Homologies Among Different Adductor Mandibulae Sections of Teleostean Fishes, With Special Regard to Catfishes (Teleostei: Siluriformes)

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ABSTRACT   The adductor mandibulae complex has been a subject of discussion and uncertainties due to a wide range of differentiations and fusions that have occurred during teleost evolution. The adductor mandibulae of numerous catfishes was studied in detail and compared with that of several other teleosts described in the literature. Our observations and comparisons demonstrate that: 1) the adductors mandibulae $A\omega$, A2, and A3 of acanthopterygians correspond, respectively, to the $A\omega$, A2, and A3 of ostariophysines; 2) the antero-dorso-lateral (A1) and the antero-ventro-lateral (A1-OST) sections of the adductor mandibulae present, respectively, in acanthopterygians and in basal ostariophysines are the result of two different patterns of differentiation of this muscle; 3) some derived ostariophysines present a lateral section of the adductor mandibulae attached to the upper jaw (A0) that is not homologous with any other section of this muscle present in any other ostariophysine or acanthopterygian fish; 4) the configuration of the adductor mandibulae present in *Diplomystes* seems to be the plesiomorphic condition for catfishes; and 5) the muscle retractor tentaculi, present in a large number of catfishes, is derived from the inner section of the adductor mandibulae (A3) and, thus, is not homologous with the lateral bundle of this muscle (A0) that inserts on the upper jaw in some derived ostariophysine fishes. J. Morphol. 243:193–208, 2000.
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In fishes, the lower jaw is raised and the mouth closed by contraction of the adductor mandibulae muscle. The basal configuration of the muscle in teleosts seems to be "a continuous muscle mass extending from the cheek to the inner surface of the mandible, with the cheek and mandibular ($A\omega$) portions separated only by a myocomma" (Gosline, 1989, p. 649) (Fig. 1A). However, from the differentiation of the single "mass muscle" has originated, in the majority of the teleosts, a complex configuration, with a large number of subdivisions or even separate muscles, as, for example, the retractor tentaculi in some catfishes (Vetter, 1878; McMurrich, 1884; Takahasi, 1925; Edgeworth, 1935; Eaton, 1948; Stix, 1956; Alexander, 1964, 1965; Winterbottom, 1974; Gosline, 1989; etc.). The complexity of the configuration of the adductor mandibulae, associated with the fact that different sections of this muscle present in the different groups of teleostean fishes are probably the result of different pathways of differentiation (Gosline, 1989), complicates questions about homology between these sections (Gosline, 1989; Adriaens and Verraes, 1996). This problem is amplified, as most studies (Takahasi, 1925; Edgeworth, 1935; Alexander, 1964, 1965; Vari, 1979; Howes, 1976, 1978, 1983a,b, 1985b, 1988; Schaefer and Lauder, 1986; Adriaens and Verraes, 1996; etc.) are devoted to the configuration of the adductor man-

dibulae in particular groups of teleostean fishes, with too few comparisons with the considerable data available in the general teleost literature. The sole significant exception is Winterbottom's (1974) work, a splendid survey of teleost myology and its possible variability. This remains a reference for many authors, although it is partially questioned by more recent articles (Vari, 1979; Howes, 1983a,b, 1985b; Gosline, 1989). Therefore, we studied in detail the configuration of the adductor mandibulae in numerous catfish and compared our results to the data in the literature about other ostariophysines, and in other teleosts, in order to establish the homologies between the different bundles present in Siluriformes, in other ostariophysines, and in teleosts in general.

MATERIALS AND METHODS

The fishes dissected (Table 1) are from the collection of the laboratory (LFEM), or were obtained from the "Musée Royal de l'Afrique Centrale" of Tervuren

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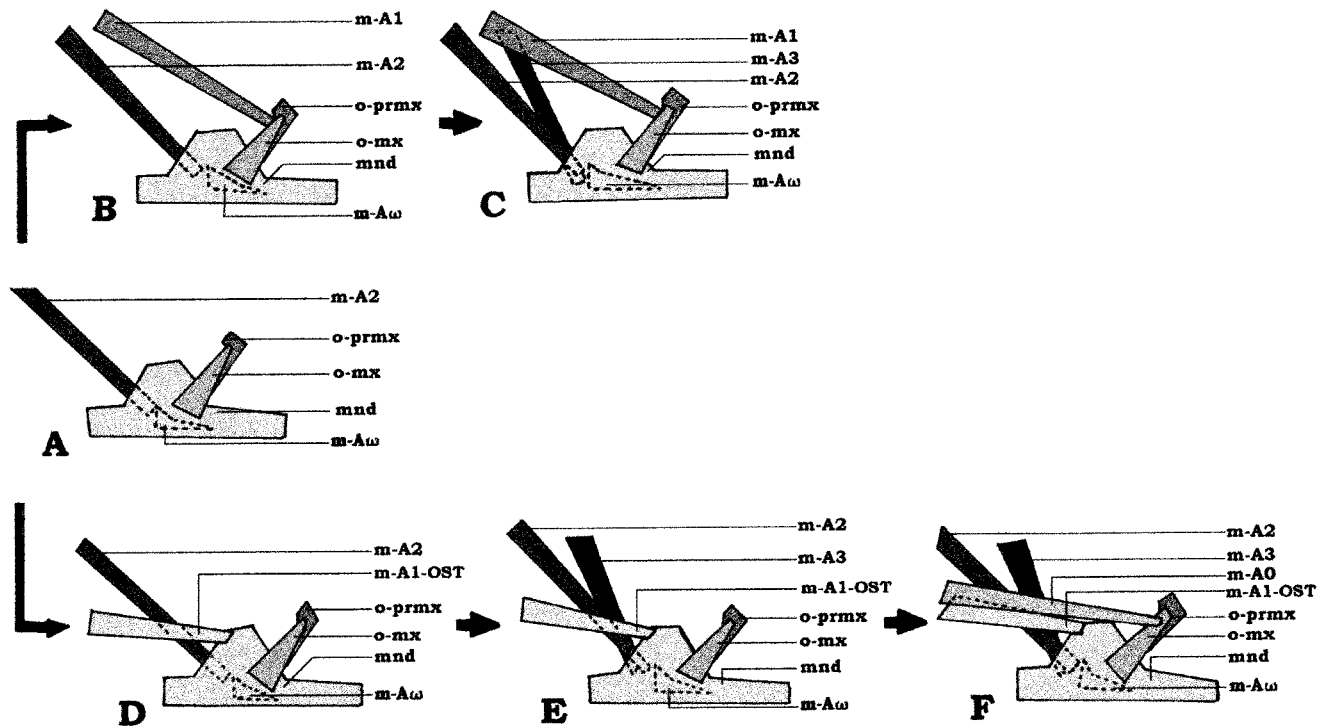E-mail: R.Diogo@student.ulg.ac.be

Fig. 1. Scheme illustrating the two patterns of adductor mandibulae differentiation of teleostean fishes (based on Gosline, 1989). **A:** Basal type in which the cheek muscle is undivided. **B:** The acanthopterygian pattern in which an *upper* part of the cheek muscle (A1 of this work) has become attached to the maxilla. **C:** Secondary differentiation in acanthopterygian fishes in which a mesial part of the cheek muscle (A3 of this work) is present. **D:** Initial differentiation in the ostariophysine pattern in which a *lower* part of the cheek muscle (A1-OST of this work) has developed a separate attachment to the back of the mandible. **E:** Secondary differentiation in ostariophysine fishes in which a mesial part of the cheek muscle (A3 of this work) is present. **F:** Differentiation in some ostariophysine fishes in which an adductor mandibulae section (A0 of this work) has developed, via the primordial ligament, an attachment to the maxilla. m-A0, m-A1, m-A1-OST, m-A2, m-A3, m-Aω, sections of the musculus adductor mandibulae; mnd, mandibula; o-mx, os maxillare; o-prmx, os praeomaxillare.

(MRAC). Anatomical descriptions were made after dissection of fresh or alcohol-fixed specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope and a camera lucida.

RESULTS

The nomenclature of the different bundles of the siluriform adductor mandibulae muscle, as in teleosts in general, has been the subject of considerable discussion. The nomenclature followed here, which does not agree with that of most authors, will stimulate discussion. The textual descriptions are complemented by Tables 2–7. These tables present the anterior and posterior insertions of the bundles, the mode of attachment to the cranium (tendinously or not), and the references to the figures where the described structures are illustrated. Recent studies (e.g., Howes, 1985a, 1988; Gosline, 1986, 1989) indicate that "the course of the ramus mandibularis seems to be a better indicator of cheek sections in the adductor mandibulae than has been generally been acknowledged" (Gosline, 1989, p. 659). Therefore, the path of this nerve tract is also described here.

Before passing to the description of the adductor mandibulae and of the course of the ramus mandibularis of the catfishes studied, we consider it appropriate to briefly present a schematic figure (Fig. 1) based in Gosline's (1989) hypothesis concerning the homologies between teleost adductor mandibulae sections (this hypothesis will be presented in more detail in the Discussion section). According to Gosline, from the basal teleostean situation of the adductor mandibulae (Fig. 1A), two types of differentiation can be distinguished. In acanthopterygians an antero-dorso-lateral part of the cheek muscle develops an attachment to the maxilla via the primordial ligament (Fig. 1B: A1). A secondary differentiation of the adductor mandibulae, mesial to all the others, is found in most acanthopterygian fishes (Fig. 1C: A3). In ostariophysines, an antero-ventro-lateral part of the cheek muscle first separates and attaches to the postero-dorso-lateral face of the mandible (Fig. 1D: A1-OST) and then, via the primordial ligament, inserts on the maxilla (Fig. 1F: A0). Apart from these divisions, another section of the adductor mandibulae, medial to all the others, could also be present in ostariophysine fishes (Fig. 1E,F: A3).

