracleithrum; pvm, prevomer; q, quadrate; sph, sphenotic; spop, suprapreopercle.

The entopterygoid forms an insertion area for the adductor arcus palatini muscle in *C. gariepinus*, but not in the others.

The relative size of the lower jaw is largest for *Gymnallabes typus* and shortest for *Clari-allabes melas*, but in the latter it is more massive. The coronoid process on the lower jaw of these species is much more developed, compared with *Clarias gariepinus* (Fig. 6A–C). The mandibular symphyseal surface in *G. typus* and *C. melas* is also larger than that in *C. gariepinus*. An additional difference between the lower jaws of these species, is the position of the teeth. The anterior lower jaw of *G. typus* is covered with posteri-

only directed teeth, almost up to the coronoid process. The dental tooth rows gradually shorten in the other two species, but are rostrally more numerous in *C. melas*.

Also, some ventrally situated bones differ between the species (Fig. 4A–C). The premaxilla is gradually becoming shorter in the series from *Gymnallabes typus* to *Clarias gariepinus*. The anterior ventral half of it in *G. typus* and *Clari-allabes melas* is covered with four to five rows of pointed, curved teeth that are directed posteriorly. The premaxillary tooth plate of *C. gariepinus* is covered more densely and with smaller teeth. The nasal sac of *G. typus* is much

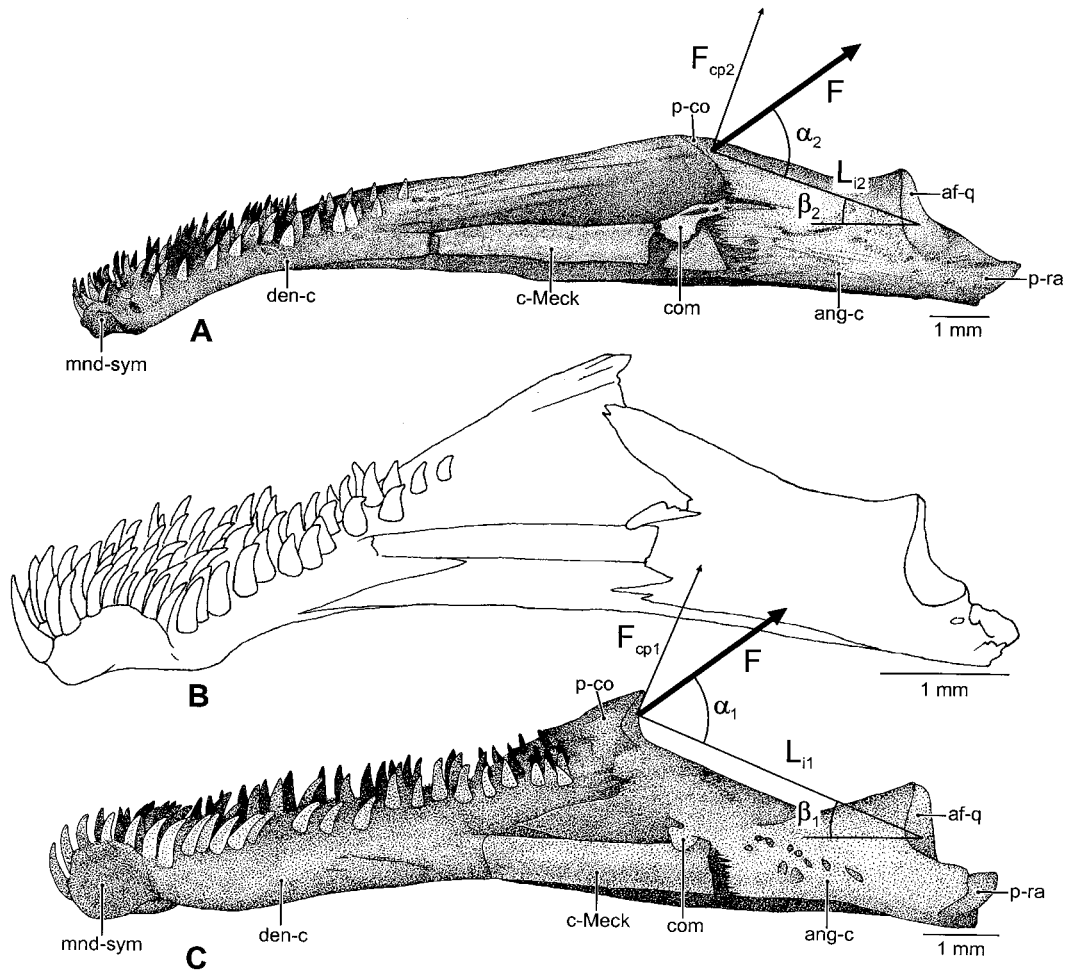


Fig. 6. Medial view of the lower jaws of **A:** *Gymnallabes typus* (217 mm TL); **B:** *Clariallabes melas* (117 mm TL); **C:** *Clarias gariepinus* (173 mm TL). The lower jaws are scaled to the same length. The higher coronoid process of *G. typus* ($\beta_1 > \beta_2$) results in a larger power arm or input length L_{i1} and vertical force vector F_{cp1} of the jaw adductor muscle compared to L_{i2} and F_{cp2} of *C.*

gariepinus, respectively ($\alpha_1 = \alpha_2$). af-q, articular facet of the mandible with the quadrate; ang-c, angulo-splenio-articulo-retroarticular complex; c-Meck, cartilago Meckeli; com, coronomeckelian bone; den-c, dento-splenio-mentomeckelium complex; mnd-sym, mandibular symphysis; p-co, coronoid process; p-ra, retroarticular process.

more supported by this bone than in *C. gariepinus*. The axe-shaped prevomer abuts the mesethmoid ventrally and interdigitates caudally with the parasphenoid through a long pointed spine. The prevomer of *C. gariepinus* has a bifurcated spine. The prevomer tooth plate of *G. typus* is laterocaudally more extended than that of *C. gariepinus*, even touching the entopterygoid. The left entopterygoid of one examined *G. typus* is even partly covered with teeth, probably as a result of its fusion with the

prevomer tooth plate. Straight conical teeth cover the prevomer tooth plate of *G. typus* and *C. melas*. The prevomer tooth plate of *C. gariepinus* is packed more densely with smaller teeth. Here, a distinction can be made between granular teeth centrally and villiform teeth at the lateral edge. The parasphenoid, the largest part of the neurocranial floor, is broader in *C. gariepinus*. It is striking to see that the braincase of *C. melas* is much broader compared to the other two species.

Gymnallabes typus is further specialized in having the anterior ceratohyal and the dorsal and ventral hypohyal greatly expanded, forming a broad surface for the origin of the hyohyoideus inferior muscle. The ventral hypohyal of *G. typus* is posteroventrally more elongated than in *Clarias gariepinus*. The dorsal hypohyal is much smaller than the previous bone but both are larger than those of *C. gariepinus*. No major differences were observed in the bones of the branchial basket and in the pharyngeal tooth plates of the three species.

Cranial myology

The adductor mandibulae of *Gymnallabes typus* is an enormous muscle, covering nearly the entire dorsolateral side of the skull. This muscle is formed by an external A_2A_3' -part and an internal, smaller A_3'' -part. One part of A_3 , hereafter referred to as A_3' , is indistinguishably fused with A_2 , whereas the medial part of A_3 , hereafter referred to as A_3'' , forms a separate muscle (Adriaens and Verraes, '96).

The bipinnate A_2A_3' muscle of *Gymnallabes typus* is nonhomogenous in that the fiber length and fiber angle differ. The fibers are arranged at mixed angles on the sheet-like tendon with the posterior fibers being shorter and more inclined. The A_2A_3' (Fig. 7A) can be subdivided into a dorsal $A_2A_3\alpha'$ -part and a ventral $A_2A_3\beta'$ -part, which are both attached to a broad aponeurosis connected to the coronoid process. The upper part, $A_2A_3\alpha'$, is attached to the ventral side of the fourth infraorbital, the complete ventrolateral ridge of the frontal, the dorsal side of the sphenotic, almost the fully dorsal side of the pterotic, the medial side of the most caudal suprapreopercle, and the rostral part of the posttemporo-supracleithrum. Some external fibers are attached to connective tissue under the skin where in *Clarias gariepinus* the fourth infraorbital is situated. $A_2A_3\beta'$ is posteriorly musculously connected with the lateral side of the suspensorium: the lowermost part of the hyomandibula, the preopercle, and the caudal side of the quadrate. The muscle fibers of the external adductor mandibulae run in such a direction that they form a transition, starting from the horizontal fibers of the $A_2A_3\beta'$ into the vertically directed fibers of $A_2A_3\alpha'$.

