Development and variation of the suspensorium of primitive Catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships

by

G. ARRATIA

BONNER ZOOLOGISCHE MONOGRAPHIEN, Nr. 32
1992

Herausgeber:
ZOOLOGISCHES FORSCHUNGSINSTITUT
UND MUSEUM ALEXANDER KOENIG
BONN

BONNER ZOOLOGISCHE MONOGRAPHIEN

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BONNER ZOOLOGISCHE MONOGRAPHIEN, Nr. 32, 1992
Preis: 35,— DM
Schriftleitung/Editor:
G. Rheinwald

Zoologisches Forschungsinstitut und Museum Alexander Koenig
Adenauerallee 150—164, D-5300 Bonn 1, Germany
Druck: Rheinischer Landwirtschafts-Verlag G.m.b.H., 5300 Bonn 1

ISBN 3-925382-34-8
ISSN 0302-671X

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CIP-Kurztitelaufnahme der Deutschen Bibliothek

Arratia, G.:

Development and variation of the suspensorium of primitive Catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships / by G. Arratia. Hrsg.: Zoolog. Forschungsinstitut und Museum Alexander Koenig, Bonn. — Bonn: Zoolog. Forschungsinst. und Museum Alexander Koenig, 1992.

(Bonner zoologische Monographien ; Nr. 32)

ISBN 3-925382-34-8

NE: GT

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INTRODUCTION

Catfishes are represented by over 2000 species assigned to about 32 families, largely distributed throughout South America, Africa, and Asia. Catfishes have traditionally been considered to exemplify a generalized morphology despite the tremendous variability of some structures between groups (Regan 1911, Alexander 1965, Howes 1983a, 1985, Arratia 1987a, 1990a, b). Phylogenetic investigations of most siluroid families have not been attempted, probably because our knowledge of this geographically widespread and morphologically diverse group is poor.

Recently, during the study of the family Diplomystidae (Arratia 1987a), I was faced with the problem of the identification of the pterygoid bones in diplomystids. I found that in some young *Diplomystes camposensis* an additional bone is present between the hyomandibula, quadrate, and metapterygoid (Arratia 1987a: 54, 98, Fig. 25A). Diplomystidae lack the bones traditionally recognized as the ectopterygoid (or pterygoid), and entopterygoid (endopterygoid or mesopterygoid); and yet some specimens may have one or two small bones. However, these do not occupy the position of the ecto- and entopterygoids in other teleosts (Arratia 1987a: 25, 40, 54, 98, 99, Figs. 6, 16, 25 A—D; Arratia & Schultze 1991: Fig. 36). As a consequence of this particular problem in diplomystids, I decided to study ontogenetic series of other catfishes to check whether the currently recognized metapterygoid, ectopterygoid, and entopterygoid of catfishes are homologous within catfishes and homologous with those of other teleosts.

I present here a detailed study of the ontogeny of the palatoquadrate and associated dermal and tendon bone pterygoids, dorsal part of the hyoid arch (hyo-symplectic), and their morphological relationships in primitive catfishes that have a small, triangular simple quadrate such as diplomystids (Diplomystidae), *Ictalurus* (Ictaluridae), and *Nematogenys* (Nematogenyidae). Further, I will compare these ontogenies to those of primitive catfishes that have a complex shaped quadrate such as *Noturus* (Ictaluridae) and *Parapimelodus* (“Pimelodidae“). However, before we can examine these ontogenies I will consider the ontogenetic studies of the suspensorium of primitive ostariophysans. Homologization of bones will follow two criteria: 1) embryonic origin and ontogeny of the bones and 2) shape, position and relationship of bones following Remane (1952); then these results will be tested in a phylogenetic context following Wiley (1981) and Ax (1987) to determine homologous and non-homologous characters. My usage of homology and non-homology follows Ax (1987: 152): “Homologous features are features in two or more evolutionary species which go back to one and the same feature of a common stem species. They may have been taken over from the stem species unchanged or else with evolutionary transformation.” “Non-homologous features in two or more evolutionary species are features which were not present in the common stem species; they were evolved independent to each other.”

METHODS

General methodology

Most specimens were cleared and double stained by the author for both cartilage and bone, following the procedure described in Schultze & Arratia (1986) and Arratia & Schultze (in press). The length of the specimens refers to the standard length, both in the text and figure captions; and the measurement was taken before clearing and staining.

Figures were prepared by the author using a Wild M5A stereo-dissecting microscope equipped with polarized light and camera lucida. Young specimens were examined with high resolution Olympus and Leitz compound microscopes, equipped with phase contrast and polarized light. Figures showing the lateral view of the left suspensorium exactly portray the position of the bones in situ and in addition, the hyomandibula maintains its precise relationship with the neurocranium. The figures were prepared while the fish was freely submerged in glycerine. The hyaline cartilage, secondary cartilage, and chondroidal regions are each differentially represented in the figures. Dermal bones and tendon bones are identified by capital letters on the illustrations.

Cladistic methodology

One set of assumptions is evaluated in this work: whether the pterygoid elements found in siluroids are modified pterygoids homologous with those of other teleosts; or whether they are new formations, and therefore non-homologous with the pterygoids of other teleosts. According to Patterson (1982), Wiley (1981), and Ax (1987), character homology should be tested in a phylogenetic context, with accepted phylogenies. If one requires accepted phylogenies to test homology, then I face the problem that there is no single publication resolving the relationships of siluroid families (the most recent study showed a polytomy among catfishes above Diplomystidae [contra Mo 1991]). There are only contributions related to a few groups (e.g., main hierarchical levels of catfishes: Grande 1987; Auchenipteridae: Ferraris 1988, Curran 1989; Diplomystidae: Arratia 1987a; Ictaluridae: Lundberg 1982; Loricarioidei: Baskin 1973, Howes 1985, Schaefer 1987, Pinna 1989; Siluridae: Bornbusch 1989; Pimelodinae: Lundberg et al. 1991 a; Pseudopimelodinae and Rhamdiinae: Lundberg et al. 1991b; Bagridae: Mo 1991), or a few characters, e.g., the Weberian complex (Chardon 1968) or the caudal skeleton (Lundberg & Baskin 1969, Arratia 1982, 1983). Based on the results of this paper, I will present the relationships of some primitive and advanced siluroids, to test the hypothesis of relationships proposed by Grande (1987) for Siluriformes, Siluroidei, and Siluroidea.

The phylogenetic techniques used in these analyses follow Hennig (1966), Wiley (1981), and Ax (1987), and were conducted using the PAUP (Phylogenetic Analysis Using Parsimony) software (version 3.0) of David L. Swofford (1990). Character states optimization used DELTRAN.

The analyses deal with two Taxa Sets. Taxa Set I was selected for ostariophysans represented by taxa selected for their presumed primitive sister group arrangement sensu Fink & Fink (1981), and Taxa Set II for a combined outgroup that includes gymnotoids and characiforms plus several primitive siluroids belonging to different families.

Two sets of characters were employed to analyse the relationships of ostariophysans (Data Set I), and catfishes (Data Set II). Data Set I consists of 131 characters and a total of 137 apomorphic character states. Data Set II consists of 75 characters and 92 apomorphic character states. Strict consensus trees were used to summarize the topologies of equally parsimonious trees.

Character determination

All characters are equally weighted and considered to be simple and independent of one another (Kluge & Farris 1969). Characters and character states are defined below. Missing data are coded as "?" in the data sets run with PAUP. The character number is followed by the character state in parenthesis (e.g., 1[1] is character state 1 of character 1).

Outgroup comparison

Outgroup comparison following Maddison et al. (1984) is used to polarize characters and ontogeny to test homology. In the present study, the primitive state of characters in Data Set I is determined by comparison to several primitive clupeocephalans, osteoglossomorphs, and elopomorphs, following Fink & Fink (1981), and in Data Set II by comparison to the gymnotoids (first outgroup) and the characiforms (second outgroup).

MATERIALS EXAMINED

Hundreds of cleared and stained specimens of different sizes were studied, as well as a large number of dry skeletons and alcoholic specimens, and serial cross sections of three trichomycterid catfishes. Institutional acronyms for specimens follow Leviton et al. (1985); except for the following collections: AG: Private collection of Dr. Atila Gosztonyi, Chubut, Argentina. PC: Private collection of the author. PU: Peabody Museum of Natural History, Yale University, New Haven, Connecticut. SIO: Scripps Institute of Oceanography, University of California, La Jolla, U.S.A. Material examined is listed below. Species are listed alphabetically within each higher taxon. The abbreviation for cleared and stained material is 'cl & st'; for examined specimens is 'sp'; for dry skeletal specimens is 'dry skel'; and for alcoholic dissected specimens is 'dissect'.

Halecomorphi

Amia calva: KU 3883, 8sp, cl & st; KU 21607, 1sp, cl & st; KU 21338, 1sp, cl & st; KU 22215, 1sp, cl & st.

Elopomorpha

Albula vulpes: UCLA W 49-122, 9sp, cl & st; UCLA W 52-122, 5sp, cl & st.
Elops affinis: UCL ST 0-29, 4sp, cl & st.
Elops hawaiensis: CAS(SU) 35103, 1sp, dry skel; CAS(SU) 35105, 1sp, dry skel.

Elops saurus: ANSP 147401, 2sp, cl & st; KU 3053, 3sp, cl & st; TCWC 0503.1, 5sp, cl & st; UMMZ 189355, 4sp, dry skel; UNC 13093, 1sp, cl & st.

Osteoglossomorpha
Hiodon alosoides: KU 7619, 6sp, cl & st; KU 9618, 3sp, cl & st.
Osteoglossum sp.: KU 22650, 2 sp, cl & st.

Clupeomorpha
Brevoortia patronus: KU 15113, 5 sp, cl & st.
Clupea harengus: PC 25986, 14 sp, cl & st.
Coilia nasus: PC 020989, 9sp, cl & st.
Denticeps clupeoides: MNHN 1960-391, 2sp, cl & st; MRAC 73-32P-4915-932, 3sp, cl & st.
Dorosoma cepedianum: KU 21802, 36sp, cl & st.
Engraulis encrasicholus: KU 19941, 8sp, cl & st.
Engraulis ringens: PC 010689, 8sp, cl & st.
Jenkinsia lamproteica: KU uncat., 10sp, cl & st.

Esocoidei
Esox americanus: KU 6041, 4sp, cl & st; KU 17864, 4sp, cl & st.
Umbra limi: KU 10370, 6sp, cl & st.

Ostariophysi
Gonorynchiformes
Chanidae:
Chanos chanos: CAS-SU 35075, 1sp, dry skel; CAS-SU 38340, 2sp, cl & st; PC uncat., 1sp, dissect; SIO 80-199, 7sp, cl & st; UMMZ 196864, 1sp, cl & st.

Gonorynchidae:
Gonorynchus abbreviatus: CAS 30993, 1sp, cl & st.

Cypriniformes

Catostomidae:
Carpiodes carpio: KU 1996, 3sp, cl & st; KU 21807, 30sp, cl & st.

Cyprinidae:
Campostoma anomalum: KU 12092, 3sp, cl & st.
Clinostomus funduloides: KU 3262, 2sp, cl & st; KU 10697, 3sp, cl & st.
Ctenopharyngodon idella: KU 21614, 1sp, dry skel; KU 22100, 1sp, dry skel.
Cyprinella lutrensis: KU 12089, 2sp, cl & st; KU 15793, 6sp, cl & st;
Cyprinella xanthicara: ASU 3642, 9sp, cl & st.
Cyprinus carpio: KU 3790, 1sp, cl & st; KU 15336, 1sp, dry skel; KU 172321, sp, dry skel; KU 21377, 1 sp, dry skel.
Dionda episcopa: KU 7427, 5sp, cl & st.
Opsariichthys bidens: CAS-SU 32512, 2sp, cl & st; CAS-SU 68907, 2sp, cl & st; PC 22, 4sp, cl & st; PC 22, 2sp, dissect.
Zacco platypus: PC 21, 10sp, cl & st.

Characiformes
Characidae:
Astyanax sp.: KU 20099, 7sp, cl & st.
Brycon argenteus: KU 10543, 2sp, cl & st; KU 10543, 2sp, dissect; PC 218, 7sp, cl & st; PC 219, 30sp, cl & st.
Cheirodon pisciculus: PC 130173, 10sp, cl & st; PC 230173, 45 sp, cl & st.
Gymnocharacinus bergi: KU 19199, 1sp, cl & st.

Distichodontidae:
Xenocharax spilurus: CAS-SU 15639, 2sp, cl & st.

Erythrinidae:
Hoplias malabaricus: KU 13636, 2sp, cl & st; KU 13636, 2sp, dissect.

Siluriformes (sensu Fink & Fink 1981)
Siluroidei
Ariidae:
Galeichthys felis: KU 19590, 10sp, cl & st; KU 19590, 1sp, dissect.
Bagre marinus: KU 3053, 3sp, cl & st; KU 3053, 1 sp, dissect; KU 21380, 1sp, dry skel.

'Bagridae':
Mystus tengara: KU 12170, 1sp, cl & st.

Bunocephalidae:
Bunocephalus coragoideus: ANSP 139313, 1sp, cl & st.

Callichthyidae:
Callichthys callichthys: KU 13722, 3sp, cl & st; KU 13724, 2sp, cl & st.

Claridae:
Clarias sp.: PC 111189, 2sp, cl & st.
Uegitglanis zammazanoi: PC 120677, 1sp, cl & st.

Diplomystidae:
Diplomystes camposensis: KU 19210, 1sp, cl & st; PC 011086b, 3sp, cl & st; PC100487, 1sp, dissect; PC 110276, 2sp, cl & st; PC 130276, 1sp, cl & st; PC 140276, 1sp, cl & st; PC 220189, 2sp, dissect.
Diplomystes chilensis: CAS (SU) 13706, 2sp, dissect; MCZ 8290, 2sp, cl & st; MNHN B.585, 1sp, dissect.
Diplomystes nahuelbutaensis: BMNH 1876-10-2:22, 1sp, dry skel; CAS-SU 55425, 1sp, cl & st; MCZ 61245, 1sp, dissect; PC 230186, 3sp, cl & st.
Olivaichthys viedmensis: AG uncat., 1sp, cl & st; PC 20279, 1sp, cl & st; FMNH 58004, 3sp, cl & st; FMNH 58004, 3 sp, radiographs.

†Hypsidoridae:
Hypsidoris farsonensis: PU 20570a-b, 1sp.

Ictaluridae:
Ameiurus catus: KU 1741, 1, dry skel; KU 8332, 2sp, cl & st; KU 10151, 3sp, cl & st; KU 10151, 1sp, dissect.
Ameiurus melas: KU 15181, 2sp, cl & st; KU 1038, 1sp, cl & st; KU uncat., 2sp, dissect.
Ictalurus furcatus: KU 1747, 1sp, dry skel; KU 11343, 1sp, dry skel; KU 15866, 1sp, dry skel; KU 21381, 1sp, dry skel.
Ictalurus punctatus: KU 9657, 9sp, cl & st; KU 15340, 1sp, dry skel; KU 15342, 1sp, dry skel; KU uncat., 50sp, cl & st; KU uncat., 85sp, cl & st; KU 4162, 2sp, dissect.
Noturus exilis: KU 17229, 61sp, cl & st; KU 17229, 2 sp, dissect.
Noturus hildebrandi: KU uncat., 12sp, cl & st.
Pylodictis olivaris: KU 1746, 3sp, cl & st; KU 2386, 1sp, dry skel; KU 10414, 3sp, cl & st; KU 13122, 1sp, dry skel; KU 15697, 2sp, cl & st; KU 16830, 2sp, cl & st; KU 17970, 1sp, cl & st; KU uncat., 1sp, dissect.

Loricariidae:
Ancistrus hoplogenus: KU 13755, 1sp, cl & st.
Hypostomus plecostomus: KU 13948, 2sp, cl & st.
Hypostomus sp.: KU 21823, 3sp, cl & st.

Loricaria uracantha: KU 17710, 2sp, cl & st.
Loricarichthys sp.: ANSP 131612, 2sp, cl & st.

Nematogenyidae:
Nematogenys inermis: PC 131, 8sp, cl & st; PC 206, 3sp, cl & st; PC 208, 2sp, cl & st; PC 30873, 6sp, cl & st; PC 230390, 4sp, cl & st; PC 051188, 1sp, dissect; PC uncat., 1sp, dissect.

'Pimelodidae':
Heptapterus mustelinus: KU 21235, 4sp, cl & st; PC 147, 1sp, cl & st; PC 147, 1sp, dissect; PC 19484, 1sp, cl & st; PC 17583, 2sp, cl & st; PC 50983, 4sp, cl & st.
Microglanis variegatus: KU 20009, 10sp, cl & st.
Parapimelodus valenciennesi: KU 21804, 10sp, cl & st; ZMH 6669, 2sp, cl & st; PC uncat., 1sp, dissect.
Pimelodella hasemani: KU 13695, 1sp, cl & st.
Pimelodella sp.: KU 137010, 3sp, cl & st.
Pimelodus maculatus: PC 271282, 2sp, cl & st.
Pimelodus sp.: KU 21805, 2sp, cl & st; PC uncat., 2sp, dissect.
Rhamdia sapo: KU 21806, 3sp, cl & st; PC 100285, 2 sp, dissect.
Rhamdia wagneri: KU 20012, 3sp, cl & st.

Schilbeidae:
Ailia coilia: KU 12156, 1sp, cl & st.
Eutropiichthys vacha: KU 12169, 1sp, cl & st.
Schilbeidae ind.: KU uncat., 4sp, cl & st.

Trichomycteridae:
Bullockia maldonadoi: KU 19371, 20sp, cl & st; PC 210986, 20sp, cl & st.
Eremophilus mutisii: CAS-SU 62927, 2sp, cl & st.
Hatcheria macraei: KU 19247, 10sp, cl & st.
Ochmacanthus reinhardti: KU 13726, 1sp, cl & st; KU 13735, 2sp, cl & st.
Trichomycterus areolatus: KU 19423, 20sp, cl & st; KU 19424, 14sp, cl & st; KU 19425, 20sp, cl & st; PC 221081, 20sp, cl & st.
Trichomycterus chiltoni: KU 19227, 9sp, cl & st.
Trichomycterus roigi: PC 230281-2, 13sp, cl & st.
Trichomycterus rivulatus: KU 19181, 3sp, cl & st; KU 19360, 2sp, cl & st.
Tridentopsis pearsoni: CAS-SU 56200, 2sp, cl & st.
Vandellia cirrhosa: AMNH 20497, 1sp, cl & st; UMMZ 205178, 10 sp, cl & st.

Gymnotoidei
Gymnotidae:
Gymnotus carapo: KU 13793, 9sp, cl & st; KU 21803, 1sp, cl & st.
Gymnotus cylindricus: KU 1869, 2sp, cl & st.

Hypopomidae:
Hypopomus brevirostris: KU 13800, 7sp, cl & st.
Hypopygus lepturus: KU 20127, 1sp, cl & st.

For other specimens used in comparative studies see list of materials in Arratia (1990a) and Arratia & Schultze (1991).

TERMINOLOGY

The differentiation of a cartilaginous plate into separate, articulating elements (Arratia 1990a, Arratia & Schultze 1990) is characterized by structural changes that produce changes in the density of the cartilage in the area where an articulation will form. The articular region itself is characterized by a change in the position of the cartilage cells, so that it appears more or less dense and fibers develop. The appearance of the future articular region under a compound microscope or stereomicroscope shows differences among species. For instance, a clear, less dense region appears where an articulation will form in trichomycterids (Fig. 1), or a more dense region than the surrounding areas will form in ictalurids. Changes in density are due to different positions and distributions of the cartilaginous cells and fibers. Secondary cartilage and chondroid bone is usually found in the articular facets of synchondral articulations of large specimens, as already established by Beresford (1981) and Smith & Hall (1991).

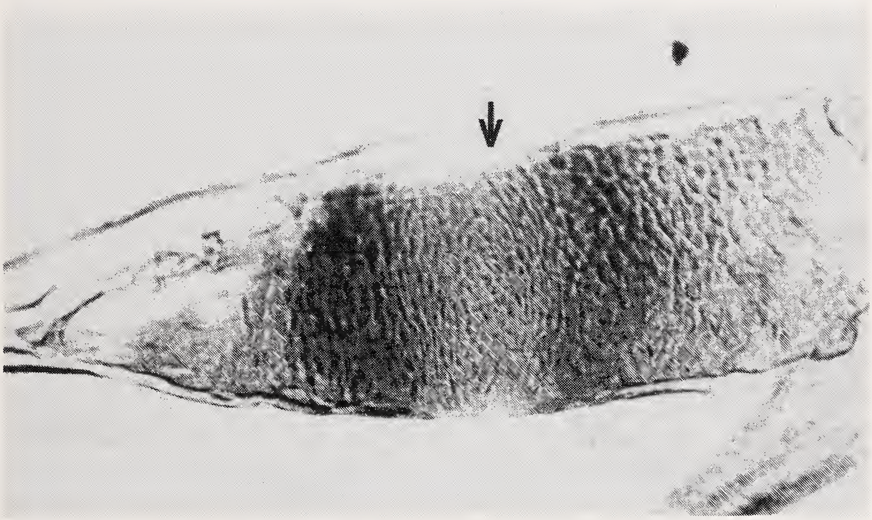

Fig.1: Pterygoquadrate portion of the hyo-symplectic-pterygoquadrate plate of *Trichomycterus areolatus* (22 mm specimen; PC 221081) illustrating the changes of the density of the cartilage where an articulation will form (indicated by an arrow) (after Arratia 1990a).
mtg: metapterygoid; q: quadrate.

The types of articulation between bones of the suspensorium differ among teleost groups. Sutures are described as serrate, dentate, harmonic, etc... following the terminology of human anatomy (Gray 1982), in the absence of a specific terminology for fishes. In the early ontogeny of teleosts, the surfaces producing a sutural joint are smooth (harmonic suture) and from this stage the suture may be modified into a dentate or serrate one, or stay as a harmonic suture (see below). Combinations of articulations are explained in the text.

I distinguish here: autopalatine from dermopalatine, true pterygoid bones (metapterygoid, ectopterygoid, and entopterygoid) sensu Arratia & Schultze (1991), rudimentary and/or sesamoid pterygoids ('entopterygoids'), and additional pterygoids (identified here as 1, 2, 3... etc).

Autopalatine

The name palatin was used by Geoffroy St. Hilaire (1824) and Cuvier & Valenciennes (1828), palatinum by Hallmann (1837), and palatine by Owen (1843, 1846, 1866) and Parker & Bettany (1877) to identify the anterior styliform ossification of the palatoquadrate that bears teeth in the perch, salmon, and other teleosts. It corresponds to a compound element formed by autopalatine and dermopalatine according to modern literature. The name auto-palatine was used first by Allis (1898: 459, Pl. 33, fig. 2) in his description and illustration of *Amia calva*. Later, auto-palatine was changed to autopalatinum (e.g., Holmgren & Stensiö 1936) or autopalatine (e.g., Stensiö 1925, Jarvik 1942).

The term autopalatine is reserved here for the anteriormost ossification of the palatoquadrate, and the term dermopalatine for a dermal ossification which develops ventrolateral to pars autopalatina of the palatoquadrate and bears dentition. Siluroids have an autopalatine; the dermopalatine is absent (see below).

Pterygoid bones

Teleostean pterygoid bones generally consist of the following:

Metapterygoid: It is a chondral bone (Parker 1873, Gaupp 1905) which originates from the posterodorsal part of the cartilaginous palatoquadrate; it overlaps laterally the hyo-symplectic cartilage early in ontogeny (gymnotoids are an exception) (see Arratia & Schultze 1991 for details). The metapterygoid in adults may be sutured (serrate, dentate, or hamonic) and/or synchondrally articulated with the quadrate and hyomandibula posteriorly; it sutures anteriorly with the entopterygoid.

The metapterygoid was identified in teleosts as temporal by Cuvier & Valenciennes (1828), as pre-tympanic by Owen (1843, 1846), and as metapterygoid by Parker & Bettany (1877). Starks (1926) labelled the metapterygoid in siluroids as pterygoid; recently, Howes & Ayanomiya Fumihito (1991) identified the siluroid metapterygoid as the posterior pterygoid. The metapterygoid in siluroids is homologous with that in other fishes (see Allis 1923, Arratia & Schultze 1991), so that there is no reason to replace the name metapterygoid by another name in siluroids.

Entopterygoid: It is a dermal bone at the medial side of the palatoquadrate, between the autopalatine anteriorly and the metapterygoid posteriorly. It supports the eye in amiids and most teleosts (for details see Arratia & Schultze 1991).

