Descriptive osteology of *Corydoras aeneus* (Siluriformes: Callichthyidae)

by

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ABSTRACT. - Both the cranial and postcranial osteology of *Corydoras aeneus* (Gill, 1858) is described based on the study of five adult specimens. The results were compared to the condition described for other loricarioid fishes. Most results corresponded with the expected pattern based on studies dealing with parts of the callichthyid osteology, although some differences were observed. One of these differences was the presence of a suprapreopercular bone, a bone that was previously unmentioned in any callichthyid species. Further, several homologies were resolved and mainly confirmed existing hypotheses. This way, for example, based on the presence of several branches of the lateral line system, the compound dorsolateral bone of the otic region was identified as the posttemporo-pterotico-supracleithrum. Further, the presence of several otoliths in the compound bone forming the neurocranial floor in the occipital region, confirmed the fact that the bone comprised out of a fusion of both basi- and exoccipital bones. This study, however failed to resolve some other questions regarding homologies (i.e., lacrymo-antorbital, suprapreopercle) pointing out the need for further ontogenetic research. In this light, this study provides the basis for this further comparative and ontogenetic research on callichthyids specifically and on loricarioids in general.

RÉSUMÉ. - Étude de l'ostéologie de *Corydoras aeneus* (Siluriformes : Callichthyidae).

L'ostéologie crâniale et postcrâniale de *Corydoras aeneus* (Gill, 1858) est décrite d'après cinq spécimens adultes. Les résultats sont comparés avec ceux des autres poissons loricarioïdes. La plupart sont en accord avec les données de la littérature, qui s'intéressaient surtout à l'ostéologie des Callichthyidae. Néanmoins, quelques différences ont été observées comme la présence d'un suprapréoperculaire, jamais observé chez aucune espèce de Callichthyidae. La majorité des homologies ont été résolues, confirmant principalement les hypothèses actuelles. L'os composé situé dorsolatéralement dans la région otique du crâne a ainsi été identifié comme l'os post-temporo-ptérotico-supracleithrum sur la présence du plusieurs branches du système de la ligne latérale. De plus, la présence du plusieurs otolithes dans l'os composé qui forme la base du crâne occipital confirme que cet os est formé d'une fusion entre les os basi- et exoccipitaux. Quelques questions concernant l'homologie restent cependant non résolues comme, par exemple, le lacrymo-antorbital ou le suprapréoperculaire), indiquant la nécessité d'une recherche ontogénétique. Cette étude est donc une base pour de futures études comparatives et ontogénétiques sur les Callichthyidae, spécifiquement, et sur les Loricarioidea, en général.

Key words. - Callichthyidae - *Corydoras aeneus* - Osteology - Morphology.

The genus *Corydoras*, belonging to the Callichthyidae, is widespread in South America (Gosline, 1940; Nijssen, 1970; Kramer and Braun, 1983) and well known among aquarists for its many ornamental species (Burgess and Quinn, 1992). *Corydoras aeneus* (Gill, 1858) is particularly a popular species in the trade of freshwater ornamental fish. It is annually bred and shipped in large quantities all over the world (Tamaru *et al*., 1997). *C. aeneus* has already been studied from both a morphological and physiological points of view (Kramer and McClure, 1980, 1981; Kramer and Braun, 1983; Huysseune and Sire, 1997) as is also the case for its reproductive biology (Kohda *et al*., 1995, 2002; Pruzsinszky and Ladich, 1998). However, despite it being commercially bred, almost nothing is known about its ontogeny. Some attention has been paid to the early ontogeny of some aspects of the head in other callichthyids (Hoedeman, 1960a), but still a lot of relevant information is lacking. The same accounts for the adult morphology: a complete overview of the cranial and postcranial morphology is absent, despite of its relevance for ongoing phylogenetic research on Loricarioidea, to which these callichthyids belong (Reis, 1998; Britto and Castro, 2002). Even though phylogenetic affinities between the families of these loricarioids is quite resolved (Schaefer, 1990; Reis, 1998; Aquino and Schaefer, 2002), as well as the generic relationships within the callichthyids (Reis, 1997, 1998), no information exists on the phylogeny of the highly diverse genus *Corydoras*. Even the monophyletic nature of this genus, comprising approximately 140 species, is uncertain, possibly partially overlapping the currently defined *Brochis* and *Aspidoras* genera (Reis, 1998). Consequently, the aim of this study is to provide a full description of the osteology of the species, as a basis for further ontogenetic research on this species, as well as to contribute to future phylogenetic studies.

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MATERIALS AND METHODS

For this study we investigated five adult specimens of *Corydoras aeneus*, obtained from an aquarium shop. The specimens were sedated and killed, using an overdose of MS-222 (3-aminobenzoic acid ethyl ester, Sigma) and afterwards cleared and stained using the technique described by Hanken and Wassersug (1981). These specimens were then investigated and drawn using a Wild M5 stereomicroscope. For the nomenclature of the skeletal elements we followed Schaefer (1990) and Reis (1998). The homology of the autopalatine with the dorsal part of a premandibular arch follows Daget (1964) and Jarvik (1980).

RESULTS AND DISCUSSION

In *Corydoras aeneus* the neurocranium is pyriform, with a small ethmoid and orbital region, broadening at the temporal region into a large occipital region.

Ethmoid region (Figs 1-3)

The mesethmoid in *Corydoras aeneus* is narrow anteriorly and broadens posteriorly (also see Fink and Fink, 1996; Arratia, 2003). It lacks cornua and broadens substantially towards its posterior margin. Although a general trend towards a reduction of the cornua is present in all catfishes (Lundberg, 1982; Schaefer, 1987), a total lack of these cornua is only present within the Callichthyidae, with the exception of the genus *Brochis*, in which extremely reduced cornua are still present (Schaefer, 1990; Reis, 1998). Hoedeman (1960a) suggested an initial formation of these cornua in *Hoplosternum* and *Callichthys*, but without further ossification, implying a reduction (presumably as a result of allometric growth). Further ontogenetic research will have to reveal whether this also holds for *C. aeneus*. On its posterior margin the mesethmoid contacts the frontals with a V-shaped suture dorsally and a W-shaped wedge with the prevomer ventrally. The posterior, V-shaped suture with the frontals in *C. aeneus* is also found in other callichthyids, in *Nematogenys inermis* and in the Scoloplacidae, but not in Loricariidae, Astroblepidae and Trichomycteridae, which reflects the plesiomorphic condition in the Loricarioidea (Schaefer, 1990). Laterally, the mesethmoid contacts the lateral ethmoids and the autopalatine ventroposteriorly. In addition, it is connected by a ligament to both the reduced premaxilla and the maxilla (Fig. 4). The presence of such ligaments is a condition which all Callichthyidae share with the Scoloplacidae, Loricariidae and Astroblepidae (Schaefer, 1990). The well developed lateral ethmoids, together with the mesethmoid, the frontal, the autopalatine and the lacrymo-antorbital, surround the nasal cavity, which is different from the situation in the Callichthyinae, where a large depression in the lateral ethmoid forms the total nasal capsule (Reis, 1998). In this cavity the free, tube-like, nasal bone encloses the anterior part of the supraorbital canal. This canal directly enters the frontal bone at the posterior margin of the nasal (Fig. 5) in contrast to the situation in the Callichthyinae where the supraorbital canal consequently first enters the lateral ethmoid (Reis, 1998). The nasal bone has the typical catfish, tube-like shape, although it only bears two pores, in contrast to the three pores found in most diplomystids and primitive loricarioids (Arratia and Huaquín, 1995). The toothless prevomer is drop-shaped and forms an elongated V-shaped suture with the parasphenoid posteriorly. An independent prevomer is, within the Loricarioidea, present in all families except the Scoloplacidae (Schaefer, 1990; Arratia, 2003).