TABLE 1. List of the specimens studied

Family	Species	Condition	Provenance	Number
Amphiliidae	*Amphilius brevis*	Alcohol	*MRAC 89-043-P-403*	1
	Amphilius brevis	Alcohol	MRAC 89-043-P-2298	1
	Amphilius brevis	Alcohol	MRAC 89-043-P-2333	1
	Amphilius brevis	Alcohol	MRAC 89-043-P-2372	1
	Amphilius jacknosi	Alcohol	LFEM	1
	Phractura brevicauda	Alcohol	MRAC 90-057-P-5145	1
	Phractura brevicauda	Alcohol	MRAC 92-125-P-362	1
	Phractura brevicauda	Alcohol	MRAC 92-125-P-386	1
	Phractura intermedia	Alcohol	MRAC 73-016-P-5888	1
Bagridae	*Bagrus bayad*	Alcohol	LFEM	1
	Bagrus docmak	Alcohol	MRAC 86-07-P-512	1
	Bagrus docmak	Alcohol	MRAC 86-07-P-516	1
Clariidae	*Clarias batrachus*	Alcohol	MRAC 94-020-P-1	1
	Clarias gariepinus	Alcohol	MRAC 93-152-P-1356	1
	Clarias gariepinus	Fresh	LFEM	2
	Clarias meladerma	Alcohol	MRAC 92-100-P-1	1
Claroteidae	*Chrysichthys auratus*	Alcohol	LFEM	3
	Chrysichthys auratus	Fresh	LFEM	3
	Chrysichthys cranchii	Alcohol	LFEM	1
	Chrysichthys nigrodigitatus	Alcohol	LFEM	2
	Chrysichthys nigrodigitatus	Fresh	LFEM	4
Diplomystidae	*Dyplomystes chilensis*	Alcohol	LFEM	2

LFEM: private collection of the "Laboratory of Functional and Evolutionary Morphology;" MRAC: collection of the "Musée Royal de l'Afrique Centrale."

Diplomystes chilensis (Figs. 1E, 2, 3, Table 2)

The adductor mandibulae of *Diplomystes chilensis* is schematized in Figure 1E. The external bundle, A1-OST, originates on the postero-lateral surface of the suspensorium (Fig. 2A). It inserts on the lateral side of the angulo-articular (Fig. 2A) and, by means of a thick tendon, on the coronomeckelian bone (Fig. 3B). The A2 originates on the dorsal surface of the neurocranium, dorsally to the A1-OST (Fig. 2A).

Anteriorly, it passes medially to it (Figs. 2A, 3A), attaching tendinously both on the coronomeckelian and the posterior part of the Aω (Fig. 3A). The deeper part of the adductor mandibulae, A3, can be subdivided into a dorsal A3-d and a ventral A3-v part (Fig. 2B). The A3-d is situated medially to the A2, its antero-dorsal fibers being separated from it by the levator arcus palatini (Fig. 2B). It originates on the lateral surface of the suspensorium (Fig. 2B) and inserts, by means of a thick tendon, on the coronomeckelian (Fig. 3B). The A3-v part attaches

TABLE 2. List of the different adductor mandibulae bundles and their insertions
in Diplomystes chilensis

| Bundles	Anterior insertion	Posterior insertion
Adductor mandibulae A1-OST	(Figs. 2A, 3B) Angulo-articular Coronomeckelian (tendon)	(Fig. 2A) Quadrate Preopercular Hyomandibular
Adductor mandibulae A2	(Fig. 3A) Coronomeckelian (tendon) Adductor mandibulae Aω (tendon)	(Fig. 2A) Pterotic (fibers + tendon) Extrascapular (fibers + tendon) Sphenotic (fibers + tendon) Frontal (fibers + tendon) Supraoccipital (fibers + tendon)
Adductor mandibulae A3-d	(Fig. 3B) Coronomeckelian (tendon)	(Fig. 2B) Quadrate Preopercular (tendon) Hyomandibular Metapterygoid
Adductor mandibulae A3-v	(Fig. 3B) Angulo-articular Adductor mandibulae A3'd	(Fig. 2B) Quadrate (tendon)
Adductor mandibulae Aω	(Fig. 3A) Coronmeckelian bone Dentary	(Fig. 3A) Adductor mandibulae A2

A

B
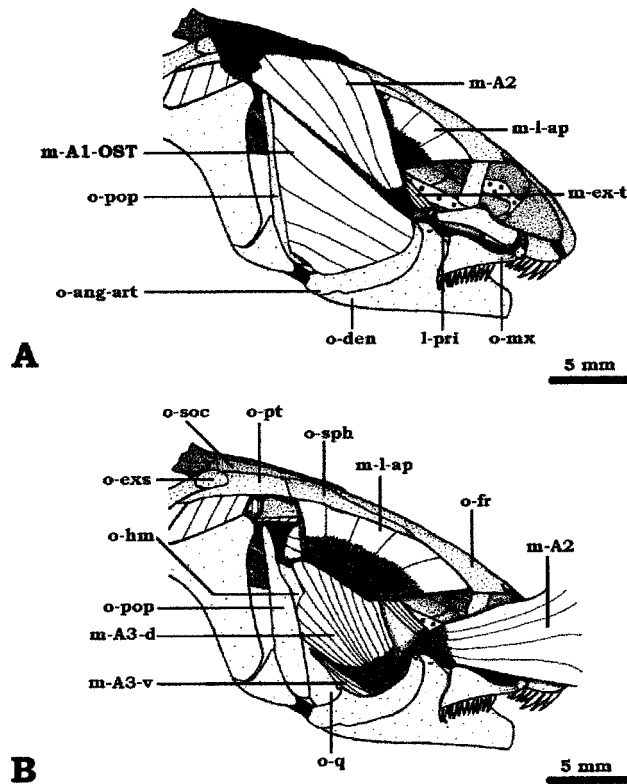
Fig. 2. Right, lateral view of the cheek musculature of *Diplomystes chilensis*, LFEM uncatalogued. **A:** Adductor mandibulae complex exposed. **B:** A1-OST and A2 folded back. l-pri, ligamentum primordium; m-A1-OST, m-A2, m-A3-d, m-A3-v, sections of the musculus adductor mandibulae; m-ex-t, musculus extensor tentaculi; m-l-ap, musculus levator arcus palatini; o-ang-art, os angulo-articulare; o-den, os dentale; o-exs, os extrascapulare; o-fr, os frontale; o-hm, os hyomandibulare; o-mx, os maxillare; o-pop, os praeoperculare; o-pt, os pteroticum; o-q, os quadratum; o-soc, os supraoccipitale; o-sph, os sphenoticum.

posteriorly on the quadrate (Fig. 2B) and anteriorly on both the angulo-articular and the tendon of the A3-d part (Fig. 3B). The Aω is lodged on the medial surface of the mandible (Fig. 3B). It runs from the tendon of the A2 to both the coronomeckelian and the dentary (Fig. 3A). The ramus mandibularis passes anteroventrally from an opening in the skull across the anterior part of the A3 and A2 sections and then branches. The main branch passes anterodorsally to the anterior part of the A1-OST and laterally to the Aω, and then between the dentary and Meckel's cartilage. The small branch passes across the A1-OST and then well forward along the outside of the mandible.

Chrysichthys nigrodigitatus (Figs. 4, 5, Table 3)

In a general way, the configuration of the adductor mandibulae of this species resembles that of *Diplomystes chilensis*. Therefore, only the principal differences between the two species will be described. In

Chrysichthys nigrodigitatus, the A1-OST inserts only on the dorso-lateral side of the angulo-articular (Fig. 4A,B,C), and not on both the angulo-articular and the coronomeckelian. Besides, the A2 originates on the lateral, and not in the dorsal, surface of the neurocranium (Fig. 4A). Lastly, in *C. nigrodigitatus* the A3 is subdivided into an A3′-d and a A3′-v part (Figs. 4C, 5B), which correspond, respectively, to the A3-d and A3-v of *D. chilensis*, but also into an A3″ section. This section situates medially to the A3′-v and A3′-d (Fig. 4C,D), being dorsocaudally separated from the latter by the levator arcus palatini (Fig. 4C,D,E). It attaches posteriorly on the anterior surface of the hyomandibular (Fig. 4E) and anteriorly on the angulo-articular (Fig. 5A). The ramus mandibularis passes anteroventrally from an opening in the skull across the anterior part of the A3″, A3′ and A2 sections and then branches. The main branch passes mesially to the A1-OST and laterally to the anterior part of the A2 and the posterior part of the Aω, and then between the dentary and Meckel's cartilage. As in *Diplomystes*, the small branch passes across the A1-OST and then well forward along the outside of the mandible.

A

B
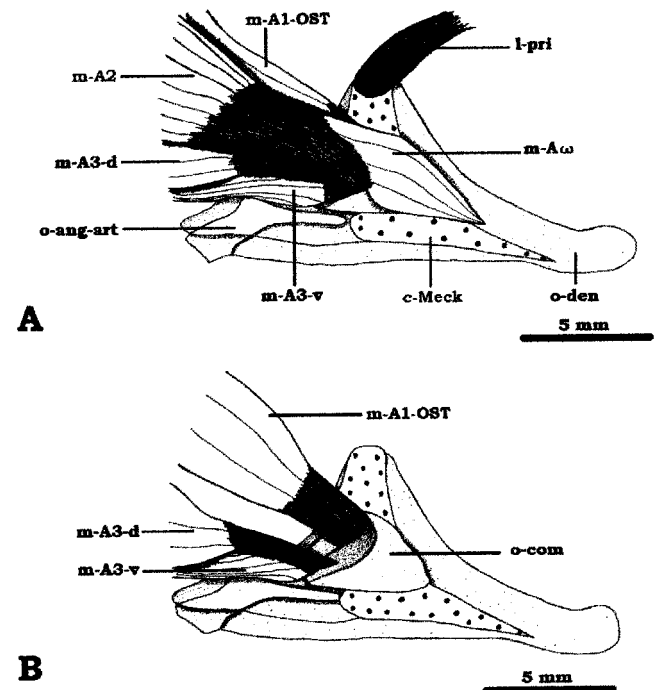
Fig. 3. Medial view of the left lower jaw of *Diplomystes chilensis*, LFEM uncatalogued. **A:** Adductor mandibulae complex exposed. **B:** A1-OST insertion on the lateral face of the mandible, Aω, A2 and ligamentum primordium removed. c-Meck, cartilago Meckeli; l-pri, ligamentum primordium; m-A1-OST, m-A2, m-A3-d, m-A3-v, m-Aω, sections of the musculus adductor mandibulae; o-ang-art, os angulo-articulare; o-com, os coronomeckelium; o-den, os dentale.