The entopterygoid in teleosts was named ptérygoidien interne or pterygoideum internum by Cuvier & Valenciennes (1828) and Hallmann (1837), and entopterygoid by Owen (1843, 1846, 1866). Therefore, the name entopterygoid was used first to identify the dermal medial pterygoid bone of the palate in actinopterygians (e.g., cypriniforms, characiforms, osteoglossomorphs, percomorphs, polypterids, lepisosteids). According to Owen (1866: Figs. 81, 98) the bone that he interpreted as entopterygoid in fishes and labelled as 23 in his figures does not have an homologous element in reptiles. Later on, the names entopterygoid or endopterygoid were used to identify the dermal medial bone of the palate in *Amia calva* by Goodrich (1930: Figs. 429, 430). Recently, Jollie (1962) used the name pterygoid to identify the medial dermal bone of the palate of fishes (e.g., salmonid: Fig. 5-1; *Lepisosteus*: Fig. 5-14E; *Amia*: Fig. 5-14F; *Eusthenopteron*: Fig. 4-31) and tetrapods (e.g., *Seymouria*: Fig. 4-26C; *Palaeogyrinus*: Fig. 4-24B; bullfrog: Fig. 4-21C). Nevertheless, it has not been demonstrated yet that the piscine entopterygoid and the tetrapod pterygoid are homologous; according to Lubosch (1907), van Kampen (1922), and de Beer (1929), the mammalian pterygoid is a composite structure.

For reasons I have not been able to find in the literature, the entopterygoid has been commonly identified as the mesopterygoid in siluroids and other ostariophysans (e.g., Regan 1911, Weitzman 1962, Fink & Fink 1981). The term mesopterygoid was created and used by Parker (1874, 1885, 1886) and Parker & Bettany (1877) for the dermal bone at the medial boundary of the palate in teleosts and tetrapods as well. (In *Galeopithecus*, Parker 1885 described and figured a bone he called mesopterygoid which exists in addition to the pterygoid, and which he also showed in the pig [1887].) Broom (1922) named mesopterygoid the region that corresponds to the pars metapterygoidea of the palatoquadrate in the sarcopterygian *Eusthenopteron* and Goodrich (1930: Fig. 407) identified the entopterygoid of *Salmo fario* as the mesopterygoid. Since the term mesopterygoid does not imply any special condition in ostariophysans and/or siluroids, I retain the term entopterygoid proposed first for teleosts.

Ectopterygoid: It is a dermal bone at the lateral or ventrolateral portion of the palatoquadrate, posterior to pars autopalatina and anterior to pars quadrata of the palatoquadrate (for details see Arratia & Schultze 1991). The ectopterygoid extends anterodorsally beyond the dermopalatine and autopalatine in primitive teleosts (e.g., Arratia & Schultze 1991: Fig. 24), but barely contacts the autopalatine in most other teleosts. Commonly, it is considered to be absent in siluroids according to Alexander (1965), Gosline (1975), and herein.

The bone was identified as adgustal by Geoffroy St. Hilaire (1824), transverse by Cuvier & Valenciennes (1828) and Agassiz (1843), pterygoideum externum by Hallmann (1837), pterygoid by Owen (1843, 1846), Parker & Bettany (1877), Regan (1911), and others in teleosts. The name ectopterygoid was used first by Owen (1866: 157) for reptiles: the ectopterygoid in lizards forms the outer boundary of the pterygo-maxillary or palatine vacuity, whereas it forms the hind boundary in crocodiles. The reptilian ectopterygoid of Owen, labelled as bone 25 (Owen 1866: 133, Fig. 98) corresponds (his interpretation) to the piscine subdivision 25 (Owen 1866: Fig. 81 = actually recognized as hyomandibula). Therefore, the reptilian ectopterygoid (bone 25) is not homologous with the piscine bone 25 sensu Owen (1866) that is the hyomandibula in fishes. The bone that actually is identified as the ectopterygoid in fishes, was named pterygoid by Owen (1843, 1846, 1866); however, pterygoid is the term that actually identifies the dermal medial pterygoid in tetrapods.

The name ectopterygoid in fishes was used first by Sagemehl (1885) in his osteological description of characiforms and since then it has been used for actinopterygians (e.g., Allis 1889, Pearson & Westoll 1979, Gardiner 1984) and sarcopterygians (e.g., Jarvik 1942, 1980). To my best knowledge the homology of the piscine ectopterygoid has never been addressed; for the purpose of the present paper, the name ectopterygoid will be used. I will deal in a separate paper with the homologization of the tetrapod and piscine ectopterygoids.

Dermo + metapterygoid: It is a compound bone formed by the ontogenetic fusion of the metapterygoid and a dermal tooth plate (e.g., *Parapimelodus*).

Ectopterygoid + subpalatine toothplate: It is a dermal, toothed bone that occupies the position of both the ectopterygoid and dermopalatine in primitive teleosts (e.g., *Eutropiichthys*). This element corresponds to the ectopterygoid of Tilak (1961); tooth plate of Gosline (1975).

Sesamoid pterygoids

Pterygoids differing in number and shape occur within the siluroids. I recognize as sesamoid 'entopterygoids' and 'ectopterygoid' any small, otherwise unnamed bone that originates as a mineralization of a ligament (=tendon bone herein) and is connected to the cranium and/or palate by ligaments and connective tissue. For the purposes of this paper the tendon-bone and/or sesamoid entopterygoid and ectopterygoid will be distinguished as 'entopterygoid' and 'ectopterygoid'. Several types of 'entopterygoids' (Fig. 2A—G) may be named according to their position, shape, and ligamentous connections; number 1 corresponds to the type having the least number of ligamentous connections; numbers 2, 3, etc., indicate the addition or change of ligamentous connections.

'Entopterygoid' type 1: (Mesopterygoid of Regan 1911, Alexander 1965.) Small, sesamoid, irregularly shaped bone, anteromedial to the processus basalis of the metapterygoid. The 'entopterygoid' type 1 is connected by ligaments (Fig. 2A) to the metapterygoid and to the vomer (occasionally present in Diplomystidae, e.g. *Olivaichthys viedmensis*).

'Entopterygoid' type 2: (Endopterygoid of Arratia et al. 1978, 'entopterygoid' of Arratia 1990a.) Small sesamoid bone forming a cup-like ossification around the distal cartilage of the autopalatine. A strong, short ligament (Fig. 2B) extends between the 'entopterygoid' type 2 and the metapterygoid. A long ligament connects the 'entopterygoid' type 2 and the anterior part of the vomer. The 'entopterygoid' is closely attached to the autopalatine by connective tissue (e.g., *Nematogenys*).

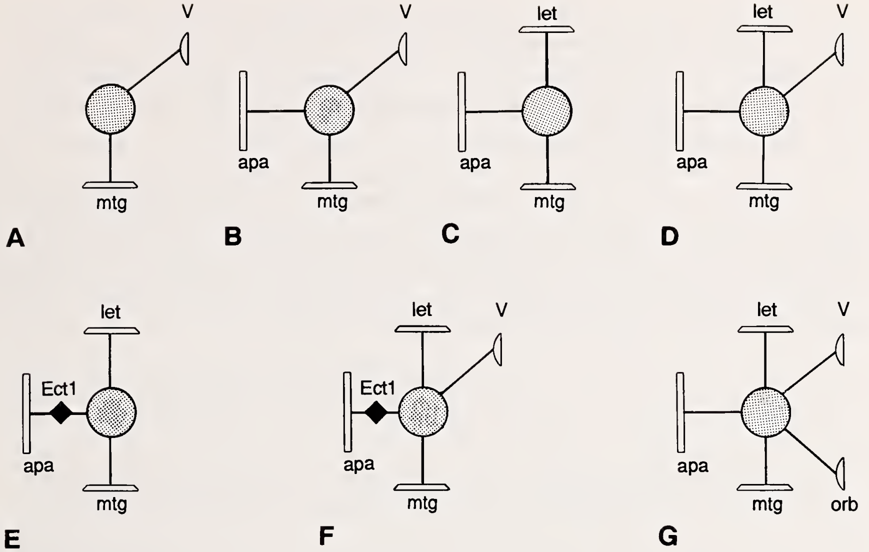

Fig.2: Diagram of the ligamentous connection of ’entopterygoid’ types 1 to 7 to palatal and cranial bones in catfishes. The circle represents an ’entopterygoid’. — A: ’Entopterygoid’ type 1; B: ’Entopterygoid’ type 2; C: ’Entopterygoid’ type 3; D: ’Entopterygoid’ type 4; E: ’Entopterygoid’ type 5; F: ’Entopterygoid’ type 6; G: ’Entopterygoid’ type 7.
apa: autopalatine; Ect 1: ’ectopterygoid’ type 1; let: lateral ethmoid; mtg: metapterygoid; orb: orbitosphenoid; V: vomer.

’Entopterygoid’ type’ 3: (Ectopterygoid of Tilak 1964.) Rudimentary splint-like, sesamoid bone between the two anterior sharp processes of the metapterygoid; metapterygoid and ’entopterygoid’ are connected by a short ligament (Fig. 2C). The ’entopterygoid’ type 3 is connected by connective tissue and ligaments to metapterygoid, autopalatine, and lateral ethmoid (e.g., *Eutropiichthys*).

’Entopterygoid’ type 4: Small, flat, slightly square sesamoid bone found anterior to the metapterygoid and medial to the autopalatine. This type of ’entopterygoid’ is linked by ligaments (Fig. 2D) to the metapterygoid, vomer, autopalatine, and lateral ethmoid (e.g., *Heptapterus, Rhamdia*, and *Noturus*).

’Entopterygoid’ type 5: (Mesopterygoid of Regan 1911, Gosline 1975, ectopterygoid of Azpelicueta et al. 1981.) Small, thick, crescentic or triangular, sesamoid bone posterior to the ’ectopterygoid’ type 1 (see below) and medial to the autopalatine. It is linked by connective tissue and ligaments (Fig. 2E) to the metapterygoid and lateral ethmoid, and by an indirect ligamentous link to the autopalatine through the ’ectopterygoid’ type 1 (e.g., *Parapimelodus*).

’Entopterygoid’ type 6: (Mesopterygoid of Jayaram 1966.) Small, flat, slightly triangular, sesamoid bone posterior to the ’ectopterygoid’ type 1 and medial to the autopalatine. The ’entopterygoid’ type 6 has connections (Fig. 2F) similar to those of ’entopterygoid’ type 5, but there is an additional ligamentous link to the vomer (e.g., *Bagre marinus* and *Galeichthys*).

’Entopterygoid’ type 7: (Endopterygoid of Lundberg 1982.) Small, triangular or square, sesamoid bone medial to the autopalatine and anterior to the metapterygoid. This type of ’entopterygoid’ is attached by connective tissue and ligaments (Fig. 2G) to the autopalatine, metapterygoid, orbitosphenoid, lateral ethmoid, and anterior portion of the vomer (e.g., *Ictalurus*).

’Ectopterygoid’ type 1: (Pterygoid of Regan 1911, palatine element number 2 of Starks 1926, fractured mesopterygoid of Gosline 1975, ectopterygoid of Rao & Lakshmi 1984.) Elongate or cup-like bone ventrally attached to the autopalatine or articulating with the anterior portion of the autopalatine; it commonly extends posterior to the distal part of autopalatine. A short, strong ligament (Fig. 2E,F) extends between ’ectopterygoid’ type 1 and ’entopterygoid’ type 6 (e.g., *Bagre marinus* and *Galeichthys*), and between ’ectopterygoid’ type 1 and ’entopterygoid’ type 5 (e.g., *Parapimelodus, Pimelodus*).

Additional pterygoids

An additional pterygoid is considered here to be a dermal bone that differs in shape and position from the metapterygoid, ectopterygoid, ’entopterygoid’ types 1 to 7, and ’ectopterygoid’ type 1. It may be an additional bone to the pterygoid series.

Pterygoid type 1: Rudimentary, flat, elongate dermal bone between the posterodorsal part of the metapterygoid and the anterior membranous outgrowth of hyomandibula. It appears fused to the metapterygoid in a few specimens of *Parapimelodus*.

Origin and ossification of bones of suspensorium

In all fishes examined, as well as other osteichthyans (see Arratia & Schultze 1991), the bones of the suspensorium have a variety of origins:

cartilaginous origin		
	mandibular arch:	autopalatine metapterygoid quadrate
	hyoid arch:	hyomandibula symplectic
dermal origin		dermopalatine tooth plates associated with palatal bones ectopterygoid

	entopterygoid
	pterygoid type 1
tendon bone origin	'entopterygoid'
	'ectopterygoid'

The bones which originate from cartilaginous arches exhibit chondral ossification, and those of dermal origin exhibit dermal ossification (that is, they do not include a cartilaginous precursor).

Ossification of the cartilaginous arches giving rise to the bones of the suspensorium begins at the surface, they therefore exhibit perichondral ossification. In addition, bones such as the hyomandibula, symplectic, metapterygoid, and quadrate may have membranous outgrowths associated with the chondral portion. These membranous outgrowths are not preformed in cartilage; they are thin, delicate ossifications that extend from the perichondral ossification.

SUSPENSORIUM OF OSTARIOPHYSANS OTHER THAN CATFISHES

Gonorynchiforms

The series of *Chanos chanos* includes 13 specimens ranging from 11 to about 850 mm standard length.

In 11—13.5 mm specimens, the mandibular and hyoid arches (Figs. 3, 4A) are cartilaginous. The dorsal part of the mandibular arch, the palatoquadrate, is an elongate cartilage that overlaps the lateral face of the dorsal limb of the hyoid arch. The palatoquadrate cartilage is continuous with the lower part of the mandibular arch, the Meckelian cartilage. The palatoquadrate broadens posteriorly and close to the

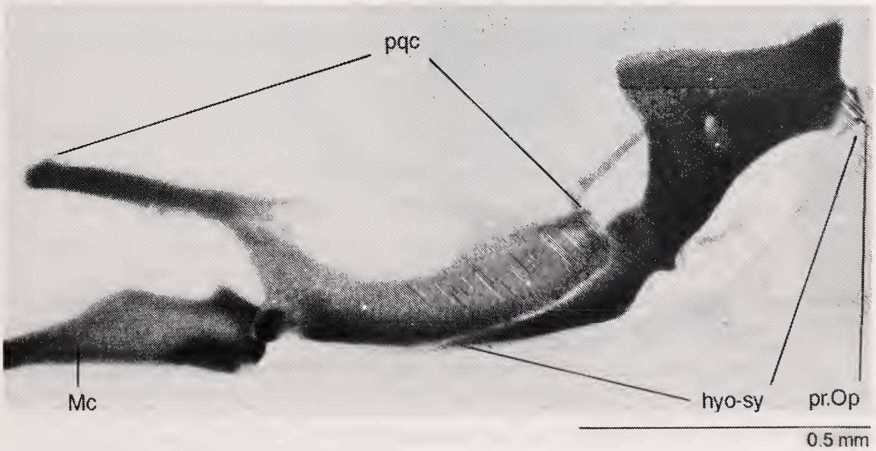

Fig.3: Suspensorium of the gonorynchiform *Chanos chanos*, lateral view (13.5 mm specimen; SIO 80-199). hyo-sy: hyo-symplectic; mc: Meckelian cartilage; pqc: palatoquadrate; pr. Op: processus opercularis.

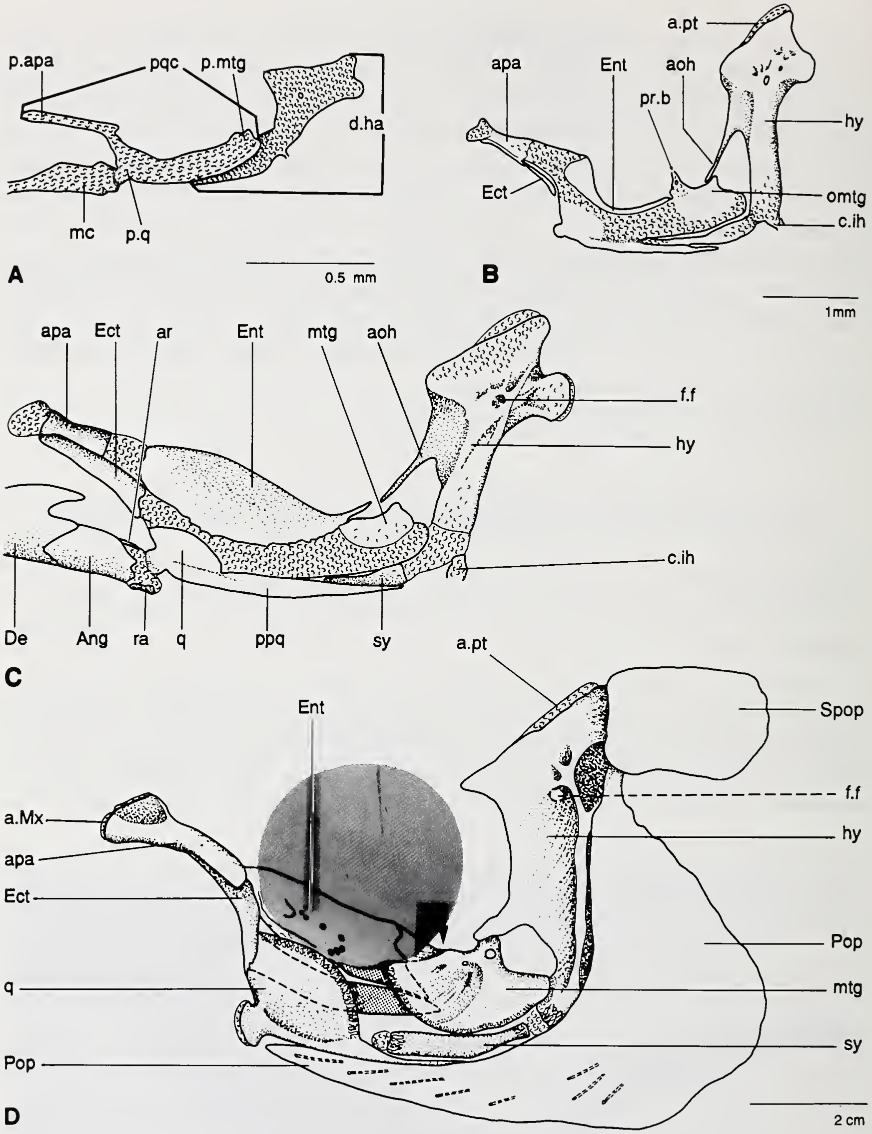

Fig.4: Suspensorium of the gonorynchiform *Chanos chanos*, lateral view and placement of the eye (dotted area). — A: 13 mm specimen (SIO 80-199); B: 16.5 mm specimen (SIO 80-199); C: 21 mm specimen (UMMZ 196864); D: 148 mm cranial length (CAS-SU 35075; after Arratia 1990a). Arrow points to a notch. Cartilage missing. Ang: angular; aoh: anterior outgrowth of hyomandibula; apa: autopalatine; a.Mx: articular facet for maxilla; a.pt: articular facet for pterotic; ar: articular; c.ih: cartilaginous interhyal; De: dentary; d.ha: dorsal limb of hyoid arch; Ect: ectopterygoid; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; mtg: metapterygoid; omtg: ossification center of metapterygoid; p.apa: pars autopalatina; p.mtg: pars metapterygoidea; Pop: preopercle; ppq: posteroventral process of quadrate; p.q: pars quadrata; pqc: palatoquadrate cartilage; q: quadrate; ra: retroarticular; Spop: suprapreopercle; sy: symplectic.

posterodorsal margin is the pars metapterygoidea which has a medial cartilaginous projection, the processus basalis. In a 13.5 mm specimen, the condylar region of the pars quadrata begins to increase in density and a fine perichondral ossification (of the quadrate) surrounds the condyle. A long, fine posteroventral process ossifies posterior to the perichondral ossification center of the quadrate.

The dorsal limb of the hyoid arch — the hyo-symplectic — is broader dorsally than ventrally and remains joined to the neurocranium by some thin cartilage. A posterior cartilaginous opercular process is present at the broadest part of the hyo-symplectic cartilage and articulates with a small, thin opercle. A small foramen for the passage of the facial nerves pierces the center of the hyo-symplectic, in the region where the hyomandibula will later ossify. The antero-ventral part of the hyo-symplectic, the future symplectic, is narrow and far from the condyle of the pars quadrata.

In specimens of about 15 mm, the dermal ectopterygoid and entopterygoid appear. The thin, elongate ectopterygoid is lateral to the palatoquadrate, whereas the entopterygoid is medial to the palatoquadrate and located between the pars autopalatina and pars quadrata.

In 16.5—17 mm specimens, the autopalatine, metapterygoid, and quadrate (Fig. 4B) are partially ossified, however they are still joined by a large quantity of cartilage. The autopalatine has a large mass of cartilage anteriorly; some cartilage also separates the autopalatine from the entopterygoid. The metapterygoid is fan shaped, with a sharp cartilaginous processus basalis extending medially from the anterodorsal margin and perforated by a small foramen. The processus metapterygoideus lateralis is small and extends dorsally to lie lateral to the anteroventral membranous outgrowth of the hyomandibula. The quadrate is a small triangle bearing a long posteroventral process that lies almost horizontal to the body axis.

A small, elongate, thin ectopterygoid is posterior and ventral to the autopalatine and ventral to the palatoquadrate cartilage. The entopterygoid is elongate, broader anteriorly than postero-ventrally and has fine arachnoid projections that extend below the palatoquadrate cartilage.

The hyomandibula is almost totally ossified but remains joined by a large cartilage to the symplectic, and by a narrow cartilage to the interhyal. An elongate, ventrally directed, membranous process develops from the anterior margin of the hyomandibula.

In a 21 mm specimen, all bones of the suspensorium (Fig. 4C) are differentiated but still joined by large remnants of the palatoquadrate cartilage. In a 111 mm specimen, the degree of ossification is higher, but large areas of cartilage are still present between the autopalatine, metapterygoid, and quadrate.

In adults the autopalatine, metapterygoid, and quadrate (Fig. 4D) are thick bones with fine perichondral ossification surrounding large areas of chondroid bone.

The autopalatine is broadest anteriorly and has a slightly concave dorsal surface where the olfactory organ rests; the whole anterior margin of the autopalatine (Fig. 4D) is coated by an articular fibrocartilage with two articular facets, one for the lateral autopalatine-maxillary cartilage, and a medial articulation continuous with the eth-

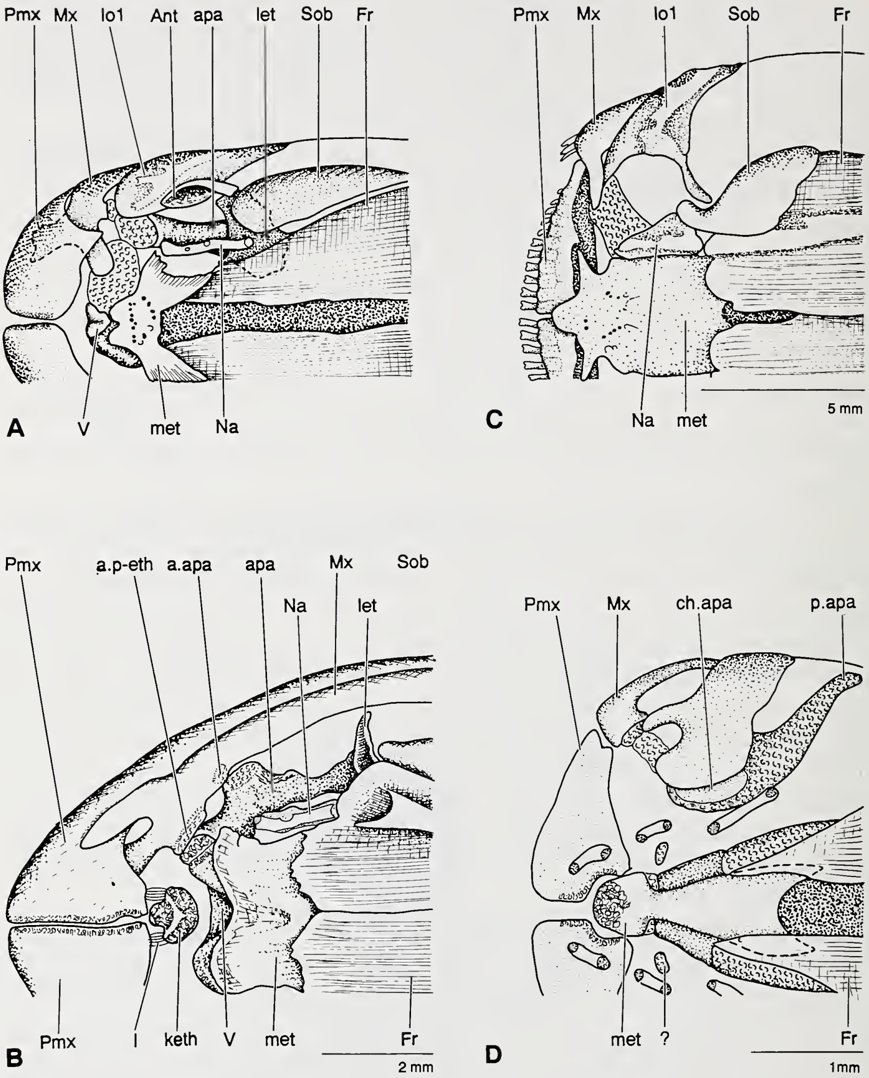

Fig.5: Relationships of the autopalatine of ostariophysans, dorsal view. — A: *Chanos chanos* (107.5 mm specimen; CAS-SU 38340); B: *Opsariichthys bidens* (74 mm standard length; PC 22); C: *Xenocharax spilurus* (94.9 mm standard length; CAS-SU 15639); D: *Hypopomus brevirostris* (133 mm total length; KU 13800). A-B, same scale.

a. apa: articular facet for autopalatine; Ant: antorbital; apa: autopalatine; a.p-eth: articular facet for preethmoidal cartilage; apa-mx: autopalatine-maxillary cartilage; ch. apa: chondroidal autopalatine; Fr: frontal; Io1: infraorbital 1; keth: kinethmoid; l: ligament; let: lateral ethmoid; met: mesethmoid; Mx: maxilla; Na: nasal; p.apa: pars autopalatina; Pmx: premaxilla; Sob: supraorbital; V: vomer; ?: unknown cartilage.