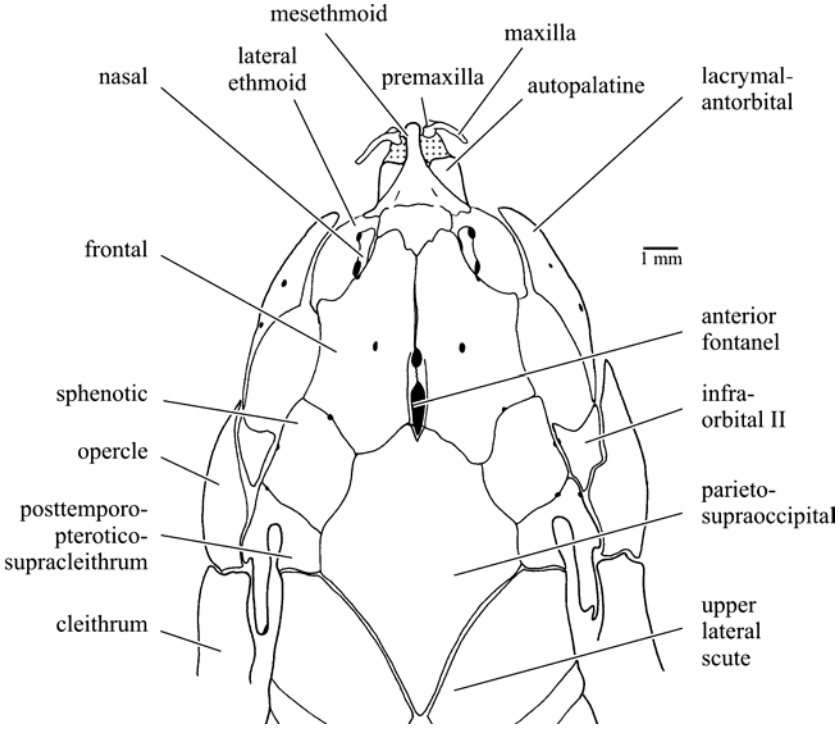

Figure 1. - Dorsal view of the skull in adult *Corydoras aeneus*. *[Vue dorsale du crâne d'un* Corydoras aeneus *adulte.]*

Orbital region (Figs 1-3)

The first bone of the infraorbital series of *Corydoras aeneus*, the lacrymo-antorbital, is a large, plate-like bone, which

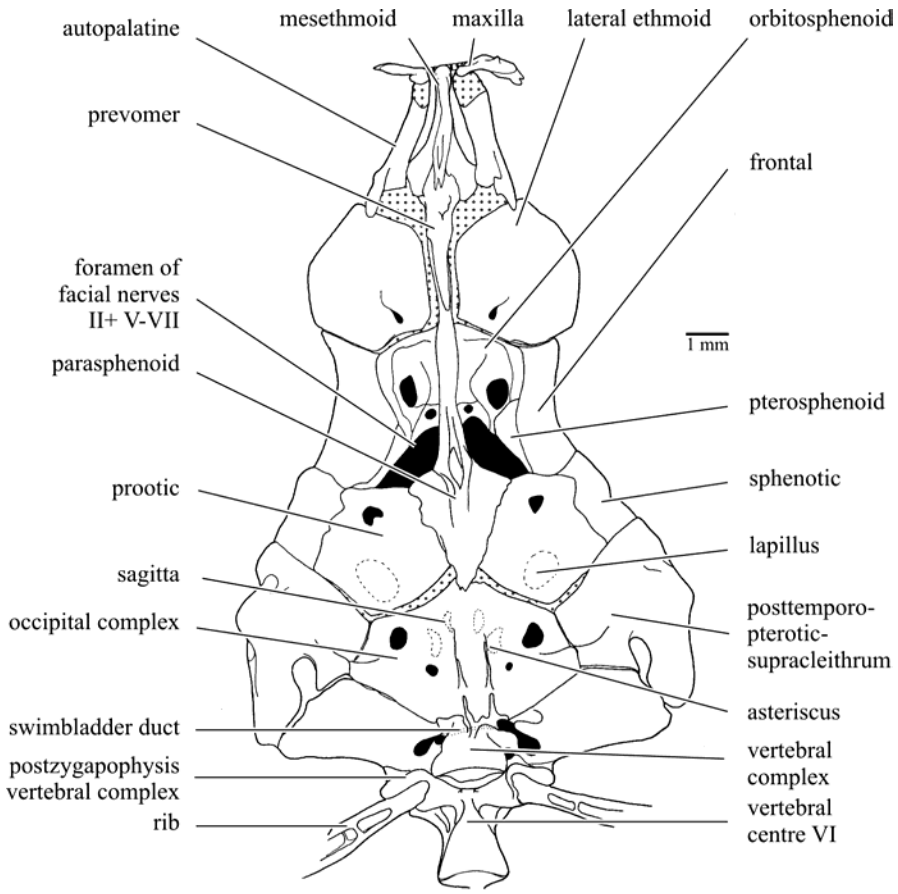

Figure 2. - Ventral view of the neurocranium in adult *Corydoras aeneus*. *[Vue ventrale du neurocrâne d'un* Corydoras aeneus *adulte.]*

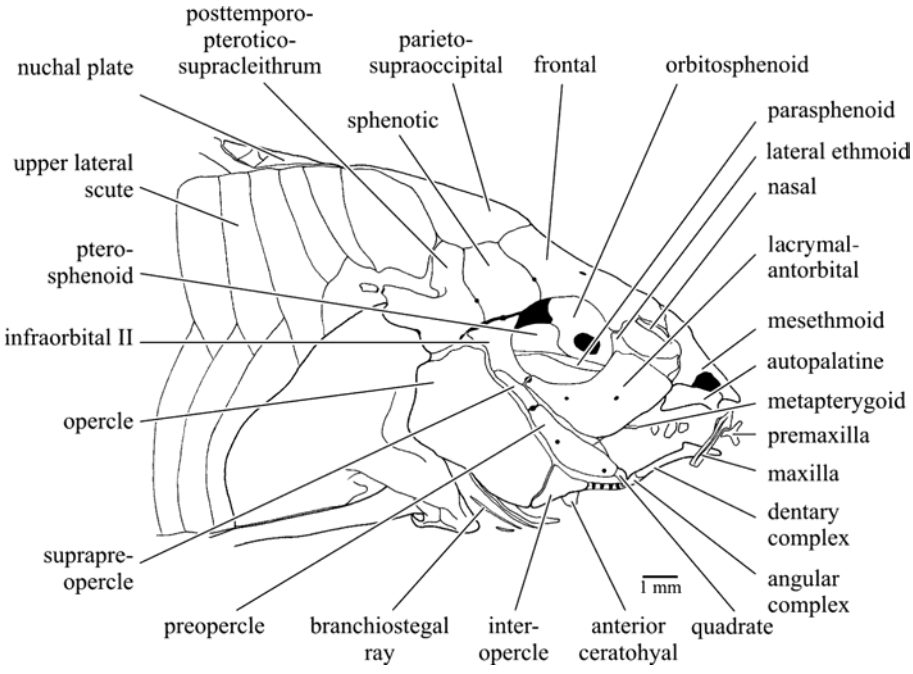

Figure 3. - Lateral view of the skull in adult *Corydoras aeneus*. *[Vue latérale du crâne d'un* Corydoras aeneus *adulte.]*

forms most of the ventral border of the orbita. This fusion of the first infraorbital bone, the lacrymal, with the antorbital bone is common among catfishes (Schaefer, 1990), but in *C. aeneus* some questions regarding the true nature and origin