The deeper part of the adductor mandibulae, A_3'' (Fig. 7C), is connected with the neurocranium and the suspensorium as well. This muscle is dorsocaudally separated from

A_2A_3' by the levator arcus palatini and is situated against the caudolateral part of the retractor tentaculi. The A_3'' muscle of *Gymnallabes typus* can also be subdivided, but in a lateral pars superficialis and a medial pars profunda. The adductor mandibulae A_3'' pars superficialis, which lies against the medial side of the levator arcus palatini, forms the biggest part of the A_3'' muscle. Posteriorly, the A_3'' is connected with the ventrolateral ridge of the frontal, just under the otic canal, the anterolateral side of the sphenotic, and the lateral side of the pterosphenoid and parasphenoid. On the suspensorium, this part of the A_3'' is attached to the caudal part of the quadrate and the anteromedial cavity of the hyomandibula. The pars profunda is caudally attached to the anteromedial membranous plate of the hyomandibula, to which the retractor tentaculi is connected more anteriorly. Rostrally, A_3'' inserts tendinously on the dorsomedial side of the angular complex, medially of the A_2A_3' tendons. Similarly, the direction of the muscle fibers of the internal adductor mandibulae ranges from a horizontal to a vertical position. The same bones of insertions of the adductor mandibulae in *G. typus* are found in *Clariallabes melas*. Compared to *Clarias gariepinus*, the adductor mandibulae A_2A_3' of *G. typus* is greatly expanded. The frontal, pterotic, and posttemporo-supracleithrum bones form new attachment sites. The insertions and morphology of the adductor mandibulae A_3'' , however, are more or less equal to those of *C. gariepinus*. However, the deeper part of the A_3'' in *G. typus*, the adductor mandibulae A_3'' pars profunda, is completely separated from the pars superficialis.

The levator arcus palatini is a flat muscle that connects the ventrolateral side of the neurocranium with the suspensorium (Fig. 7B) and separates A_2A_3' posteriorly from the A_3'' muscle. In *Gymnallabes typus*, the levator arcus palatini is mainly attached to the ventrolateral side of the frontal, but also on the anterolateral part of the sphenotic and the caudolateral part of the lateral ethmoid. The levator arcus palatini of *Clarias gariepinus* (Adriaens and Verraes, '97a: Fig. 7B) extends more to the front and covers the complete ventrolateral side of the latter bone. With regard to the suspensorium, there is a partly muscular and aponeurotic connection on the rostral crest of the hyomandibula, whereas in *C. gariepinus*, the attachment is only aponeurotic. The sphenotic of *G. typus*

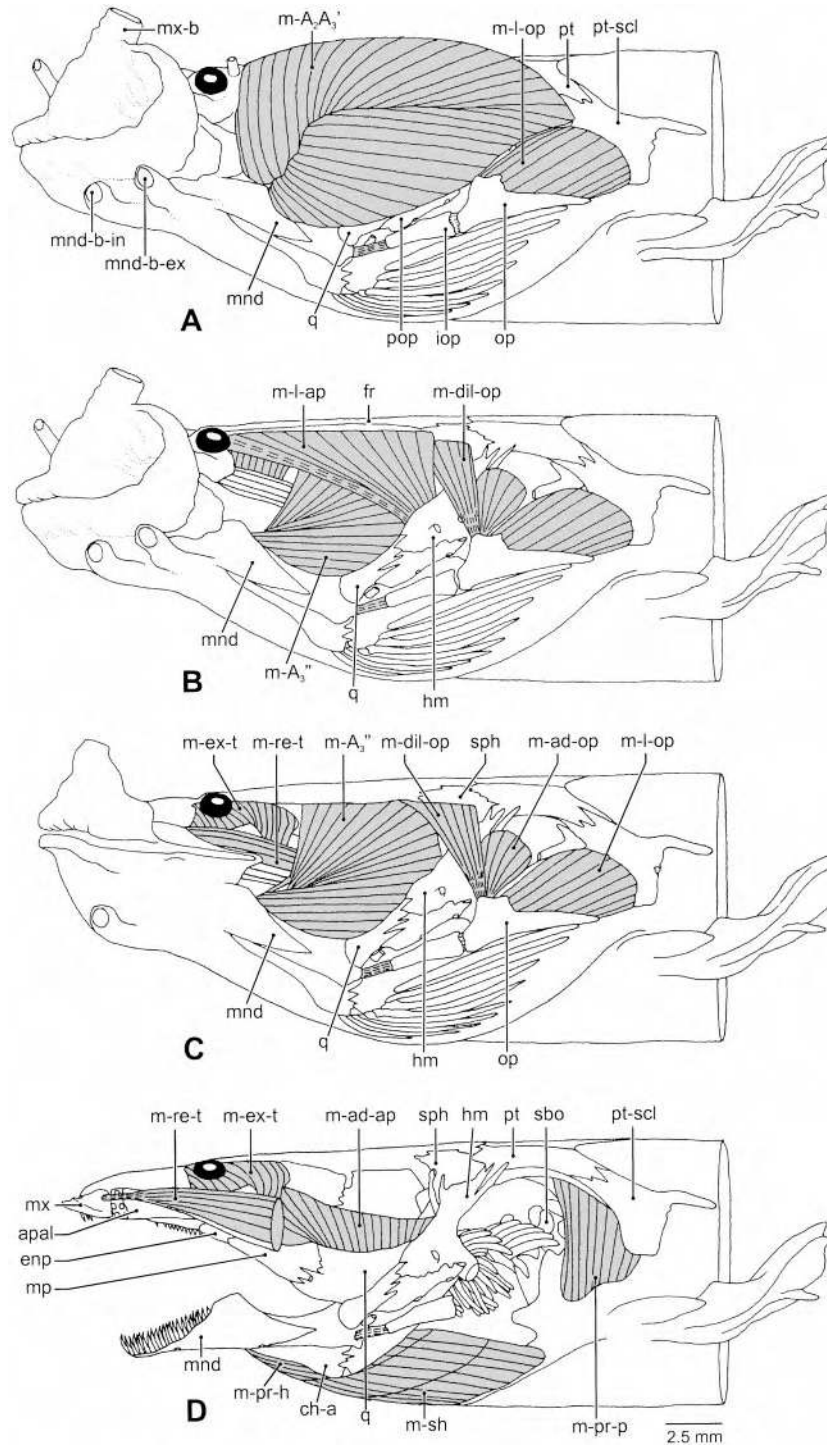


Figure 7

forms an additional insertion area, whereas an attachment on the fourth infraorbital and the quadrate, as is the case in *C. gariepinus*, is missing. Contraction of this muscle abducts the suspensorium and causes an expansion of the orobranchial cavity.

The adductor arcus palatini, the antagonist of the previous muscle, connects the neurocranium with the dorsal rim of the suspensorium (Fig. 7D), lining the mouth cavity laterodorsally. The adductor arcus palatini lies medially of the caudal part of the retractor and extensor tentaculi. The muscle fibers of the adductor in *Gymnallabes typus* originate mainly on the lateral side of the parasphenoid, but also on the pterosphenoid and the orbitosphenoid. On the suspensorium, the muscle is inserted on the medial side of the hyomandibula rostral plate and on the full medial edge of the quadrate. The adductor arcus palatini consists of sparsely tendinous parts, which are most prominent in *Clariallabes melas*, running parallel with the muscle fibers. The fibers run in a transversal plane, with the rostral fibers more obliquely oriented. The metapterygoid and entopterygoid are additional attachment sites in *Clarias gariepinus*, the former bone only for *C. melas*.

The opercular muscles comprise three muscles. The flattened dilatator operculi, being the most rostral one, covers the upper lateral side of the hyomandibula. The rostral part of the dilatator operculi is situated between the adductor mandibulae A_3'' and the levator arcus palatini. The dilatator operculi of *Gymnallabes typus* (Fig. 7C) starts

from the posteroventral part of the frontal, the lower lateral part of the sphenotic and the upper lateral part of the hyomandibula. The muscle fibers run mainly dorsoventrally and insert tendinously on the dorsal process of the opercle, close to the articulation with the hyomandibula. This muscle is shorter and not attached to the lateral ethmoid as in *Clarias gariepinus*, where the fibers are more horizontally oriented (Adriaens and Verrees, '97a: Fig. 7C).

The adductor operculi (Fig. 7C) is a thicker, shorter muscle connecting the dorsocaudal ridge of the hyomandibula with the opercle. In *Clarias gariepinus*, this muscle lies in a cavity of the hyomandibula, which is absent in *Gymnallabes typus*. Dorsocaudally this muscle is also attached to connective tissue, which covers the dorsolateral side of the suprabranchial cavity. The adductor operculi is covered anteriorly by the dilatator operculi. The adductor inserts musculously on the medial side of the opercular dorsal process, caudolaterally of the opercular process of the hyomandibula, as is the case in *C. gariepinus*. The muscular insertion of this muscle and the tendinous insertion of the dilatator operculi on the opercle seem to be fused with each other.