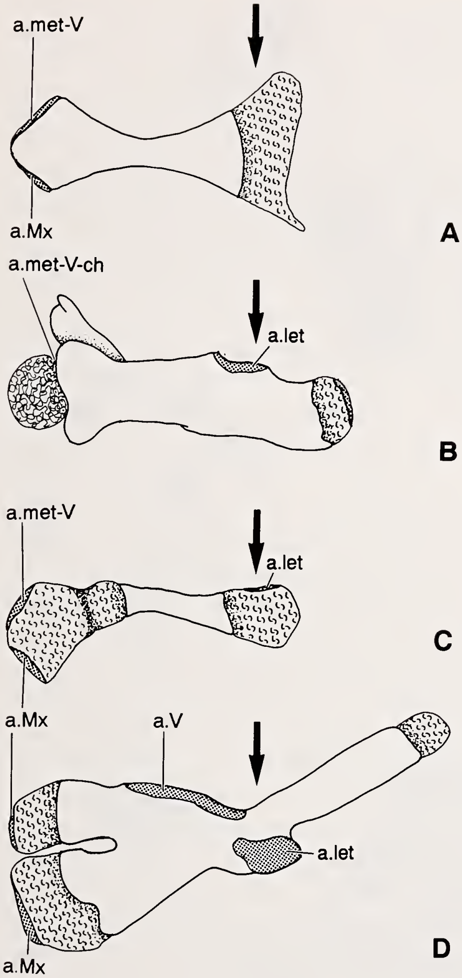

Fig.6: Articulatory surfaces of the autopalatine, left side, for cranial bones in ostariophysans. Arrows point to the position of the lateral ethmoid. — A: *Chanos chanos*; B: *Opsariichthys bidens*; C: *Xenocharax spilurus*; D: *Diplomystes camposensis*.
a.let: articular surface for lateral ethmoid; a.met-V: articular surface for mesethmoid and vomer; a.met-V-ch: articular surface for cartilaginous or chondroidal preethmoidal element connecting with mesethmoid and vomer; a.Mx: articular surface for maxilla; a.V: articular surface for vomer.

moidal cartilage. This ethmoidal chondroidal region is dorsal to the vomer and anteroventral to the mesethmoid. The autopalatine-maxillary cartilage is derived from the pars autopalatine, and is therefore not an ethmoidal element. (It was identified as an ethmopalatal cartilage by Fink & Fink 1981.) Both cartilages, the autopalatine-maxillary and the ethmoidal, become fibrocartilaginous during growth.

Anteriorly, the autopalatine (Figs. 5A, 6A) indirectly articulates with the lateral portion of the maxilla, and medially the autopalatine directly articulates with the neurocranium through the ethmoidal secondary cartilage or chondroidal region between the vomer

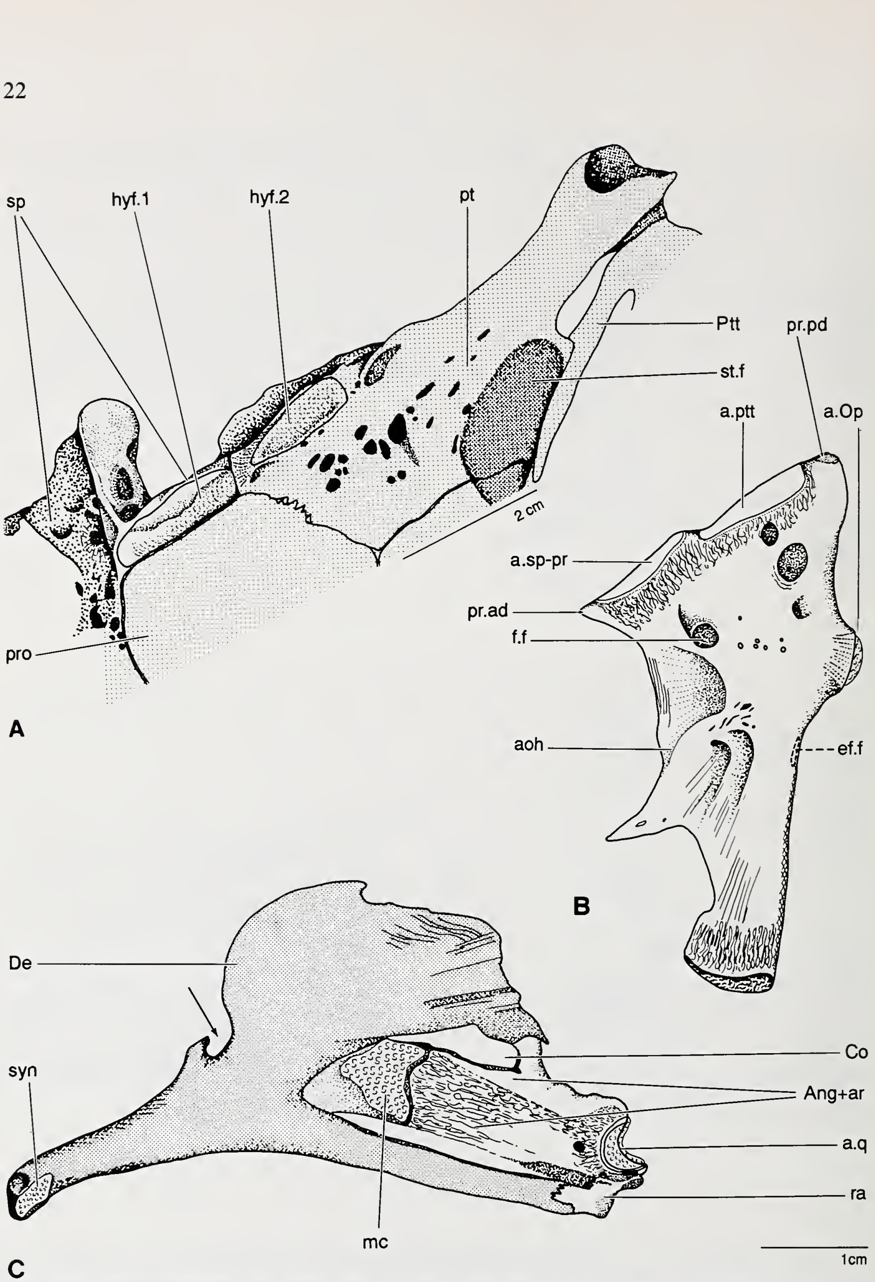

Fig.7: Part of the suspensorium and lower jaw of *Chanos chanos* (148 mm cranial length; CAS-SU 35075). — A: Lateral region of the neurocranium, ventral view; B: Hyomandibula, medial view; C: Posterior part of the lower jaw, lateral view. A, B, same scale. Arrow points to a notch.

Ang+ar: angulo-articular; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; a.pt: articular facet for pterotic; a. sp-pr: articular facet for autosphenotic and prootic; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; hyf. 1-2: hyomandibular fossae 1-2; ef. f: foramen for exit of hyoideomandibular nerve trunk; f.f: foramen for passage of hyoideomandibular nerve trunk; mc: Meckelian cartilage; Ptt: posttemporal; pr.ad: processus anterodorsalis; pr.pd: processus posterodorsalis; pro: prootic; pt: pterotic; ra: retroarticular; sp: sphenotic; st.f: subtemporal fossa; syn: symphyseal surface.

and mesethmoid. The autopalatine does not articulate with the lateral ethmoid. The autopalatine-maxillary cartilage also laterally contacts infraorbital 1. The autopalatine sutures with the entopterygoid medially and ventrally, and with the ectopterygoid laterally and ventrally. The elongate, sharp, anterior portion of the ectopterygoid extends below the autopalatine.

The entopterygoid is slightly concave dorsally. It sutures with the autopalatine anteriorly, with the ectopterygoid and quadrate laterally, and with the metapterygoid posteriorly and medially. The suture between the entopterygoid and quadrate is relatively longer than in other teleosts, whose entopterygoids mainly suture with the ectopterygoids. In a lateral view of the suspensorium, the ectopterygoid is shaped like a boomerang; however, the whole bone is a complex shape, bearing a posterior projection medial to the quadrate and metapterygoid (Fig. 4D). Laterally, there is a schindylesis between the ectopterygoid and the anterior margin of the quadrate.

The metapterygoid is a small chondral bone without membranous outgrowths. It is joined by connective tissue to the anteroventral outgrowth and the anteroventral margin of the hyomandibula.

The quadrate has a fan-shaped body and a long posteroventral process. There is no medial groove for the symplectic, and the latter does not reach the body of the quadrate. The quadrate condyle articulates with the articular portion of a partially fused angular-articular-retroarticular (Fig. 7C). (This fusion was only observed in the largest specimen; only the angular and articular are fused in young specimens.) The quadrate condyle is expanded laterally and medially, with two slightly convex facets separated by a slight depression. The lateral facet is larger than the medial one. These articular facets fit in corresponding slightly concave facets of the articular; the angular and retroarticular portions of the jaw are excluded from the actual articulation. The posteroventral process of the quadrate is medial to the preopercle and sutured to it.

The hyomandibula (Figs. 4D, 7B) is the largest bone of the suspensorium. The main chondral portion is broader dorsally than ventrally. It bears two articular facets for the hyomandibular fossae of the neurocranium (Table 1). The larger anterior facet articulates with sphenotic (or autosphenotic) and prootic, and the posterior one with the pterotic (Fig. 7A). Both fossae are oval-shaped and separated by a notch. The anterior fossa is mainly formed by the autosphenotic; the prootic forms only the medial boundary, the pterotic forms the posterior border. The anterior facet is lower on the neurocranium than the posterior one, because the dorsal margin of the hyomandibula is obliquely ascending to the posterior.

The posterior margin of the hyomandibula bears a short opercular process for articulation with the opercle. Ventrally, the hyomandibula synchondrally articulates with the symplectic and interhyal. Posterolaterally the hyomandibula is overlapped by the anterior margin of the suprapreopercle and the preopercle.

The hyoideomandibular nerve trunk (Fig. 7B) penetrates the hyomandibula on the medial face, and then runs through the bone to exit the posterior margin, ventral to the opercular process. During ontogeny the foramen for the facial nerve which first opens laterally, becomes closed laterally (compare Figs. 4A—C, D).

Tab.1: Single or double articulation of the hyomandibula with cranial bones in some adult ostariophysans. Abbreviations for bones: phs: pterosphenoid; pro: prootic; pt: pterotic; sp: sphenotic. Bold types indicate fusion of bones.

	Single articulation				Double articulation					
					Anterior facet			posterior facet		
Chanos					-	sp	pro	-	-	pt
Carpiodes					phs	sp	pro	sp	pro	pt
Ctenopharyngodon					phs	sp	pro	sp	pro	pt
Cyprinus					phs	sp	pro	sp	pro	pt
Notropis					phs	sp	pro	sp	pro	pt
Ospariichthys					phs	sp	pro	sp	pro	pt
Ptychochceilus					phs	sp	pro	sp	pro	pt
Zacco					phs	sp	pro	sp	pro	pt
Cheirodon	-	sp	pro	pt						
Hoplias	-	sp	pro	pt						
Xenocharax	-	sp	pro	pt						
Bagre	-	sp	-	pt						
Callichthys	-	sp	-	pt						
Diplomystes	phs	sp	pro	pt						
Galeichthys	-	sp	-	pt						
Heptapterus	-	sp	-	pt						
Hypostomus	-	sp	-	pt						
Ictalurus	-	sp	-	pt						
Nematogenys	-	**sp**	**pro**	pt						
Noturus	-	sp	-	pt						
Ochmacanthus	-	sp	pro	pt						
Olivaichthys	phs	sp	pro	pt						
Parapimelodus	-	sp	-	pt						
Pylodictis	-	sp	-	pt						
Rhamdia	-	sp	-	pt						
Trichomycterus	-	**sp**	**pro**	pt						
Gymnotus	phs	sp	pro	pt						
Hypopomus	phs	sp	pro	pt						

The symplectic (Fig. 4D) is an elongate bone that in adults only articulates with the hyomandibula. The interhyal also articulates with the cartilage between the hyomandibula and symplectic.

The main ontogenetic changes in the suspensorium of *Chanos chanos* include: 1) the transformation of a semi-mobile joint between autopalatine and entopterygoid to a suture; 2) the development of a suture between the anterior part of the ectopterygoid and autopalatine; and 3) the posterior growth of the ectopterygoid medial to the metapterygoid.

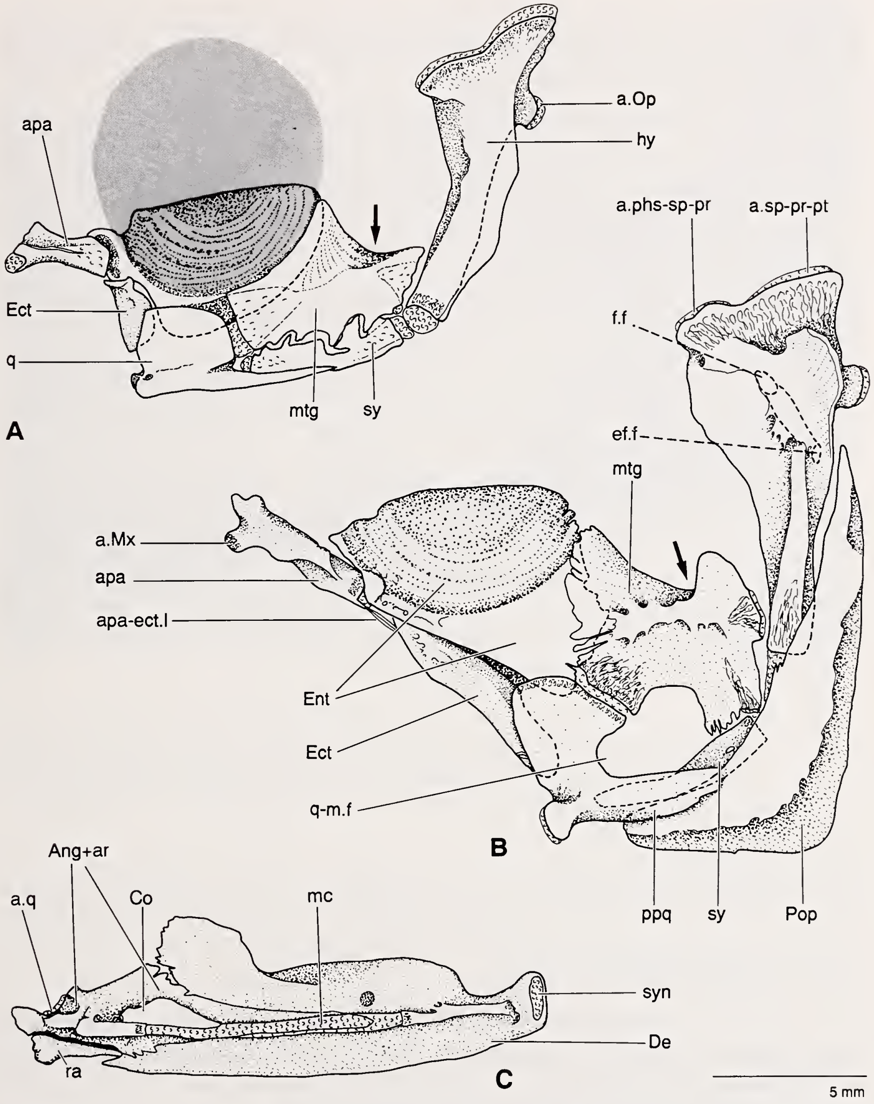

Fig.8: Suspensorium and lower jaw of *Opsariichthys bidens*; dotted area represents the position of the eye. — A: Suspensorium, lateral view (26.5 mm standard length; PC 22); B: Suspensorium, lateral view (120 mm standard length; CAS-SU 32512); C: Lower jaw, medial view (120 mm standard length; PC 32512). Arrows point to a notch. Scale applies to the entire figure.

Ang+ar: angulo-articular; a.Mx; articular facet for maxilla; a.Op: articular facet for opercle; apa: autopalatine; apa-ect.l: autopalatine-ectopterygoid ligament; a.phs-sp-pr: articular facet for pterosphenoid, sphenotic, and prootic; a.sp-pr-pt: articular facet for autosphenotic, prootic, and pterotic; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; Ect: ectopterygoid; Ent: entopterygoid; ef.f: exit of hyoideomandibular nerve trunk; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; mtg: metapterygoid; Pop: preopercle; ppq: posteroventral process; q: quadrate; q-m.f: quadrate-metapterygoid fenestra; ra: retroarticular; sy: symplectic; syn: symphyseal surface.

Cypriniforms

The series of *Opsariichthys bidens* includes 10 specimens ranging from 26.5 mm to 118 mm standard length.

In a 26.5 mm specimen, all bones of the suspensorium (Fig. 8A) are perichondrally ossified; however, they retain a large quantity of cartilage inside the ossification. The autopalatine is small, with a tube-like body that broadens slightly posteriorly and anteriorly bears a concave articular facet for the maxilla. A thin, dorsal membranous outgrowth extends from the main body of the bone. The posterior cartilage of the autopalatine nests into a concave, broad articular facet of the entopterygoid. The entopterygoid forms the medial margin of the suspensorium and dorsomedially is largely concave; it also lies medial to the quadrate and metapterygoid.

The small, stout ectopterygoid anteriorly forms a thick margin that ventrally partially surrounds the articular facet of the entopterygoid. The posterior part of the ectopterygoid is less robust and medial to the quadrate.

The metapterygoid is the largest bone derived from the palatoquadrate cartilage. It bears a sharp, large processus basalis dorsally separated from the posterior margin of the bone by a notch. The posterior margin of the metapterygoid bears two short processes, each with an articular surface; the dorsal one abuts the anteroventral margin of the hyomandibula, the ventral one articulates with the cartilage between the hyomandibula and symplectic. The ventral margin of the metapterygoid is unusual in that it has a dentate suture with the symplectic (Fig. 9).

The quadrate has an almost fan-shaped body, with a moderately long posteroventral process. The symplectic does not reach the body of the quadrate. The condylar articulation for the lower jaw is anteriorly directed, in a plane almost horizontal to the neurocranium. This condyle articulates with the articular portion of the angulo-articular (Fig. 8A—C) of the lower jaw.

The hyomandibula (Fig. 8A) is vertically elongate; it has a lateral membranous outgrowth that extends along almost the entire length of the bone. There is a well-developed opercular process at the posterior margin, but any trace of an anterior process of the hyomandibula is lacking.

There are remarkable ontogenetic changes in the shape of some elements in the suspensorium and the lower jaw in *Opsariichthys.* The dentate suture between metapterygoid and symplectic begins to disappear in specimens of about 30 mm, and the form of the quadrate begins to change in specimens of about 30 mm.

In a 118 mm specimen, the autopalatine is well ossified; it anteriorly bears two articular surfaces (Figs. 5B, 6B, 8B); a lateral one for the maxilla and a medial one for the preethmoidal cartilage. There is also a small dorsomedial articular surface for the lateral ethmoid, close to the posterior end of the autopalatine. Posterolaterally, the autopalatine (Fig. 8B) has a small process where the short autopalatine-ectopterygoid ligament attaches. Posteriorly, the autopalatal fibrocartilage articulates with a medial concave facet on the entopterygoid.

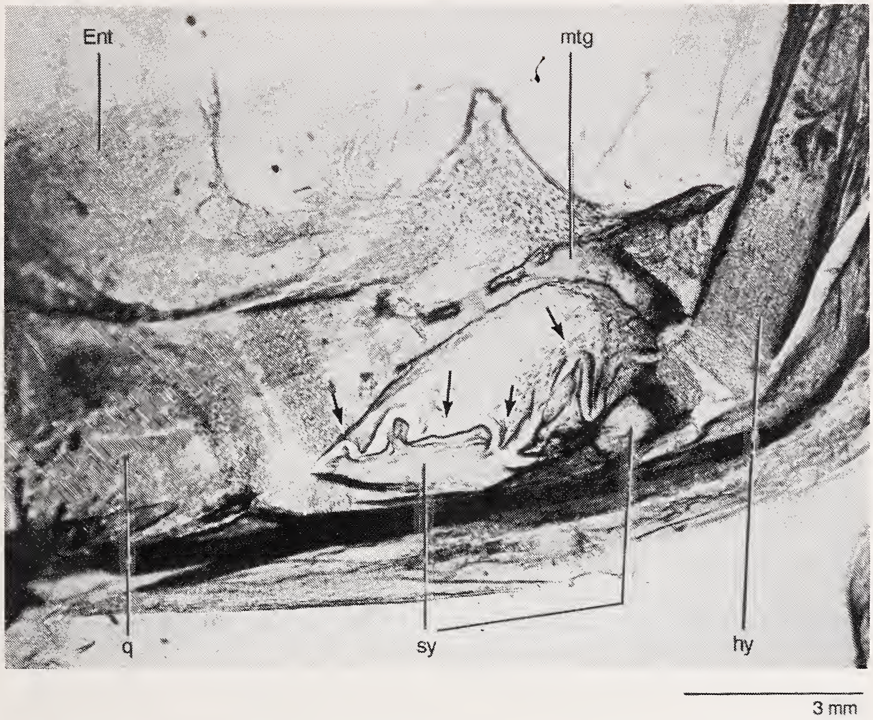

Fig.9: Lateral view of the suspensorium of *Opsariichthys bidens* illustrating the presence of a dentate suture between metapterygoid and symplectic that is indicated by arrows (26.5 mm standard length; PC 22).
Ent: entopterygoid; hy: hyomandibula; mtg: metapterygoid; sy: symplectic; q: quadrate.

The large entopterygoid slightly overlaps the posterior part of the autopalatine, which is unusual among teleosts. The posterior part of the entopterygoid is medial to the metapterygoid, and to a small area to the quadrate.

The elongate, blade-like ectopterygoid does not reach the autopalatine anteriorly, and it is medial to the quadrate posteriorly. A suture between the ectopterygoid and quadrate is missing, instead a short ligament connects them.

The metapterygoid is a large bone, with serrate or dentate anterior and posteroventral margins. It has a well developed processus basalis, separated by a notch from the posterior part of the bone. Anteroventrally, there is a synchondral joint between the metapterygoid and quadrate. A deep notch (part of the wall of the quadrate-metapterygoid fossa) separates the articular border with the quadrate from the serrated posteroventral margin. The posterior margin bears two articular surfaces; the dorsal one for the anteroventral part of the hyomandibula, the ventral one for the cartilage between the hyomandibula, symplectic, and interhyal.

The quadrate has a complex shape. The main body is separated by a deep notch from the posteroventral process; this process is broad and lateral to part of the anterior process of the preopercle. The quadrate also forms part of the quadrate-metapterygoid fenestra.

The articular facet of the lower jaw (Fig. 8C) is composed of two well-developed convex surfaces separated by a notch; this condylar surface lies within the posteriorly directed, broad surface of the articular, that is almost smooth. The articular portion of the angulo-articular is small relative to the angular. The retroarticular is well-developed and doesn't reach the articular facet of the jaw.

The hyomandibula (Fig. 8B) of adults, retains the shape present in young individuals (Fig. 8A), but its dorsal margin is less inclined than in young individuals. There are two facets articulating with the neurocranium (Table 1). The anterior facet articulates with the pterosphenoid, sphenotic, and prootic; the posterior one with the autosphenotic, prootic, and pterotic. Anteriorly, the hyomandibula has a moderately large membranous outgrowth; posteriorly, there is a well-developed opercular process; laterally, there is a well-developed, but thin, membranous outgrowth.