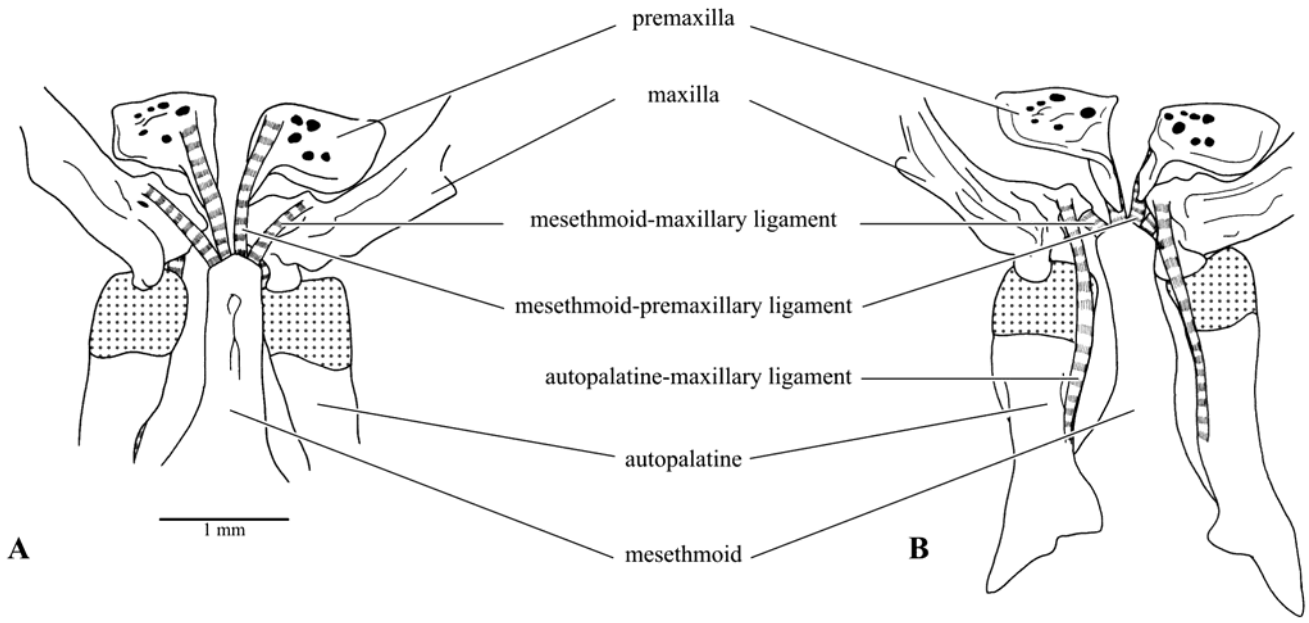

Figure 4. - Mesethmoid-palatine-maxillary mechanism in adult *Corydoras aeneus*. **A**: Dorsal view ; **B**: ventral view. *[Mécanisme méseth - moide-palatin-maxillaire chez un* Corydoras aeneus *adulte.* ***A** : Vue dorsale ; **B** : Vue ventrale.]*

of the infraorbital bones remain. A first question is whether this bone really is the lacrymo-antorbital, merely an expansion of the lacrymal bone or whether both lacrymal and/or antorbital are totally absent (Schaefer, 1990; Reis, 1998; Arratia, 2003). Subsequently, the homologies of the remaining infraorbital bones and of possible fusions within this series remain unclear. Regardless, the first two infraorbitals have become plate-like in all Callichthyidae, a condition which they share with more primitive non-siluriform teleosts, and some other Siluriformes (e.g., *Clarias gariepi - nus* (Adriaens *et al*., 1997)). In general, in Siluriphysi, the infraorbital series is reduced to tube-like bones bearing the infraorbital canal. Plate-like infraorbitals are therefore believed to be secondarily derived (Fink and Fink, 1996). The lacrymo-antorbital bears the first part of the infraorbital canal with two of its sensory pores. This canal further continues through the smaller second infraorbital bone (Fig. 5). Furthermore, the anterior extension of this infraorbital canal into the first bone of the series occurs in *Corydoras*, *Aspido - ras* and *Brochis* but is not present in other callichthyid species (Schaefer, 1990; Britto, 1998; Reis, 1998). On its dorso-posterior margin the second infraorbital broadens and connects both the sphenotic, of which the dermal part is in fact the last infraorbital bone (Gosline, 1975), and the post-temporo-pterotico-supracleithrum. The orbital skull roof is formed by the two large frontal bones, separated posteriorly by the anterior cranial fontanel. This fontanel is divided into two openings by the ossified epiphyseal bridge and is elongated posteriorly. As in the genera *Hoplosternum*, *Megalechis*, *Lepthoplosternum*, *Dianema* and *Brochis* the anterior fontanel enters the parieto-supraoccipital bone in *C. aeneus* (Reis, 1998). The fontanel itself is minute, in contrast to that in other callichthyids, where a larger fontanel is present (Schaefer, 1990; Reis, 1998). In astroblepids, scoloplacids and loricariids, however, no open cranial fontanels are found. The frontals further contact the sphenotics laterally and the orbito- and pterosphenoid ventrally. The frontals, as in other teleosts, bear the supraorbital canal, but in *C. aeneus* an additional central pore is present (Fig. 5). According to Reis (1998) this pore represents the parietal branch of that canal in other Siluriformes. Arratia and Huaquín (1995), however, report the absence of a parietal branch as a loricarioid synapomorphy, but, they, on the other hand, do report the presence of an epiphyseal branch in several loricarioids. Therefore, and based on the position and orientation of this pore we believe it to be homologous with this epiphyseal branch. The wall of the orbital region is formed by the anterior orbito- and the posterior pterosphenoid, which both ventrally contact the orbital floor at the level of the parasphenoid. The orbito-, and pterosphenoid in *C. aeneus* all possess the typical shape found in other Siluriformes (Schaefer, 1990; Reis, 1998; Arratia, 2003). The orbitosphenoid is hour-glass-shaped in ventral view and holds a large foramen. The parasphenoid is fairly narrow anteriorly and bears two elongated, anterior processes (in between lies the prevomer). Posteriorly, it broadens widely at the level of the prootics, further ending in a narrow, sharp region. Anteriorly, the bone shows a strong, midline ridge. The posterior “wings” of the parasphenoid suture with both prootic bones and the posterior tip connects to the occipital bone complex. Further, the

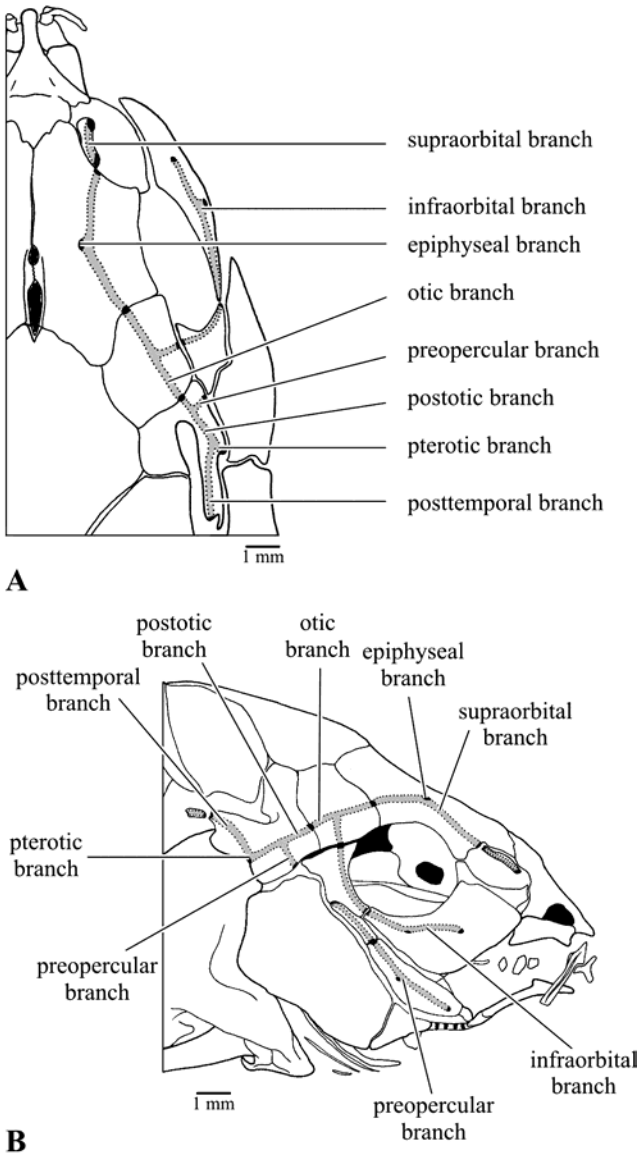

Figure 5. - Cranial lateral line system in adult *Corydoras aeneus*. **A**: Dorsal view ; **B**: ventral view. *[Système de la ligne latérale chez un* Corydoras aeneus *adulte. **A** : Vue dorsale ; **B** : Vue ventrale.]*

bone is much broader than what is described for all Corydoradinae in Reis (1998). In between the orbitosphenoid, pterosphenoid, parasphenoid and prootics, as in most Siluriformes, the combined foramen for the fasciculus opticus and the trigemino-facial nerve is situated. A connection between the parasphenoid and pterosphenoid, thereby splitting the foramen in an orbital and trigemino-facial fenestra, is absent.