The levator operculi is the most solid of the three opercular muscles. In *Gymnallabes typus* (Fig. 7C), this muscle originates on the caudolateral edge of the pterotic, the complete rostral rim of the posttemporo-supracleithrum, and partly on the connective tissue lining the dorsolateral wall of the suprabranchial cavity. The posttemporo-supracleithrum of *G. typus* forms a new attachment site compared with the other two species and results in a more inclined levator muscle. Ventrally, the levator operculi inserts almost on the entire upper ridge of the opercle.

Ventrally situated cranial muscles show peculiar differences as well. The hyoid bars are connected with the lower jaws by a large, compact muscle, the protractor hyoidei. At the ventral face of the head, rostrally of the isthmus, this muscle is seen as a U-shape (Fig. 1B). The ventral side of the lower jaw, except caudally, is completely covered by it. The protractor consists of a ventral part (Fig. 8A), penetrated by the mandibular barbels, and a dorsal part (Fig. 8B). Caudally, the muscle fibers originate on the ventrolateral side of the anterior ceratohyal, lateral to the attachment of the hyohyoideus infe-

Fig. 7. Lateral view of the head musculature of *Gymnallabes typus* (238 mm TL). **A:** Skin and barbels are removed. **B:** External jaw muscle is removed. **C:** Levator arcus palatini is removed. **D:** Internal jaw muscle and opercular muscles are removed. The caudal part of the retractor tentaculi is cut away. apal, autopalatine; ch-a, anterior ceratohyal; enp, entopterygoid; fr, frontal; hm, hyomandibula; iop, interopercle; m- A_2A_3' , external part of the adductor mandibulae muscle; m- A_3'' , internal part of the adductor mandibulae muscle; m-ad-ap, adductor arcus palatini muscle; m-ad-op, adductor operculi muscle; m-dil-op, dilatator operculi muscle; m-ex-t, extensor tentaculi muscle; m-l-ap, levator arcus palatini muscle; m-l-op, levator operculi muscle; mnd, mandible; mnd-b-ex, external mandibular barbel; mnd-b-in, internal mandibular barbel; mp, metapterygoid; m-pr-h, protractor hyoidei muscle; m-pr-p, protractor pectoralis muscle; m-re-t, retractor tentaculi muscle; m-sh, sternohyoideus muscle; mx, maxilla; mx-b, maxillary barbel; op, opercle; pop, preopercle; pt, pterotic; pt-scl, posttemporo-supracleithrum; q, quadrate; sbo, suprabranchial organs; sph, sphenotic.

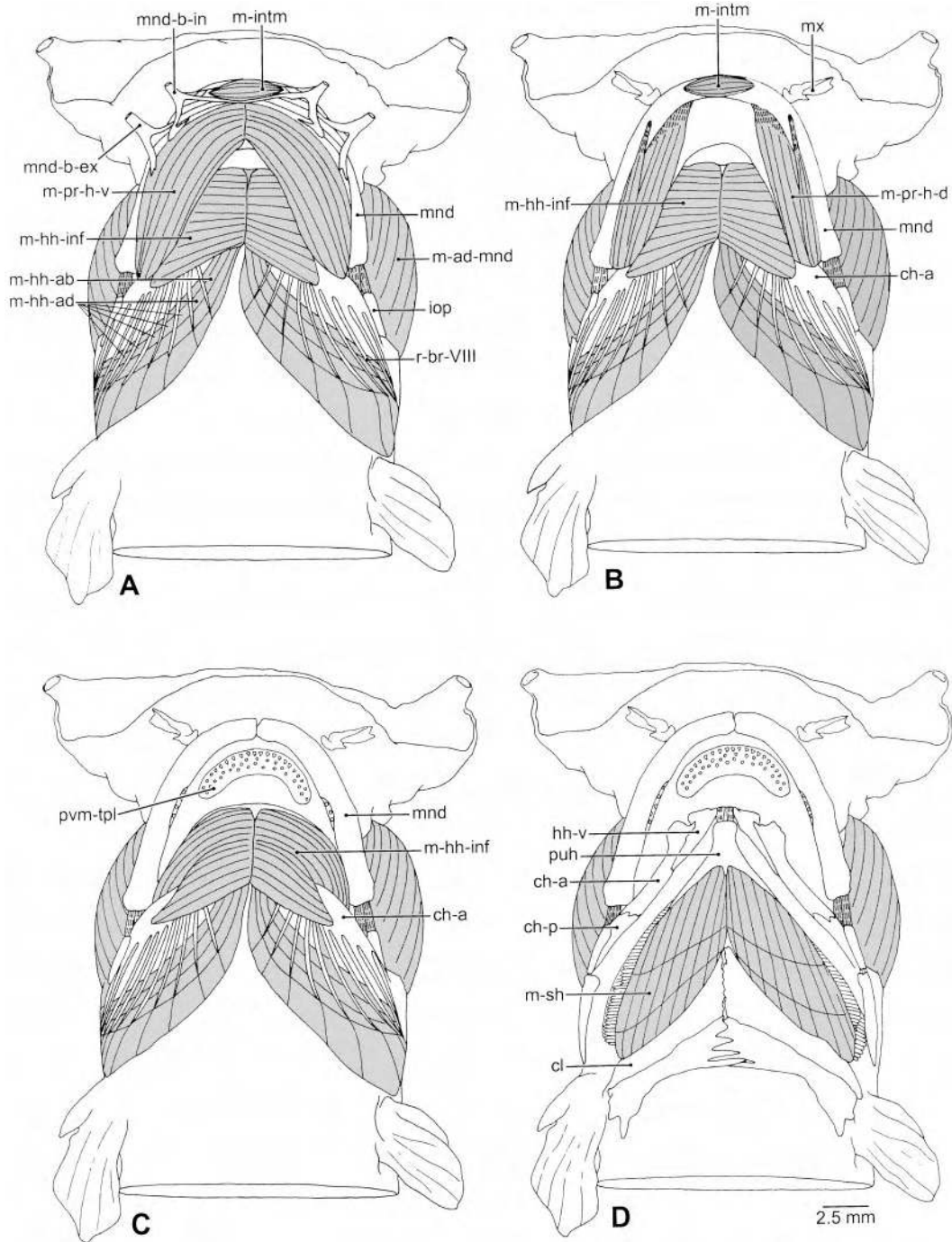


Fig. 8. Ventral view of the head musculature of *Gymnallabes typus* (238 mm TL). **A:** Skin and barbels are removed. **B:** Ventral part of the hyoid protractor is removed. **C:** Hyoid protractor and connective tissue between the jaws are removed. **D:** Hyohyoideus inferior is removed. ch-a, anterior ceratohyal; ch-p, posterior ceratohyal; cl, cleithrum; hh-v, ventral hypohyal; iop, interopercle; m-ad-mnd, adductor mandibulae muscle; m-hh-ab, hyohyoideus abductor muscle; m-hh-ad, hyohyoidei

adductores muscles; m-intm, intermandibularis muscle; mnd, mandible; mnd-b-ex, external mandibular barbel; mnd-b-in, internal mandibular barbel; m-hh-inf, hyohyoideus inferior muscle; m-pr-h-d, protractor hyoidei pars dorsalis muscle; m-pr-h-v, protractor hyoidei pars ventralis muscle; m-sh, sternohyoideus muscle; puh, parurohyal; pvm-tpl, prevomerale tooth plate; r-br-VIII, branchiostegal ray VIII.

rior. The left and right ventral parts are rostrally connected with each other by an aponeurosis, which is tightly connected with the lower jaws. The dorsal part consists of two parts, which cannot be distinguished from each other caudally. It is the medial part of the protractor hyoidei dorsalis of *Gymnallabes typus* that differs substantially with that of *Clarias gariepinus*. In the latter, the contralateral parts of it are connected with each other in the medial plane by an aponeurosis (Adriaens and Verraes, '97c: Fig. 6B). In *G. typus*, however, the two parts are not connected with each other, but are attached to the caudal side of the lower jaws.

Another hyoid muscle of *Gymnallabes typus*, the hyohyoideus inferior (Fig. 8C), shows a different morphology. This muscle covers the ventral side of the anterior ceratohyal and the ventral and dorsal hypohyal, and consists of a rostral and a caudal part. No such a distinction, however, is seen in *Clarias gariepinus* (Adriaens and Verraes, '97c: Fig. 8A). The contralateral fibers are medially connected to an aponeurosis. The rostral part in *G. typus* is thicker and caudolaterally not only connected with the anteroventral side, but also with the lateral side of the anterior ceratohyal.