TABLE 3. List of the different adductor mandibulae bundles and their insertions
in Chrysichthys nigrodigitatus

Bundles	Anterior insertion	Posterior insertion
Adductor mandibulae A1-OST	(Fig. 4A,B,C) Angulo-articular (fibers + tendon)	(Fig. 4A,B) Quadrate Preopercular Hyomandibular
Adductor mandibulae A2	(Fig. 5B) Angulo-articular (tendon) Adductor mandibulae Aω (tendon)	(Fig. 4A) Pterotic (tendon) Sphenotic (fibers + tendon)
Adductor mandibulae A3'-d	(Fig. 5C) Coronmeckelian (tendon)	(Fig. 4C) Quadrate Preopercular Hyomandibular
Adductor mandibulae A3'-v	(Fig. 5C) Angulo-articular	(Fig. 4C) Quadrate (tendon)
Adductor mandibulae A3"	(Fig. 5A) Angulo-articular (tendon)	(Fig. 4E) Hyomandibular
Adductor mandibulae Aω	(Fig. 5A,B) Dentary	(Fig. 5A,B) Adductor mandibulae A2

Bagrus docmac (Figs. 6, 7, Table 4)

There are only two significant differences between the adductor mandibulae of *Bagrus docmac* and that of *Chrysichthys nigrodigitatus*. The A3′-d of *B. docmac* can be subdivided into a large, A3′-d-1, and a small, A3′-d-2, subdivision (Figs. 6B, 7C), inserted, respectively, on the posterior and postero-dorsal edges of the coronomeckelian bone (Fig. 7C). Besides, in *B. docmac* the A3″ bifurcates anteriorly, attaching not only on the angulo-articular, as in *C. nigrodigitatus*, but also on the primordial ligament (Figs. 6C, 7A). The path of the ramus mandibularis of *B. docmac* is quite similar to that of *C. nigrodigitatus*.

Clarias gariepinus (Table 5)

The configuration of the adductor mandibulae of this species is described here, although it was previously studied by Adriaens and Verraes (1996), because of problems of different nomenclature and some minor differences between our observations and their descriptions. There are three significant differences between the adductor mandibulae of *Clarias gariepinus* and that of *Chrysichthys nigrodigitatus*. The Aω, present in *C. nigrodigitatus*, is lacking in *C. gariepinus* (see fig. 7 of Adriaens and Verraes, 1996). In *C. gariepinus* the A3′ (A3″-s of Adriaens and Verraes, 1996) is not subdivided into a A3′-d and a A3′-v part, and attaches not only on the lateral surface of the suspensorium, but also on the neurocranium, namely, on the sphenotic, pterosphenoid, and frontal (see fig. 5C of Adriaens and Verraes, 1996). Lastly, the A1-OST (A2A3′b of Adriaens and Verraes, 1996) and the A2 (A2A3′a of Adriaens and Verraes, 1996) are fused anteriorly in *C. gariepinus* (see fig. 7C of Adriaens and Verraes, 1996). In a general way, the path of the ramus mandibularis of *C. gariepinus* resembles that of *C.*

nigrodigitatus. However, in *C. gariepinus*, at the insertion site of the adductor mandibulae complex on the lower jaw the main branch of the ramus passes anteriorly to all the sections of this muscle, and not between the A2 and Aω and the A1-OST (as described above, the Aω is lacking in this species).

Phractura brevicauda (Figs. 8, 9, Table 6)

The configuration of the adductor mandibulae of *Phractura brevicauda* is rather simple. The A1-OST is subdivided into a lateral A1-OST-1 and a medial A1-OST-2 part. Both originate on the lateral side of the suspensorium and insert on the dorso-lateral surface of the angulo-articular (Fig. 8). The A2, which lies medially to the A1-OST, attaches caudally on the preopercular and rostrally on the medial surface of the mandible (Fig. 9). The deeper bundle of the adductor mandibulae, A3, runs from the external side of the suspensorium (Fig. 8) to the coronomeckelian bone (Fig. 9). The path of the ramus mandibularis of *P. brevicauda* is quite similar to that of *Chrysichthys nigrodigitatus*.

Amphilius brevis (Figs. 10, 11, Table 7)

Contrarily to *Phractura brevicauda*, the configuration of the adductor mandibulae of this species is rather complicated. In fact, in *Amphilius brevis* this muscle is differentiated in nine bundles. The A1-OST-1, A1-OST-2, A1-OST-3, and A1-OST-4 are somewhat similar: they originate on both the neurocranium and the suspensorium — except A1-OST-2, which originates only on the neurocranium — and insert on the lateral side of the dentary (Fig. 10A,B). The A1-OST-5, situated ventrally to these bundles, runs from the ventro-lateral edge of the suspensorium to the postero-dorsal surface of the mandible (Fig. 10C). With regard to the A2, it
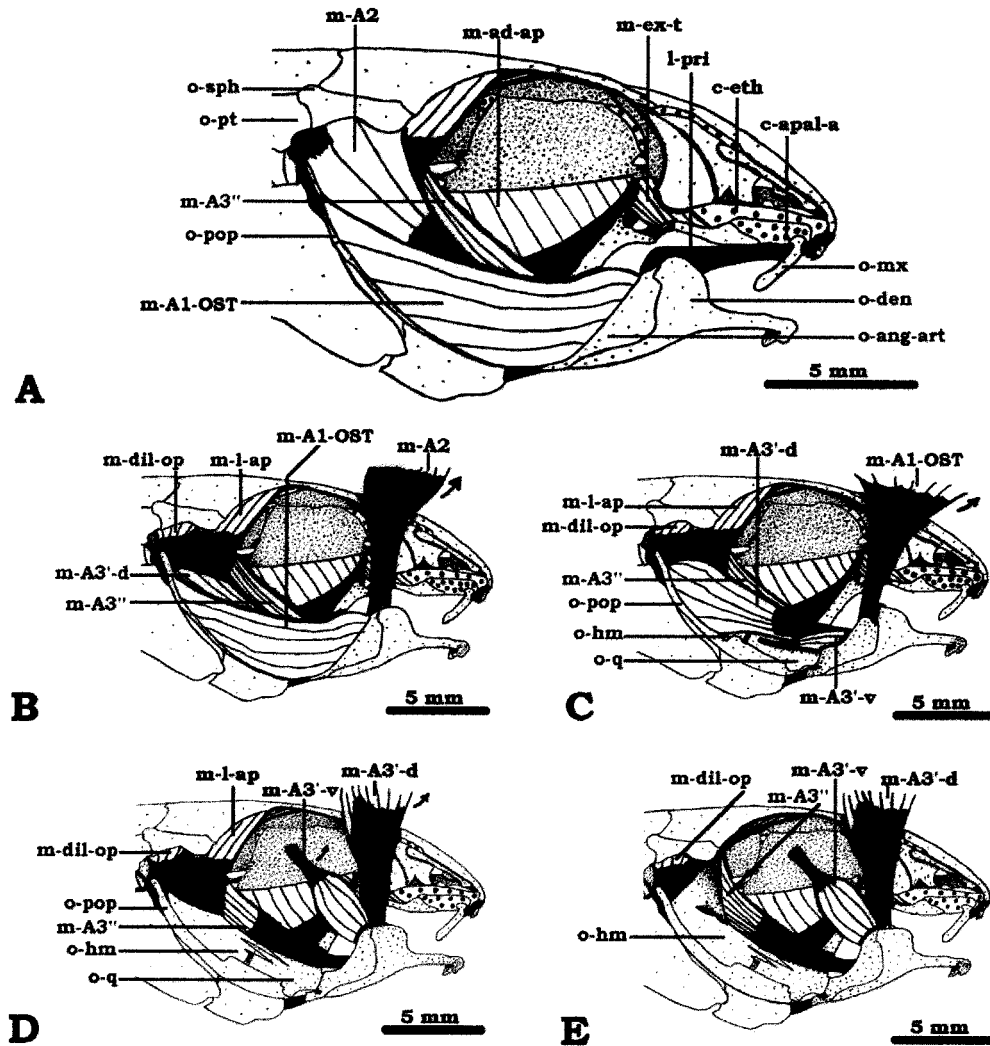
Fig. 4. Right, lateral view of the cheek musculature of *Chrysichthys nigrodigitatus*, LFEM uncatalogued. **A:** Adductor mandibulae complex exposed. **B:** Ligamentum primordium removed and A2 folded back. **C:** A2 removed and A1-OST folded back. **D:** A3′-d and A3′-v folded back and A1-OST removed. **E:** Levator arcus palatini removed. c-apal-a, cartilago autopalatinus anterior; c-eth, cartilago ethmoideus; l-pri, ligamentum primor-dium; m-A1-OST, m-A2, m-A3′-d, m-A3′-v, m-A3″, sections of the musculus adductor mandibulae; m-ad-ap, musculus adductor arcus palatini; m-dil-op, musculus dilatator operculi; m-ex-t, musculus extensor tentaculi; m-l-ap, musculus levator arcus palatini; o-ang-art, os angulo-articulare; o-den, os dentale; o-hm, os hyomandibulare; o-mx, os maxillare; o-pop, os praeoperculare; o-pt, os pteroticum; o-q, os quadratum; o-sph, os sphenoticum.

is connected posteriorly to both the neurocranium and the suspensorium (Fig. 10C), and anteriorly to the postero-medial side of the dentary (Fig. 11A). The A3, situated medially to the A2, can be subdivided into a dorsal A3-d, a ventro-lateral A3-v-1 and a ventro-medial A3-v-2 part (Fig. 10D,E). The A3-d runs from the preopercular and hyomandibular (Fig. 10D) to the coronomeckelian (Fig. 11B). The A3-v-1 and A3-v-2 parts originate on the quadrate (Fig. 10D,E), and insert, respectively, on the postero-dorsal surface of the dentary and on the postero-medial side of the angulo-articular (Fig. 11B). The path of the ramus mandibularis of *A. brevis* resembles that of *Chrysichthys nigrodigitatus*.