Otic region (Figs 1-3)

The floor of this region is formed by the posterior tip of the parasphenoid, flanked by the prootic bones. These square-shaped prootics further connect to the sphenotics and posttemporo-pterotico-supracleithrum laterodorsally and to the occipital complex posteriorly. The prootics enclose the utricle with the lapillus and furthermore bear a large foramen. These foramina are not homologous to the auditory foramen (Schaefer, 1987), although their true purpose remains unknown. The lateral margins of the otic region are made up by the sphenotics that are also square and make additional contact with the parieto-supraoccipital dorsally and the posttemporo-pterotico-supracleithrum posteriorly. In the sphenotics, both supraorbital and infraorbital canal come together into the otic canal, which exits the sphenotic at its posterior margin and continues into the posttemporo-pterotico-supracleithrum. The latter bone has often been described as the fusion of both supracleithrum and pterotic with the absence of the posttemporal (Regan, 1911; Lundberg, 1975), while other authors described it as the fusion between a compound supracleithrum (supracleithrum, posttemporal and an ossified Baudelot's ligament) and pterotic (Schaefer and Lauder, 1986; Schaefer, 1987, 1990; de Pinna, 1993; Reis, 1998). A compound nature of this bone is also supported by the presence of several segments and branches of the lateral line system (Schaefer and Aquino, 2000). At about one-third of the bone length, the preopercular canal branches off and from that point on the otic canal continues in the postotic canal, from which, at about two-thirds of the bone length, a first postotic branch, the pterotic branch, branches off. The canal then continues through the remaining one-third of the bone into the posttemporal branch and leaves the bone at its posterior margin (Fig. 5). The presence of both the preopercular and pterotic branch indeed confirm the fact that the pterotic bone is included in this bony complex since both branches are generally inherent to the pterotic (Schaefer and Aquino, 2000). This situation, in which only one postotic branch (the pterotic branch) is present, occurs in all Corydoradinae. In other callichthyid species two postotic branches are present (Schaefer and Aquino, 2000). Furthermore, the presence of a posttemporal branch confirms the presence of the posttemporal bone in the complex. Further, in *Corydoras aeneus*, the posttemporo-pterotico-supracleithrum also bears a large articular cavity for the articulation of the pectoral girdle with the skull. Finally, it remains unclear whether the epiotic bones have disappeared during the development of *C. aeneus* or whether they have become incorporated within other bone complexes (Arratia, 2003).

Occipital region (Figs 1-3)

The skull roof in this region is formed by one, large, compound bone, the parieto-supraoccipital. The fusion of the dermal parietal bones and perichondral supraoccipital bones during ontogeny is typical for Siluriphysi (Bamford, 1948; Lundberg, 1975; Fink and Fink, 1996). Here, the bone neither bears a posterior fontanel nor latero-sensory canals

and has a large posterior process which contacts the nuchal plate and the first pair of laterodorsal bony scutes. The neurocranium floor in this region is formed by the compound occipital bone, a fusion between the basi- and exoccipitals. Within the Loricarioidea, a similar fusion only occurs in Scoloplacidae and Callichthyidae (Reis, 1998). Evidence for the presence of the basioccipital bone within the complex is found in the position of the bone contacting the parasphenoid anteriorly and articulating with the centre of the first vertebrae posteriorly, where it forms the posterior rim of the neurocranium (Rojo, 1991). Another indication is the fact that the bone encapsulates the asteriscus. Similar, the encapsulation of the sagitta confirms the presence of the exoccipitals within the bone complex. Further, this bone contacts the complex vertebral centrum and its outgrowths on its posterior side and the posttemporo-pterotico-supracleithrum through the ossified Baudelot's or trans-scapular ligament on its dorsolateral side [for a nomenclature on this structure, see Lundberg (1975), Fink and Fink (1981), Schaefer (1987) and Reis (1998)].

Maxillary bones (Figs 1-4)

The highly reduced premaxillary bone is toothless in adult specimens of *Corydoras aeneus* and bears a small dorsal process. The absence of teeth on the premaxilla is common to all callichthyids, although teeth are present in the early stages of *C. aeneus* (Machado-Allison and Garcia, 1986; Huysseune and Sire, 1997). The maxillary bone is also reduced to a small bone lacking dentition and supporting the maxillary barbel. In *C. aeneus* the bone is comma-shaped and bears a small process on its postero-lateral face. The bone articulates with the autopalatine through two articular

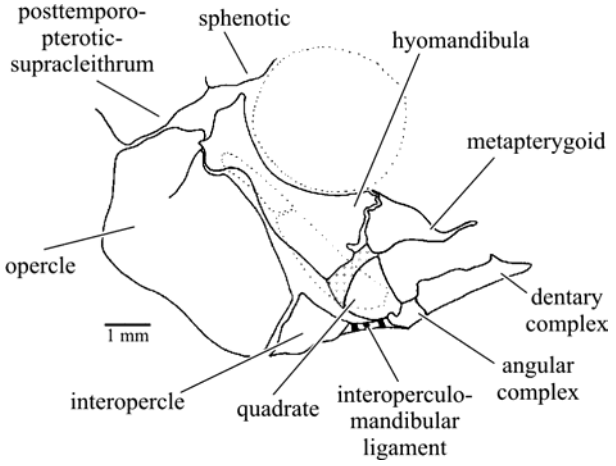

Figure 6. - Lateral view of the right suspensorium, opercular and lower jaw in adult *Corydoras aeneus* (dotted lines represent removed eye, preopercular and suprapreopercular). *[Vue latérale du suspensorium droit, de l'opercule et de la mâchoire inférieure chez un* Corydoras aeneus *adulte (les lignes pointillées représen - tent l'œil, le préopercule et le suprapréopercule enlevés).]*

facets which creates a hinge-joint. Both premaxillary and maxillary bones are ligamentously connected to the mesethmoid and next to that another ligament connects the maxillary bone to the palatine. A similar highly mobile and reduced premaxilla is present in all Callichthyidae. The fact that this increased mobility is caused by a ligamentous junction with the mesethmoid is a character shared with Astroblepidae and Loricariidae, but not with Scoloplacidae (Schaefer and Lauder, 1986). The shape and function of the maxillary bone (small, toothless and supporting the maxillary barbel) is the same as in all Siluriformes, with the exception of the Diplomystidae and †Hypsidoridae (Grande, 1987; Fink and Fink, 1996; Grande and de Pinna, 1998; Arratia, 2003). Also the presence of a pair of palatine condyles on the bone is common to all Siluriformes, except Astroblepidae and *Helogenes*-species (de Pinna, 1993). The bone's postero-lateral process serves as an insertion site for the musculus retractor tentaculi.