Finally, the sternohyoideus of *Gymnallabes typus* (Fig. 8D), which seems to be larger than in *Clarias gariepinus*, connects the pectoral girdle with the hyoid bars through the parurohyal. The cleithrum bears a rostrally directed wing to which the sternohyoideus is attached. This muscle is composed of three myomeres separated by two myocommata. The rostral myomere is the largest, whereas in *C. gariepinus*, the maximum length of the three myomeres is equal (Adriaens and Verraes, '97c: Fig. 8C). Furthermore, the myocommata are positioned less inclined than in *C. gariepinus*.

No differences were observed in the other cranial muscles of the three species, such as the extensor and retractor tentaculi, the hyohyoideus abductor, and the hyohyoidei adductores.

Suprabranchial organs

The suprabranchial organs (Fig. 7D) consist of an anterior and a posterior structure, situated on the second and fourth epibranchials, respectively. The anterior structure is always smaller than the posterior one. Both organs of *Gymnallabes typus* are much more reduced, but less in *Clariallabes melas* com-

pared with *Clarias gariepinus*. The anterior suprabranchial structures of *G. typus* are either absent or consist only of one vesicle, whereas that of *C. melas* counts two to three vesicles. The suprabranchial organs of *C. gariepinus* are most developed and reach the skull more posteriorly.

Postcranial skeleton

A comparison of the three species with each other reveals that tail length is allometric. The mean number of caudal vertebrae increases from 38 (*Clarias gariepinus*) to 64 (*Gymnallabes typus*). The number of abdominal vertebrae is approximately the same for *Clariallabes melas* and *G. typus*, but slightly more for *C. gariepinus*. *Gymnallabes typus* (Fig. 2A) exhibits 76 to 80 vertebrae (maximum 17 abdominal and 64 caudal vertebrae). These numbers are lower than those of the *G. typus* specimens (123 mm and 195 mm TL) described by Poll ('77), who counted 89 vertebrae, 15 of which are abdominal and 74 caudal. The urogenital porus (which is situated anteriorly of the pelvic girdle in one aberrant specimen) is positioned ventrally between vertebrae 14 to 17. The number of abdominal vertebrae of *G. typus* is variable as observed in some other clariids. *Clariallabes melas* (Fig. 2B) exhibits 65 to 71 vertebrae (maximum 17 abdominal and 54 caudal vertebrae), whereas *C. gariepinus*. (Fig. 2C) has 59 vertebrae (56 to 63 [Teugels, '86b]) (maximum 21 abdominal and 40 caudal vertebrae) (Table 1). In addition, the abdominal vertebrae are more compressed in an anteroposterior direction in *C. gariepinus*, and least in *G. typus*. Articulation facets between the vertebrae are most pronounced in *G. typus*. The neural and haemal spines of *G. typus* are more inclined toward the back with the first haemal spine (left and right haemal spine fused distally) originating between vertebrae 14 and 17. In *C. melas* (in two of the three specimens) and in *C. gariepinus*, these haemal spines are situated more in the front, at vertebrae 12 or 13. From the first, second, or third to the ninth, tenth, or eleventh vertebrae, 8 to 10 pleural ribs connect the lateral parapophyses of *G. typus*, occasionally followed by a rudimentary one, floating in the abdominal wall. The parapophyses of the second vertebra are the longest, whereas those of the first vertebra are hardly developed (Fig. 3A). The parapophyses of the anterior abdominal vertebrae of *C. gariepinus* are much larger than in the other two species. *Clariallabes melas* has 10 or 11 pairs of

ribs and *C. gariiepinus* 12. The distance between the pterygiophores and the vertebral column increases, together with an increasing body height, in the series from *G. typus* to *C. gariiepinus*. One or two pterygiophores are present between successive neural and haemal spines. The number of pterygiophores, for instance for every 30 vertebrae, slightly decreases from *G. typus* to *C. gariiepinus*.

The number of dorsal and anal fin rays of *Gymnallabes typus* does not lie within the specified intervals defined by Poll ('77), but varies between 99 to 109 dorsal fin rays and 84 to 94 anal fin rays. Only the proximal radials of the pterygiophores of both fins are ossified and osseous distal radials are absent, except in some *G. typus* where tiny bones can be seen. The caudal fin of *G. typus* has a maximum total (principal plus procurrent) of 19 fin rays. The maximum numbers of dorsal, anal, and caudal fin rays of *Clariallabes melas* observed is 97, 82, and 21, respectively. For *Clarias gariiepinus*, these numbers are 74, 59, and 29. The caudal skeleton of *G. typus* differs intraspecifically in the number of hypurals fused with each other, ranging from two to all. The parhypural is not fused with the ventral hypurals. The hypurals of the caudal skeleton of observed *C. gariiepinus* are not fused with each other (except in one specimen), whereas they are in *C. melas*.

The pectoral fins of *Gymnallabes typus* have mostly a nonserrated spine and seven fin rays that articulate with three proximal radials of which the most anterior is less ossified. The number of pectoral fin rays in *Clariallabes melas* and *Clarias gariiepinus* is, respectively, 7–9 and 9–10. Their pectoral spines are serrated at both sides. No major differences were seen in the pectoral girdles of the three species, except that the girdle in *C. melas* consists of more massive bones and that the anterior rim of the cleithrum has a concave shape in *G. typus*. Similarly, the Weberian apparatus in *C. melas* is more strongly built. The pelvic fins of all three species exhibit six fin rays, which articulate with the basipterygium of the pelvic girdle; osseous radials are absent. The morphology of the basipterygium is the same in the three species. The length of the paired and caudal fins, in relation to body length, increases in the series, whereas the length of the dorsal and anal fins decreases. Paired and unpaired fins have bifurcated rays, but the

dorsal and anal fin rays are only split at the caudal part of the fin. These fin rays are not divided to their base.

DISCUSSION

The differences seen in the three species, *Gymnallabes typus*, *Clariallabes melas*, and *Clarias gariiepinus*, cannot be attributed to the difference in developmental stage, although the studied species represent fishes of differing body lengths. The studied fishes showed within their species essentially no obvious allometric growth in overall skull morphology. The jaw muscles in a 167 mm TL *G. typus*, for instance, have a similar morphology as in a 238 mm TL adult. Therefore, it appears acceptable to compare species of a different length with each other on the basis of their skeleton and cranial myology.

The impact of the enlargement of the adductor mandibulae and its effect on the overall skull is discussed. It is also considered whether skull remodeling (narrowing of the neurocranium as a result of the increase of the jaw adductors) is related with body elongation.

Significance of larger jaw muscles in Gymnallabes typus

When *Gymnallabes typus* is put in an aquarium without ground cover, it hastily senses the bottom with its lips and barbels. While it is swimming, it bends its head and pushes its mouth against the bottom as if it were searching for an opening. A burrowing *G. typus*, however, has not been reported so far in the literature and neither has it been seen during our observations, either in gravel or in sand. It should be feasible, however, bearing in mind that the related but more elongated *Channallabes apus* can burrow themselves in mud (Lambert, '60; Matthes, '64) or in gravel (personal observation). Although the suprabranchial organs of *G. typus* are considerably reduced compared with those of *Clarias gariiepinus*, it still strongly depends on atmospheric respiration in oxygen-poor water. It was also seen in the aquarium that *G. typus*, which were put together in a group, seemed to be fond of each other, rubbing their skins on one another and nesting closely together on the bottom. A totally different behavior was observed when only two individuals were kept together. They assumed quite aggressive fights, which involved biting each other's tails and grasping movements of the mouth.

The food habits of *Gymnallabes typus* have not been reported yet. Only Matthes ('64) carried out a stomach analysis on one specimen of 75 mm. The stomach content consisted of some sand, one ostracod, one hydracrid, and a few insect larvae. Personal stomach analyses on the specimens caught in their natural habit revealed sand, insect larvae, snail shells, fish scales, termites, a horsehair worm, and plant material. Although they probably prey on anything that is edible, the short gut of *G. typus* indicates mainly a carnivorous diet. According to Matthes ('64), other eel-like clariids, such as *Dolichallabes microphthalmus* and *Channallabes apus*, are omnivorous. Presenting *G. typus* with live prey, such as mealworms (*Tenebrio molitor*), fly larvae, water fleas (*Daphnia pulex*), earthworms (*Lumbricus terrestris*), zebra fish (*Danio rerio*), but also canned mackerel, was successful. When it was predated live fishes, voracious *G. typus* attained a high initial speed. It seemed that food with an easily dispersible flavor, such as fresh salmon or canned mackerel, was most favored, but whether they locate their food primarily by cutaneous senses or by olfaction is unknown. Sometimes, *G. typus* takes up sand, which it will spit out later, possibly partly filtered, explaining the presence of some sand in the stomach. When the mouth gape is wide, the mouth folds are stretched and form a funnel, an advantage for sucking up small invertebrates and preventing potential food from escaping.