DISCUSSION

The principal aim of this work is to discuss the identity of the different adductor mandibulae sections present in the Siluriformes. It is first necessary to recognize the different sections of this muscle in the ostariophysines and in teleosts in general. Thus, the discussion will be divided in four parts: 1) the configuration of the adductor mandibulae in teleostean fishes in general; 2) the configuration of this muscle in Ostariophysi; 3) the identity and the homology of the different sections in catfishes; and 4) the special problem of the muscle retractor tentaculi, which is a differentiation of the adductor mandibulae present in a large number of catfishes
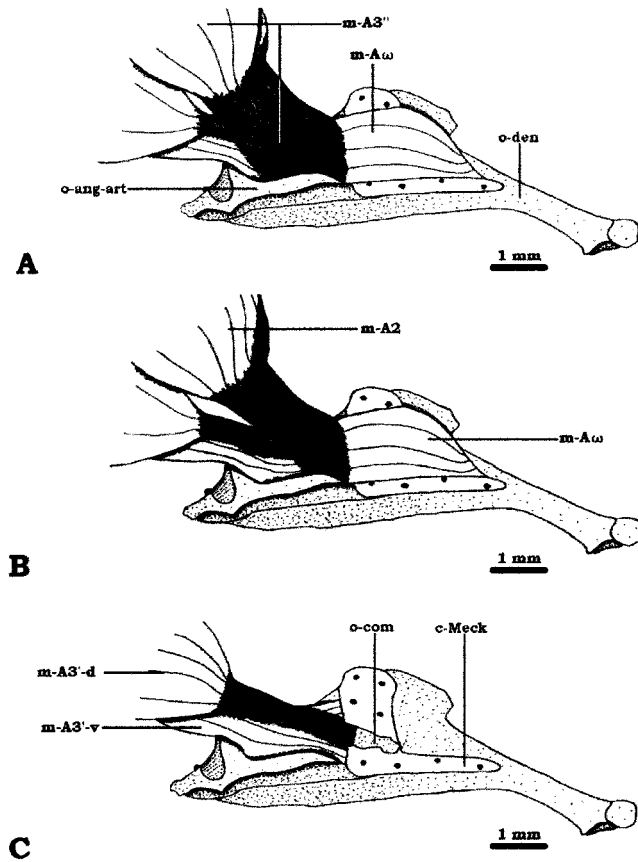
Fig. 5. Medial view of the left lower jaw of *Chrysichthys nigrodigitatus*, LFEM uncatalogued. **A:** Adductor mandibulae complex, except to the A1-OST, exposed. **B:** A3″ removed. **C:** Aω and A2 removed. c-Meck, cartilago Meckeli; m-A2, m-A3′-d, m-A3′-v, m-A3″, m-Aω, sections of the musculus adductor mandibulae; o-ang-art, os angulo-articulare; o-com, os coronomeckelium; o-den, os dentale.

and which has been the subject of considerable discussions.

Configuration of the Adductor Mandibulae in Teleostean Fishes in General

Gosline (1989) noted that, in teleostean fishes, there are "two basically different pathways of differentiation in the cheek part of the adductor mandibulae," which are illustrated in Figure 1. Figure 1A represents the teleostean basal situation of the adductor mandibulae: an undivided cheek muscle attached to the mesial face of the mandible and the Aω already differentiated (the presence of an Aω is an actinopterygian plesiomorphy [Lauder, 1980] and this section was probably the first adductor mandibulae bundle to separate as a distinct entity [Edgeworth, 1935; Winterbottom, 1974; Lauder, 1980]). This situation is observable, for example, in *Salvelinus* (Lauder and Liem, 1980) and also in *Hiodon*, *Elops*, and *Clupea* (Gosline, 1989).

From this configuration, two types of differentiation are possible. In acanthopterygians, an antero-dorso-lateral part of the cheek muscle (A1, see below) appears to have developed an attachment to the maxilla via the primordial ligament (Fig. 1B) (Gosline, 1989). This situation seems to be plesiomorphic for acanthopterygians and is present, for example, in *Aulopus* (Lauder and Liem, 1983; Gosline, 1986, 1989) and *Neoscopelus* (Winterbottom, 1974). A secondary differentiation of the adductor mandibulae (A3, see below), mesial to all the others, is found in most acanthopterygian fishes (Fig. 1C).

In ostariophysines an antero-ventro-lateral (A1-OST, see below) part of the cheek muscle separates and attaches to the postero-dorso-lateral face of the mandible (Fig. 1D) (Gosline, 1989). This section is

TABLE 4. *List of the different adductor mandibulae bundles and their insertions in* Bagrus docmac

| Bundles	Anterior insertion	Posterior insertion
Adductor mandibulae A1-OST	(Fig. 6A) Angulo-articular (fibers + tendon)	(Fig. 6A) Quadrate Preopercular Hyomandibular
Adductor mandibulae A2	(Fig. 7B) Angulo-articular (tendon) Adductor mandibulae Aω (tendon)	(Fig. 6a) Pterotic (tendon) Sphenotic (tendon) Frontal (tendon)
Adductor mandibulae A3'-d-1	(Fig. 7C) Coronomeckelian (tendon)	(Fig. 6B) Quadrate Metapterygoid Hyomandibular
Adductor mandibulae A3'-d-2	(Fig. 7C) Coronmeckelian (tendon)	(Fig. 6B) Preopercular
Adductor mandibulae A3'-v	(Fig. 7C) Angulo-articular	(Fig. 6B) Quadrate (tendon)
Adductor mandibulae A3″	(Figs. 6C, 7A) Angulo-articular (tendon) Primordial ligament (tendon)	(Fig. 6C) Hyomandibular
Adductor mandibulae Aω	(Fig. 7A,B) Dentary	(Fig. 7B) Adductor mandibulae A2
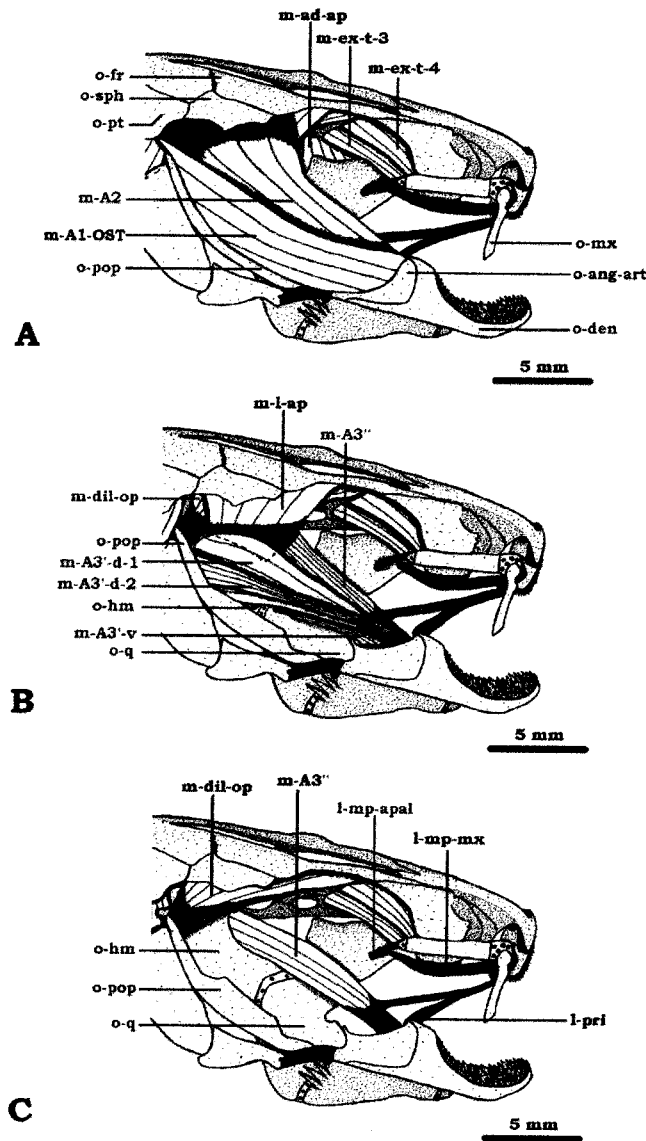
Fig. 6. Right, lateral view of the cheek musculature of *Bagrus docmac*, MRAC 86-07-P-512. **A:** Adductor mandibulae complex exposed. **B:** A1-OST, A2 and adductor arcus palatini removed. **C:** A3′-d-1, A3′-d-2, A3′-v and levator arcus palatini removed. l-mp-apal, ligamentum metapterygoideo-autopalatinum; l-mp-mx, ligamentum-metapterygoideo-maxillare; l-pri, ligamentum primordium; m-A1-OST, m-A2, m-A3′-d-1, m-A3′-d-2, m-A3′-v, m-A3″, sections of the musculus adductor mandibulae; m-ad-ap, musculus adductor arcus palatini; m-dil-op, musculus dilatator operculi; m-ex-t-3, m-ex-t-4, sections of the musculus extensor tentaculi; m-l-ap, musculus levator arcus palatini; o-ang-art, os angulo-articulare; o-den, os dentale; o-fr, os frontale; o-hm, os hyomandibulare; o-mx, os maxillare; o-pop, os praeoperculare; o-pt, os pteroticum; o-q, os quadratum; o-sph, os sphenoticum.

effectively present in all the catfishes studied here (see, for example, Figs. 2A, 3A,B,C, 4A, and 8), namely, in *Diplomystes*, which presents the plesiomorphic condition of the adductor mandibulae of these fishes (see below). This situation, where only an A1-OST, an A2, and an Aω are present, found, e.g., in *Salminus* and *Hepsetus* (Characiformes),

seems (contra Fink and Fink, 1981) to be plesiomorphic for ostariophysine fishes (Vari, 1979; Howes, 1983a, 1985b; Gosline, 1989). The antero-ventro-lateral division of the adductor mandibulae present in these fishes seems to have developed as a "supplementary system for raising the mandible" (Gosline, 1989). Apart from this division, another section of the adductor mandibulae, mesial to all the others (A3, see below), is also present in most ostariophysines (Figs. 1E,F) (McMurrich, 1884; Takahasi, 1925; Edgeworth, 1935; Nawar, 1955; Alexander, 1964, 1965; Munshi and Singh, 1967; Osse, 1969; Ballintijn et al., 1972; Winterbottom, 1974; Vandewalle, 1975; Gijsen and Chardon, 1976; Howes, 1976, 1983a, 1985b; Vari, 1979; De La Hoz and Chardon, 1984; Schaefer and Lauder, 1986; Aguilera, 1988; Gosline, 1989; Adriaens and Verraes, 1996; etc.) and in all catfish studied in this work (see, e.g., Figs. 2–11).