The foramina for both the entrance and exit of the ramus hyoideomandibularis of the facial nerve (Fig. 8B) are medial. The nerve is enclosed in a short bony tube that opens to the posterior margin of the hyomandibula, ventral to the opercular process.

The suspensorium of *Opsariichthys* and *Zacco* are similar; however, the suture between the metapterygoid and symplectic observed in young specimens of *Opsariichthys* was not observed in young specimens of *Zacco*, and the quadrate-metapterygoid foramen is smaller in *Zacco* than *Opsariichthys*. The suspensorium of other cyprinids, as well as other cypriniforms, has the same general pattern described above for *Opsariichthys*. However, there is some variation in the shape and size of some bones and in the number of additional chondroids or bones between the autopalatine, the maxilla, and the ethmoidal region (e.g., Ramaswami 1955 a, b, 1957, Nelson 1969, Sawada 1982, Mayden 1989).

Characiforms

Two specimens of *Xenocharax* were studied. Their standard lengths are 75.9 and 94.9 mm. For more information and variation of the suspensorium among distichodontids see Daget (1961, 1967) and Vari (1979).

The autopalatine (Fig. 10A) is a small bone, rod-like, and slightly expanded posteriorly. It is mostly anterior to the lateral ethmoid. Anteriorly, the autopalatine bears a large, broadly-expanded cartilage (intermediating body that during ontogeny becomes the submaxillary cartilage of Bertmar 1959). In the 75.9 mm specimen, the cartilage is simple, whereas in the 94.9 mm specimen, the cartilage has differentiated into two distinct regions: an articular cartilage that nests into the anterior part of the autopalatine and an expanded part or the maxillary-autopalatine cartilage (Fig. 5C) that provides the contact between the suspensorium and the neurocranium and maxilla. Medially, the maxillary-autopalatine cartilage is tightly joined to the vomer and the cartilaginous area between the vomer and mesethmoid. Laterally, the maxillo-autopalatine cartilage articulates with the maxilla; anteriorly, the cartilage rests on the posterodorsal part of the premaxilla. Posteriorly, the autopalatine bears a large, oval-shaped cartilage that is

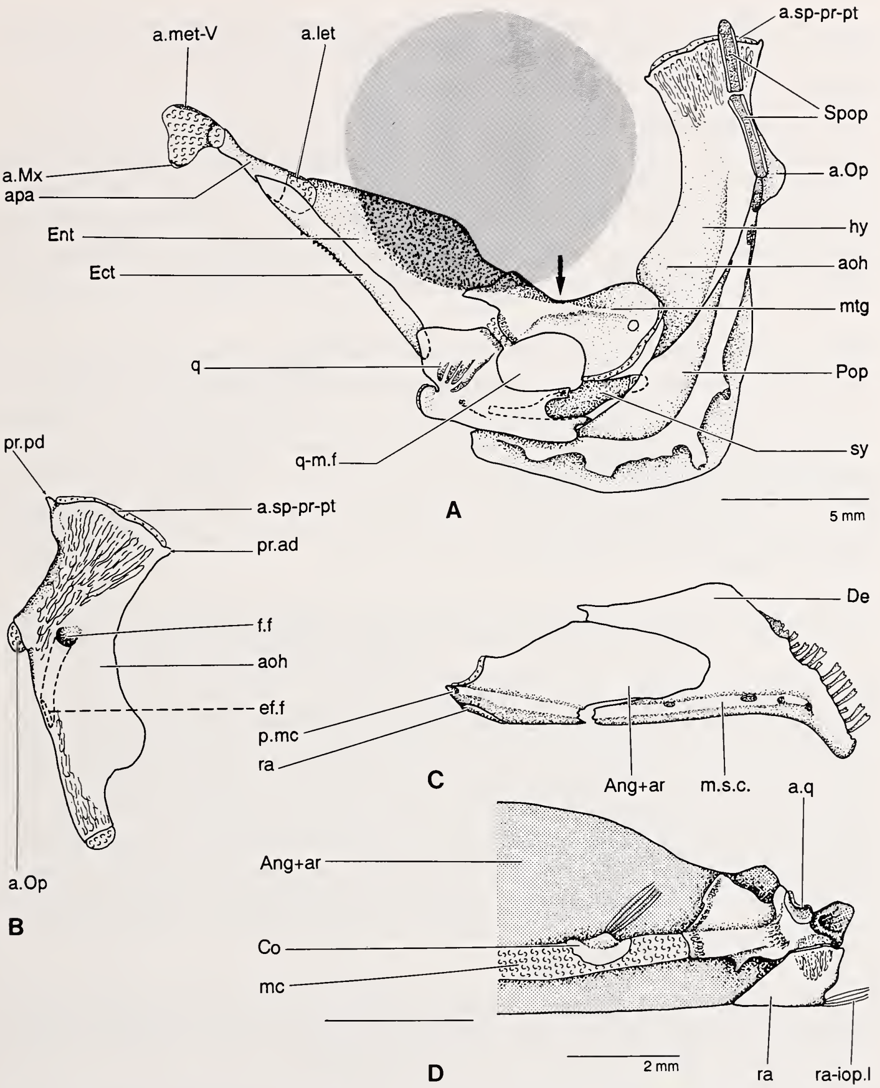

Fig.10: Suspensorium, preopercle, and lower jaw of *Xenocharax spilurus* (94.9 mm; CAS-SU 15639); dotted area represents the position of the eye. — A: Suspensorium, lateral view. Arrow points to a notch; B: Hyomandibula, medial view; C: Lower jaw, lateral view; D: Posterior part of lower jaw, medial view. A—C, same scale. Ang+ar: angulo-articular; a.let: articular facet for lateral ethmoid; a. met-V: articular facet for cartilage joining mesethmoid and vomer; a.Mx: articular facet for maxilla; aoh: membranous outgrowth; a.Op: articular facet for opercle; apa: autopalatine; a.sp-pr-pt: articular facet for sphenotic, prootic, and pterotic; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; Ect: ectopterygoid; ef.f: exit of hyoideomandibular nerve trunk; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; m.s.c.: mandibular canal; mtg: metapterygoid; p.mc: posterior opening of mandibular canal; Pop: preopercle; pr.ad: processus anterodorsalis; pr.pd: processus posterodorsalis; q: quadrate; q-m.f: quadrate-metapterygoid fenestra; ra: retroarticular; ra-iop.l: retroarticular-interopercular ligament; Spop: suprapreopercle; sy: symplectic.

dorsal to both the ectopterygoid and entopterygoid, and articulates with the lateral ethmoid. Posteriorly, the autopalatine is attached to the ectopterygoid. The autopalatine is not sutured to the entopterygoid.

The entopterygoid (Fig. 10A) is a large, thin bone, that is slightly concave dorsally. Laterally it is linked by connective tissue and a ligament to the ectopterygoid, and medially, there is a small suture with the quadrate and metapterygoid. The ectopterygoid extends from below the autopalatine to the quadrate; anteriorly it is a half-tube which encloses the posterior part of the autopalatine; posteriorly it is blade-like and medial to the quadrate. The ectopterygoid bears small teeth along half of its anterior margin.

The quadrate is similar in shape to that of large *Opsariichthys* (compare Figs. 8B, 10A), and the broad posteroventral process partially covers the lateral face of the anterior part of the preopercle. The quadrate-metapterygoid foramen is more or less oval-shaped, and of moderate size. The quadrate sutures anterodorsally and medially with the entopterygoid, and anteriorly with ectopterygoid. There is a synchondral joint between the posterodorsal corner of the main portion of the quadrate and the metapterygoid. There is a condylar joint between the angulo-articular (Fig. 10C—D) of the lower jaw and the quadrate.

The metapterygoid (Fig. 10A) also is similar to that of *Opsariichthys*, but the posterior processes are separated in *Opsariichthys*, but they are united to form a broad articular surface extending along the posterior margin of the metapterygoid in *Xenocharax.*

The hyomandibula (Fig. 10A, B) is a dorsoventrally long, narrow bone. It retains regions of chondroid bone and secondary cartilage close to the neurocranial articular surface, and along a narrow region close to the posterior margin. The slightly broad anterior region is membranous. Dorsally, there is only one narrow, long articular surface, almost horizontal to the neurocranium. Anteriorly it articulates with the sphenotic and prootic, and posteriorly with the pterotic. About half way up the posterior margin of the hyomandibula is a rudimentary opercular process bearing a small, round articular surface. Ventrally, the hyomandibula articulates with the symplectic and interhyal.

The medial foramen for the hyoideomandibular nerve trunk (Fig. 10B) is almost in the middle of the bone. The nerve runs through a short tube in the hyomandibula exiting to the posterior margin, ventral to the opercular process.

The symplectic (Fig. 10A) is elongate, almost reaching the condylar region of the quadrate.

The suspensorium of *Hoplias* shows the general pattern of the suspensorium as in *Xenocharax*; however, *Hoplias* differs from *Xenocharax* and other characiforms in the presence of an almost triangular autopalatine (Fig. 11) that ventrally bears a small toothplate (see below). The autopalatine is a small bone that anteromedially has a short articular surface for the vomer, and a long facet for the lateral ethmoid posterodorsally. Posterolaterally, the autopalatine is sutured to the ectopterygoid. Laterally, the autopalatine articulates with the maxilla; and in addition, a short ligament keeps both bones

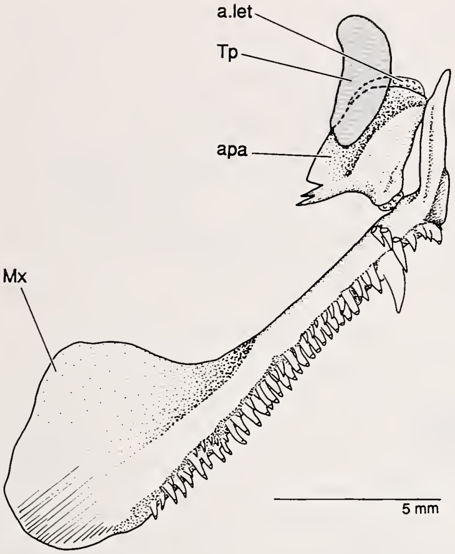

Fig.11: Anterior part of the suspensorium and maxilla of *Hoplias malabaricus*, ventral view (100 mm standard length; KU 13636).
a.let: articular facet for lateral ethmoid; apa: autopalatine; Mx: maxilla; Tp: toothplate (dotted).

in position. The autopalatine is dorsal to the entopterygoid; these bones do not articulate and are not linked by a ligament.

In *Hoplias*, the toothplate is attached by a ligament to the ventral part of the vomer and dorsal part of the autopalatine. This plate was called accessory ectopterygoid tooth plate by Weitzman (1964). It is anterior to but not associated with the ectopterygoid; the numerous, conical teeth face their antimeres medially; however, the toothplates are not sutured to each other. This small dentate bone is not a dermopalatine because this element is missing in primitive ostariophysans; therefore, this element is considered here to be a new formation. The name toothplate is used to avoid confusion with either the dermopalatine, or the subautopalatine toothplate of catfishes.

Gymnotoids

The suspensorium of gymnotoids has been extensively illustrated by Chardon & de la Hoz (1974), who proposed a classification of the group based on the suspensorium. Here I will only address a few points.

The anterior part of the palatoquadrate — the pars autopalatina — does not differentiate into an autopalatine in most gymnoids (Fig. 12A); however, it does in *Hypopomus* (Fig. 12B, D). In *Hypopomus*, anteriorly the suspensorium is connected to the premaxilla by a ligament; laterally, the pars autopalatine articulates with the maxilla. A small, round cartilage between the autopalatine and lateral ethmoid is present in *Hypopomus*. This cartilage is free. The ectopterygoid is absent. The large entopterygoid occupies the position of the ectopterygoid of other teleosts. Among gymnotoids, the dorsal projection of the entopterygoid (Fig. 12A, B) exhibits different degrees of development. This dorsal projection articulates with the lateral ethmoid, the cartilage between the lateral

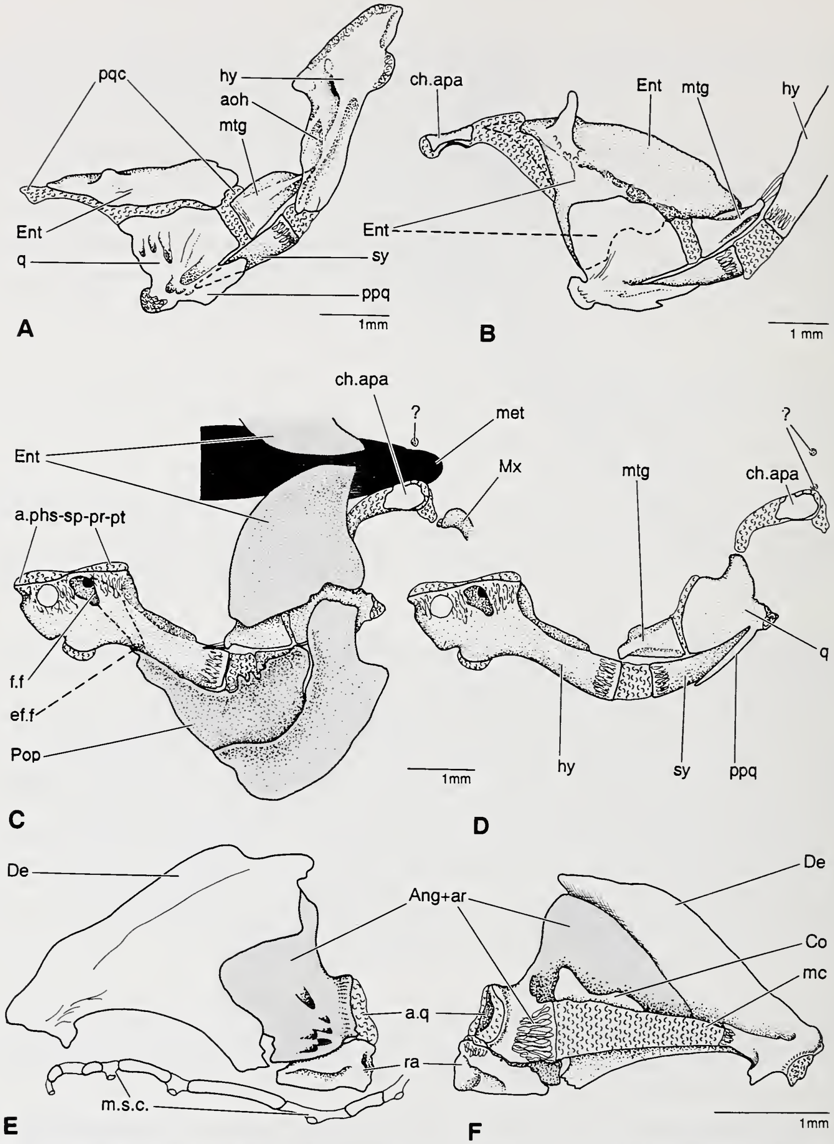

Fig.12: Suspensorium and lower jaw of gymnotoids. — A: *Gymnotus carapo*, lateral view (80 mm specimen; KU 13793); B—F: *Hypopomus brevirostris* (72 mm specimen; KU 13800); B: Suspensorium, lateral view; C: Suspensorium and related bones, medial view; D: Chondral elements of the suspensorium, medial view; E: Lower jaw, lateral view; F: Lower jaw, medial view. C—F same scales.

Ang + ar: angulo-articular; aoh: membranous outgrowth; apa: chondral autopalatine; a. phs-sp-pr-pt: articular facet for pterosphenoid, sphenotic, prootic, and pterotic; a.q: articular facet for quadrate; ch. apa: chondroidal autopalatine; Co: coronomeckelian bone; De: dentary; Ect: ectopterygoid; ef.f: exit of hyoideomandibular nerve trunk; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; Iop: interopercle; mc: Meckelian cartilage; m.s.c.: mandibular canal; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Pop: preopercle; ppq: posteroventral process; pqc: palatoquadrate; q: quadrate; ra: retroarticular; sy: symplectic; ?: unknown cartilage.

ethmoid and orbitosphenoid, and/or the orbitosphenoid alone. Both right and left entopterygoids project medially and almost contact each other, ventral to the parasphenoid, in *Hypopomus*. The entopterygoids, however, do not project below the parasphenoid so extensively in *Gymnotus*. The metapterygoid in *Hypopomus* is small and slightly triangular. The posterodorsal part of the metapterygoid is medial to the hyomandibula and has a ligamentous connection between the metapterygoid and the posterior ceratohyal.

The quadrate (Fig. 12A—F) of gymnotoids articulates with the articular part of the angulo-articular and with the large retroarticular. Part of the quadrate condyle rests on the retroarticular when the fish closes its mouth.

The hyomandibula (Fig. 12A, B; Table 1) of gymnotoids has only one articular surface for the neurocranium; it articulates anteriorly with the pterosphenoid, sphenotic, and prootic, and posteriorly with the pterotic. Only a single hyomandibular facet is observed in the cranium, and the facet narrows posteriorly between the sphenotic-prootic region and the pterotic. I have not had the opportunity to examine specimens larger than 220 mm. Examination of larger specimens will be necessary to verify whether there is a change from a single articular facet to two articular facets during growth.

The hyoideomandibular nerve trunk (Fig. 12C, D) medially enters the hyomandibula and exits at the posterior margin of the bone, ventral to the opercular process.

Let us now examine the situation in catfishes.

SUSPENSORIUM OF CATFISHES

Regan (1911) used the presence or absence of certain pterygoid bones as distinguishing features of particular catfish families. Furthermore, he also used the type of pterygoid (the 'ectopterygoid') and entopterygoid (the 'entopterygoid') articulation to separate subfamilies within the Bagridae; and the presence or absence of the 'ectopterygoid' to separate genera within the Pimelodidae. He also mentioned the ligamentous connections of some pterygoid bones to the autopalatine, vomer, lateral ethmoid, and orbitosphenoid for some families. The connections he mentioned differ between groups; for example, ligaments join the 'entopterygoid' to the metapterygoid and vomer in *Diplomystes* (considered an unique feature by Alexander 1965; I will present contrary evidence here), whereas ligaments join the 'entopterygoid' to the metapterygoid and lateral ethmoid in the Doradidae.

From Regan (1911) to Fink & Fink (1981), the literature shows a variety of shapes and positions for bones that have been variously called the pterygoid or ectopterygoid, and others that have been called the entopterygoid, endopterygoid or mesopterygoid; all of which makes it difficult to precisely identify the elements. The question arises as to which of these bones are homologous within catfishes, and homologous with other

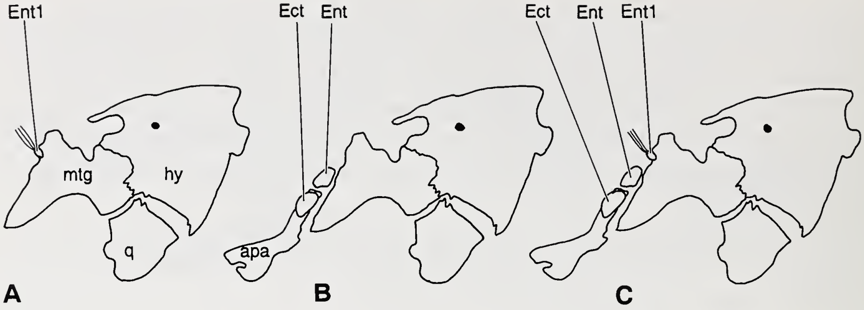

Fig.13: Identification of the dermal pterygoid bones in a diagrammatic medial view of the suspensorium of diplomystids according to various authors. — A: Regan (1911); B: Fink & Fink (1981); C: present paper. apa: autopalatine; Ect: ectopterygoid; Ent: entopterygoid; Ent1: 'entopterygoid' type 1; hy: hyomandibula; mtg: metapterygoid; q: quadrate.

teleosts. Gosline (1975: 3) distinguished two problems concerning the names applied to the bones of catfishes (1) nomenclatural and (2) zoological (the difficulty in identification of elements between divergent taxa). Figure 13A—C, based on diplomystids, illustrates both problems. Regan (1911) and Fink & Fink (1981), agreed only in the identification of the metapterygoid. In addition, the ligamentous connections of the metapterygoid are somewhat different from that stated by Regan (see Arratia 1987a, and below for diplomystids).

According to Regan (1911: 7) the ectopterygoid is absent in *Diplomystes*, a small entopterygoid is present (Fig. 13A) that connects the metapterygoid to the vomer, and furthermore the metapterygoid is anteriorly attached to the autopalatine and medially to the orbitosphenoid. Alexander (1965) and Fink & Fink (1981) agreed that the ectopterygoid and entopterygoid are both present in *Diplomystes*, but the element which Fink & Fink (1981: Fig. 32B) identified as the entopterygoid is not homologous with the entopterygoid of Regan (1911) and Alexander (1965). This is because the entopterygoid of Fink & Fink lacks the ligamentous connection to the cranium and has a unique position in relation to the autopalatine. I have only seen a few specimens that have had the entopterygoid like that described by Regan (Fig. 13A, C).

When this type of 'entopterygoid' is present, it is in addition to two other bones that correspond to the ectopterygoid and entopterygoid of Lundberg (as cited in Gosline 1975) and Fink & Fink (1981). The entopterygoid described by Regan and Alexander is commonly absent; and when it is present, is very small. The bone forming a cup-like ossification around the distal cartilage of the autopalatine has been labelled as the mesopterygoid or endopterygoid (Regan 1911, Lundberg cited in Gosline 1975, Fink & Fink 1981); whereas Alexander (1965: Fig. 4, top) labelled it as the ectopterygoid. I have named this bone as bone 4 (Arratia 1987a), following McMurrich (1884a). The 'entopterygoid' is often absent from one or both sides of the body and so is the ectopterygoid of Fink & Fink (1981). I considered this element not to be homologous with the entopterygoid, because its position and relationships differ from those of other teleosts (Arratia 1987a).

In my opinion, the identification of the pterygoid bones in catfishes is difficult for a variety of reasons: some elements are not consistently present, some are so enlarged that they occupy what would otherwise be the position of two or three pterygoid bones in other teleosts (see below), some have ligamentous connections that vary between groups, and some elements are new formations such as the rudimentary dermal pterygoids.

In addition, siluroids may have between three (e.g., diplomystids, parapimelodids) and zero (e.g., trichomycterids, callichthyids some ictalurids, synodontids) pterygoid elements. These elements include sesamoid 'entopterygoid' types 1—7 and additional pterygoid type 1. The fact that some siluroids have more than two dermal and/or tendon bones and sesamoid pterygoids shows that the palatal region of those siluroids differs from other ostariophysans. It is extremely difficult to determine which pterygoids are homologous with the traditionally recognized dermal ectopterygoid or dermal entopterygoid of other ostariophysans without developmental studies. My attempt to establish homology for the additional dermal and/or sesamoid pterygoids of siluroids with the ectopterygoid of other ostariophysans failed when considering only the macromorphology of the suspensorium. However, to surrender and consider the sesamoid 'entopterygoid' types 1—7 as just the entopterygoid, is too simplistic an ap-

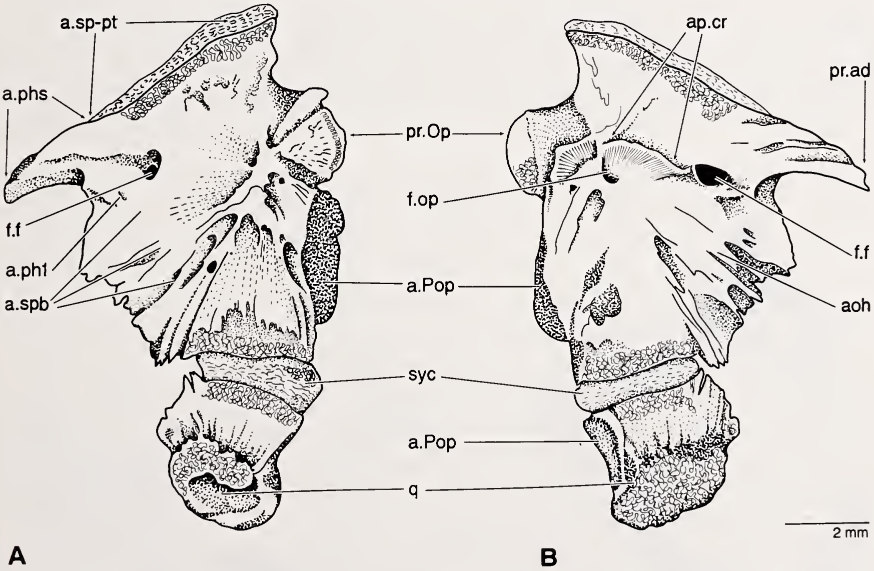

Fig.14: Posterior part of the suspensorium of *Diplomystes camposensis.* (Disarticulated specimen; PC 110276). — A: medial view; B: external view.
a.lj: articular facet for lower jaw; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; ap. cr: levator autopalatini crest; a. ph1: attachment area of pharyngobranchial 1; a.phs: articular facet for pterosphenoid; a.Pop: articular facet for preopercle; a. spb: attachment area for pseudobranch; a.sp-pt: articular facet for sphenotic and pterotic; f.f: foramen for passage of hyoideomandibular nerve trunk; f.op: foramen for passage of ramus opercularis; hy: hyomandibula; pr. ad: processus anterodorsalis; pr. Op: processus opercularis; q: simple quadrate; syc: symplectic cartilage.

proach. The sesamoid 'entopterygoid' types 1—7 are not strictly identical with the entopterygoid of other ostariophysans, and the relationships of the 'entopterygoid' with the surrounding elements differs between the catfish groups. It is therefore important to define the 'entopterygoid' type according to its ligamentous connections, because these connections differ in the palatal region of catfishes. Examples of the variation in the 'entopterygoid' include the following: a large bone contacting the hyomandibula posteriorly, the lateral ethmoid anteriorly and projecting lateral to autopalatine (e.g., *Amplyceps mangois*; Tilak 1967); a small crescentic bone (e.g., in 'pimelodids'); the 'entopterygoid' is absent (e.g., in trichomycterids; Arratia 1990a).