The three basic feeding modes of the anguillids occur also in *Gymnallabes typus*, i.e., 1. suction of food; 2. grasp and shake, which entails grasping of larger items in the mouth while shaking head and body, thereby tearing off small pieces; and (3) rotational or spin feeding, which entails grasping of larger items in the mouth and spinning on the long axis, thereby tearing larger prey items into smaller pieces (Helfman and Clark, '86). The first feeding mode in *G. typus*, suction of food, was observed with *Daphnia*. As an experiment, a large piece of frozen salmon was tied to a weight in the aquarium. The meat could not be torn easily, but *G. typus* was able to jerk off small pieces of the larger item by grasping and shaking its head. Most of the time, the body swung itself in a U-shaped position, before grasping the food. Rotational feeding was not as pronounced as was observed in the eel by Helfman and Clark ('86) and was combined with the sec-

ond mode of feeding. *Gymnallabes typus* did not manage to tear off pieces out of a big chunk of salmon, which was presented free in the aquarium, by shaking its head. It took it in its wide-open mouth instead and returned to its hiding place where it started processing the food. This extensive meal resulted in an enormous swollen belly. Apparently, these fishes are well suited to this kind of feeding behavior. The number of empty stomachs encountered could be explained by the fact that *G. typus* do not have to feed continuously, because the large dimensions of the prey enable them to eat a considerable amount of food in a short period, reducing their need to forage. Another explanation could be that captured specimens were kept alive for a while before being put in formalin, so that their stomach content was already digested.

Stomach analyses of *Clariallabes melas* revealed only fish scales, whereas the stomach of *Channallabes apus* contained one grasshopper and plant material. *Clarias gariepinus* in general is also an omnivorous scavenger whose food consists mainly of fishes, terrestrial invertebrates, aquatic insects, and zooplankton (Groenewald, '64; Clay, '79). Spin feeding in *C. gariepinus*, as mentioned by Helfman and Clark ('86), is not a plausible feeding form for fish with a fusiform body. In general, it can be stated that in nature clariids tend to feed on almost any food with a preference for animal material (Clay, '79).

The adult skull of *Gymnallabes typus* (Fig. 3A) shows characteristics that correspond with the other anguilliform clariids such as *Channallabes apus* (personal observation) and *Dolichallabes microphthalmus* (Poll, '42b). There is no bony protection above the jaw muscles, nor is there one between the neurocranium and the parapophyses of the fourth vertebra. The nasal sac is partly covered by the nasal bone, the infraorbital bones are small and tubulous, the eyes are reduced, and there is a wide gap between the fourth infraorbital and the suprapreopercle, both of which are small bones. The neurocranial bones of *Clarias gariepinus* (Fig. 3C), in contrast, form a closed, broad roof, whereas the neurocranial width of *Clariallabes melas* (Fig. 3B) is situated in between. The most conspicuous feature of the head of *G. typus* is its enormous jaw muscles, which nearly cover the entire dorsolateral side of the head. It is primarily the external part of

the jaw muscle that reduces in the series from *G. typus* to *C. gariepinus* (Fig. 9A–C). The relative enlargement of these muscles in *G. typus* was possible because the broadened aponeurosis in the bipinnate jaw muscle provided a larger attachment side for additional fibers. The increase of the larger jaw muscles has an impact on a major part of the skull. The frontals narrow, for instance, and the fourth infraorbital and suprapreopercle are more reduced and separated from each other to make room for the invasion of the jaw adductors. These smaller jaw muscle-surrounding bones allow a more extensive growth of the external jaw muscles during development, but it cannot be deduced from adult specimens whether the larger jaw muscles induce a reduced neurocranium, or vice versa. The larger jaw musculature is not directly the driving force behind all the cranial differences, because the reduction of the cranial bones also appears in places where they are not susceptible to being affected by the larger jaw muscles. For example, the caudal side of the skull roof in *G. typus* (Fig. 3A) is much shorter than in *C. gariepinus* (Fig. 3C) and the ethmoid region is less covered with bone. Similarly, a relation between the size of the eyes and the jaw muscles seems to be present. With the enlargement of the jaw muscles, the eye size as well as the circumorbital bones decrease and the eyes shift gradually in a more anteromedial position (Fig. 3C–A).

In Figure 3, the distance between the rostral tip of the premaxilla and the caudal side of the braincase (exoccipital), or the rostral tip of the premaxilla and the fourth parapophysis (the latter is defined as the neurocranial length in this text), is scaled to the same length. In doing so and by comparing the three skulls, we see that the positions of the sutural connections between some neurocranial medial bones (e.g., mesethmoid, frontal, parieto-supraoccipital) are approximately the same. Apparently, the enlargement of the jaw muscles does not change the positions of the contact zones between these bones.

Some features of the head of *Gymnallabes typus* indicate a relatively stronger bite potential compared with *Clarias gariepinus*. First, *G. typus* can generate a stronger force on the lower jaw because of the larger physiological cross section of the jaw muscles by the attachment of additional fibers. Moreover, the anterior muscle fibers are im-

planted at higher angles on the aponeurosis, producing a much higher moment. As a result, the resultant force vector of the jaw muscle is rotated counterclockwise and results in a relatively larger vertical vector component compared to *C. gariepinus* for the same contraction (Fig. 9C–A). In addition, this muscle is extremely enlarged posterodorsally of the head, but also extends more toward the front of the lateral side of the frontal. The anteriormost upper and lower fibers of the external adductor insert at the highest angles on the tendinous skeleton. Here, the high angle fibers may provide a greater holding force.

A second indication for a more powerful bite is the position of the teeth. The examined specimens illustrate that the teeth of the lower jaw are positioned more posteriorly, thus closer to the lower jaw articulation, when the jaw muscles increase (Fig. 6A–C). The position of the prevomer teeth shows a similar trend (Fig. 4C–A). The lateral processes of the prevomer of *Gymnallabes typus* are extended more posteriorly, by which the teeth are positioned more in the back, even touching the entopterygoid. Moreover, the left entopterygoid of one examined specimen is partly covered by teeth, whereas usually the entopterygoid of catfishes does not have teeth (Arratia, '92). Teeth in *G. typus* and *Clariallabes melas* are not as densely packed as in *Clarias gariepinus* and are much larger, penetrating deeper into the prey.

A third indication for a stronger bite is the size of the coronoid process of the lower jaw to which the external jaw muscle is attached. This process is higher in *Gymnallabes typus* and *Clariallabes melas* than in *Clarias gariepinus* (Fig. 6A–C). A higher coronoid process implicates a longer power arm and produces a relatively greater vertical force vector component of the jaw muscle for the same contraction. The elevation of the coronoid process is not exclusively correlated with larger jaw muscles, as is clearly illustrated by the coronoid process of *C. melas*, which is similarly developed as in *G. typus*, but the jaw adductors are not. Furthermore, the coronoid process of *G. typus* is situated more in the front compared with the lower jaw length of *C. gariepinus* and also causes a greater moment for the same contraction force of the jaw muscle.

Differences in some cranial muscles of *Gymnallabes typus* involved in mouth open-