The situation represented in Figure 1E is found in most characiforms (Alexander, 1964, 1965; Gijsen and Chardon, 1976; Howes, 1976, 1983a, 1985b; Vari, 1979; Gosline, 1989; etc.) and in a large number of gymnotiforms (Fink and Fink, 1981; Howes, 1983a, 1985b), and seems to be plesiomorphic for the siluriforms (see below).

In a large number of ostariophysine fishes, namely, in all cypriniforms (Winterbottom, 1974; Fink and Fink, 1981; Howes, 1983a, 1985b; Gosline, 1989; etc.), in some characiforms (Alexander, 1964, 1965; Howes, 1976, 1983a, 1985b; Vari, 1979; Gosline, 1989; etc.), in most gonorynchiforms (Fink and Fink, 1981; Howes, 1985a; Gosline, 1989), and in a large number of gymnotiforms (Chardon and De La Hoz, 1973; Howes, 1983a; De La Hoz and Chardon, 1984; Aguilera 1988), a superficial differentiation of the external section (A1-OST) attaches, via the primordial ligament, to the upper jaw as a new section (A0, see below) of the adductor mandibulae (Fig. 1F) (Gosline, 1989).

This hypothesis about the evolution of the configuration of the adductor mandibulae in ostariophysine fishes contradicts Takahasi (1925) and Fink and Fink (1981). These authors consider that the presence of a lateral section of this muscle attached to the upper jaw is the plesiomorphic situation for these fishes and that "the conditions in some Characiformes and in Siluriformes are hypothesized to be secondary reductions from a primitive attachment to the maxilla" (Fink and Fink, 1981). However, this opinion is contestable. As reminded by Howes (1983a), not only in "some Characiformes," but in the large majority of these fishes the most lateral section of the adductor mandibulae attaches to the mandible, and not to the upper jaw. In fact, Alexander's (1964), Vari's (1979), and Gosline's (1989) studies support the idea that the attachment of the adductor mandibulae on the upper jaw is probably a derived character of some characiforms, probably associated with the small-mouth and/or

the protrusile upper jaw conditions in some specialized species of this group. Moreover, in some Gymnotiformes (*Gymnotus*) the outer part of the adductor mandibulae inserts mainly onto the outer face of the lower jaw, with only a few fibers inserting on the primordial ligament (Howes, 1983a). Moreover, in the morphologically primitive gonorynchiform *Chanos* (Rosen and Greenwood, 1970; Fink and Fink, 1981), the most external bundle of the adductor mandibulae inserts both on the external face of the mandible and on the maxilla (Howes, 1985b; Gosline, 1989). Most other Gonorynchiformes (more specialized than *Chanos*), exhibit a superficial, completely independent bundle attached to the upper jaw, probably associated with their small-mouth condition, like in characiforms (see above) (Gosline, 1989). Finally, in almost all catfish the most external section of the adductor mandibulae attaches to the mandible (see Figs. 2, 4, 6, 8, and 10 and descriptions of McMurrich, 1884; Takahasi, 1925; Edgeworth, 1935; Eaton, 1948; Nawar, 1955; Munshi, 1960; Alexander, 1965; Winterbottom, 1974; Howes, 1983a,b, 1985b; Schaefer and Lauder, 1986, 1996; Gosline, 1989; Schaefer, 1990; Mo, 1991; Adriaens and Verraes, 1996; etc.). Thus, in agreement with Alexander (1964, 1965), Vari (1979), Howes (1983a, 1985b), and Gosline (1989), the insertion of the most superficial section of the adductor mandibulae on the mandible seems to be the plesiomorphic condition for ostariophysines. The differentiation of a section attached, via the primordial ligament, to the upper jaw seems, thus, to be a derived condition for these fishes (Fig. 1), probably associated with derived characters such as a small mouth and/or protrusile upper jaw.

There has been some controversy in the past concerning the reliability of the path of the ramus mandibularis to identify subdivisions of the adductor mandibulae. According to Edgeworth (1935) and Winterbottom (1974), the path of this nerve tract is an "unreliable character" to recognize the different adductor mandibulae sections, since "it may pass: external to the adductor mandibulae (e.g., *Salmo*, *Clupea*); external to A2 (e.g., *Pleuronectes*); between A2 and A3 (e.g., *Scomber*, *Cyprinus*, *Esox*); external to A1 and internal to A2 and A2A3 (e.g., *Ictalurus*, *Galeichthys*) and internal to A3 (*Zoaces*)" (Winterbottom, 1974). However, recent studies (e.g., Howes, 1985a, 1988; Gosline, 1986, 1989) indicate that "the course of the ramus mandibularis seems to be a better indicator of cheek sections in the adductor mandibulae than has been generally been acknowledged" (Gosline, 1989). According to Gosline (1989) "much of the previously assumed variability in the course of the ramus mandibularis disappears once it is realized that the cheek sections of the adductor mandibulae in acanthopterygians and ostariophysines are not homologous." The present study supports this last idea. Apart from some minor shifts, the path of the ramus mandibularis of all the

catfish examined is quite alike, usually separating the anterior part of the external section of the adductor mandibulae, A1-OST, from the anterior part of the A2 and/or posterior part of the Aω. This type of course of the ramus resembles that of the characiforms and cypriniforms described by Gosline (1989), in which this nerve tract passes between the anterior parts of the A1-OST and A2. The study of the path of the ramus mandibularis thus supports Gosline's (1989) hypothesis concerning the homologies of the adductor mandibulae sections among ostariophysines (see above).
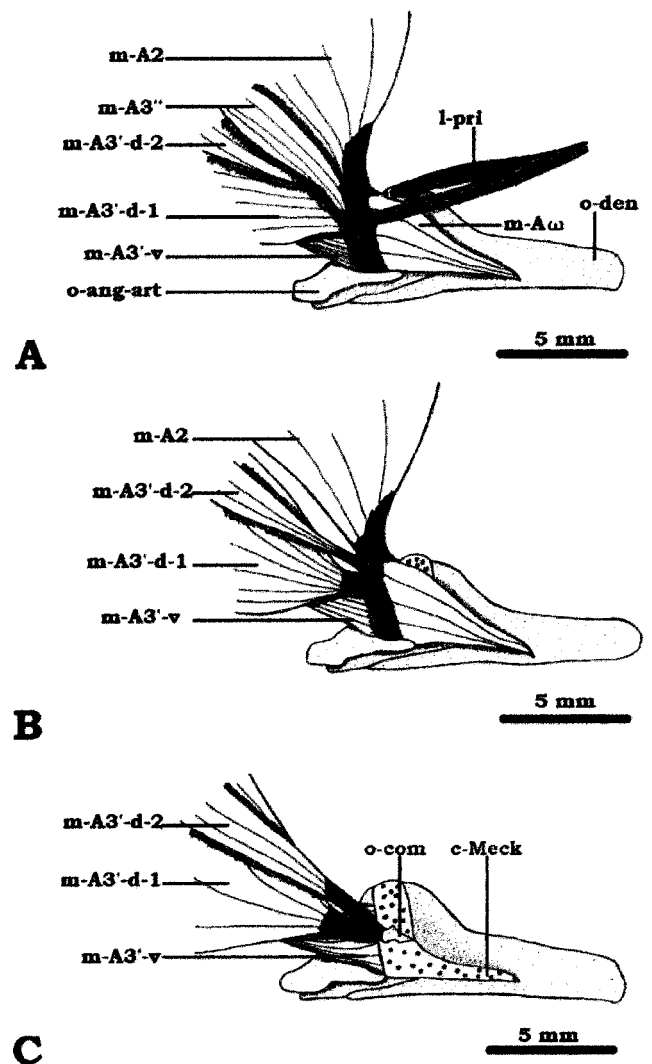
Fig. 7. Medial view of the left lower jaw of *Bagrus docmac*, MRAC 86-07-P-516. **A:** Adductor mandibulae complex, except the A1-OST, exposed. **B:** A3″ and ligamentum primordium removed. **C:** Aω and A2 removed. c-Meck, cartilago Meckeli; l-pri, ligamentum primordium; m-A2, m-A3′-d-1, m-A3′-d-2, m-A3′-v, m-A3″, m-Aω, sections of the musculus adductor mandibulae; o-ang-art, os angulo-articulare; o-com, os coronomeckelium; o-den, os dentale.

TABLE 5. List of the different adductor mandibulae bundles and their insertions in Clarias gariepinus

Bundles	Anterior insertion	Posterior insertion
Adductor mandibulae A1-OST	Angulo-articular (fibers + tendon)	(Adriaens and Verraes, 1996: Fig. 5A) Quadrate
(A2A3'β of Adriaens and Verraes, 1996)	(the anterior part of this bundle is fused with the anterior part of the A2)	Preopercular Hyomandibular
Adductor mandibulae A2	Angulo-articular (fibers + tendon)	(Adriaens and Verraes, 1996: Fig. 5A) Supraopercular
(A2A3'α of Adriaens and Verraes, 1996)	(the anterior part of this bundle is fused with the anterior part of the A1)	Sphenotic Infraorbital IV
Adductor mandibulae A3'	(Adriaens and Verraes, 1996: Fig. 7B,C)	(Adriaens and Verraes, 1996: Fig. 5C) Quadrate Hyomandibular Frontal
(A3"-s of Adriaens and Verraes, 1996)	Coronomeckelian (tendon)	Sphenotic Pterosphenoid
Adductor mandibulae A3" (A3"-p of Adriaens and Verraes, 1996)	(Adriaens and Verraes, 1996: Fig. 7A,B,C) Angulo-articular (tendon)	Hyomandibular

Identity of the Adductor Mandibulae Sections in Ostariophysine Fishes

There are two patterns of differentiation in the jaw musculature of teleosts (Fig. 1). Thus, neither the external section of the adductor mandibulae plesiomorphically present in ostariophysines (A1-OST) nor the section derived from it, present in a large number of these fishes (A0), correspond to the bundle that attaches to the upper jaw in acanthopterygians (A1) (Fig. 1). Gosline (1989) considered that Vetter's (1878) A1, A2, A3, and Aω should be retained for acanthopterygians. Thus, the section that attaches to the upper jaw in acanthopterygian fishes should be called A1, since it corresponds to Vetter's A1 in *Perca*. The two sections that are homologous (see below) throughout the teleosts (Aω and A2) (Fig. 1), correspond, respectively, to Vetter's Aω and A2 in *Perca*. Finally, the mesial section of the adductor mandibulae present in a great number of acanthopterygians (A3) (Fig. 1C) corresponds to Vetter's A3 in *Perca*.