The absence of the symplectic bone has been traditionally accepted for catfishes; nevertheless, Howes (1983a: Fig. 23) illustrated the presence of a small cartilaginous symplectic between the hyomandibula and quadrate in *Hypophthalmus*. In a few large specimens of *Diplomystes camposensis* (Fig. 14A, B; see below), I have found a large dense cartilage exhibiting some ossification. This cartilage is between the hyomandibula and quadrate. I therefore consider it to be the remnant of the symplectic cartilage. In all siluroids there is a large cartilage between the hyomandibula and quadrate.

A small, triangular quadrate lacking an ossified anterior pterygoid process (identified herein as simple quadrate; Figs. 14A, B, 15A) is present in some siluroids such as diplomystids, ictalurids, and nematogenyids (Arratia 1990a: Fig. 12A, B), and modified slightly (to become longer) in loricariids and callichthyids (Arratia 1990a: Figs. 13A, B). In other catfishes, there is a complex-shaped element (Fig. 15B) with two well ossified chondral regions similar to those of both the quadrate and an ossified anterior pterygoid process; a membranous outgrowth may develop between both regions during

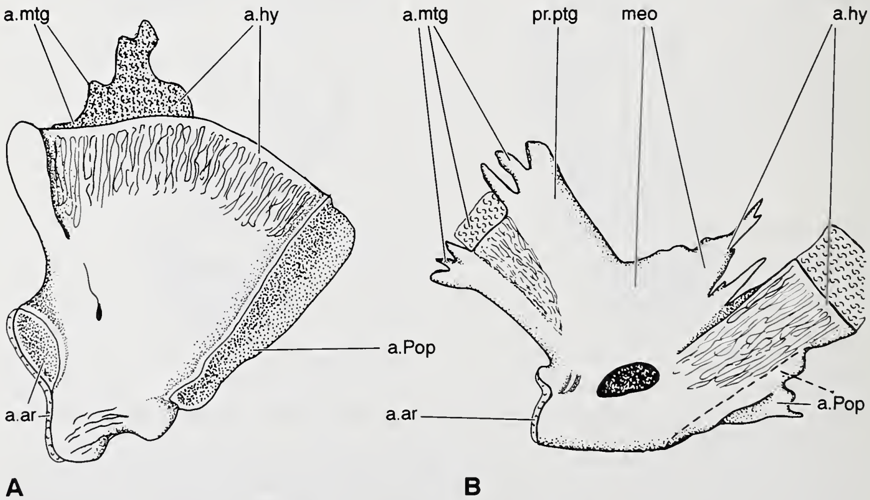

Fig.15: Quadrate of catfishes. — A: Simple quadrate; B: Complex quadrate.
a.ar: articular facet for articular; a.hy: articular facet for hyomandibula; a.mtg: articular facet for metapterygoid; a. Pop: articular facet for preopercle; pr. ptg: processus pterygoideus; meo: membranous outgrowth.

ontogeny. I have named this element the complex quadrate (Arratia 1990a); it has been named as bifid quadrate by Ferraris (1988) and Lundberg et al. (1991). The presence of a simple quadrate or a complex quadrate results in an important difference in the placement of the metapterygoid (Arratia 1990a; see below).

I cannot describe the morphology of the suspensorium for all catfishes. I therefore intend to present what I have learned studying growth series of many individuals of a few species of catfishes. It may be instructive to remember that the confusion of Gosline (1975) in trying to understand the suspensorium of catfishes, is a reality for everyone who compares several catfish groups.

In the next section I will first describe the suspensorium of some siluroids with a simple quadrate: the diplomystids *Diplomystes* and *Olivaichthys*, the fossil hypsidorid *Hypsidoris*, the ictalurid *Ictalurus*, and the nematogenyid *Nematogenys*. This section is then followed by the description of fishes with a complex quadrate: the ictalurid *Noturus*, the ’pimelodids’ *Heptapterus, Rhamdia*, and *Parapimelodus*, and the schilbeid *Eutropiichthys.*

Siluroids with a simple quadrate

Diplomystids

As already established by Arratia (1987a: 25, 54, 97—99), the pterygoid series in diplomystids is variable in number and often varies between the left and right sides. Therefore, for the purposes of this paper, I have chosen *Diplomystes* specimens with a ’complete’ suspensorium and compare them with that of the Argentinean diplomystid *Olivaichthys viedmensis.*

The series of *Diplomystes* includes four specimens of *D. chilensis*, 12 cleared and stained specimens of *D. camposensis*, and six specimens of *D. nahuelbutaensis.* The specimens range from 23 mm to 210 mm standard length. The series of *Olivaichthys* examined includes five cleared and stained specimens, ranging from 28 to 206 mm.

In a 23 mm specimen of *Diplomystes*, the suspensorium is partially ossified. The autopalatine (Fig. 16A) is separate from the hyo-symplectic-pterygoquadrate plate; the partially ossified elements are still joined by large areas of cartilage. The anterior cartilage of the autopalatine is bifid anteriorly and the elongate medial projection overlaps the maxilla. A small, semi-cylindrical ectopterygoid is attached to the posteroventral part of the autopalatine. This small bone (which may or may not be present) does not have the position or relationship of the ectopterygoid of most other teleosts, and I therefore described it as an additional pterygoid (Arratia 1987a). However, upon studying more material (particularly of *Chanos* and *Xenocharax*) I must accept that this element is a reduced ectopterygoid. This is because the ectopterygoid in primitive ostariophysans and diplomystids is partially or mostly ventral to the autopalatine (see Figs. 4D, 10A). Another small, rudimentary pterygoid (which may or may not be present) arises as a cup-like dermal ossification around the distal part of the cartilaginous, rod-like autopalatine. This ossification is interpreted here as the entopterygoid through comparison with the entopterygoid in gonorynchiforms, cypriniforms, and characiforms.

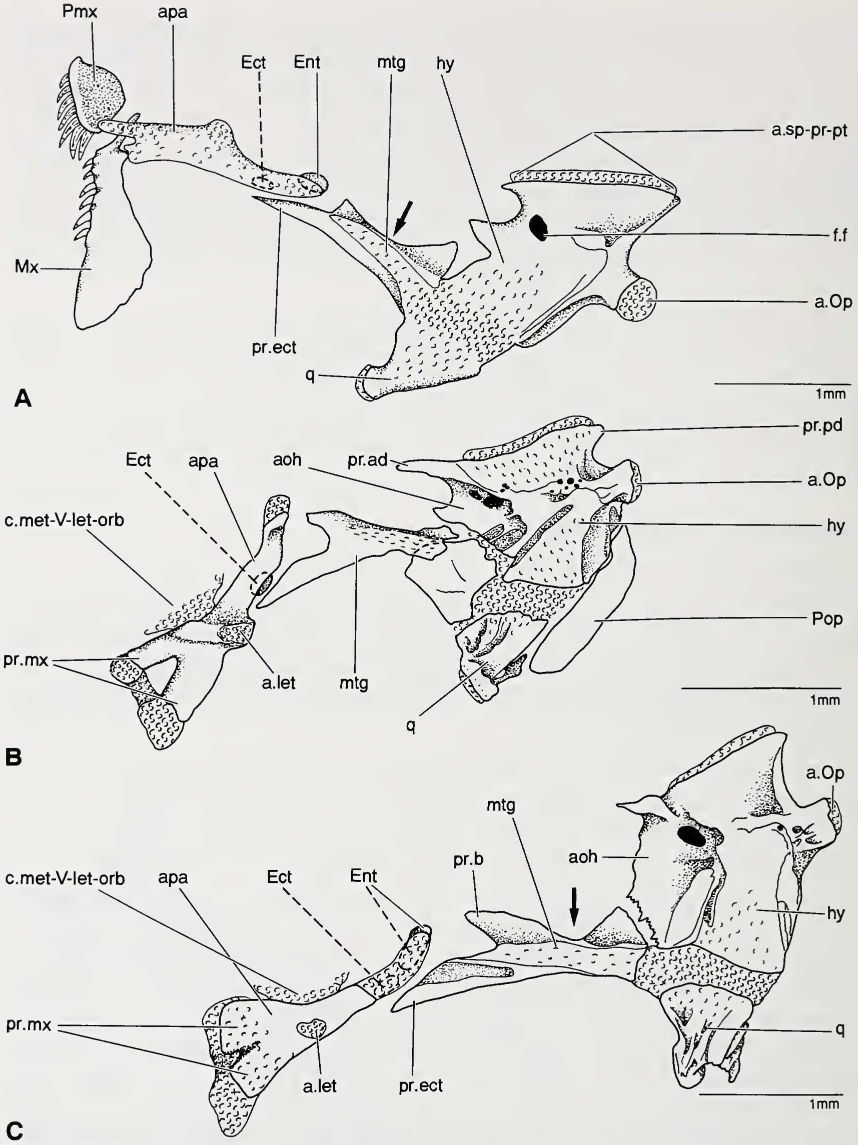

Fig.16: Suspensoria of diplomystids, lateral view. — A: *Diplomystes nahuelbutaensis* (23 mm standard length; PC 230186); B: *Diplomystes camposensis* (28 mm standard length; after Arratia 1987); C: *D. camposensis* (about 29 mm standard length; after Arratia 1987). Arrows point to a notch.

apa: autopalatine; a.let: articular facet for lateral ethmoid; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; a.sp-pr-pt: articular facet for sphenotic, prootic, and pterotic; apa: autopalatine; c. met-V-let-orb: cartilage joining mesethmoid, vomer, lateral ethmoid, and orbitosphenoid; Ect: ectopterygoid; Ent: entopterygoid; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mtg: metapterygoid; Mx: maxilla; Pop: preopercle; pr.ad: processus anterodorsalis; pr.b: processus basalis; pr. ect: processus ectopterygoideus; Pmx: premaxilla; pr.mx: processus maxillaris; pr.pd: processus posterodorsalis; q: quadrate.

The metapterygoid is elongate, with a central rod of ossifying cartilage, and with a well ossified, elongate processus ectopterygoideus. Medially, the bone is thinly ossified. There is a slight notch separating the sharp, short processus basalis from the posterodorsal flange of the bone. Metapterygoid, quadrate, and hyomandibula are broadly joined by cartilage of the hyo-symplectic-pterygoquadrate plate.

The simple, triangular quadrate is mainly ossified at its condylar articular facet with the lower jaw, and posteroventrally, at the articular facet with preopercle.

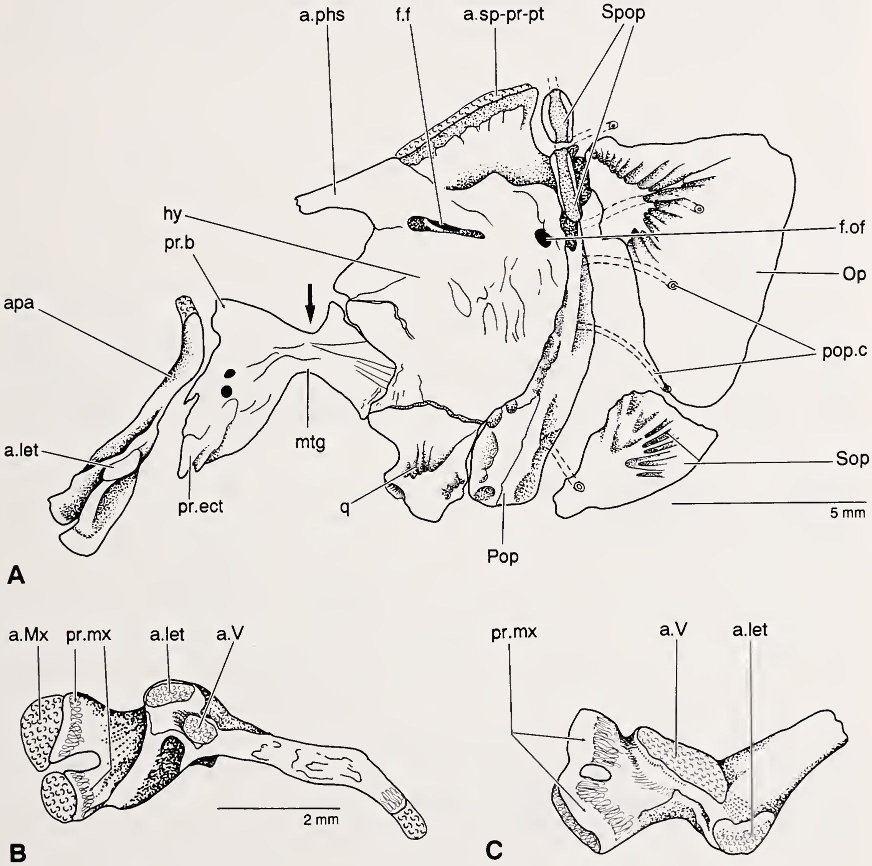

Fig.17: Suspensorium in diplomystids (after Arratia 1987a). — A: Suspensorium of *Diplomystes camposensis*, lateral view; note the absence of entopterygoid and ectopterygoid; B: Autopalatine of *D. camposensis*, right side, dorsal view; C: Autopalatine of *D. chilensis*, left side, dorsal view. Arrow points to a notch.
a.let: articular facet for lateral ethmoid; a.Mx: articular facet for maxilla; apa: autopalatine; a.phs: articular facet for pterosphenoid; a.V: articular facet for vomer; a.sp-pr-pt: articular facet for sphenotic, prootic, and pterotic; f.f: foramen for passage of hyoideomandibular nerve trunk; f.rop: foramen for ramus opercularis; hy: hyomandibula; mtg: metapterygoid; Op: opercle; Pop: preopercle; pop. c: preopercular canal; pr.b: processus basalis; pr.ect: processus ectopterygoideus; pr.mx; processus maxillaris; q: quadrate; Sop: subopercle; Spop: suprapreopercle.

The hyomandibula is a broad bone, with a long articular facet covered with cartilage and articulating with the sphenotic and pterotic. A small, short, sharp, membranous outgrowth extends anteriorly. Posteriorly, there is an elongate, massive opercular process and an elongate sutural surface at the posterolateral margin of the hyomandibula, below the opercular process. A small levator arcus palatini crest is present close to the posterior margin of the bone. A single foramen for both the entrance and exit of the facial nerve pierces the bone, close to the anterodorsal corner of the hyomandibula.

In a 28 mm specimen of *D. camposensis*, there is a large bone (Fig. 16B) on both sides of the body between the hyomandibula, quadrate, and metapterygoid and it was identified as ?metapterygoid by Arratia (1987a: 54, Fig. 25A). Based on my more recent

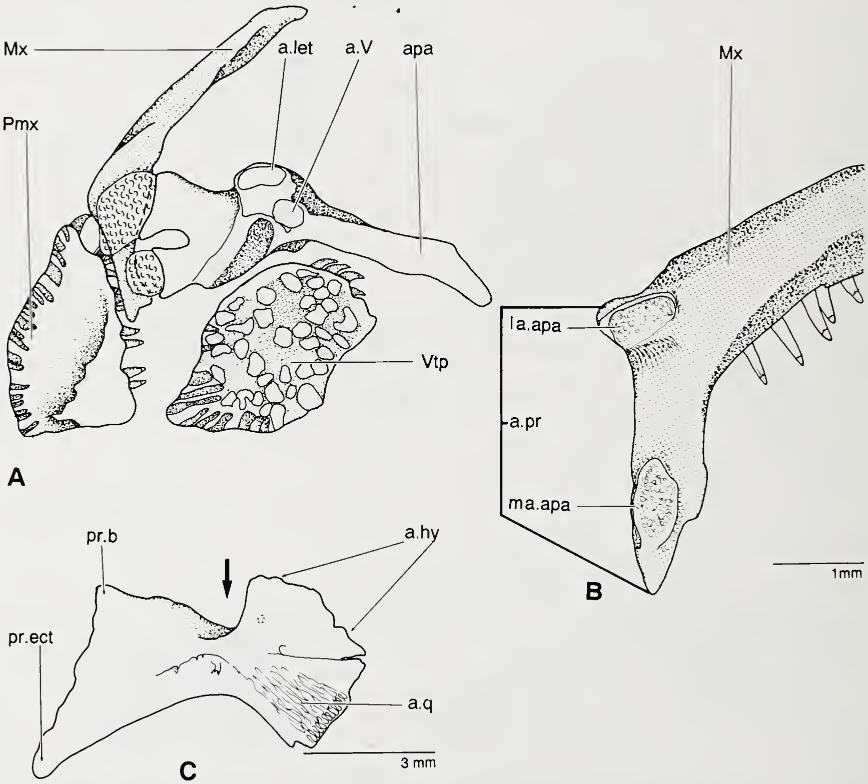

Fig.18: Elements of the suspensorium and maxilla in diplomystids. — A: Autopalatine and surrounding bones in *Diplomystes camposensis*, dorsal view (after Arratia 1987a); B: Anterior part of maxilla in *D. nahuelbutaensis* (CAS-SU 55425); C: Metapterygoid in *D. nahuelbutaensis*, lateral view (CAS-SU 55425). Arrow points to a notch.

a.let: articular facet for lateral ethmoid; a.hy: articular surface for hyomandibula; apa: autopalatine; a.pr: articular process of maxilla; a.q: articular surface for quadrate; a.V: articular facet for vomer; la.apa; lateral articular facet for autopalatine; ma.apa: medial articular facet for autopalatine; Mx: maxilla; Pmx: premaxilla; pr. b: processus basalis; pr.ect; processus ectopterygoideus; Vtp: vomerine toothplate.

comparative studies, I now consider this element as a result of a fracture of the hyosymplectic-pterygoquadrate plate, which has grown as a separate element. This fractured piece may be part of the metapterygoid by origin or part of the anterior membranous outgrowth of the hyomandibula. In a 29 mm specimen of *D. camposensis*, all of the bones of the suspensorium are well ossified but retain large areas of cartilage at the anterior and posterior tips (Fig. 16C) of the autopalatine, and within the hyomandibula, quadrate, and metapterygoid.

The main changes observed in specimens ranging between 24 and 29 mm length are the increase in the ossification, the loss of contact between the anterior cartilage of the autopalatine and the premaxilla, the enlargement of the membranous outgrowth of the hyomandibula, and the development of the levator arcus palatini crest (Fig. 16A—C).

In large specimens of *Diplomystes*, the autopalatine (Figs. 17A, B, 18A, 19A, B) is an elongate, somewhat sigmoidal bone that is more broad anteriorly than posteriorly. Anteriorly, this bone has two articular maxillary processes (Figs. 17B, 19A, B) that may fuse to produce a single elongate articular facet (Fig. 17C). When the two processes are separate, the lateral one is slightly broader than the medial one. The maxillary processes of the autopalatine articulate with two small processes of the maxilla that bear articular facets on the maxilla (Fig. 19B). The anterior fibrocartilage(s) of the autopalatine is lateral to the premaxilla. Dorsally, the autopalatine may have a crest ending in the articular process for the lateral ethmoid, which is dorsolateral. The vomerine process of the autopalatine is dorsomedial; it has an elongate, ovoid articular facet in *Diplomystes chilensis* (Fig. 17C), whereas the facet is comparatively smaller in *D. camposensis* (Fig. 17B).

The posterior part of the autopalatine (Figs. 17B, C, 18A) is elongate — longer than the anterior portion — in *Diplomystes camposensis*, and comparatively shorter in *D. chilensis* and *D. nahuelbutaensis*. The posterior part (Fig. 18A) is directed medially, and does not overlap the metapterygoid as it does in most siluroids (see below). The posterior fibrocartilage of the autopalatine is elongate and oval shaped and the entopterygoid (when present) fits onto the posteroventral part of this fibrocartilage via connective tissue. I have not seen any ligaments uniting the posterior part of the autopalatine with the neurocranium.

The ectopterygoid (Figs. 19A, B) — when present — is a small, oval, thin, plate-like bone firmly attached by connective tissue to the posteroventral part of the autopalatine. The entopterygoid (Fig. 19A, B) is a cup-like bone partially surrounding the posteroventral end of the autopalatine and in addition to the cup-like part, a small oval plate of thin bone extends posteriorly.

The metapterygoid (Figs. 17A, 18C) is strongly ossified and has a complex shape. The bone is markedly notched dorsally and ventrally, therefore it is broader at both ends than in the mid-section. The anterior portion projects medially as a sharp processus basalis, and projects laterally in a sharp, broad ectopterygoid process. This process occupies the position of the ectopterygoid in other teleosts. Anteriorly, there is a short ligamentous connection between the ectopterygoid process and the autopalatine, and the processus basalis is connected by ligaments mainly to the vomer but also to the

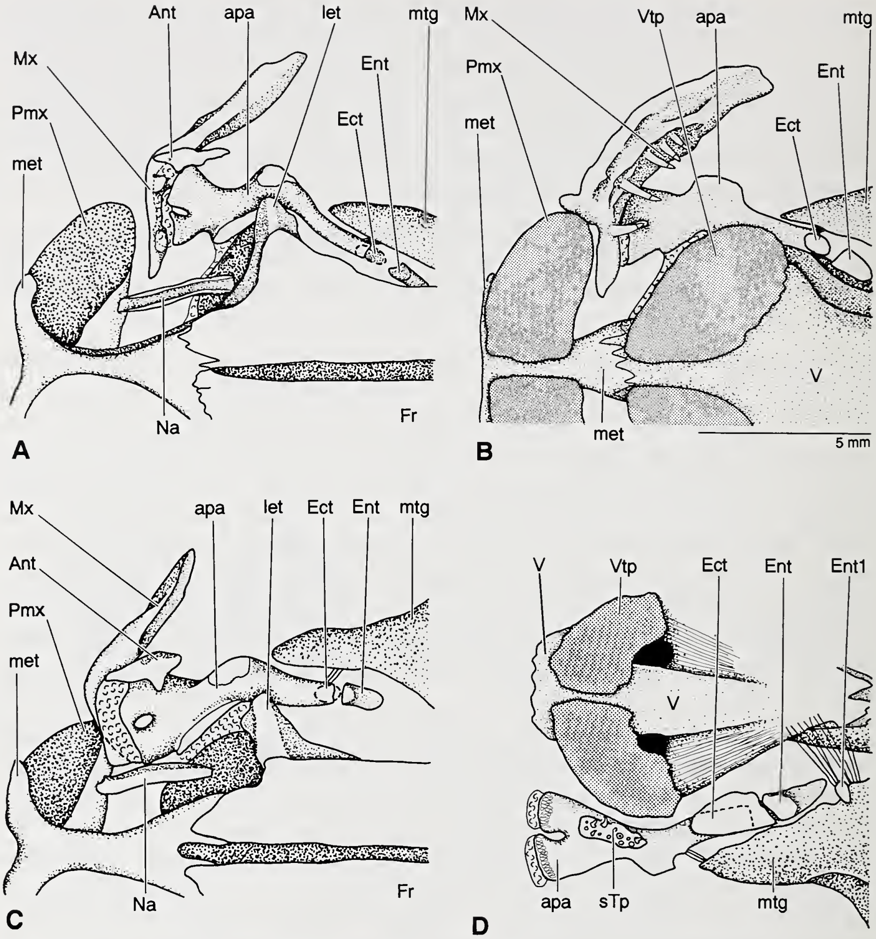

Fig.19: Autopalatine and surrounding bones in diplomystids. — A: *Diplomystes camposensis*, dorsal view; B: *D. camposensis*, ventral view; C: *Olivaichthys viedmensis*, dorsal view (FMNH 58004); D: *O. viedmensis*, ventral view (PC 20279). A—D, same scale.
Ant: antorbital; apa: autopalatine; Ect: ectopterygoid; Ent: entopterygoid; Ent1: 'entopterygoid' type 1; Fr: frontal; let: lateral ethmoid; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Na: nasal; Pmx: premaxilla; sTp: subautopalatine toothplate; V: vomer; Vtp: vomerine toothplate.

parasphenoid. Posteriorly, the metapterygoid is mainly sutured (sutura limbata) to the hyomandibula. However, it also synchondrally articulates with the quadrate and symplectic cartilage. In some large specimens the symplectic cartilage is almost gone. Grande (1987: 35) reported the presence of "what appears to be a large foramen" in the metapterygoid of one diplomystid specimen and in †*Hypsidoris*; I did not find this foramen in the diplomystid specimens I examined, but there are a variable number of

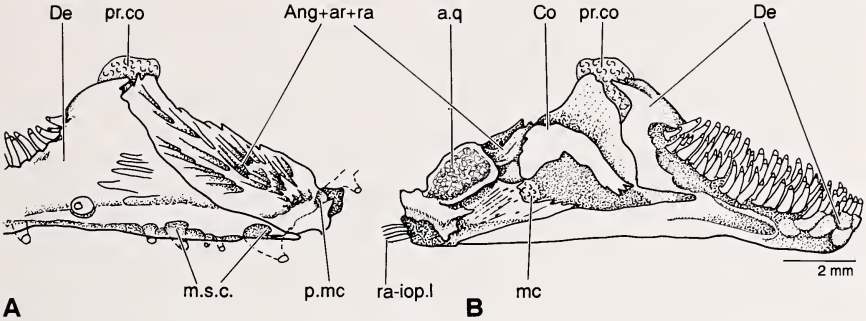

Fig.20: Lower jaw of *Diplomystes camposensis* (slightly modified from Arratia 1987a). — A: Posterior part, lateral view; B: Medial view.
Ang+ar+ra: angular, articular, and retroarticular fused; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; mc: Meckelian cartilage; m.s.c.: mandibular sensory canal; p.mc: posterior opening of the mandibular sensory canal; pr.co: cartilaginous coronomeckelian process; ra-iop.l: retroarticular-interopercular ligament.

small foramina that may be present or completely absent within species. It seems likely then, that Grande simply described yet another variant.