Premandibular arch (Figs 1-4)

The autopalatine is rod-shaped and straight, with a flat lateral surface. It bears a small posterior process, which contacts the lateral ethmoid, a shape which is different from that in less advanced catfish families like Diplomystidae and †Hypsidoridae (Grande, 1987; Schaefer, 1990; Arratia, 1992). Anteriorly the bone bears a large cartilaginous condyle for articulation with the maxillary bone, to which it is also ligamentously connected. The posterior process, on the other hand, bears no cartilaginous tip and is small compared to primitive catfishes (Arratia, 1992; Reis, 1998), but not as small as in *Callichthys* (Reis, 1998). The absence of this cartilaginous tip is variably present among catfishes, but common to all non-nematogenyid loricarioids (de Pinna, 1993). The process serves as the insertion site of the musculus extensor tentaculi (Fink and Fink, 1981; Reis, 1998).

Mandibular arch (Figs 3, 6-7)

The metapterygoid bone is nearly triangular and has a narrow, elongated, anterior process that ends near the autopalatine. This process is single in *Corydoras*, as it is in *Aspidoras* and *Brochis*, whereas, in *Callichthys*, it is bifurcated (Reis, 1998). The metapterygoid itself was first described as a fusion of ecto-, ento- and metapterygoid by Howes and Teugels (1989), although other authors reported the ecto- and entopterygoid to be absent (Regan, 1911; Arratia, 1990; Reis, 1998). In addition, the hypothesis by Howes and Teugels (1989) was, due to the lack of ontogenetic evidence, contradicted by Arratia (1992), who thus defined the bone as being the metapterygoid only. The bone further contacts the hyomandibula on its posterior margin through a serrated suture, as in all Corydoradinae (Reis, 1998). The metapterygoid is also joint synchondrally to the quadrate

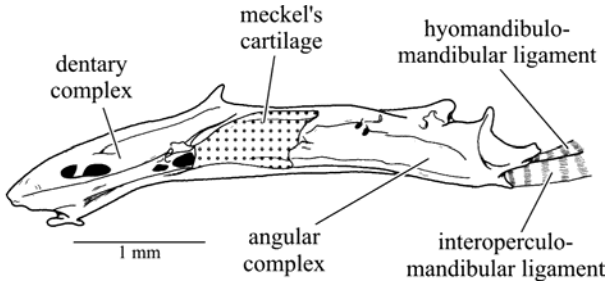

Figure 7. - Medial view of the right lower jaw in adult *Corydoras aeneus*. *[Vue médiale de la mâchoire inférieure droite chez un* Corydoras aeneus *adulte.]*

bone and ligamentously attached to the lateral ethmoid. The quadrate bone is a simple, small, triangular bone, the typical condition found in Diplomystidae, as well as in most Siluriformes (Arratia, 1992; Reis, 1998). The bone connects synchondrally to both the metapterygoid and the hyomandibula. On its postero-ventral margin it articulates with the angular bone complex. This complex is considered to consist of the fused angular, the articular and the retro-articular bone (Arratia, 2003). This compound bone is small, not canal-bearing, and connected to the dentary bone complex. It articulates with the quadrate dorsally and is ligamentously connected with both the interopercule and posterior ceratohyal bone. The angular bone complex further bears a laminar coronoid process, which serves as an insertion site for parts of the musculus adductor mandibulae complex (Reis, 1998). The last bone of the mandibular arch is another compound bone called the dentary complex. The bone is a fusion of the mento-meckelium and the dental bone. It forms the main part of the lower jaw and is toothless in adult specimens of *Corydoras aeneus*, a condition that is different from that in the early ontogenetic stages (Huysseune and Sire, 1997). It bears a small process antero-medially for insertion of the intermandibular muscle. Further it medially encloses the Meckel's cartilage. The fact that the Meckel's cartilage is small and that no coronomeckelian bone is present are conditions the Callichthyidae share with Astroblepidae, Loricariidae, Trichomycteridae and several other non-loricarioid catfishes (de Pinna, 1993). As in the angulo-retroarticular, the dentary complex does not bear a part of the preoperculo-mandibular branch of the lateral line system, a condition shared by all Loricarioidea, except *Nematogenys inermis* (Schaefer, 1990).

Hyoid arch (Figs 6, 8-9)

The hyomandibula articulates with the neurocranium through the sphenotic and posttemporo-pterotico-supracleithrum. It also bears a large process on its dorso-posterior margin for the articulation with the opercule. The perichondral part of the hyomandibula is long and bears a bony plate on its ventro-anterior side, which contacts the metapterygoid and quadrate. On its medial side the bone articulates with the rest of the hyoid arch through the small interhyal bone. This interhyal articulates with the posterior ceratohyal, which, in turn, synchondrally contacts the anterior ceratohyal. The anterior ceratohyal has a twisted surface with a medial, bony outgrowth and articulates with three branchiostegal rays on its medial posterior margin and with the larger, fourth ray on its lateral posterior margin. The anterior part of the hyoid

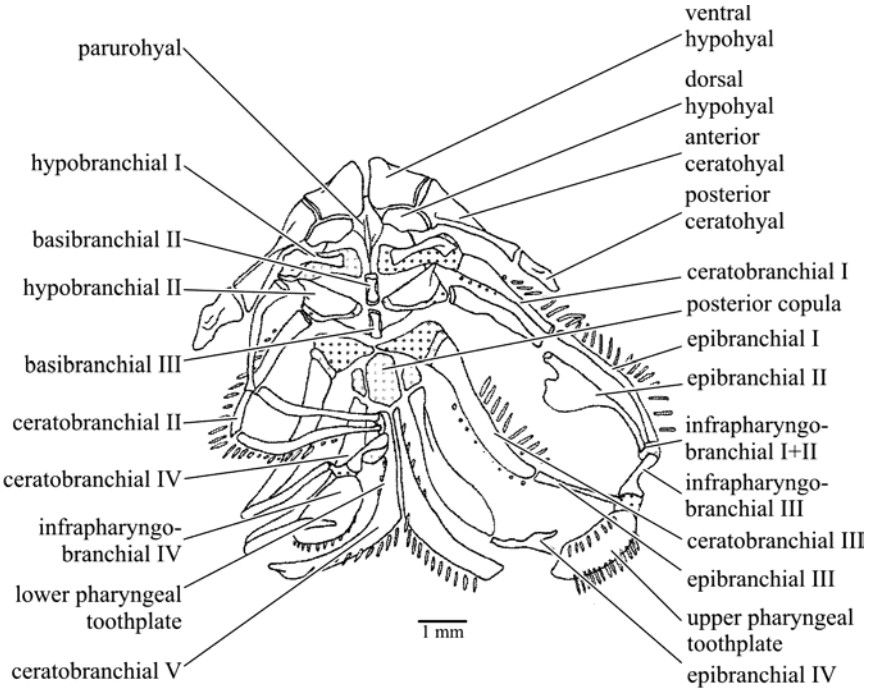

Figure 8 - Dorsal view of the hyoid arch and branchial basket in adult *Corydoras aeneus*. *[Vue dorsale de l'arc hyoïde et des arcs branchiaux chez un* Corydoras aeneus *adulte.]*

arch consist of both a ventral and a dorsal hypohyal, both square-shaped and articulating with the ventral, plate-like parurohyal. The presence of both dorsal and ventral hypohyals in *Corydoras aeneus* and in most other Corydoradinae (Reis, 1998) is in contrast to other Loricarioidea. According to Arratia and Schultze (1990) most catfishes have two pairs of hypohyals, except for Trichomycteridae, Loricariidae and Callichthyidae, which is contradicted by our findings. The former study, however, was solely based on observations on *Callichthys*, where indeed only the ventral hypohyals are present (Arratia and Schultze, 1990; Reis, 1998). Schaefer (1987) confirms this and mentions a loss of the dorsal hypohyal only in Trichomycteridae and Loricariidae, but contrary to Arratia and Schultze (1990), he also mentions a similar loss in Astroblepidae.