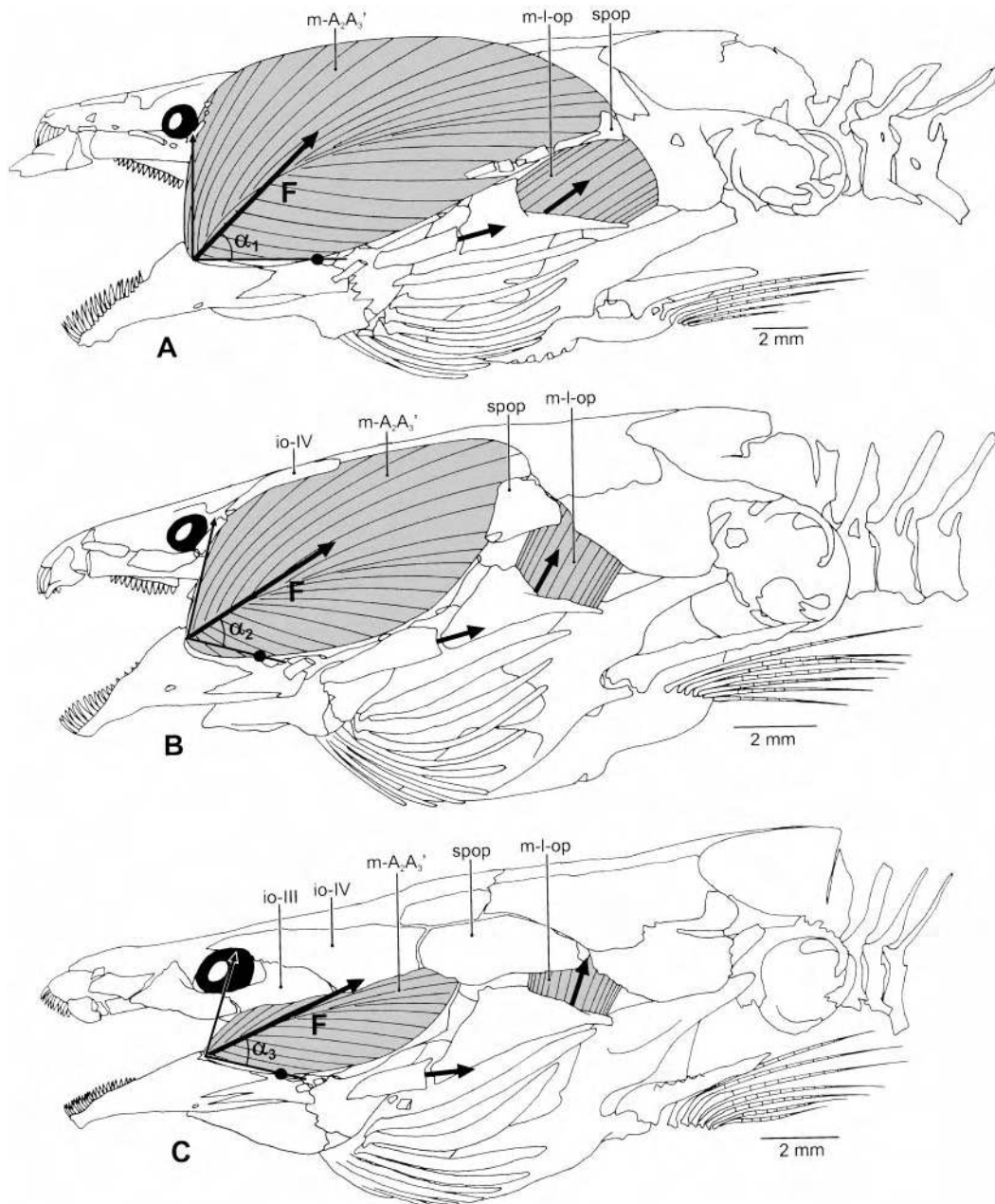


Fig. 9. Lateral view of the skull and superficial jaw adductor and opercular levator muscles of **A:** *Gymnalabes typus*, **B:** *Clariallabes melas*, **C:** *Clarias gariepinus*. F indicates the approximate resultant force vector of the external jaw adductor exerted on the lower jaw

($\alpha_1 > \alpha_2 > \alpha_3$). io-III, infraorbital III; io-IV, infraorbital IV; m-A₂A₃', external part of the adductor mandibulae muscle; m-l-op, levator operculi muscle; spop, suprapreopercle.

ing have been found as well. These mainly concern the levator operculi, the dorsal part of the protractor hyoidei, and the sternohyoideus. They may be principally modified to enable a larger gape and to open the mouth more quickly, but also to compensate the greater resistance caused by the larger jaw muscles during jaw depression. A first adaptation concerns one of the opercular muscles, the levator operculi (Fig. 9A). Normally, contraction of this muscle results in an upward rotation of the opercle around its articulation with the hyomandibula. This action plays an important role in the opercular mouth opening mechanism (Aerts and Verreaes, '84). The rotation is coupled with a retraction of the interopercle, which in its turn pulls at the retroarticular process of the lower jaw, which results in a depression of the lower jaw. Since the suprapreopercle of *G. typus* is much smaller than that of *Clarias gariepinus*, the attachment area is also smaller. This shifts the levator operculi to the posttemporo-supracleithrum, which is located more posteriorly. The muscle fibers are, therefore, more inclined than in *C. gariepinus* (Fig. 9C). As a result of this posterodorsal displacement of the opercular levator attachment site, its main resultant force vector is rotated so that it forms an acute angle with the dorsal rim of the opercle. The muscle fibers are also longer than those of the other two species, due to the longer distance to be bridged. Both features, more inclined and larger fibers, may imply a gain in mechanical advantage of the opercular four bar system. The levator operculi of *G. typus* is almost oriented to the line of action between the lower jaw and the opercle;

therefore, contraction of this muscle results in a relatively larger retraction of the interopercle. Additionally, the opercular process of the hyomandibula of *G. typus* is directed more ventrally and has a straight facet instead of an obliquely oriented process with a more rounded facet as in *C. gariepinus*. The more vertical position of the opercular process also explains the shorter, more ventrally directed dilatator and adductor operculi muscles of *G. typus*.

A second adaptation to generate a larger mouth opening force on the lower jaws is the attachment of the protractor hyoidei dorsalis, which is situated on the ventral side of the head (Fig. 8B). Contraction results in elevation of the hyoid bars during closing of the mouth, but also in a depression of the lower jaw when the hypaxial and sternohyoideus muscles are contracted simultaneously. The anterior attachment site of the protractor muscle in the series from *Gymnallabes typus* to *Clarias gariepinus* shifts toward the midline of the skull (Fig. 10A–C). The contralateral dorsal parts of the protractor hyoidei of *G. typus* are separately attached to the caudal side of the lower jaw. In *C. gariepinus*, however, both parts of this muscle are connected with each other in the sagittal plane and on the caudal side of the lower jaws. Therefore, the resultant force vector of the protractor hyoidei dorsalis of *G. typus* is rotated more toward the sagittal plane than that of *C. gariepinus*. The morphology of the protractor of *Clariallabes melas* is intermediate in the one dissected specimen. Apparently, there is no correlation between the mediolateral shift of the anterior protractor muscle fibers and the length of the lower

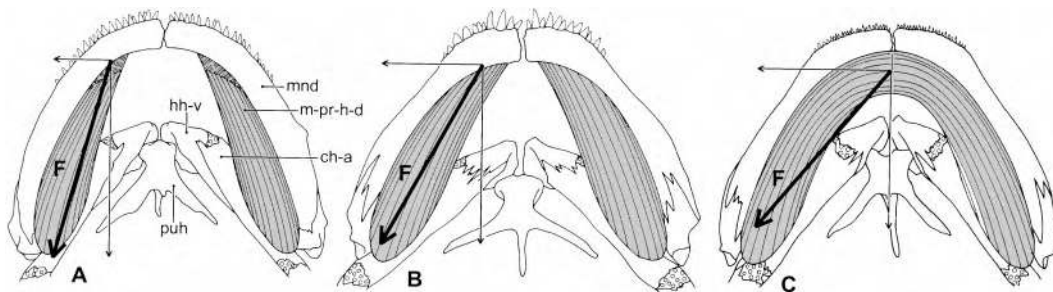


Fig. 10. Schematic ventral view of the dorsal part of the hyoid protractor muscle of **A:** *Gymnallabes typus*, **B:** *Clariallabes melas*, **C:** *Clarias gariepinus*. F indicates the approximate resultant force vector of the dorsal hyoid protractor muscle exerted on the lower jaw. The

lengths of the lower jaws are scaled to the same length. ch-a, anterior ceratohyal; hh-v, ventral hypohyal; mnd, mandible; m-pr-h-d, protractor hyoidei pars dorsalis muscle; puh, parurohyal.

jaws, because the jaws of *C. melas* are shorter than those of *C. gariepinus*. A correlation, however, may exist between the hyoid protractor morphology and the size of the jaw muscles.

Third, the sternohyoideus of *Gymnallabes typus* (Fig. 8D) seems to be longer as well, causing a larger depression (or retraction) of the hyoids. And, finally, the enlargement of the posterior fibers of the adductor mandibulae reduces the relative stretching of the individual posterior fibers as the lower jaw is depressed, thus compensating for a larger gape.