The quadrate (Figs. 14A, B, 17A) is short, compact, and lacks the chondral or membranous pterygoid process described for other siluroids (Arratia 1990a), as well as the membranous posterior process present in other ostariophysans. Anteroventrally, the quadrate articulates through a slightly convex surface (it is not a true condyle) with the articular portion of the angulo-articulo-retroarticular (Fig. 20A, B; Arratia 1987a: Figs. 7A—C, 15A, C, 26A—F); however, an additional articular facet may be found in some large individuals (Arratia 1987a: Fig. 26E). Anterodorsally, the quadrate articulates through a short synchondral joint with the metapterygoid. Dorsally, the quadrate articulates with the hyomandibula through the symplectic cartilage and posteroventrally the quadrate is sutured with the preopercle.

In large specimens, the hyomandibula (Figs. 14A, B, 17A) is a broad, short bone whose anterior membranous outgrowth is large and well ossified. The dorsal margin of the membranous outgrowth of the hyomandibula forms the processus anterodorsalis which extensively articulates (bone-to-bone) with the pterosphenoid. This bone-to-bone articulation may be longer than the cartilaginous articular facet for the autosphenotic, prootic, and pterotic, resulting in a remarkably long syndesmotic joint between the processus anterodorsalis of the hyomandibula and the pterosphenoid. Arratia (1987a) considered this double articulation (diarthrosis and syndesmosis) of the hyomandibula with the pterosphenoid, sphenotic, prootic, and pterotic as an advanced feature of the Diplomystidae within the Siluroidei.

The hyomandibula articulates ventrally with a thick symplectic cartilage and anteriorly with the quadrate through a short dentate suture. The dentate suture is so short that it may be represented by only one or two indentations. The metapterygoid overlaps the hyomandibula through a wide lateral articulation over the anterior membranous outgrowth of the hyomandibula producing a lap joint or sutura limbata. Posteriorly, the hyomandibula articulates with the opercle through the opercular process, and the hyomandibula is sutured to the dorsal limb of the preopercle. On its medial face, the hyomandibula has a small area for the attachment of the first pharyngobranchial; the pseudobranch is almost vertical to the anterior membranous outgrowth.

The levator arcus palatini crest, horizontal to the lateral face of the hyomandibula, is well-developed in *Diplomystes chilensis* and *D. nahuelbutaensis*, whereas is rudimentary in *D. camposensis* (Arratia 1987a: Figs. 6B, 16, 25D). The development of the crest results in different patterns of exit of the hyoideomandibular nerve trunk (Fig. 21A, B) on the lateral surface of the bone. This nerve pierces the hyomandibula medially, and runs a short distance through the bone to exit just ventral to the levator arcus palatini

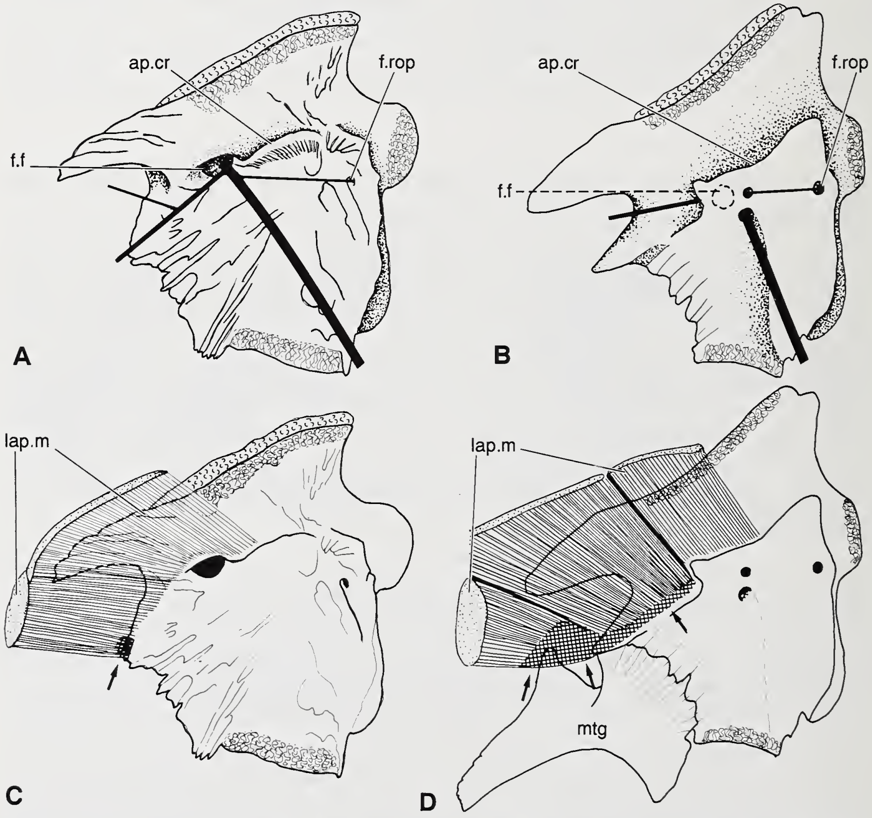

Fig.21: Hyoideomandibular nerve trunk and levator arcus palatini muscle and its tendinous attachment (indicated by arrows) in diplomystids. — A: Trajectory of the hyoideomandibular nerve trunk on the lateral aspect of hyomandibula in *Diplomystes camposensis* (after Arratia 1987a); B: Trajectory of the hyoideomandibular nerve trunk in *D. chilensis* (after Arratia 1987a); C: Levator arcus palatini muscle in *D. camposensis* (PC 220189); D: Levator arcus palatini muscle in *D. chilensis* (CAS-SU 13706).
ap.cr: levator arcus palatini crest; f.f: foramen for passage of hyoideomandibular nerve trunk; f.rop: foramen for ramus opercularis; lap.m: levator arcus palatini muscle; mtg: metapterygoid.

crest in *D. nahuelbutaensis*. It then branches into the ramus hyomandibularis, the ramus opercularis, and an anterior ramus that bifurcates into a small ramus innervating the levator arcus palatini muscle, and another ramus that runs anteriorly and may innervate the lateral portion of the eye and/or the skin. In *D. chilensis*, the facial nerve bifurcates inside the levator arcus palatini crest, therefore the ramus hyoideomandibularis and ramus opercularis have separate exits. In *D. camposensis*, the lateral opening of the hyoideomandibular nerve trunk is exposed, because the levator arcus palatini crest is rudimentary. The ramus opercularis runs posteriorly, pierces the hyomandibula and exits posteromedially to innervate the opercle. The hyoideomandibular nerve trunk runs laterally and may penetrate the hyomandibula at its posteroventral corner and exit medially, or it may just run through a small foramen between the hyomandibula, quadrate and preopercle.

In addition to the differences in the size of the levator arcus palatini crest and arcus palatini process, there are differences in the development of the levator arcus palatini muscle. In *Diplomystes camposensis*, which has a rudimentary crest and process, the muscle (Fig. 21C) is thin and has a small tendinous attachment to the levator arcus palatini process. The muscle inserts on the sphenotic and frontal, but not on the lateral ethmoid. In addition, the levator arcus palatini muscle of *D. camposensis* has two sections weakly distinguishable laterally. In contrast, three sections are observed in *D. chilensis* (Fig. 21D), the anteriormost one is well-developed, thick, and tendinously attached to the levator arcus palatini process of the hyomandibula and metapterygoid; the other two sections are thin and attached at the dorsal margin of the levator arcus palatini crest; the insertion of the muscle is similar to that of *D. camposensis*.

The suspensorium of *Olivaichthys viedmensis* has the same general pattern of that of *Diplomystes*. Some differences are as follows. The autopalatine of *Olivaichthys* bears one or two large articular fibrocartilage surfaces anteriorly that reach the posterolateral corner of the premaxilla (Fig. 19C, D); both bones are linked by a short piece of connective tissue. A small, flat, 'entopterygoid' type 1 is present anteromedial to the dorsomedial process of the metapterygoid in a single specimen. I have not observed a subautopalatine toothplate in young specimens, but in large specimens a patch (or patches) with conical teeth enlarges throughout growth (although it sometimes may be absent); this toothplate is not fused to the autopalatine. Only in one specimen of *Diplomystes chilensis* did Arratia (1987a: 24) observe a small subautopalatine toothplate with six conical teeth.

The ligamentous connections among the bones of the suspensorium of diplomystids may vary (Arratia 1987a: 26); nevertheless, the following ligaments are observed: there is a ligament connecting the quadrate, autopalatine, and maxilla as in other catfishes (see below) that in diplomystids joins the ligamentum primordiale and inserts broadly on the posteromedial face of the maxilla. The dorsomedial part of the processus basalis of the metapterygoid is linked through a broad ligament to the vomer (mainly) and also to the parasphenoid. A short ligament extends between the ectopterygoid process of the metapterygoid and the autopalatine (ligament 17 of Ghiot et al. 1984). The 'entopterygoid' type 1 — when present — lacks ligamentous connections with the lateral ethmoid, orbitosphenoid, and autopalatine (Figs. 2A, 19D); but is linked to the vomer. Anteriorly, the autopalatine is joined by short ligaments and/or connective tissue to the antorbital laterally and lateral ethmoid medially. In its middle region, the autopalatine is ligamentously linked to the metapterygoid and quadrate, and posteriorly to the orbitosphenoid.

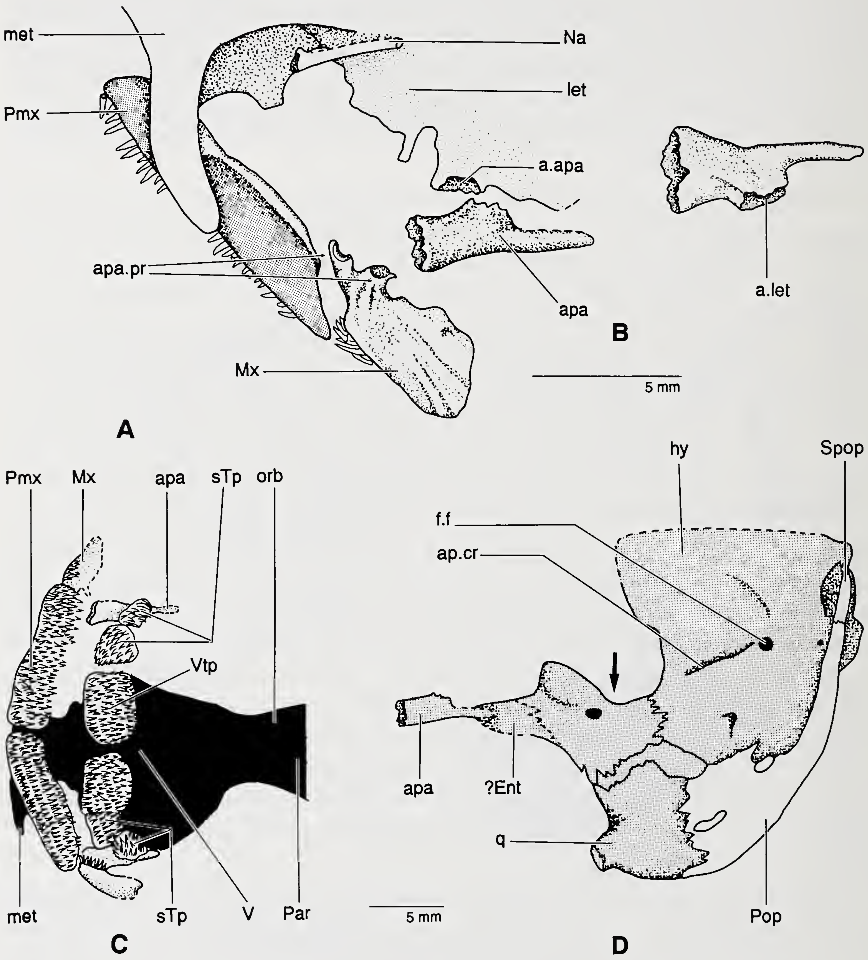

Fig.22: Suspensorium of †*Hypsidoris farsonensis* (after Grande 1987). — A: Dorsal view of autopalatine, maxilla, and premaxilla; B: Dorsal view of the autopalatine; C: Autopalatine and surrounding bones, ventral view; D: Restoration of the suspensorium, lateral view. Arrow points to a notch.
a.apa: articular facet for autopalatine; a.let: articular facet for lateral ethmoid; apa: autopalatine; apa.pr: autopalatinal process; ap.cr: levator arcus palatini crest; ?Ent: ?entopterygoid; hy: hyomandibula; let: lateral ethmoid; met: mesethmoid; Mx: maxilla; Na: nasal; orb: orbitosphenoid; Par: parasphenoid; Pop: preopercle; Pmx: premaxilla; q: quadrate; Spop: suprapreopercle; sTp: subautopalatine toothplate; V: vomer; Vtp: vomerine toothplate.

†Hypsidorids

The description of the suspensorium of †*Hypsidoris farsonensis* from the Eocene of the Green River Formation is based on Grande's (1987) reconstruction and my reinterpretation of some of his characters.

The autopalatine (Fig. 22A, B) is expanded anteriorly to probably form two articular facets for articulation with the two facets of the maxilla. Although the double articulation between the maxilla and autopalatine is also present in diplomystids (compare Figs. 18A, B, 19A—C, 22A), †*Hypsidoris* lacks the long anterior maxillary process that completely separates the autopalatine from the premaxilla in diplomystids. The autopalatine of †*Hypsidoris* (Fig. 22C), like that of *Olivaichthys*, may have reached the posterolateral corner of the premaxilla. The posterior part of the autopalatine — unlike that of diplomystids and nematogenyids — seems to be dorsal to the entopterygoid (Fig. 22D) and not medial to the metapterygoid. Grande (1987: Fig. 4) illustrated the autopalatine as bearing an articular facet for the lateral ethmoid; it is unknown though, whether the autopalatine of †*Hypsidoris* also articulated with the vomer. Two small subautopalatine toothplates (named as accessory ectopterygoid toothplates by Grande 1987) are present. One is ventral to the autopalatine, the second is between the ventral part of autopalatine and the lateral margin of the vomer (Fig. 22C).

A small, slightly elongate entopterygoid is present. The entopterygoid has been interpreted by Grande (1987) as probably being sutured with the metapterygoid. This condition is unlikely, when you compare it with other primitive siluroids. In large ictalurids and some pimelodids (see below) the entopterygoid and metapterygoid may be close to each other and become indented or serrated, but they are linked to each other by a ligament. With the available information, I am unable to establish whether this entopterygoid is a dermal or a sesamoid pterygoid as found in extant siluroids above the level of the Diplomystidae.

Grande (1987) could not find an ectopterygoid in †*Hypsidoris* and he expected that it could be hidden by other bones. I hypothesize that †*Hypsidoris* does not have an ectopterygoid.

The metapterygoid (Fig. 22D) is a slightly rectangular bone which bears a pronounced processus basalis that is separated by a deep notch from the posterodorsal part of the bone as in diplomystids, but it is missing the ectopterygoid process found in diplomystids and other primitive siluroids (compare Figs. 17A, 19C, 22D). Another possibility is that the bone labelled by Grande (1987) as the entopterygoid, is really the broken ectopterygoid process of the metapterygoid.

It is unclear whether †*Hypsidoris* has a simple or complex quadrate, because small individuals have not been studied. The quadrate of †*Hypsidoris* is similar in shape to that of adult *Pylodictis*; although the quadrate of *Pylodictis* develops a small projection anteriorly during ontogeny, the origin of the bone is similar to the simple quadrate in diplomystids, ictalurids, and nematogenyids. With the available information, I therefore hypothesize that †*Hypsidoris* has a simple quadrate.

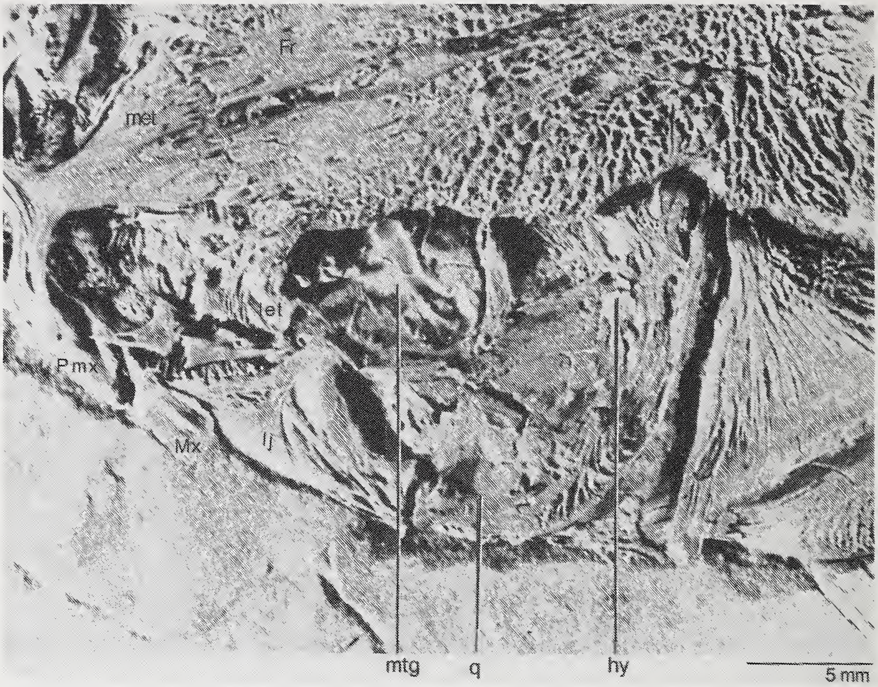

Fig.23: Head of †*Hypsidoris farsonensis*, dorsolateral view (Peel of holotype PU 20570a).
Fr: frontal; hy: hyomandibula; let: lateral ethmoid; lj: lower jaw; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Pmx: premaxilla; q: quadrate.

The large hyomandibula (Figs. 22D, 23) is incompletely known; its dorsal margin is covered by other bones in specimens studied by Grande (1987). The levator arcus palatini crest is smaller than in diplomystids and closer to the anteroventral portion of the bone than the dorsal portion (compare Figs. 14B, 21A, B, 22D). The facial nerve runs through a canal inside the bone according to Grande's restoration (1987). This would be different than diplomystids (compare Figs. 21A, B, 22D), and is remarkably curious because there is a visible lateral foramen for the facial nerve in the hyomandibula.

Ictalurids

The development of the suspensorium of catfishes with a simple quadrate is based on a detailed description of *Ictalurus punctatus*. The series of *I. punctatus* examined included 146 cleared and stained specimens, ranging from 6 mm total length through 65 mm standard length, in addition to numerous large individuals prepared as dry skeletons and cleared and stained material.

In 6 mm total length specimens (one day after hatching), the elements of the suspensorium (Fig. 24A) as well as those of the branchial arches are cartilaginous. The pars autopalatina is a large plate of cartilage bearing the maxillary barbel laterally. The maxillary barbel is not preformed in hyaline cartilage, and the position and distribution of its cellular elements differs from the cartilaginous areas of the suspensorium. The pars autopalatina and the hyo-symplectic-pterygoquadrate plate are broadly separated from each other. The hyo-symplectic-pterygoquadrate plate is synchondrotic with the ventral portion of the hyoid arch, as well as the Meckelian cartilage, and the endocranium. The

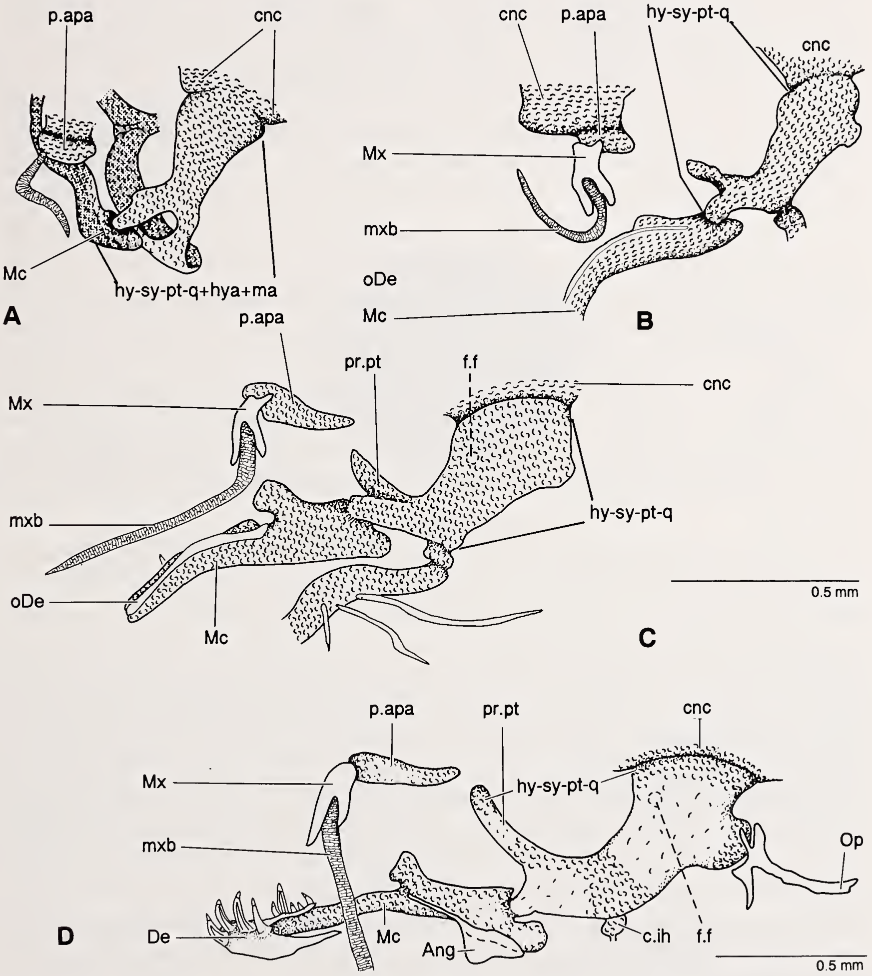

Fig.24: Sequence of the development of the suspensorium in *Ictalurus punctatus*, lateral view (KU uncat.). — A: 6 mm total length; B: 7 mm total length; C: 8.5 mm total length; D: 9 mm total length. A—C same scale. Ang: angular; De: dentary; c.ih: cartilaginous interhyal; cnc: cartilaginous neurocranium; f.f: foramen for passage of hyoideomandibular nerve trunk; hy-sy-pt-q: hyo-symplectic-pterygoquadrate plate; hy-sy-pt-q+hya+ma; hyo-symplectic-pterygoquadrate plate synchondrotic with the ventral limb of hyoid arch and mandibular arch; mc: Meckelian cartilage; Mx: maxilla; mxb: maxillary barbel; oDe: ossification center of dentary; Op: opercle; p.apa: pars autopalatina; pr.pt: processus pterygoideus.

hyo-symplectic-pterygoquadrate plate has a short anterior cartilaginous pterygoid process.