Branchial arches (Figs 8-9)

In *Corydoras aeneus*, the branchial basket bears the typical siluriform configuration in which five branchial arches are present. Only basibranchials II and III are present as distinct, ossified elements. The posterior copula remains cartilaginous. Ossified hypobranchials I and II are present, whereas separate hypobranchials III and IV show no ossification. The fifth hypobranchial is absent. The ceratobranchials of all five arches are well ossified, bearing cartilaginous tips (with exception of the posterior tip of the fifth one). All ceratobranchials support hemibranchs. The fifth ceratobranchial bears the lower pharyngeal tooth plate and is the only ossified bone in this arch. The first four epibranchials are very variable in shape, with the second and fourth bearing an uncinate process. All four are fully ossified and bear hemibranchia. Furthermore, the two first epibranchials are synchondrally connected to each other distally. They contact the ossified third infra-pharyngobranchial bone through a fused cartilaginous first and second infrapharyngobranchial. The latter is synchondrally connected to the third epibranchial and to the fourth infrapharyngobranchial. This fourth infrapharyngobranchial is connected to the fourth epibranchial bone and supports the upper pharyngeal tooth plate.

Opercular series (Figs 3, 5)

The opercular series consist of the opercular, interopercular, preopercular and suprapreopercular bones. This condition differs within different groups of catfishes and even loricarioids. In Loricariidae, for example, the interopercular bones have been lost entirely. The opercule itself is large, more or less triangular, and is connected to the interopercule on its ventro-anterior margin. It also bears a process for the articulation with the hyomandibula on its dorso-anterior margin. In Astroblepidae and Loricariidae this articulation shifts towards the dorsal side of the opercular bone (Schaefer, 1987, 1988). The interopercule is a small, triangular bone, which is ligamentously connected to the lower jaw at the level of the angulo-retroarticular bone. Dorso-anteriorly from the interopercule and anterior to the ventral part of the opercule, lies the preopercule. This bone, present in all loricarioid families, bears part of the preopercular canal with two of its pores, one centrally and one anteriorly, which are homologue to pores 4 and 5 in *Diplomystes* (Schaefer,

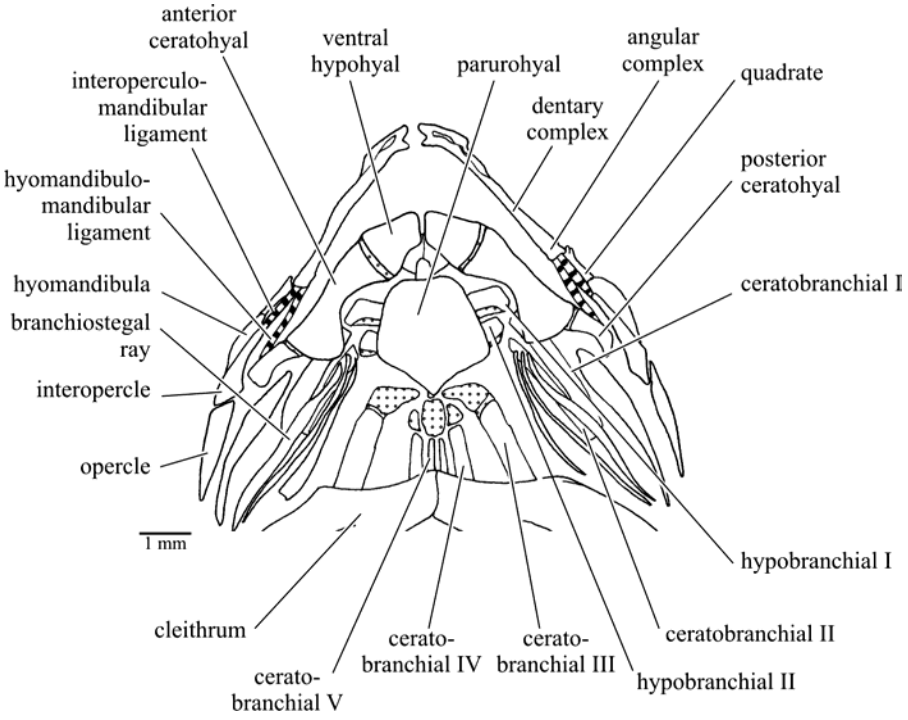

Figure 9. - Ventral view of the mandibular arch, hyoid arch and branchial basket in adult *Corydoras aeneus*. *[Vue ventrale de l'arc mandibulaire, de l'arc hyoïde et des arcs branchiaux chez un* Corydoras aeneus *adulte.]*

1988). The part of the preopercular canal running through the preopercle and suprapreopercle in *Corydoras aeneus*, as in all Callichthyidae, does no longer connect to the part of the preopercular canal that is present in the posttemporo-pterotico-supracleithrum. In *Nematogenys inermis* and in several non-loricarioid catfishes, this canal continues into the mandible and is consequently referred to as the preoperculo-mandibular branch. In trichomycterids, on the other hand, the preopercular canal is extremely reduced and does not even enter the preopercule, but remains limited to an opening in the pterotic bone (Baskin, 1972; Schaefer, 1988). Finally, the presence of a suprapreopercular bone in *C. aeneus*, is a condition that has never been mentioned within the Callichthyidae but which was present in all specimens examined. Therefore, further ontogenetic research will focus on the development of this bone, attempting to reveal whether this bone is truly homologous to the suprapreopercular bone found in other fish groups.

Weberian apparatus (Fig. 2)

In *Corydoras aeneus* the Weberian apparatus is part of a complex structure, comprising a fusion between several vertebrae. Normally, the complex vertebral centre of the Weberian apparatus is a fusion of the second to the fifth vertebral centres in all Siluriformes, except *Diplomystes*, where the fifth centre is excluded from the complex (Arratia, 1987; Fink and Fink, 1996). Additionally, in Loricarioidea the first vertebral centre is also fused to the complex (Schaefer, 1990; Reis, 1998). Coburn and Grubach (1998), however, discovered, after ontogenetic research, that in *C. paleatus* only three vertebrae are fused within the complex and that the first two vertebrae are missing. The gas bladder is divided into two chambers which are encapsulated in the expansions of the transversal processes of this complex centrum. Laterally to the compound centre, two foramina are situated through which passes the duct that connects these two chambers. Gas bladder contact with the external medium occurs through an aperture in the posttemporo-pterotico-supracleithrum, covered by a hollow expansion bearing the latero-sensory canal. This condition is possibly homologous to the condition found in Astroblepidae and Loricariidae, where the aperture is completely covered by the posttemporo-pterotico-supracleithral bone (Reis, 1998). The connection between the gas bladder and inner ear is made up of one compound bone referred to as the compound tripus (Schaefer, 1990). The compound tripus found in *C. aeneus* was suggested to be a fusion between the tripus, intercalarium, scaphium and interossicular ligament, typically found in all Siluriformes, but with the loss of the claustrum in Callichthyidae (Schaefer, 1990; Reis, 1998). However, since Coburn and Grubach (1998) mention the loss of the first two vertebrae, their derivatives (claustrum, scaphium and intercalarium) are also missing and their results show the tripus to be a myoseptal tripus (formed in the paravertebral sac and the dorsal myoseptum of vertebra-III).