Several skeletal differences between the three skulls may as well be related to the larger size of the jaw musculature. A first adaptation concerns a stronger interdigitation of the suspensorium with the neurocranium. In the series from *Gymnallabes typus* to *Clarias gariepinus*, the interdigitation becomes gradually less pronounced. The hyomandibula of *C. gariepinus* has only one upward process, articulating with the sphenotic and followed by a cartilaginous articulation ridge (Fig. 5C). The hyomandibula of *G. typus* and other anguilliform clariids have several processes. Both the sphenotic and pterotic of *G. typus* have a number of lateral descending processes, which articulate with the hyomandibula (Fig. 5A,B). These additional processes may be an adaptation for the larger jaw adductor muscles. Indeed, the posterior hyomandibula processes as well as the jaw musculature of *Clariallabes melas* are less developed than in *G. typus*. The long posterior hyomandibula processes are obliquely oriented in the direction of the lower jaw articulation point. These additional processes may prevent a forward or backward movement of the hyomandibula during depression or elevation of the lower jaws, as well as dislocation through torque forces. Also, the hyomandibula shifts gradually posteriorly in the series from *C. gariepinus* to *G. typus* (Fig. 4C–A). Moreover, its rostral membranous plate shortens and this results in longer jaw muscle fibers because their insertion area is partly situated on this plate. The hyomandibula of *G. typus* is also higher, articulating closer to the midline of the skull. A higher suspensorium can enable a larger lateral displacement of its ventral margin and thus an orobranchial volume increase, than a shorter one for the same rotation angle (Adriaens and Verraes, '94) (Fig. 11A–B). In addition, a longer mandible

results in a larger mouth opening for the same rotation angle of the lower jaw. The position of the lower jaw articulation socket of *G. typus* is situated lower compared with *C. gariepinus*. Generating a larger force on the lower jaw requires also a better-fixed articulation with the quadrate. An adaptation, therefore, is the lower jaw socket of *G. typus* and *C. melas*, which has a deeper curve than in *C. gariepinus* (Fig. 6A–C).

The described arrangements in *Gymnallabes typus*, which result in a relatively greater adductive force and a larger gape, may reflect, therefore, dietary specialization in anguilliform clariids in general. However, stomach analyses of *G. typus* (this study), other extreme eel-like clariids (Matthes, '64), and *Clarias gariepinus* (Groenewald, '64; Clay, '79) have revealed no particular dietary difference. According to these data, although restricted for the anguilliform species, all of these catfishes seem to be opportunistic feeders. This may provide the answer to the question why skull remodeling has taken place in smaller, but elongated clariids. The relative increase of the gape and adductive forces may have compensated for the reduction of the skull and enabled the clariids to retain their feeding preferences. A larger number of stomach analyses on anguilliform clariids, however, is required to make this a solid argument.

Anguilliform body and skull size vs. larger jaw muscles

The bodies of the three clariid species become more elongated in the series from *Clarias gariepinus* to *Gymnallabes typus* and the number of the caudal vertebrae increases (Fig. 2C–A). It has been statistically demonstrated in *Fundulus* that the caudal region is the site of modifications in the number of vertebrae (Ford, '33 in Gabriel, '44), apparently in the region where the somites last form. Elongation means either a reduction in the relative diameter for a given mass, an increase in the relative length, or both, the latter probably being applicable for the three species. As the bodies of the three clariid species become more anguilliform, the dorsal and anal fins gradually enlarge and are ultimately confluent with the caudal fin. In the latter, more hypurals are fused with each other when the body elongates, ending up in a single plate as in *Channallabes apus*. The paired fins reduce relative to the total body length (Fig. 2C–A), as was noted by earlier authors (Boulenger, '07; Pellegrin,

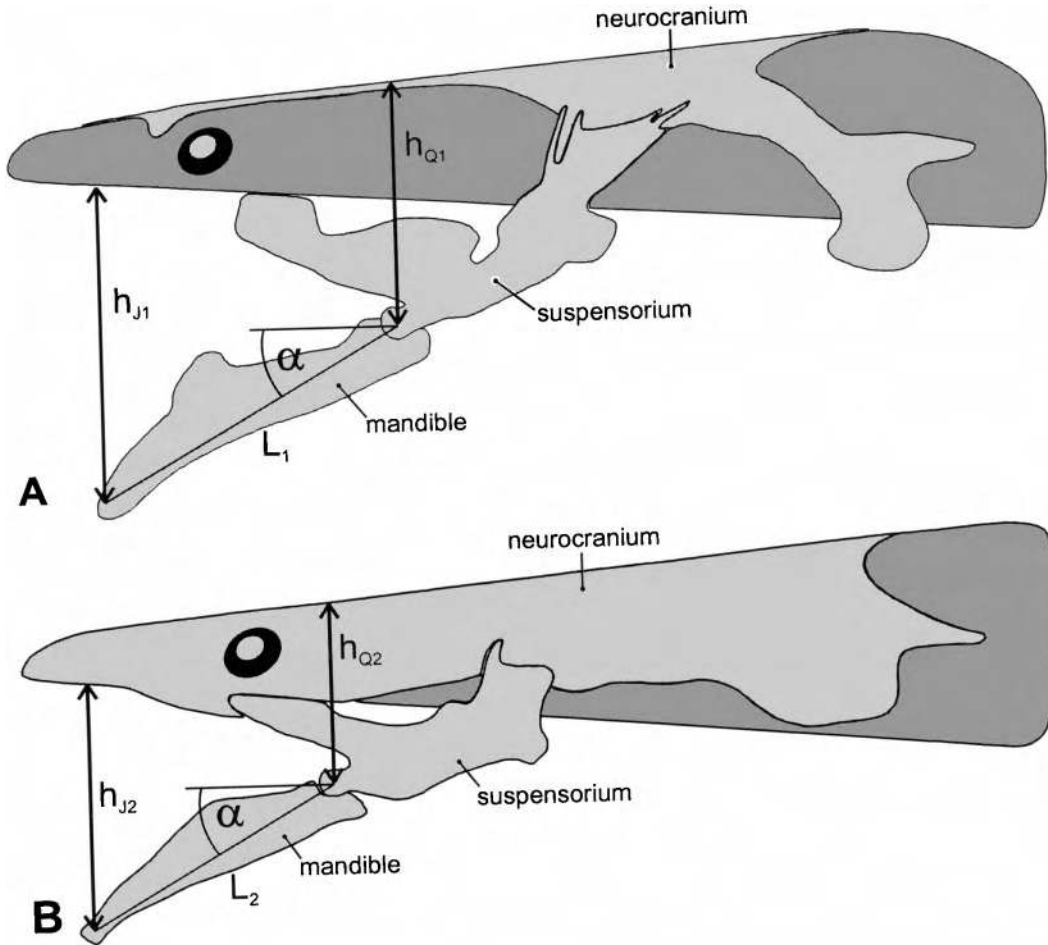


Fig. 11. Schematic view of the position of the suspensorium in relation to the skull of **A**: *Gymnallabes typus* and **B**: *Clarias gariepinus*. The distance h_{Q1} and L_1 in *G.*

typus is relatively larger than h_{Q2} and L_2 in *C. gariepinus*, respectively. This results in a relatively larger mouth opening ($h_{J1} > h_{J2}$).

'27; David, '35; Poll, '77), but this does not occur in relation to the cranial length (Fig. 9A–C).

Anguilliform clariids are equipped with much larger jaw muscles compared with their fusiform relatives, and intermediate forms such as *Clariallabes melas* can be easily found among the Clariidae. Both characteristics, anguilliform body versus hypertrophied jaw muscles, and thus feeding mode, may in some way be correlated with each other. This study and literature on clariids, however, seem to reveal that the relation between the jaw muscle size and the degree of anguilliformism (or the number of vertebrae) in clariids is not consistent. A re-

markable example to illustrate this is *Tanganikallabes mortiauxi*, endemic to Lake Tanganyika (Poll, '43). The neurocranium of *T. mortiauxi* is extremely narrow (Poll, '43: Fig. 1), but its external morphology looks like that of *C. melas*. Based on the approximate number of dorsal fin rays, i.e., 70 (Poll, '43), the number of vertebrae should be much lower than in an anguilliform clariid. Other examples, such as *Clarias salae* or the smaller *Clarias submarginatus*, have a number of vertebrae similar to *C. melas*, but their lateral skull roof bones are not reduced (Teugels, '86b). *Channallabes apus* also shows that the relation between the degree of anguilliformism and the size of the jaw

muscles is inconsistent or that the size of the jaw muscles does not gradually increase when vertebrae are added. Also, two examined clariids (124 and 239 mm TL) originally determined as *Gymnallabes typus*, have a broader neurocranium than we see in *G. typus*, almost identical with that of *C. melas*, but the number of vertebrae (81) is greater than in *G. typus*. It is, therefore, not understood whether a relation exists between the increasing jaw muscles and elongation in clariids. It can be said that such a relation is not present in other siluroids on the basis of a superficial survey conducted by Howes ('83), which indicated a mean number of 40–45 vertebrae among siluroids, whereas only some members of the Clariidae have exceptionally high numbers. However, it is certain that eel-like clariids always have hypertrophied jaw muscles, whereas almost all nonanguilliform clariids have much smaller ones. Strikingly, in the Mastacembelidae or spiny eels the size of the jaw muscles decreases when the body elongates, as opposed to what we see in clariids. Microphthalmic and cryptophthalmic mastacembeloids have expanded their jaw muscles but have the lowest number of vertebrae (Travers, '84).