But, as mentioned by Gosline (1989), "the question arises of what to call the cheek sections of ostariophysine fishes, if the designations A1, A2 and A3 are retained for acanthopterygians." This author

suggested three hypotheses to resolve this problem: 1) use purely descriptive terms for the adductor mandibulae sections of the Ostariophysi; 2) use diagnostic designations other than A1, A2, A3, and Aω that are homologous, or at least represent parallel developments, within the ostariophysines; 3) try to adapt Vetter's designations, starting from that one cheek section (Fig. 1: A2) homologous throughout teleosts.

Gosline chose to adopt the first hypothesis. However, we consider that the utilization of purely descriptive terms can be very complicated. In some ostariophysines, e.g., *Amphilius* (Table 7; Figs. 10, 11), there are nine different adductor mandibulae sections. It is too difficult to relate them with descriptive terms like "external part of the external division of the adductor mandibulae," "external part of the internal division of the adductor mandibulae," etc. Moreover, it is also very confusing, as no rule was previously established for the use of these descriptive names. Therefore, it is possible to give to the same bundle an endless number of different names, which will enormously complicate further morphological comparisons. The same problem will result if we use previously unestablished diagnostic

TABLE 6. List of the different adductor mandibulae bundles and their insertions in
Phactura brevicauda

| Bundles	Anterior insertion	Posterior insertion
Adductor mandibulae A1-OST-1	(Fig. 8) Angulo-articular (fibers + tendon)	(Fig. 8) Preopercular (tendon)
Adductor mandibulae A1-OST-2	(Fig. 8) Angulo-articular (fibers + tendon)	(Fig. 8) Preopercular Quadrate
Adductor mandibulae A2	(Fig. 9) Angulo-articular (tendon)	Preopercular
Adductor mandibulae A3	(Fig. 9) Coronomeckelian (tendon)	(Fig. 8) Preopercular (tendon) Hyomandibular Quadrate
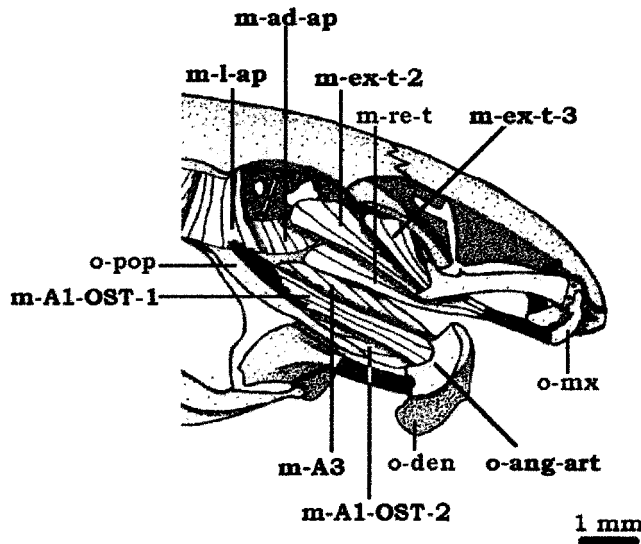
Fig. 8. Right, lateral view of the cheek musculature of *Phractura brevicauda*, MRAC 90-057-P-5145 (the A2 is not shown, since it is hidden mesially to the A1-OST). m-A1-OST-1, m-A1-OST-2, m-A3, sections of the musculus adductor mandibulae; m-ad-ap, musculus adductor arcus palatini; m-ex-t-2, m-ex-t-3, sections of the musculus extensor tentaculi; m-l-ap, musculus levator arcus palatini; m-re-t, musculus retractor tentaculi; o-ang-art, os angulo-articulare; o-den, os dentale; o-mx, os maxillare; o-pop, os praeoperculare.

designations other than A1, A2, A3, and Aω to describe the adductor mandibulae sections present in ostariophysines. Besides, two of the adductor mandibulae sections present in ostariophysines clearly correspond to the A2 and Aω of acanthopterygian fishes (Fig. 1). Thus, there is no reason (and it is not correct) to give them names other than A2 and Aω.

Therefore, we adopted Gosline's third hypothesis and called the ostariophysine adductor mandibulae sections A2 and Aω that corresponded to the A2 and
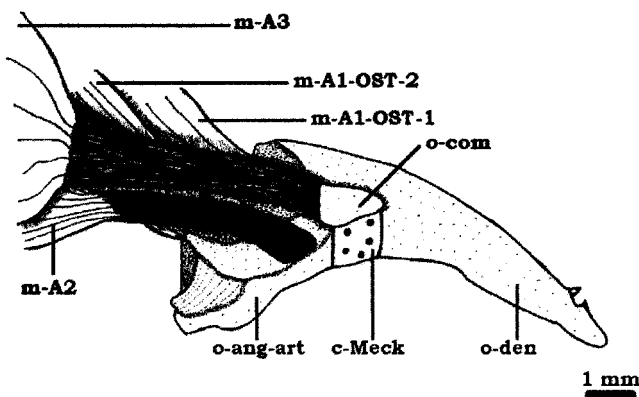

Fig. 9. Medial view of the left lower jaw of *Phractura brevicauda*, MRAC 92-125-P-362. c-Meck, cartilago Meckeli; m-A1-OST-1, m-A1-OST-2, m-A2, m-A3, sections of the musculus adductor mandibulae; o-ang-art, os angulo-articulare; o-com, os coronomeckelium; o-den, os dentale.

TABLE 7. *List of the different adductor mandibulae bundles and their insertions in* Amphilius brevis

Bundles	Anterior insertion	Posterior insertion
Adductor mandibulae A1-OST-1	(Fig. 10A) Dentary	(Fig. 10A) Pterotic (tendon) Preopercular (tendon) Sphenotic (tendon) Frontal (tendon)
Adductor mandibulae A1-OST-2	(Fig. 10A) Dentary (tendon)	(Fig. 10A) Sphenotic (tendon) Frontal (tendon)
Adductor mandibulae A1-OST-3	(Fig. 10B) Denary (tendon)	(Fig. 10B) Sphenotic Frontal Preopercular Hyomandibular
Adductor mandibulae A1-OST-4	(Figs. 10B, 11B) Dentary (tendon)	(Fig. 10B) Sphenotic Preopercular Hyomandibular
Adductor mandibulae A1-OST-5	(Fig. 10C) Dentary	(Fig. 10C) Quadrate Preopercular Hyomandibular
Adductor mandibulae A2	(Fig. 11A) Dentary (tendon)	(Fig. 10C) Frontal Sphenotic Hyomandibular Preopercular
Adductor mandibulae A3-d	(Fig. 11B) Coronomeckelian (tendon)	(Fig. 10D) Preopercular Hyomandibular
Adductor mandibulae A3-v-1	(Fig. 11B) Dentary	(Fig. 10D) Quadrate
Adductor mandibulae A3-v-2	(Fig. 11B) Angulo-articular	(Fig. 10E) Quadrate (tendon)

Aω of acanthopterygians (Fig. 1). As to A3, the situation is more delicate. The A3 is lacking in both the teleostean (Fig. 1A), acanthopterygian (Fig. 1B), and ostariophysine (Fig. 1D) basal configuration of the adductor mandibulae, being present, however, in a large number of acanthopterygians (Fig. 1C) and ostariophysines (Fig. 1E,F) (see above). The A3 of these two groups are very much alike. They are the most mesial adductor mandibulae sections, they normally attach posteriorly to the lateral face of the suspensorium and anteriorly to the mesial face of the mandible (Winterbottom, 1974), and they present a quite similar configuration and orientation of their fibers (Fig. 1C,E). Therefore, the A3 of acanthopterygians and ostariophysines are the result of parallel independent specializations that occurred in these two groups and are, thus, homoplastic structures (Fig. 1). From a practical nomenclatural point of view, the name A3, retained for acanthopterygian fishes (Fig. 1C) (see above), can also be (and, in our opinion, must be) used to describe the most mesial section of the adductor man-
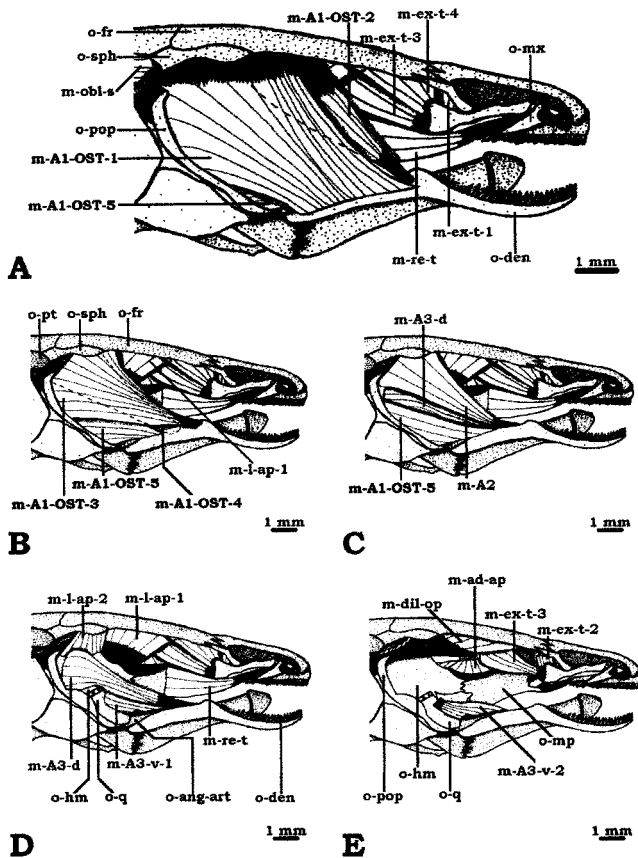
Fig. 10. Right, lateral view of the cheek musculature of *Amphilius brevis*, MRAC 89-043-P-2298. **A:** Adductor mandibulae complex exposed. **B:** A1-OST-1, A1-OST-2, and musculus obliquus superior removed. **C:** A1-OST-3 and A1-OST-4 removed. **D:** A1-OST-5 and A2 removed. **E:** A3-d, A3-v-1, retractor tentaculi, levator arcus palatini, and the sections 1 and 4 of the extensor tentaculi removed. m-A1-OST-1, m-A1-OST-2, m-A1-OST-3, m-A1-OST-4, m-A1-OST-5, m-A2, m-A3-d, m-A3-v-1, m-A3-v-2, sections of the musculus adductor mandibulae; m-ad-ap, musculus adductor arcus palatini; m-dil-op, musculus dilatator operculi; m-ex-t-1, m-ex-t-2, m-ex-t-3, m-ex-t-4, sections of the musculus extensor tentaculi; m-l-ap-1, m-l-ap-2, sections of the musculus levator arcus palatini; m-obl-s, musculus obliquus superioris; m-re-t, musculus retractor tentaculi; o-ang-art, os angulo-articulare; o-den, os dentale; o-fr, os frontale; o-hm, os hyomandibulare; o-mp, os metapterygoideum; o-mx, os maxillare; o-pop, os praeoperculare; o-pt, os pteroticum; o-q, os quadratum; o-sph, os sphenoticum.

dibulae present in the great majority of ostariophysine fishes (Fig. 1E,F). In fact, this is a usual procedure for similar structures developed in parallel. It seems to be logical, and facilitates comparisons: the "retractor tentaculi" (see below) and the "elastic string apparatus" (Chardon, 1968) of catfish, and the "maxillary barbels," present in different groups of fishes, e.g., Siluriformes and Cypriniformes, are good examples of this procedure.