Vertebral column (Figs 2, 10-11)

In the specimens examined, the total number of vertebrae, including the first five incorporated in the Weberian apparatus, was 28. This number equals that found in several other *Corydoras* and callichthyid species, and is one more than the number found in Scoloplacidae and some Loricariidae (e.g. *Otocinclus, Hypoptopoma*) (Schaefer, 1990). Britto (2000) mentions the presence of 28-31 vertebrae in several *Aspidoras*-species, which corresponds to the 27-32 vertebrae described by Regan (1911) for the family of the Callichthyidae. The first articulating vertebra, the sixth vertebra, has two large parapophyses that articulate with the complex centrum of the Weberian apparatus. These parapophyses further support a large, hollow rib, which contacts the first ventrolateral bony scutes behind the pectoral girdle. Vertebrae 7-12 each carry a small, thin rib. The presence of such a large, hollow rib on the parapophysis of the sixth vertebral centre, followed by several small ribs is typical for all Callichthyidae (Regan, 1911; Hoedeman, 1960b; Reis, 1998; Britto, 2000). In contrast to Hoedeman (1960b) mentioning only four to five of these small ribs in *Corydoras*-species, six were found here. The number of caudal vertebrae is 14, of which, in the first three to four, the haemal spines are

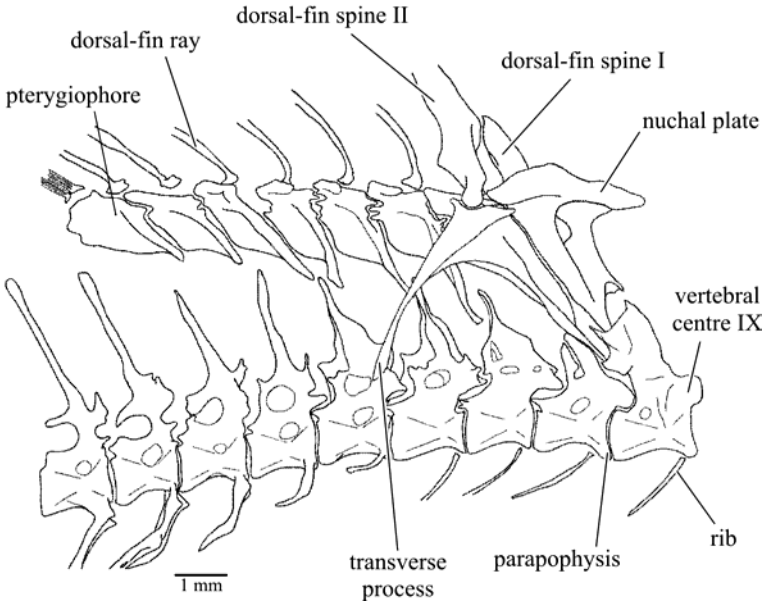

Figure 10. - Lateral view of the dorsal fin skeleton in adult *Corydoras aeneus*. *[Vue latérale du squelette de la nageoire dorsale chez un* Corydoras aeneus *adulte.]*

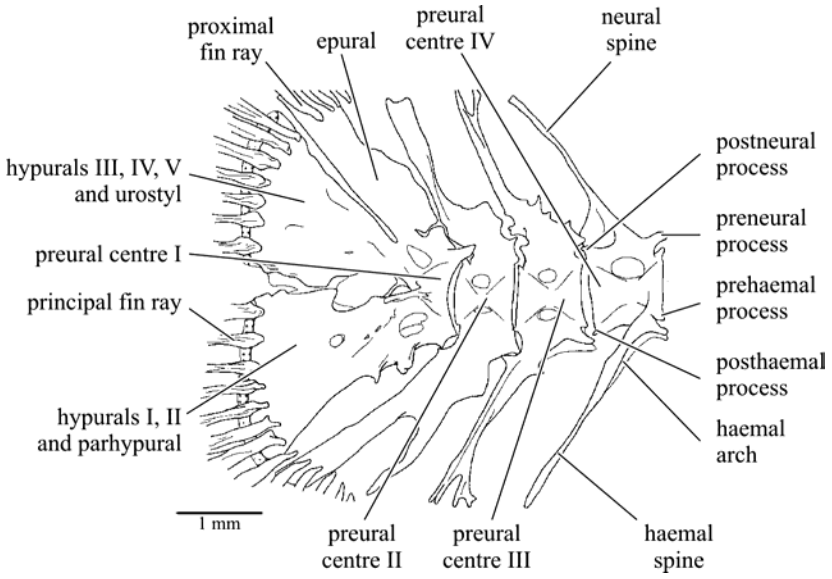

Figure 11. - Lateral view of the caudal fin skeleton in adult *Corydoras aeneus*. *[Vue latérale du squelette de la nageoire caudale chez un* Corydoras aeneus *adulte.]*

expanded and plate-like. These haemal spines are ventroposteriorly oriented, thus forming a protective, posterior wall for the abdominal cavity. Furthermore, the last preural vertebra is incorporated within the ural complex together with the last vertebra, the first ural vertebra (Lundberg and Baskin, 1969).

Dorsal fin (Fig. 10)

In *Corydoras aeneus* the dorsal fin bears a first small fin ray, modified to serve a spine-locking mechanism, followed by a second, large one (Alexander, 1965). After this, seven branched dorsal fin rays are present, of which the last is split up to its base. The pterygiophores of these spines plus the first five fin rays are connected to the 10th to 13th vertebral neural spine. The first pterygiophore bears a large transverse process, which connects to the lateral body scutes. In Callichthyids, this process is further ligamentously connected to the sixth rib, whereas in scoloplacids, astroblepids and loricariids, this ligament ossifies into a lateral bone (Schaefer, 1990). Preceding the first dorsal fin spine, a nuchal plate is present, which is connected to the ninth vertebra and contacts the parieto-supraoccipital at its anterior side. The condition where two fin spines with seven fin rays are present, as is the case here, fits the plesiomorphic nine fin rays found in *Diplomystes* (Alexander, 1965). Although most authors do not count the first modified fin spine, the number of remaining true fin rays fits our findings. Seven fin rays, with the last ray branched up to the base, corresponds with the original description of *C. aeneus* by Gill (1858) and of other *Corydoras*-species (Isbrücker and Nijssen , 1973, 1992; Nijssen, 1970). The number of dorsal fin rays is a character of great taxonomic value within the Corydoradinae and a number of 7-9 is determinative for *Corydoras*-species, whereas a number of 10 or more is determinative for species belonging to *Brochis* (and different from the plesiomorphic siluriform condition). The distinction between *Aspidoras*, on the one hand, and *Corydoras* and *Brochis*, on the other hand can also be done based on dorsal fin morphology. Here, a lack of contact between the nuchal plate and the posterior process of the parieto-supraoccipital is held as being typical for *Aspidoras*-species (Reis, 1996). Within the Loricarioidea, all families have the plesiomorphic siluriform number of branched dorsal fin rays, except for the Scoloplacidae, where a reduction of the number has occurred and only four are present (Reis, 1998).

Anal fin

The anal fin consists of a single unbranched and seven branched fin rays. The bases of the first four rays articulate with the haemal spines of vertebrae 20 to 22. The number of fin rays (n = 7) found in *Corydoras aeneus* corresponds with the number given in the original description by Gill (1858), although the presence of a possible eighth branched ray is

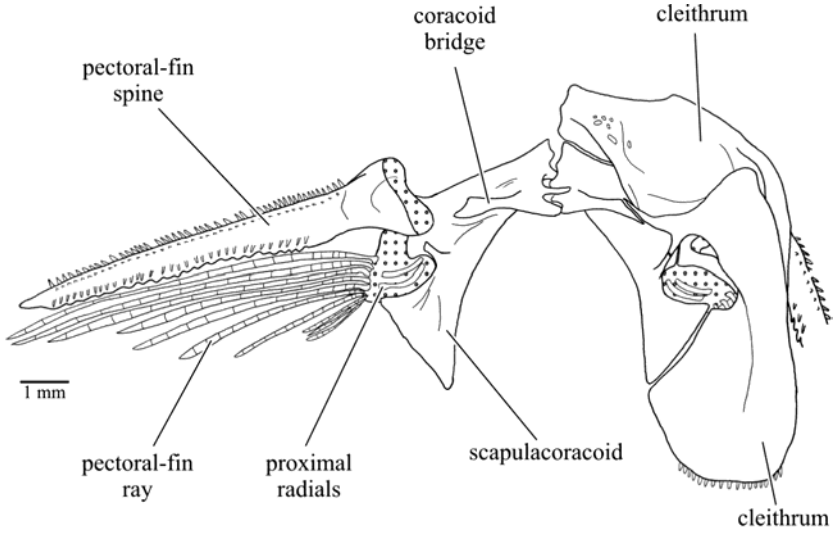

Figure 12. - Dorsal view of the pectoral girdle in adult *Corydoras aeneus* with the cleithrum removed on the left side. *[Vue dorsale de la ceinture pectorale chez un* Corydoras aeneus *adulte, cleithrum gauche enlevé.]*

mentioned. The presence of a single, unbranched, anal fin ray is a derived condition within the Callichthyidae, which only occurs in some *Corydoras*-species and all *Leptho - plosternum*-species. Among the Loricarioidea, this condition is also found in Scoloplacidae, Astroblepidae and Loricariidae, in contrast to trichomycterids and *Nematogenys iner - mis*, where two unbranched rays are present (Reis, 1998).