In 7 mm total length specimens (two days after hatching), a well ossified, small maxilla (Fig. 24B) articulates laterally with the pars autopalatina; the maxillary barbel is associated with the maxilla. There are changes in the cartilage of the areas where the articulation for quadrate and articular bone and hyomandibula and interhyal will form; there is a small cartilaginous opercular process in the dorsoposterior margin of the hyo-symplectic-pterygoquadrate plate and the pterygoid process is more elongate. Still the Meckelian cartilage forms one unit anteriorly, but it is not synchondrotic with the hyoid arch as it is in trichomycterids (Arratia & Schultze 1990: Fig. 15A—D). At this stage, the Meckelian cartilage develops a dorsal process which I identified as the coronoid cartilage in diplomystids (Arratia 1987a); there is a long, thin, and narrow dermal ossification above and lateral to the Meckelian cartilage; this corresponds to the dentary.

In 8.5 to 9 mm total length (3 or 4 days after hatching), the anterior part of the elongate pars autopalatina (Fig. 24A, B) has expanded medially and lies ventral to the endocranium, in the region where the future lateral ethmoid will form. At this stage, the pars autopalatina appears synchondrotic with the ethmoidal region in some specimens, whereas both parts are separate in other specimens (Fig. 24C—D). The main changes are the growth of the pars autopalatina and pars pterygoquadrata, resulting in these elements becoming closer. The coronoid process of the Meckelian cartilage enlarges considerably, as does the dentary (which bears one or a few teeth). Three slender, ossified, branchiostegal rays are associated with the cartilaginous ventral portion of the hyoid arch.

In 10 to 10.5 mm total length (5 days after hatching) there are significant changes in the structure of the hyo-symplectic-pterygoquadrate plate. Although only a single cartilaginous element is observed, the regions of the future metapterygoid, hyomandibula, and quadrate (Fig. 25A) are identifiable because of the change in density of the cartilaginous cells. This change in density is also true of the future articular bone in the Meckelian cartilage. The pars autopalatina and pars pterygoquadrata continue their elongation and become closer to each other. The pars autopalatina is separate from the ethmoidal cartilage. Similarly, the hyomandibular region is separate from the endocranial cartilage. There is complete separation between the pars pterygoquadrata and the Meckelian cartilage, and between the interhyal cartilage and the hyo-symplectic-pterygoquadrate plate. The retroarticular begins to ossify at the posterior margin of the Meckelian cartilage; the symphyseal articulation separating the Meckelian cartilage into left and right elements is formed. The dentary enlarges considerably, to produce two processes posteriorly, the coronoid process and the long posteroventral process, which is closer to the retroarticular.

In 11.7—12 mm standard length (7 days after hatching) the main change is the beginning of the ossification of the autopalatine. A small 'entopterygoid' appears between 12 and 13 mm standard length (about 9 days after hatching). The bone begins to form in the rod of connective tissue that links the metapterygoid, lateral ethmoid, vomer, and autopalatine. At this stage, the hyomandibula and quadrate begin to be finely,

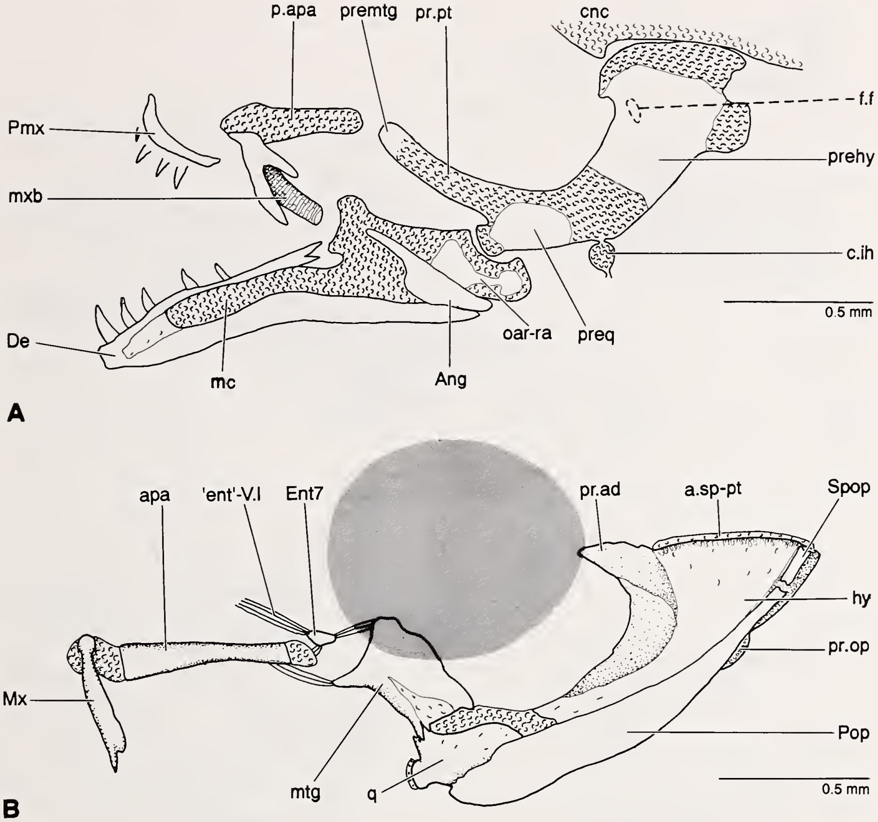

Fig.25: Suspensorium of *Ictalurus punctatus*, lateral view (KU uncat.) and position of eye (dotted area). — A: 10 mm standard length; B: 54 mm standard length.
Ang: angular; apa: autopalatine; a.sp-pt: articular facet for sphenotic and pterotic; c.ih: cartilaginous interhyal; cnc: cartilaginous neurocranium; De: dentary; Ent7: 'entopterygoid' type 7; 'ent'-V.l: 'entopterygoid'-vomer ligament; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mc: Meckelian cartilage; mtg: metapterygoid; Mx: maxilla; mxb: maxillary barbel; oar-ra: ossification center of articular and retroarticular; p.apa: pars autopalatina; prehy: preformed hyomandibula; premtg: preformed metapterygoid; preq: preformed quadrate; Pmx: premaxilla; Pop: preopercle; pr.ad: processus anterodorsalis; pr.op: processus opercularis; pr. pt: processus pterygoideus; q: quadrate; Spop: suprapreopercle.

perichondrally ossified. Between 14 and 15.5 mm standard length all of the bones of the suspensorium are ossified despite the presence of large cartilaginous areas between them. From this stage on, the main changes are related to the ossification of the bones, and the appearance of ligaments replacing the connective tissue between 'entopterygoid' and metapterygoid, the 'entopterygoid' and the lateral ethmoid (ligament 2 of Ghiot et al. 1984), the 'entopterygoid' and the vomer, and 'entopterygoid' and autopalatine. In addition, the metapterygoid is linked to the lateral ethmoid (ligament 18 of Ghiot et al. 1984).

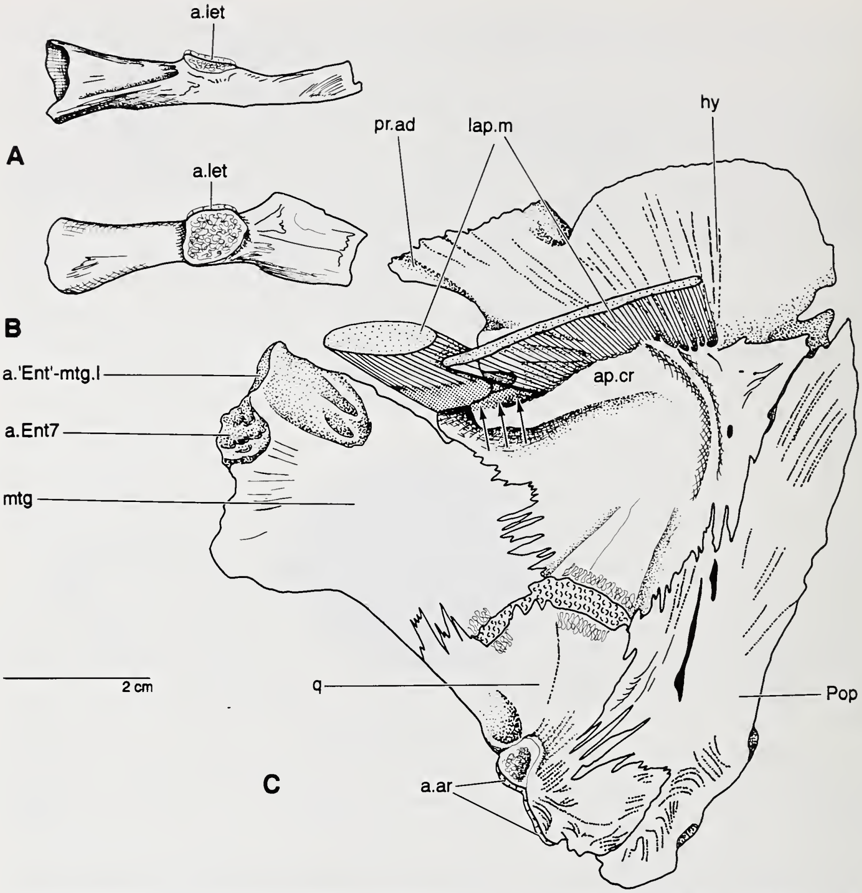

Fig.26: Suspensorium of *Ictalurus punctatus* (KU 21429). — A: Autopalatine, left side, dorsal view; B: Autopalatine, medial view; C: Posterior part of the suspensorium, levator arcus palatini muscle and its tendinous area (indicated by arrows), and preopercle.
a. ar: articular facet for articular; a.Ent7: sutural surface for 'entopterygoid' type 7; a.'Ent'-mtg.l: attachment surface for 'entopterygoid'-metapterygoid ligament; a.let: articular facet for lateral ethmoid; ap.cr: levator arcus palatini crest; hy: hyomandibula: lap.m: levator arcus palatini muscle; mtg: metapterygoid; Pop: preopercle; pr.ad: processus anterodorsalis; q: quadrate.

In specimens of about 50 mm length and larger (Figs. 25B, 26A—C) the autopalatine — which is rod-like — articulates with the lateral ethmoid. The 'entopterygoid' enlarges and gets closer to the metapterygoid; such that both bones may suture during growth. The arcus palatini process of the hyomandibula is well ossified and large. The levator arcus palatini muscle, divided into two sections of different sizes, attaches to the process and the levator arcus palatini crest; and this muscle inserts onto the autosphenotic and frontal.

The anterior part of the suspensorium in ictalurids has interesting differences between species. The highest number of ligamentous connections of the 'entopterygoid' is found

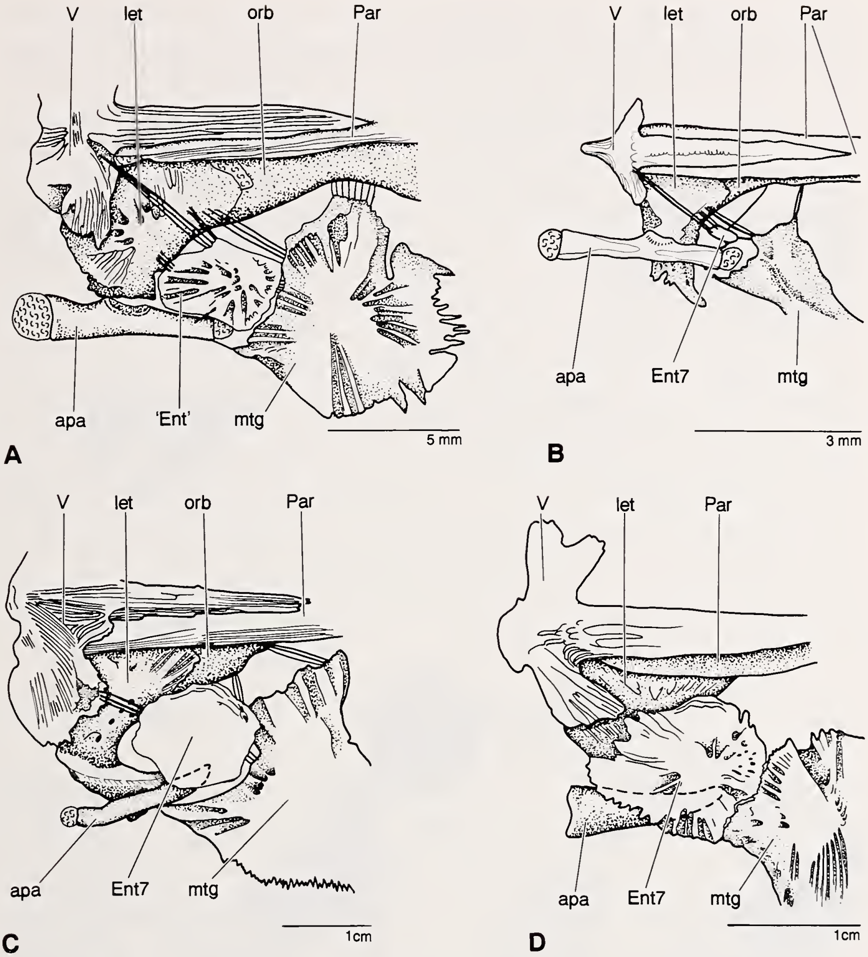

Fig.27: Anterior part of the suspensorium in ventral view of some ictalurids. — A: *Ameiurus melas* (135 mm standard length; KU 103843); B: *Ictalurus punctatus* (59 mm standard length; KU 9657); C: *Pylodictis olivaris* (KU 1746, KU 10414, and KU 15697); D: *Ictalurus furcatus* (81 mm standard length; KU 21381); ligaments omitted.
apa: autopalatine; 'Ent': 'entopterygoid'; Ent7: 'entopterygoid' type 7; let: lateral ethmoid; mtg: metapterygoid; orb: orbitosphenoid; Par: parasphenoid; V: vomer.

in *Ameiurus melas* (Fig. 27A); a high number is also found within the ictalurids (type 7). An 'entopterygoid' is missing in *Prietella* (Lundberg 1982). The 'entopterygoid' is in close contact with the metapterygoid, vomer, and lateral ethmoid in some individuals of *Ictalurus* and *Pylodictis*; it may even be sutured to the metapterygoid and vomer in large specimens. Another difference is that in *Ameiurus, Ictalurus*, and *Pylodictis* (Fig. 27A—C), the autopalatine does not extend dorsal to the metapterygoid, but only dorsal to the 'entopterygoid'; whereas in *Noturus* the autopalatine extends dorsal to the metapterygoid — the condition commonly found in siluroids (see below). A well-developed lateral process is lateral to the metapterygoid in *Pylodictis* and some species of *Ictalurus*; in these species, the levator arcus palatini muscle also attaches on the lateral process of the metapterygoid.

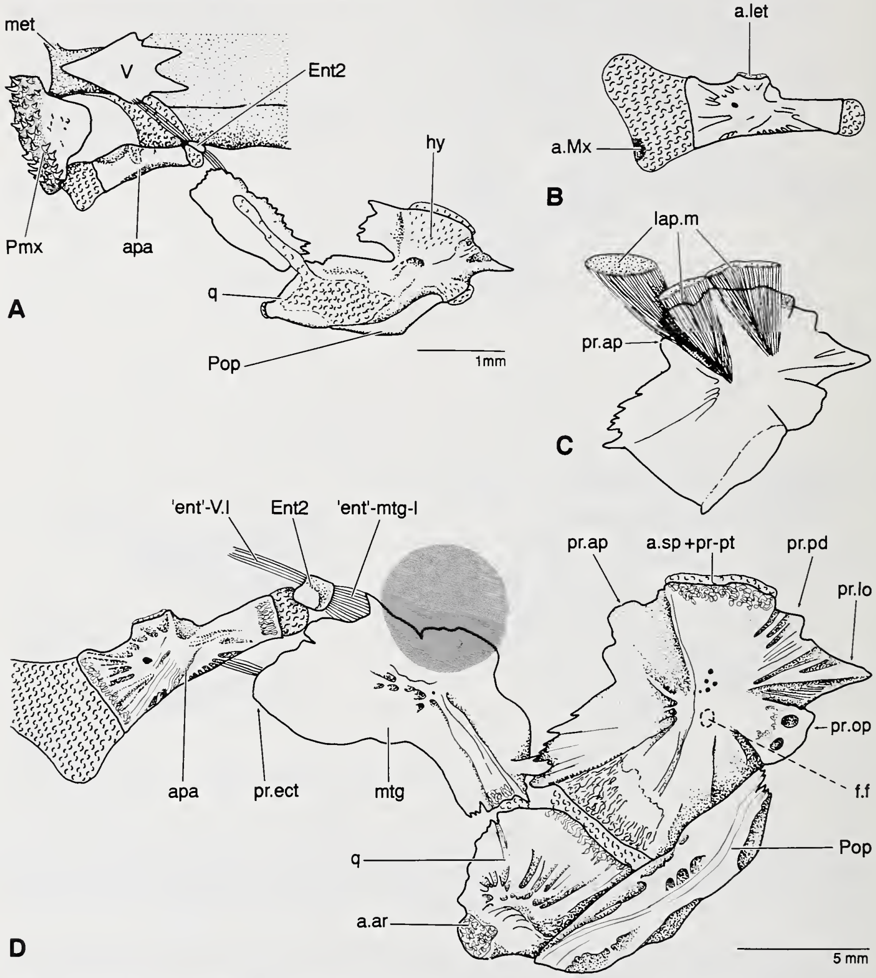

Fig.28: Suspensorium of *Nematogenys inermis*; dotted area represents the position of eye. — A: Suspensorium, ventral view (31.8 mm standard length; PC 131); B: Autopalatine, left side, dorsal view (about 200 mm; PC 30873); C: Insertion of levator arcus palatini muscle on lateral aspect of hyomandibula; D: Suspensorium, lateral view (about 200 mm; PC 30873). B—D same scale.

a. ar: articular facet for articular; a.let: articular facet for lateral ethmoid; a.Mx: articular facet for maxilla; apa: autopalatine; a.sp + pr-pt: articular facet for sphenotic + prootic and pterotic; Ent2: 'entopterygoid' type 2; 'ent'-mtg-l: 'entopterygoid'-metapterygoid ligament; 'ent'-V.l: 'entopterygoid'-vomer ligament; f.f: foramen for passage of hyoideomandibular nerve trunk; lap.m: levator arcus palatini muscle; met: mesethmoid; mtg: metapterygoid; Pmx: premaxilla; pr.ap: processus anterodorsalis; pr.ect: processus ectopterygoideus; Pop: preopercle; pr. lo: processus levator operculi; pr.op: processus opercularis; pr.pd: processus posterodorsalis; q: quadrate.

Nematogenyids

General information on the suspensorium of *Nematogenys inermis* may be found in Arratia (1990a: 207); here I will provide additional information.

The elements of the suspensorium form similarly to those of *Ictalurus*, but the position and size of bones of the suspensorium and cranium vary.

The autopalatine (Figs. 28A, D, 29A, B) is broader anteriorly than posteriorly, similar to the condition present in diplomystids and †*Hypsidoris*. The anterior cartilage of the autopalatine is large and lies in a dorsolateral cavity of the premaxilla. Laterally, the small maxilla articulates through two small articular processes with the anterior cartilage. At about half of the length of the autopalatine is an elongate articular facet for the lateral ethmoid and vomer; there is a direct articulation between the autopalatine and lateral ethmoid, and an indirect articulation via cartilage with the vomer. There is a mass of fibrocartilage at the posterior end of the autopalatine; it is closely attached by connective tissue with a small cup-like sesamoid bone, the 'entopterygoid' type 2. This 'entopterygoid' is connected by a short ligament to the metapterygoid, and by a long ligament to the vomer. Neither an ectopterygoid or an 'ectopterygoid' are present.

The metapterygoid forms similarly to that of diplomystids and *Ictalurus* (compare Figs. 16A—C, 25A, B, 28A). The metapterygoid (Fig. 28A, D) is the largest element of the palatoquadrate; dorsally it has a small notch separating the anterior region from the posterior one. The anterior region produces a sharp, short processus basalis. Ventro-

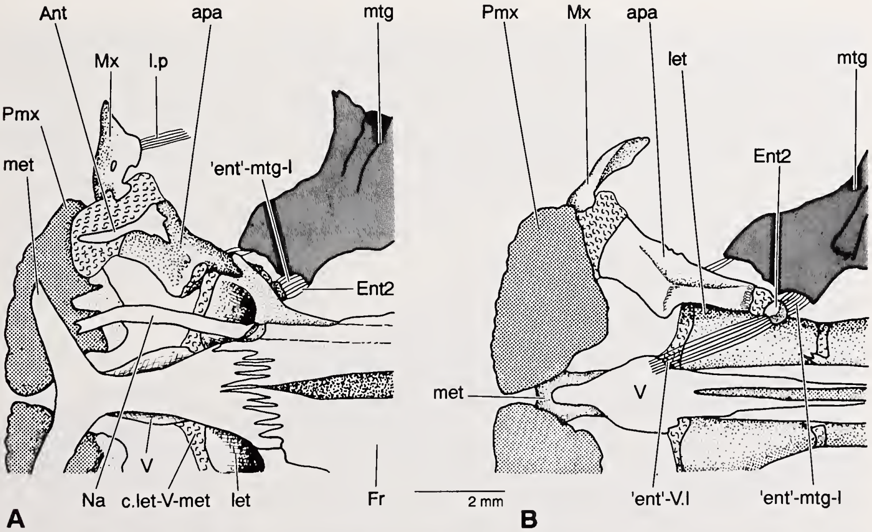

Fig.29: Autopalatine and surrounding bones in *Nematogenys inermis* (PC 30873). — A: Dorsal view; B: Ventral view; A,B same scale.

Ant: antorbital; apa: autopalatine; c.let-V-met: cartilage joining lateral ethmoid, vomer, and mesethmoid; Ent2: 'entopterygoid' type 2; 'ent'-mtg.l: 'entopterygoid'-metapterygoid ligament; 'ent'-V.l: 'entopterygoid'-vomer ligament; Fr: frontal; let: lateral ethmoid; l.p: ligamentum primordiale; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; Na: nasal; Pmx: premaxilla; V: vomer.

anteriorly, the metapterygoid projects a broad ectopterygoid process, that is lateral to the posterior portion of the autopalatine. The metapterygoid is loosely sutured with the hyomandibula. Most of the metapterygoid is membranous bone; the chondral region is elongate, narrow, and lies posteroventrally. There is an articulation between this chondral portion of the metapterygoid and the cartilaginous symplectic region between the hyomandibula and quadrate that is lost in some adult specimens. The suture between the metapterygoid and quadrate is not present, unlike other primitive siluroids. In addition, *Nematogenys* lacks a suture between the hyomandibula and quadrate.

The simple quadrate is a small bone, but a little larger than that in diplomystids. It bears large articular facets for the hyomandibula, preopercle, and the articular portion of the fused angulo-articulo-retroarticular (Fig. 30A, B). The main elements of this fusion of the angulo-articulo-retroarticular are the chondral ones; the angular is only a small ossification that may never contact the retroarticular portion of the Meckelian cartilage.

The hyomandibula has a moderately large, anterior, membranous outgrowth. Posterodorsally, there is a sharp elongate process — the processus levator operculi — just dorsal to the opercular process. A horizontal levator arcus palatini crest is not present, but a nearly vertical ridge for attachment of the levator arcus palatini muscle is present. The levator arcus palatini muscle (Fig. 28C) is subdivided into three portions. The largest or anterior one extends from the small levator arcus palatini process to the frontal, staying well separate from the lateral ethmoid; the other two portions are thin and extend from the lateral aspect of the hyomandibula to the autosphenotic.

The posteroventral margin of the hyomandibula is sutured to the preopercle. The dorsal margin of the hyomandibula articulates synchondrally with the pterotic and sphenotic + prootic. The pterosphenoid is not included in this cranial fusion as it was in trichomycterids. A small pseudobranch, with a few branchial lamellae, is associated with the medial aspect of the hyomandibula. The first pharyngobranchial is missing,

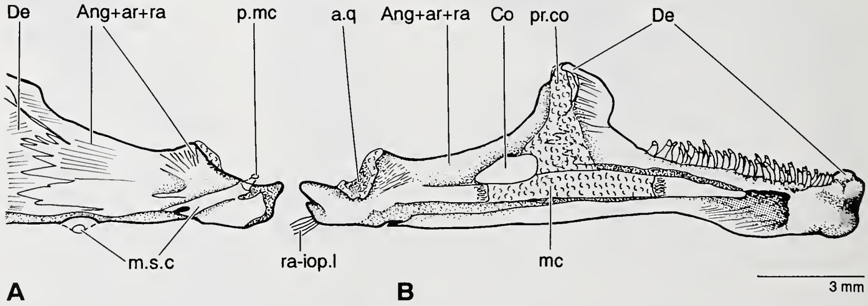

Fig.30: Lower jaw in *Nematogenys inermis* (PC 30873). — A: Posterior part, lateral view; B: Medial view. Ang + ar + ra: angular, articular and retroarticular fused; a.q: articular facet for quadrate; Co: coronomeckelian bone; De: dentary; mc: Meckelian cartilage; m.s.c.: mandibular sensory canal; p.mc: posterior opening of the mandibular sensory canal; pr.co: cartilaginous coronomeckelian process; ra-iop.l: retroarticular- interopercular ligament.

therefore there is no lateral attachment of this element to the hyomandibula like in diplomystids.