As to the A1 and the A1-OST, the situation is quite different, and more complicated, due to the definition of "homologous," which remains far from being clear (Gould, 1988; Hall, 1994; Beaumont,

1998). The most widespread definition of the term homologous in vertebrate biology is "descended from the same ancestral structure." But the question of the definition of "structure" arises. For example, if we consider the adductor mandibulae section (A2) present in basal teleostean fishes (Fig. 1A) as a single structure, we can consider that the A1 and the A1-OST that result from two different patterns of differentiation of this section (see above) (Fig. 1B,D) are homologous. However, if we consider the fibers of this section as individual structures, the A1 and A1-OST are not homologous, since they are derived, respectively, from its dorso-lateral (Fig. 1B) and ventro-lateral (Fig. 1D) fibers. However, for purely nomenclatural purposes, both considerations lead to the same result. In fact, even if these sections are considered homologous, they should not be given the same name, since they are the result of divergent evolutionary steps, which have led to quite different structures (Fig. 1B,D). Thus, to distinguish the dorso-lateral adductor mandibulae section present in basal acanthopterygians (Fig. 1B) termed A1 (see above) from the ventro-lateral adductor mandibulae section of basal ostariophysines, and following Vetter's (1878) nomenclature, in which as a more lateral section it should be attributed an inferior number (the ventro-lateral adductor mandibulae section present in basal ostariophysine fishes is lateral to the A2), we decided to call the ventro-lateral section of ostariophysines A1-OST (Fig. 1D).

The lateral adductor mandibulae section that attaches to the upper jaw in some ostariophysines (Fig. 1F: A0) — e.g., all cypriniforms, some characiforms, most gonorynchiforms and a large number of gymnotiforms (see above) — can be considered, to some extent, homoplastic with the A1 of acanthopterygians (Fig. 1B), since both are attached to the maxilla. However, the similarities between
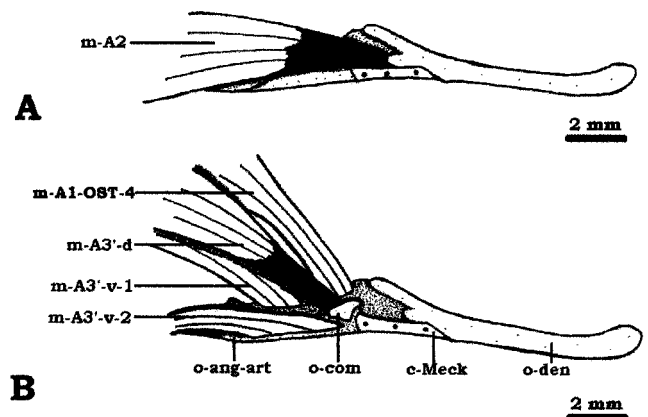

Fig. 11. Medial view of the left lower jaw of *Amphilius brevis*, MRAC 89-043-P-403. **A:** Only the A2 is illustrated. **B:** Only the A1-OST-4, A3-d, A3-v-1 and A3-v-2 are illustrated. c-Meck, cartilago Meckeli; m-A1-OST-4, m-A2, m-A3-d, m-A3-v-1, m-A3-v-2, sections of the musculus adductor mandibulae; o-ang-art, os angulo-articulare; o-com, os coronomeckelium; o-den, os dentale.

these two structures are merely confined to this attachment, because their posterior attachment and configuration are somewhat different (Gosline, 1989). To be consistent with Vetter's nomenclature (see above), and since it is external to the A1-OST (Fig. 1F), this section will be termed A0 (Fig. 1F) (the "OST" is not necessary, since the name A0 has not yet been used to describe any other adductor mandibulae section). The diagnostic designation A0 was never used by Vetter (1878), for a very simple reason: Vetter used only the designations A1, A2, A3, and Aω since he considered that the A1 of acanthopterygians corresponded to the most external adductor mandibulae section of Cypriniformes (A0 of this work). So, in his descriptions of the adductor mandibulae of cypriniforms, Vetter called the A1-OST, A2, and A3 of this work, respectively, A2, A3′ and A3″. Therefore, the section that he called A2 in the acanthopterygian *Perca*, he termed A3 in the cypriniforms *Barbus* and *Cyprinus* (Gosline, 1989).

This misinterpretation was followed by most authors. Thus, the A0 of this work was usually called A1 (or A1-a) (Takahasi, 1925; Ballintijn et al., 1972; Chardon and De La Hoz, 1973; Winterbottom, 1974; Vandewalle, 1975; Howes, 1978; Fink and Fink, 1981; De La Hoz and Chardon, 1984; Aguilera, 1988; etc.). Similarly, the sections A1-OST, A2, A3 (or A3′), and A3″ (of this work) of ostariophysines were often called, respectively, A2 (Takahasi, 1925; Ballintijn et al., 1972; Vandewalle, 1975; Aguilera, 1988; Adriaens and Verraes, 1996; etc.), A3 (or A3′) (Takahasi, 1925; Ballintijn et al., 1972; Vandewalle, 1975; Adriaens and Verraes, 1996; etc.), A3″ (or A3″-s) (Takahasi, 1925; Adriaens and Verraes, 1996; etc.), and A3″-p (Adriaens and Verraes, 1996).

However, to complicate this question still more, many authors that studied mainly ostariophysine fishes without an A0, as, for example, the siluriforms or most characiforms (e.g., McMurrich, 1884; Stix, 1956; Alexander, 1964, 1965; Gijsen and Chardon, 1976; Howes, 1976, 1983a, 1985b; Schaefer and Lauder, 1986; etc.) used the name A1 to designate the A1-OST of this work (because, as the A0 is absent, the A1-OST is the outermost adductor mandibulae section of these fishes). Therefore, they used the names A2 and A3 to designate, respectively, the A2 and A3 of this work. Other authors, e.g., De La Hoz and Chardon (1984), who studied *Sternopygus macrurus*, a gymnotiform ostariophysine fish that possesses a configuration of this muscle similar to that illustrated in Figure 1F, decided to call A1-a and A1-b, respectively, the A0 and A1-OST of this work and, therefore, to call (correctly, in our opinion) A2 and A3, respectively, the A2 and A3 of this work.

All this confusion about the identity of the adductor mandibulae sections is, thus, nearly exclusively due to a sole defect: the study of the configuration of this muscle in only one group of fishes, without comparisons with other groups. The procedure followed in this work is an attempt to avoid the repetition of this defect.

Adductor Mandibulae of Catfish

In the basal adductor mandibulae configuration for ostariophysines, this muscle is divided into three sections, namely, the Aω, the A1-OST, and the A2 (Fig. 1D). But what is the basal situation for catfish? Howes (1983a, 1985b), Schaefer and Lauder (1986), and Gosline (1989) consider that the plesiomorphic adductor mandibulae configuration for these fishes is seen in *Diplomystes*, of the Diplomystidae, the most primitive catfish family (Eigenmann, 1890; Regan, 1911; Alexander, 1965; Chardon, 1968; Lundberg and Baskin, 1969; Gosline, 1975; Fink and Fink, 1981; Arratia, 1987, 1992; Mo, 1991; etc.). For Howes (1983a, 1985b), Schaefer and Lauder (1986), Arratia (1987), and Gosline (1989) the adductor mandibulae of *Diplomystes* is an almost undifferentiated muscle. However, careful study of this muscle in *Diplomystes chilensis* (Figs. 2, 3) reveals that it is divided into four well-distinguishable sections, namely, the Aω, A1-OST, A2, and A3, the latter being subdivided in a dorsal (A3-d) and a ventral part (A3-v) (Figs. 2, 3). But, despite the presence of these sections and subsections, we agree with these authors that the plesiomorphic adductor mandibulae configuration of siluriforms is that present in *Diplomystes*. We give two arguments to support this hypothesis.

First, the adductor mandibulae of this genus presents a configuration quite similar to that present in certain archaic Characiformes, e.g., *Hoplerythrinus* (Gijsen and Chardon, 1976: Figs. 2, 3, 6), and Gymnotiformes, e.g., *Sternopygus* — considered the most primitive gymnotiform by Fink and Fink (1981). The sole exception is that the latter possesses an adductor mandibulae section attached to the lacrimal (De La Hoz and Chardon, 1984: Figs. 14, 15).