Not only do we see a relative enlargement of the external jaw adductors when the body becomes more elongate, but the maximum attainable body size decreases as well. The known maximum length for *Clarias gariepinus* is 1.5 m (Teugels, '86a), for *Clariallabes melas* 260 mm (Poll, '41), and for *Gymnallabes typus* 238 mm. Thus the absolute size of the cranium decreases in the series from *C. gariepinus* to *G. typus* (Fig. 2C–A). On first thought, the maximum attainable skull size may be correlated with changes in the arrangement of the jaw adductor musculature and skull roof bones. Indeed, readings in the literature on clariids (e.g., David, '35; Poll, '41, '42a,b, '43, '57, '77; Greenwood, '61; Teugels, '86b; Teugels et al., '90) reveal that larger jaw muscles only occur in small adult skulls. Teugels ('86b) has noted in his description of each *Clarias* species whether the fourth infraorbital and suprapreopercle are separated and reduced. Apparently, mainly the small fishes (maximum 300 mm) of the subgenus *Brevicephaloides* consist of species that have separated lateral skull roof bones, as a result of larger jaw muscles. An exception to this rule is *Dinotopterus*. Some adult fishes (> 1 m) of this genus are character-

ized by a gap between the fourth infraorbital and suprapreopercle (the supraorbital and dermosphenotic of Greenwood) (Greenwood, '61).

The larger jaw muscles of *Gymnallabes typus* and other anguilliform clariids cannot be related to a decrease in absolute skull size alone. Noneel-like clariid species with an adult, closed skull roof of <2 cm corroborate this statement. *Clarias* species, such as *Clarias alluaudi* or *Clarias albopunctatus*, e.g., also have a closed skull roof as does *Clarias gariepinus* (Teugels, '86b), but are much smaller in adult life. Therefore, this trait cannot be viewed as related to small size alone. In addition, the degree to which a muscle fiber may be stretched depends on its absolute length, i.e., on the number of sarcomeres of which it is composed. Thus the length of the jaw muscle fibers in a 2 cm or slightly smaller anguilliform skull is apparently not limited in restricting the excursion range of the jaw adductors, as these fibers may be even smaller in a similar sized closed skull roof like that of *C. alluaudi*.

We could also think that relatively more space leaves scope for the development of additional structures in larger skulls. The meristic characters such as the number of branchial filaments, the number of gill rakers, or the number of olfactory lamellae of *Clariallabes melas* are slightly higher than those of *Gymnallabes typus*, but increase sharply in *Clarias gariepinus*, as does the skull size of these species. Although the series confirms the statement, meristic characters of the head of *Clarias* species (Teugels, '86b) corroborate that there is no relation with skull size. As the absolute size of the skull decreases, the relative size of the braincase and the semicircular canals (inner ear), deduced from the size of the prootics, do not change. An exception is *C. melas*, of which the parasphenoid, forming the anterior braincase, and the prootics are slightly broader (Fig. 4B). In addition, the relatively smaller skull of *G. typus* is less strongly connected with the postcranial skeleton, making it easier for the head to maneuver. The ventromedial ridge of the parieto-supraoccipital of *G. typus*, on which the epaxial muscles are attached, is much shorter than in *C. gariepinus*. Moreover, the transscapular process abuts only the rostral side of the fourth parapophysis (Fig. 3A), whereas in the other two species, this process reaches it in the middle (Fig. 3B,C).

The reduction of neurocranial bones in clariids apparently influences the location of the head sensory canals during development. In most Siluriformes, the infraorbital canal branches off from the supraorbital canal in the sphenotic bone (Arratia and Huaquín, '95). *Gymnallabes typus* and *Clariallabes melas* have this bifurcation in the frontal bone. This is also the case in the two examined *Channallabes apus*, although not in the skull drawn by Poll ('77). The shift of this sensory canal bifurcation is related to the width of the neurocranium and, therefore, to the size of the jaw musculature. The anterior displacement of the point of branching into the frontal also occurs in a few other catfishes (see Lundberg, '82). Yet, the infra- and supraorbital canal fusion does not always occur in the frontal when the neurocranium is narrow. In *Diplomystes camposensis*, e.g., the infraorbital still bifurcates in the sphenotic (Arratia and Gayet, '95: Fig. 5). In addition, the preopercular canal of *G. typus* is situated more in the back of the skull as a consequence of the reduced post-temporo-supracleithrum and suprapreopercular bones. The reduction of the neurocranial bones may also cause the absence of side branches or a decrease in the number of surface pores of the sensory canals. The ant-orbitals of *C. apus* and *G. typus* do not bear a sensory canal as in *C. melas* and *Clarias gariepinus*. Also, the number of pores of the cranial lateral line system of *G. typus* is reduced. For instance, the preoperculo-mandibular canal consists of seven pores, whereas *C. gariepinus* has two pores extra.

The reduced neurocranium of anguilliform clariids has been interpreted as a juvenile trait of their predecessors (Poll, '42a, '77; Greenwood, '56). The expression of juvenile traits in the adult would have been caused by a retarded somatic development (neoteny), which would have played an important role in the development of morphological adaptations in anguilliform clariids. It is currently impossible, however, to discuss the implications of paedomorphosis on clariid ontogeny, mainly because of the lack of information on the embryonic development of the anguilliform clariid skull.

Interrelationships of anguilliform clariids?

The series of Boulenger ('07) and Pellegrin ('27), illustrated here by four species, has been interpreted by several other authors (a.o., Poll, '41, '42a, '77; Greenwood, '56; Lambert, '60) as an evolutionary trend toward an

increased elongation in some clariids. Their assumption that a separate lineage as such would exist is unrealistic. First, selecting a handful of species from a large and complex group of a variety of species is not sufficient to prove such a trend. Second, by constructing the orthogenetic series, the importance of external fish morphology is overemphasized. This study has demonstrated, however, the presence of a nongradual trend in the examined skulls. The cranium of *Clariallabes melas* is not an entirely intermediate form between *Gymnallabes typus* and *Clarias gariepinus*, some of its skull bones being more massive. If the presumed trend were consistent, it would have been legitimate to expect an even further reduced skull in the most elongated *Channallabes apus* (108 vertebrae), but the latter's neurocranium is slightly broader than that of *G. typus*. In addition, the suprabranchial organs of *C. apus* are larger and the number of abdominal vertebrae (23) and ribs (18) is higher than in *G. typus*.

It is suggested here that the orthogenetic series of Boulenger may be rather a reflection of highly diverse species. Based on the aberrant forms in asymmetry, meristic counts, and absence of an organ, which were encountered during this study, the least that can be said is that the examined clariids can be regarded as variable specimens. For example, a left-right asymmetry in the number of pterygoids is seen in the 217 mm TL *Gymnallabes typus*, which also lacks the first ceratobranchial. Also, the parieto-supraoccipital of the 214 mm TL *G. typus* is not fused in the middle, as is normally the case. Several aberrant characters in the other species were also revealed. *Channallabes apus* has two separate ventral median fins instead of one anal fin, *Clariallabes melas* is missing a right pelvic fin, and *Clarias gariepinus* a right suprapreopercle. Fused vertebrae were present in most of the specimens. In order to define some of these characters as an abnormal condition, however, more extensive research is required.

The monophyletic nature of the Clariidae has not yet been demonstrated (Teugels, '96), and the taxonomy of most genera, the anguilliform clariids in particular, needs further exploration. A phylogenetic analysis of the Clariidae, which is lacking in the literature, could verify the old hypothesis of Boulenger that predecessors of primitive fishes, such as *Heterobranchus* and most *Clarias*, would

have evolved into progressively anguilliform clariids. This is the subject of ongoing research. Also, the existence of a correlation between the size of the jaw muscles versus body shape in clariids could be ascertained once a phylogenetic tree is established.

CONCLUSIONS

Although only a few specimens have been investigated, several conclusions can be drawn. First, the adductor mandibulae of some anguilliform clariids (e.g., *Gymnallabes typus*) is substantially more developed and the neurocranium is much narrower than in the nonanguilliform *Clarias gariepinus*. Second, several morphological adaptations, both skeletal and muscular, can be regarded as being related to a more powerful biting potential and a wider gape. A stronger bite is performed by a larger physiological cross section of the jaw muscles, a stronger interdigitation between the hyomandibula and the neurocranium, the prevomer and mandibular teeth being positioned closer to the lower jaw articulation, and a higher coronoid process. The enlargement of the adductor mandibulae, levator operculi, and the sternohyoideus also enables increase of the gape. It is not understood, however, whether a relation exists between the size of the jaw muscles and the shape of the body. Third, although some morphological features of the intermediate anguilliform *Clariallabes melas* fit well into the trend, this does not apply to all morphological characters. For instance, the Weberian apparatus and the braincase are relatively broader, and the lower jaw is shorter. Moreover, the pterygoid bones of *C. melas* are different.

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