Adipose fin

The adipose fin consists of a single spine, derived from a small dorsal bony plate.

The homology of this spine initially was unclear. The spine could be considered as a transformed bony scute or a true fin ray that is covered by these dermal plates. Hoedeman (1960b), however, mentions the presence of "two strong muscle bundles" used for erection of the spine in Callichthyinae, which would mean that the spine in *Corydoras*, although not movable in the Corydoradinae, is homologous to a fin ray.

Caudal skeleton (Fig. 11)

As mentioned before, in many Siluriformes and Cypriniformes, the first preural vertebra is fused to the complex centre of the caudal skeleton (Lundberg and Baskin, 1969). The caudal skeleton in *Corydoras aeneus* is of the pleurostyl type and consists of two bony plates. The dorsal plate is formed by a fusion of the urostyl and the dorsal hypurals III, IV and V, a fusion which, as well as the development of a plate-like lamina on the epural (the neural spine of the first preural centre), could be revealed by preliminary ontogenetic data. The ventral plate comprises the parhypural and hypurals I and II. Hypurals II and III are variably fused on their left and/or right side or on neither side. The fact that the dorsal hypurals are also fused to the compound centre is common to all loricarioids, except for *Nematogenys inermis* (Schaefer, 1990). The number of principal rays is 7/7, which is common among *Corydoras* species (Isbrücker and Nijssen, 1973, 1992). Surprisingly, the number found here differs from that given in the original *C. aeneus* description by Gill (1858) (n = 6/6). Further, both the neural and haemal spine of the preural vertebral centre II are heavily ossified and branched. This state is, to a lesser extent, also present in the preural vertebral centre III.

Pectoral girdle (Fig. 12)

The pectoral girdle consists of the cleithrum, which articulates with the supracleithrum, part of the posttemporopterotico-supracleithrum and embedded in the skull. The

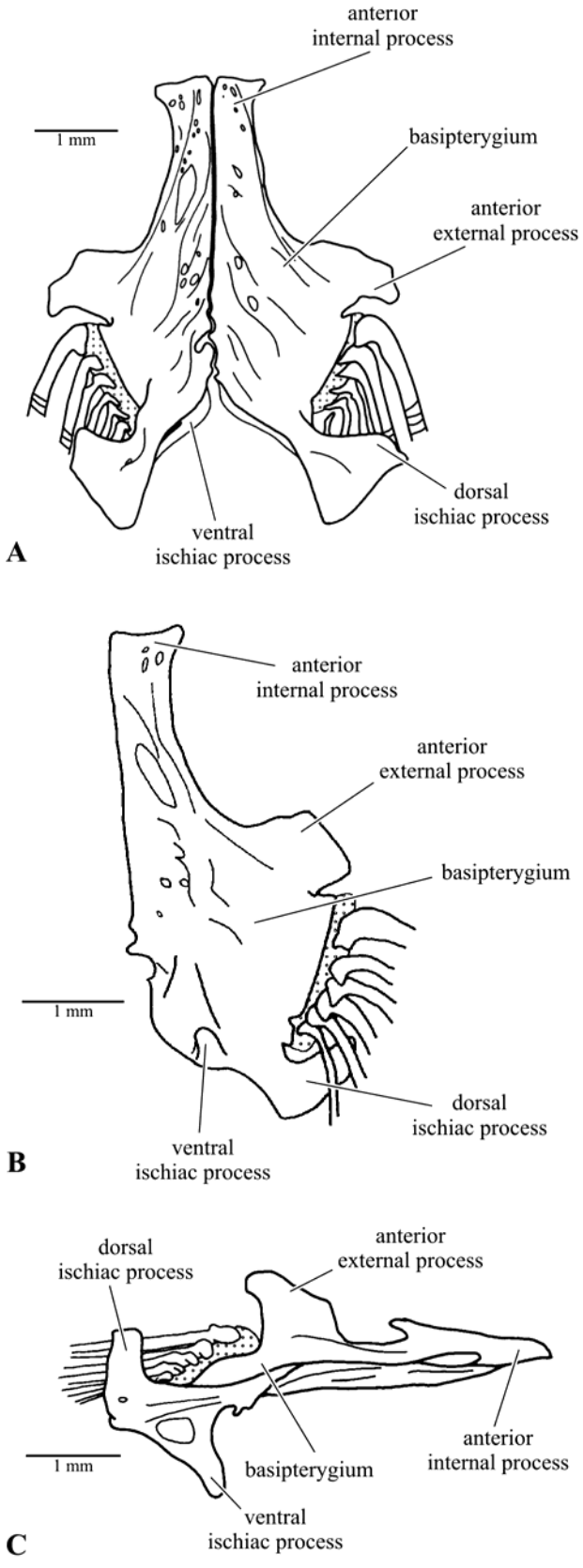

Figure 13. - Pelvic girdle in adult *Corydoras aeneus*. **A**: Dorsal view ; **B**: Ventral view ; **C**: Lateral view. *[Ceinture pelvienne chez un* Corydoras aeneus *adulte. **A** : Vue dorsale ; **B** : Vue ventrale ; **C** : Vue latérale.]*

cleithral bones are medially connected by a simple suture. The ventral part of the pectoral girdle consists of the scapulocoracoid. As in all Siluriformes the scapulocoracoid bone is a compound bone, comprising the scapula, the coracoid and the mesocoracoid. In Callichthyidae, the posterior process of this scapulocoracoid and of the cleithrum are sutured behind the articulation of the fin with the girdle, this way forming a bony shield around the entire base of that fin (Reis, 1998). The scapulocoracoid bones also connect ventrally, but in contrast to the cleithral bones, here a heavily interdigitating suture is present. Cleithrum and scapulocoracoid are connect medially by means of a coracoid bridge (see also Diogo *et al*., 2001). The pectoral spine is pungent as in all Corydoradinae (this in contrast to the Callichthyinae), bears serrations on both its anterior and posterior face and a large articulation head, which also suits a spine locking mechanism (Hoedeman, 1960b; Alexander, 1965). Ten branched rays together with two proximal radials are present.

Pelvic girdle (Fig. 13)

The pelvic girdle consists of two basipterygia, which bear both an internal and an external anterior process. The homology of both these processes was questioned by Shelden (1937), and both were referred to as "projections". Since no obvious motivation was given to support this idea, we do not follow his views on this matter and consider them to be the internal and external process. The internal process is well developed and bears a small dorsal lamina. The presence of a dorsal lamina on the internal process is a typic callichthyid feature (Reis, 1998). Second, the external process also bears a lamina, which, in *Corydoras aeneus* is connected to a scute of the lower, lateral series of bony scutes, by means of connective tissue (Reis, 1998). A third laminar process is present on the ischiac process, where it connects to the ventral tip of a scute of the lower, lateral series (Reis, 1998). This ischiac process is further divided into a dorsal and a ventral process, of which the dorsal part is bent laterally. These callichthyid features in the pelvic girdle are possibly related to reproductive strategies (Reis, 1998). Furthermore, the pelvic fin bears six branched rays.

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