Second, from the configuration of the adductor mandibulae of *Diplomystes*, it is theoretically possible to "build" the adductor mandibulae of any other catfish studied in the present work. According to Alexander (1965), the configuration of this muscle is strongly related to the form of the head. So, in fishes with a narrow cranial roof, the levator arcus palatini is situated very close to the mesial line, and the adductor mandibulae cannot extend mesially to this muscle. The inverse occurs in fishes with a large cranial roof: they present thick adductor mandibulae sections mesially to the levator arcus palatini. Following Alexander's hypothesis, we can, starting from the configuration of the adductor mandibulae of *Diplomystes*, easily arrive at the configuration present in the other catfishes studied and, therefore, determine the identity of the different adductor mandibulae sections of these fishes (Fig. 12). **F12**

In *Diplomystes* (Fig. 12A) the cranial roof is narrow. Therefore, the levator arcus palatini is near to
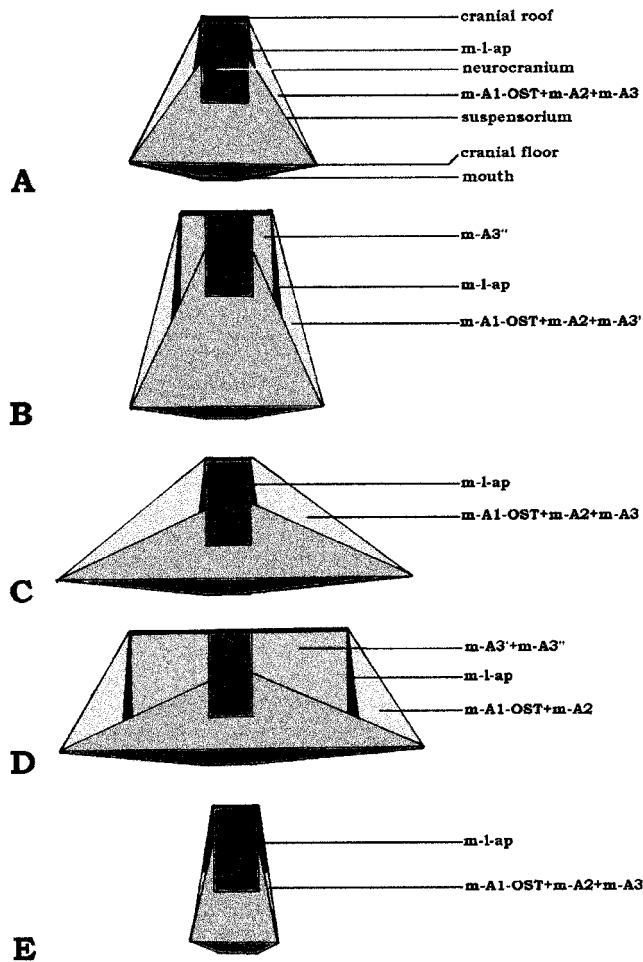
Fig. 12. Scheme illustrating the relation between the shape of the skull, the levator arcus palatini, and the adductor mandibulae (see Discussion) in: **A:** *Diplomystes*; **B:** *Chrysichthys* and *Bagrus*; **C:** *Amphilius*; **D:** *Clarias*; **E:** *Phractura*. m-A1-OST, m-A2, m-A3, m-A3′, m-A3″, sections of the musculus adductor mandibulae; m-l-ap, musculus levator arcus palatini.

the mesial line and the A3 is almost entirely lateral to this muscle (see Fig. 2B).

In *Bagrus* and *Chrysichthys* (Fig. 12B) the cranial roof is broader than that of *Diplomystes*. Thus, one part of the adductor mandibulae A3, the A3″, is situated mesially to the levator arcus palatini. The other adductor mandibulae sections are rather like to those of *Diplomystes* (Figs. 4–7, cf. Figs. 2, 3).

Amphilius (Fig. 12C) presents a very broad cranial floor. As in *Diplomystes*, the adductor mandibulae A3 is external to the levator arcus palatini. However, the area situated laterally to this muscle is much larger than that of *Diplomystes*, which leaves place to a much thicker A1-OST and A2. Therefore, the A1-OST is differentiated in five thick subsections, four of them being attached to the neurocranium (Fig. 10, cf. Fig. 2). *Amphilius* possesses a very flat head, adapted to a benthic lifestyle. The mandible is depressed dorso-ventrally, which probably ex-

plains the absence of the Aω (Fig. 11, cf. Fig. 3). In the specific case of this genus, the tendon of the A2, which is associated with the Aω in *Diplomystes*, *Bagrus*, and *Chrysichthys*, migrates anteriorly, attaching to the dentary (Fig. 11, cf. Figs. 3, 5, 7).

In *Clarias* (Fig. 12D), the cranial roof is very broad, but less than the cranial floor. Consequently, the levator arcus palatini is quite far to the mesial line, and the A3′ and A3″ situate mesially to this muscle. The Aω is missing, probably for the same reason that it is missing in *Amphilius* (see above). As a result, in the specific case of *Clarias*, the tendon of the A2 associates to that of the A1-OST.

Phractura (Fig. 12E) presents a very narrow cranial roof and floor. So, in this genus, the A3 is completely external to the levator arcus palatini. All the adductor mandibulae sections are very narrow, and none of them attaches onto the neurocranium (Fig. 8). As in *Clarias* and *Amphilius*, the mandible of *Phractura* is depressed dorso-ventrally (although, contrary to these genera, the head of *Phractura* is not flattened), and the Aω is missing. However, in this genus the anterior insertion of the A2 has not suffered any spatial modification in relation to the genera where the Aω is present (Fig. 19, cf. Figs. 3, 5, 7).

The configuration of the adductor mandibulae of *Diplomystes* thus seems to represent the plesiomorphic catfish situation. In fact, the configuration of this muscle present in the Siluriformes described in the literature (McMurrich, 1884; Takahasi, 1925; Edgeworth, 1935; Eaton, 1948; Nawar, 1955; Stix, 1956; Alexander, 1965; Winterbottom, 1974; Howes, 1983a,b, 1985b; Schaefer and Lauder, 1986, 1996; Schaefer, 1990; etc.) can also be easily explained as the result of slight modifications of that present in this genus.

However, the assumption that the configuration of the adductor mandibulae of *Diplomystes* probably represents the plesiomorphic catfish situation raises an interesting question: is the attachment of the adductor mandibulae to the dorsal surface of the neurocranium a plesiomorphic character for the Siluriformes?

The few authors who analyzed this question (Lundberg, 1970; Howes, 1983b; Mo, 1991) considered that the origin of the adductor mandibulae on the dorsal surface of the neurocranium should be considered as a derived character, independently developed in certain catfish groups. However, we consider that this character is, probably, plesiomorphic for catfish. The origin of this muscle on the dorsal surface of the neurocranium is present in the diplomystids (Fig. 2), cetopsids, malapterurids, ictalurids, plotosids, amblycipitids, clariids, and bagrids (see the descriptions of McMurrich, 1884; Stix, 1956; Lundberg, 1970; Gosline, 1975; Howes, 1983b; Arratia, 1987; Mo, 1991; Cabuy et al., 1999). Therefore, this character is distributed in African, Australian, Asiatic, South American, and North American cat-

fishes (the ictalurids were artificially introduced in the Europe and, thus, this continent should not be counted for this purpose) and in four of the six families considered by Mo (1991) as the most primitive of the Siluriformes (Diplomystidae, Cetopsidae, Malapteruridae, and Ictaluridae). Since this character seems not to be directly associated with a parallel or convergent evolution for the adaptation to a certain type of life — the different groups where it is present do not have, in any way, the same ecological preferences — it seems likely that it would represent a plesiomorphy for catfish. It should be noted, however, that this question could only be clarified with further comparisons with non-siluriform outgroups.

Origin of the Retractor Tentaculi of Catfish

Numerous catfish possess a muscle that attaches to the maxillary (see, e.g., Figs. 8, 10), which is usually called the retractor tentaculi, since its contraction pulls the distal end of this bone backward, thus retracting the maxillary barbel (Nawar, 1955; Alexander, 1965; Singh, 1967; Gosline, 1975; Fink and Fink, 1981; Howes, 1983a,b, 1985b; Schaefer and Lauder, 1986, 1996; Schaefer, 1990; Mo, 1991; Adriaens and Verraes, 1996, 1997; etc.). The question of the origin of this muscle has been controversial, and, since it is narrowly associated with the adductor mandibulae, it will be briefly discussed here. Certain authors, e.g., Takahasi (1925), Edgeworth (1935), and Winterbottom (1974), consider that it is derived from the most external adductor mandibulae section present in the Siluriformes (A1-OST) (Fig. 1E). Thus, it would be homologous with the adductor mandibulae A0 (Fig. 1F) of other ostariophysine fishes, since, as does the latter, it inserts on the maxillary (cf. Figs. 8, 10 to Fig. 1F). However, other authors, e.g., McMurrich (1884), Eaton (1948), Alexander (1965), Howes (1983a), and Adriaens and Verraes (1997), consider that the retractor tentaculi results from the differentiation of the adductor mandibulae A3, since it does not occupy the same spatial position as the A0 of other ostariophysines: it is situated mesially to all the other adductor mandibulae sections, whereas the A0 is the most lateral section of this muscle.

The present study strongly supports the latter hypothesis. In *Diplomystes* (Fig. 2) and *Chrysichthys* (Fig. 4), there is no association between the adductor mandibulae and the maxillary, the primordial ligament is present, and the retractor tentaculi is absent. In *Bagrus*, the innermost adductor mandibulae section (A3″), originated on the lateral face of the suspensorium, presents an anterior tendon that is associated with the primordial ligament and that, through the latter, attaches to the maxillary bone (Fig. 6). This situation is also found in the bagrid *Mystus* (Munshi, 1960) and the pimelodids *Megalonema* (Howes, 1983a) and *Pseudopimelodus* (Al-

exander, 1965). In *Amphilius* (Fig. 10), *Clarias* (Adriaens and Verraes, 1996: Fig. 5) and *Phractura* (Fig. 8), as in most catfish that possess a retractor tentaculi (McMurrich, 1884; Takahasi, 1925; Edgeworth, 1935; Eaton, 1948; Alexander, 1965; Munshi, 1960; Singh, 1967; Singh and Munshi, 1968; Gosline, 1975; Ghiot, 1978; Howes, 1983a,b, 1985b; Ghiot et al., 1984; Mo, 1991 and Schaefer, 1990; etc.), this muscle, originated on the lateral face of the suspensorium, is situated mesially to all the adductor mandibulae sections, and is attached to the maxillary through an anterior tendon, while the primordial ligament is absent. Thus, it seems clear that the retractor tentaculi results from the differentiation of the innermost adductor mandibulae section (A3) attached, via the primordial ligament, to the maxillary. As considered by Howes (1983a), this differentiation probably occurred independently in different catfish lineages, since the basic conditions for its development are present in some bagrids and pimelodids, two generalized catfish families from which many other Siluriformes families probably derived (Chardon, 1968).

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