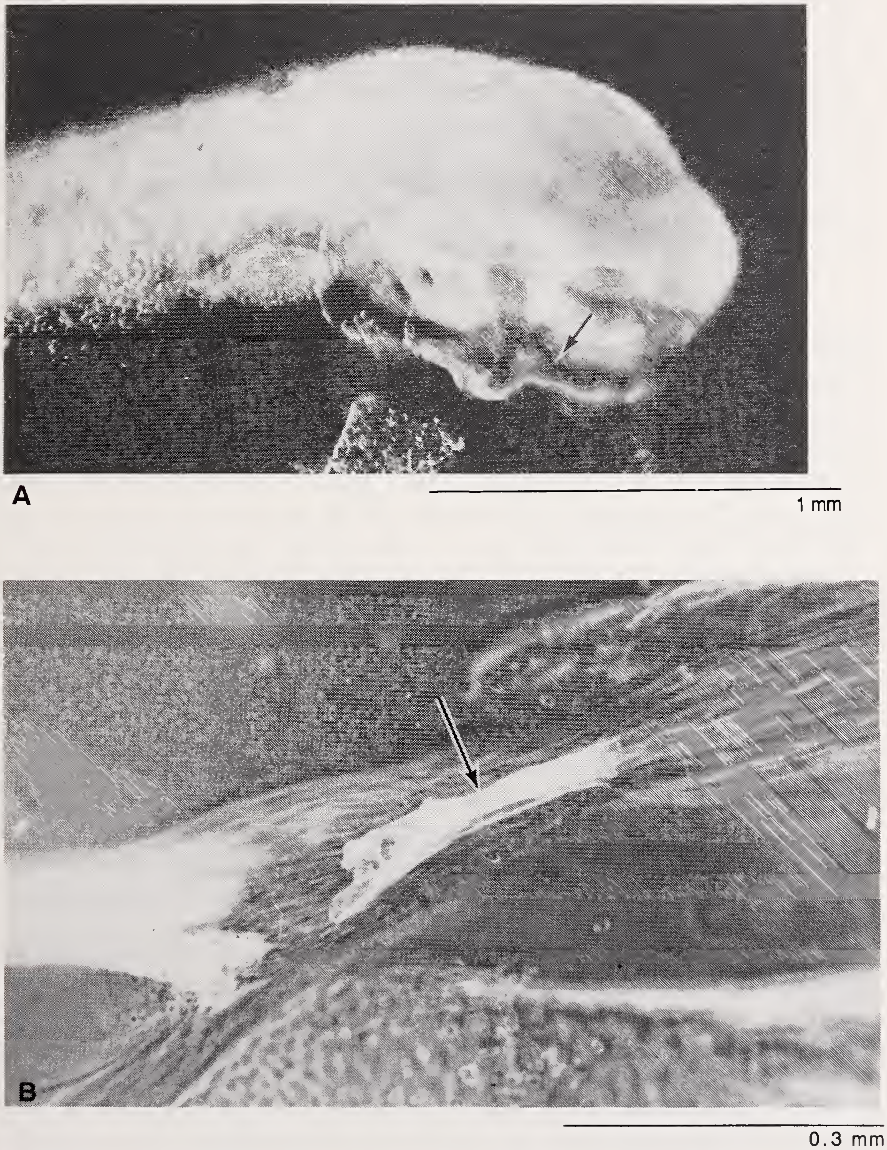

Fig.31: Suspensorium of *Noturus*. — A: *N. hildebrandi*, lateral view (5.5 mm total length; KU uncat.). Arrows point to the hyo-symplectic-pterygoid plate plus Meckelian cartilage; B: *Noturus exilis* (14 mm standard length; KU 17229). Arrows point to the 'entopterygoid' chalcifying in the ligament.

The ramus hyoideomandibularis of the facial nerve medially penetrates the hyomandibula and passes through a short tube inside the bone, emerging at the ventrolateral corner of the bone, as in ictalurids and most catfishes.

Ariids

The pterygoid series of *Bagre* and *Galeichthys* differs from those above described for catfishes with a simple quadrate. The small 'ectopterygoid' forms as an ossification in the ligament extending between the 'entopterygoid' and autopalatine; the the ligament becomes separated into two short ligaments, one between the 'entopterygoid' and 'ectopterygoid' and another between the 'ectopterygoid' and autopalatine. The small 'entopterygoid' is connected by ligaments and/or connective tissue with the lateral ethmoid, vomer, and metapterygoid.

Siluroids with a complex quadrate

Ictalurids

The two series of *Noturus* examined include 12 cleared and stained specimens of *Noturus hildebrandi* between 5.5 mm total length and 12.5 mm standard length, and 61 specimens of *Noturus exilis* ranging between 13.6 and 78 mm standard length. There are no major differences in the development of the suspensorium and hyoid arch between *Trichomycterus* (Arratia 1990a) and *Noturus*; however, the minor differences are of interest. In general, these differences are in the speed of ossification and the appearance of dermal elements as correlated with age (and represented by length).

In 5.5 mm specimens of *Noturus hildebrandi*, the hyoid and mandibular arches (Fig. 31A) are synchondrotic. The 'articulation' between the Meckelian cartilage and pars quadrata is produced by a fold of the cartilage. The only ossified bone at this stage is the cleithrum.

In 13.6 mm specimens of *Noturus exilis* the hyomandibular-symplectic-pterygoquadrate plate, the hyoid arch, and the pars autopalatina (Fig. 32A) are partially perichondrally ossified. The sesamoid 'entopterygoid' type 4 (anteriorly adjacent to the metapterygoid) is already ossified in the ligament linking the metapterygoid and vomer (Fig. 31B). There is no evidence that this 'entopterygoid' is the result of a fracture of the metapterygoid as suggested by Gosline (1975). The hyo-symplectic-pterygoquadrate plate is partially separated from the cranium. The anterior, membranous outgrowth of the hyomandibula is large. The quadrate complex is perichondrally ossified at the condylar region; anteriorly it also has a small membranous ossification. The metapterygoid has a thin, flat, membranous process (the ectopterygo-quadrate process) that is posterolateral to the autopalatine, occupying the position of the ectopterygoid in other teleosts. No lateral metapterygoid process was observed. The autopalatine is long and narrow. It is largely cartilaginous anteriorly, whereas the mid-section of the posterior part is partially surrounded by a fine perichondral ossification. The articular facet for the lateral ethmoid is about midway along the length of the bone. A ligament connects the posterior part of the autopalatine to the anterodorsal part of the metapterygoid.

The process of ossification then progresses and no major changes are observed in larger specimens. For example, in 16.1 mm specimens, changes in the density of the cartilage are observed in those regions that will later become synchondral articulations. The hyomandibula is largely ossified and articulates with the neurocranium. The metaptery-

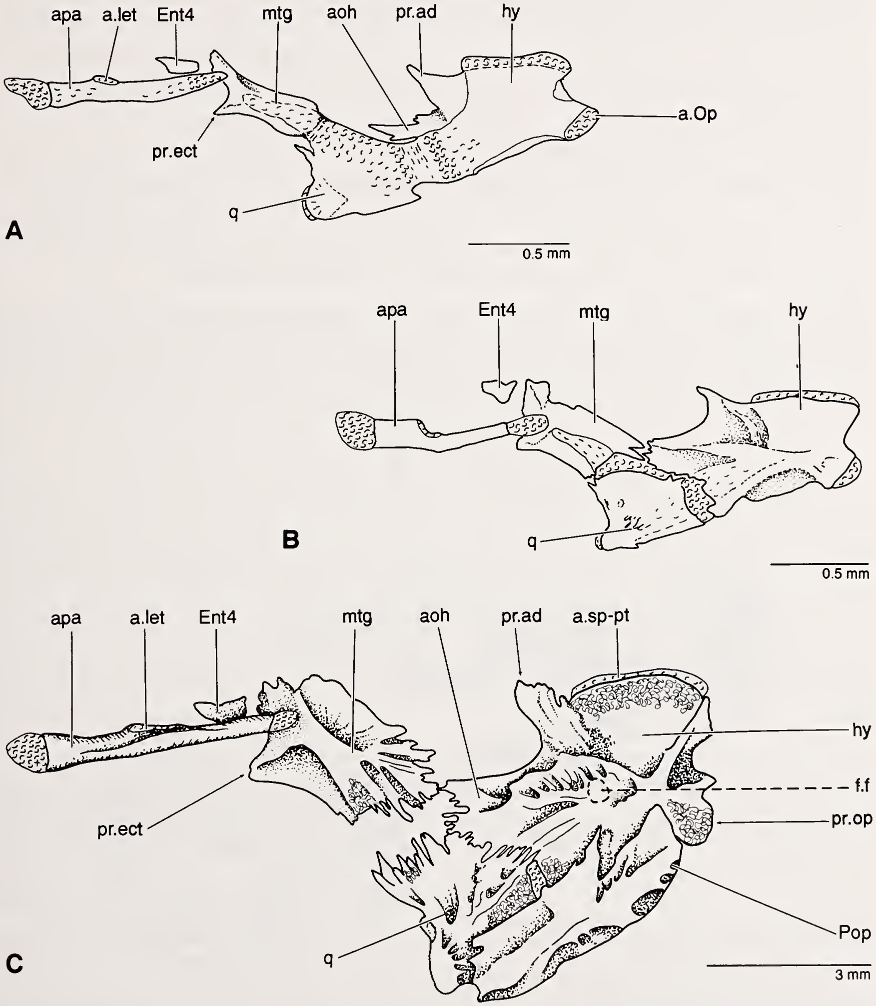

Fig.32: Developmental sequence of the suspensorium of *Noturus exilis*, lateral view (KU 17229). Ligaments omitted. — A: 13.6 mm standard length; B: 26.7 mm standard length; C: 73.9 mm standard length; the metapterygoid is slightly displaced dorsally to show its sutural and synchondral surfaces.
a.let: articular facet for lateral ethmoid; aoh: anterior membranous outgrowth; a.Op: articular facet for opercle; apa: autopalatine; a.sp-pt: articular facet for sphenotic and pterotic; Ent4: 'entopterygoid' type 4; f.f: foramen for passage of hyoideomandibular nerve trunk; hy: hyomandibula; mtg: metapterygoid; Pop: preopercle; pr.ad: processus anterodorsalis; pr.ect: processus ectopterygoideus; pr. op: processus opercularis; q: quadrate.

goid produces a posterodorsal process that faces the anterior membranous outgrowth of the hyomandibula.

In specimens of about 27 mm, the membranous regions of hyomandibula, complex quadrate, and metapterygoid (Fig. 32B) continue to enlarge. In 40—50 mm specimens, cartilaginous regions are only found between the hyomandibula and quadrate, and between the quadrate and metapterygoid. The metapterygoid enlarges dorsally and laterally through membranous projections or processes; its posterodorsal process produces serrations which articulate (sutura serrata) with the anterior membranous outgrowth of the hyomandibula, and just barely with the quadrate. The ’entopterygoid’ type 4 does not change markedly in shape or relationships throughout ontogeny.

The changes observed in specimens of 50—74 mm are the enlargement of the sutural regions between the anterior membranous outgrowth of the hyomandibula, the dorsal region of the quadrate and the posterodorsal process of the metapterygoid (Fig. 32C). The autopalatine becomes mostly ossified, although the anterior region retains a large nodule of cartilage and the posterior region has a smaller cartilage.

In 78 mm specimens the anterior part of the autopalatine has a large, oval or round cartilage. The two articular facets of the maxilla articulate with this nodule of cartilage and in addition, they are joined to the autopalatine by ligaments. The antorbital is in

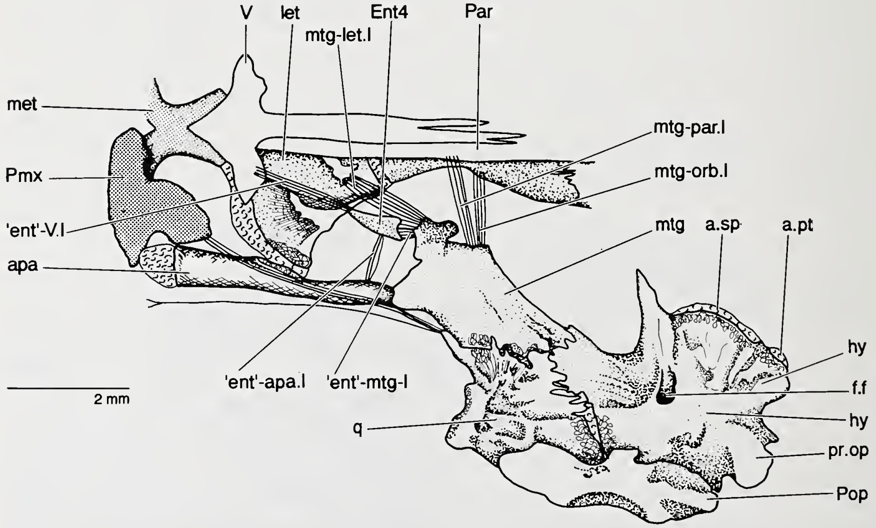

Fig.33: Suspensorium and its relationships in *Noturus exilis* (78 mm standard length; KU 172929) in ventral view of the premaxilla and anterior cranial bones.
apa: autopalatine; a. pt: articular facet for pterotic; a. sp: articular facet for sphenotic; Ent4: ’entopterygoid’ type 4; ’ent’-apa. l: ’entopterygoid’-autopalatine ligament; ’ent’-mtg. l: ’entopterygoid’-metapterygoid ligament; ’ent’-V. l: ’entopterygoid’-vomer ligament; f.f: forament for hyoideomandibular nerve trunk; hy: hyomandibula; let: lateral ethmoid; met: mesethmoid; mtg: metapterygoid; mtg-let. l: metapterygoid-lateral ethmoid ligament; mtg-par. l: metapterygoid-paraspehnoid ligament; mtg-orb.l: metapterygoid-orbitosphenoid ligament; Par: parasphenoid; Pmx: premaxilla; Pop: preopercle; pr. op: processus opercularis; q: quadrate; V: vomer.

close contact with this nodule of cartilage; it is attached to the posteromedial facet of the maxilla, the autopalatine, and the lateral ethmoid, as well as the nasal and/or premaxilla.

The complex quadrate is heavily ossified posteriorly, as well as in its articular region with the articular (lower jaw); whereas the anterodorsal part is thin and has numerous fine ridges. The complex quadrate articulates anteriorly through a short synchondral joint with the metapterygoid. The posteroventral region of the quadrate forms an articular facet for the preopercle.

The hyomandibula (Fig. 33) is a short, broad bone and its membranous outgrowth is comparatively smaller than that in *Trichomycterus areolatus* (Arratia 1990a). Dorsally the hyomandibula may have its elongate articular facet divided into three portions:

1) the dorsal portion of the anterior membranous outgrowth that articulates bone-to-bone in a groove of the sphenotic;
2) a long, cartilaginous surface for the sphenotic; and
3) a posterior, cartilaginous surface for the pterotic.

Only a few large specimens have three articular regions; portions two and three are usually combined. Posteriorly, the hyomandibula has a condylar articulation with the opercle, whereas it is sutured to the preopercle. Anteroventrally, the hyomandibula articulates synchondrally with the complex quadrate through the symplectic cartilage and anteriorly sutures (sutura dentata) with the quadrate and metapterygoid.

A long ligament extends branches from the quadrate to each of the following: the metapterygoid, autopalatine, premaxilla, and maxilla. The ligamentum primordiale is independent of this ligament as in *Trichomycterus areolatus* (Arratia 1990a). Several ligaments link the metapterygoid to surrounding bones: a broad ligament joins the metapterygoid to the orbitosphenoid, another ligament joins the metapterygoid to the lateral ethmoid, a third short ligament joins the metapterygoid to the 'entopterygoid' type 4. The 'entopterygoid' type 4 is linked through four separate ligaments to the metapterygoid, autopalatine, lateral ethmoid, and vomer. This 'entopterygoid' type 4 is consistently present.

The 'entopterygoid' type 4 of *Noturus* has fewer ligamentous connections (Fig. 2D) than the 'entopterygoid' in *Ameiurus melas* (Fig. 27A) and in *Ictalurus punctatus* (Figs. 2G, 27B). *Noturus* differs from *Ictalurus* and *Pylodictis* in the lack of a ligamentous connection between 'entopterygoid' and the orbitosphenoid.

'Pimelodids'

Heptapterus and *Parapimelodus* are currently included in the family Pimelodidae (e.g., Ringuelet et al. 1967, Eschmeyer 1990), in the subfamily Rhamdiinae (Lundberg et al. 1991); however, the 'Pimelodidae' are paraphyletic with respect to the Ariidae (see below).

Two patterns of the suspensorium are described below. First that of *Heptapterus mustelinus* is described, followed by that of *Parapimelodus valenciennesi*. The series of *Heptapterus mustelinus* examined included 12 cleared and stained specimens ranging in size from 27 mm to 185 mm standard length.

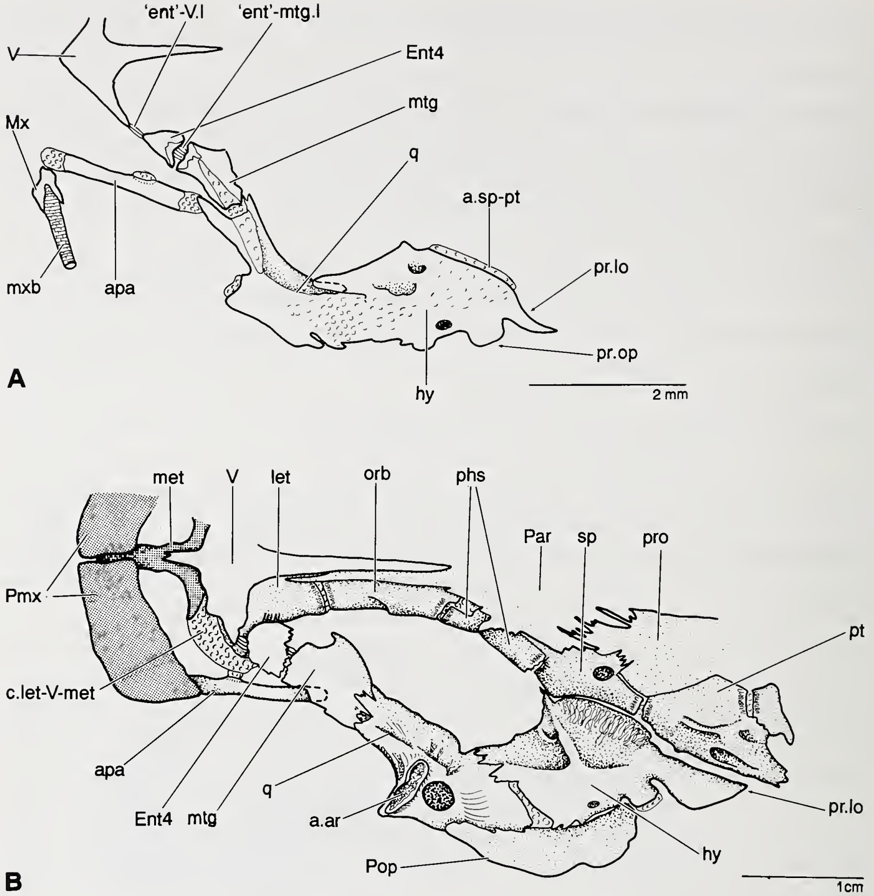

Fig.34: Suspensorium and its relationships in *Heptapterus mustelinus*. — A: Ventral view, 27 mm standard length (PC 50983); B: Ventral view, 185 mm standard length (PC 19484).
a.ar: articular facet for articular; apa: autopalatine; a.sp-pt: articular facet for sphenotic and pterotic; c.let-V-met: cartilage joining lateral ethmoid, vomer, and mesethmoid; Ent4: 'entopterygoid' type 4; 'ent'-mtg. l: 'entopterygoid'- metapterygoid ligament; 'ent'-V. l: 'entopterygoid'- vomer ligament; hy: homandibula; let: lateral ethmoid; met: mesethmoid; mtg: metapterygoid; Mx: maxilla; mxb: maxillary barbel; orb: orbitosphenoid; Par: parasphenoid; phs: pterosphenoid; Pmx: premaxilla; Pop: preopercle; pro: prootic; pr.lo: processus levator operculi; pr. op: processus opercularis; pt: pterotic; sp: sphenotic; q: quadrate; V: vomer.

In the 27 mm specimen of *Heptapterus*, every bone (Fig. 34A) of the palatoquadrate, hyoid, and branchial arches are already differentiated and partially ossified. The autopalatine is not connected by ligament or connective tissue to the metapterygoid during any stage of growth. The 'entopterygoid' type 4 is attached by a short ligament to the anterior part of the metapterygoid and by a little longer ligament to the lateral wing of the anterior part of the vomer. I could not find a ligament between the 'entopterygoid' and lateral ethmoid, except in large individuals. The 'entopterygoid' lies ventral to the lateral cartilage of the lateral ethmoid. Both an ectopterygoid and 'ectopterygoid' are absent. The metapterygoid (Fig. 34A) is slightly elongate; anteriorly it is heavily ossified and has a broad surface for the attachment of the 'entopterygoid'-metapterygoid ligament. The metapterygoid and hyomandibula are not sutured to each other during any stage of growth (Fig. 34A, B); both bones are completely separate due to the enlargement of the quadrate. A similar pattern is observed in other 'pimelodids' such as *Rhamdia, Pimelodus*, and *Parapimelodus*. The quadrate has an anterior, elongate, slightly-broad pterygoid process. The anterior membranous outgrowth of the hyomandibula is small in both young and adult individuals; the processus levator operculi is well developed.

The main ontogenetic changes of the bones of the suspensorium are related to size and position. For example, in large specimens the anterior part of the autopalatine rests largely on the dorsal face of the premaxilla. The medial articular facet of the autopalatine (Fig. 34B) articulates with the lateral ethmoid and with the ethmoidal cartilage joining the vomer, lateral ethmoid, and mesethmoid (as in diplomystids); a direct contact between the vomer and autopalatine is missing.

In large specimens the 'entopterygoid' (Fig. 34B) may articulate with the lateral ethmoid during growth, and a dentate and/or serrate sutural joint may form between the 'entopterygoid' and metapterygoid. Although the metapterygoid partly supports the eye, the eye is mainly resting on soft tissue between the suspensorium and neurocranium. A similar pattern is present in *Rhamdia*. The anterior membranous outgrowth of the hyomandibula is small and projects anteroventrally. Posterodorsally, the hyomandibula has a long, well-developed processus levator operculi (as it does in *Rhamdia*) that may extend nearly to the posterior end of the pterotic. The hyomandibula articulates mainly with the autosphenotic, and less extensively with the pterotic. The hyoideomandibular nerve trunk enters the hyomandibula medially and exits ventral to the opercular process.

The series of *Parapimelodus valenciennesi* examined included 12 cleared and stained specimens, ranging in size from 28—190 mm. In a 28 mm specimen, every bone of the palatoquadrate, hyoid and branchial arches has already differentiated and ossified; there are, however, slight changes in the shape of some bones during growth. The hyomandibula is dorsoventrally elongate and anteriorly has a moderate membranous outgrowth. The complex quadrate (Fig. 34A) has two well-defined parts: the posteroventral one articulates synchondrally with the hyomandibula and the anterior chondral process borders the membranous outgrowth of the hyomandibula and the metapterygoid. Anteriorly, the ectopterygoid process of the metapterygoid extends lateral to the autopalatine (Fig. 35A, B). The metapterygoid occupies the position that the ectopterygoid, entopterygoid, and metapterygoid occupy in other ostariophysans. The metapterygoid of *Parapimelodus* bears teeth on the medial surface of the broad, strong dorso-medial projection. From this observation it is evident that an early fusion between the chondral metapterygoid and a dermal toothplate has produced a compound dermo+metapterygoid bone (Fig. 35B, C).

In some young and adult specimens, a small, elongate additional pterygoid type 1 (Fig. 35A) is present between the ventral part of the anterior membranous outgrowth of the hyomandibula and the dermo+metapterygoid; in other specimens, the pterygoid type 1 fuses to the dermo+metapterygoid. This additional pterygoid is apparently not a fracture of the dermo+metapterygoid.

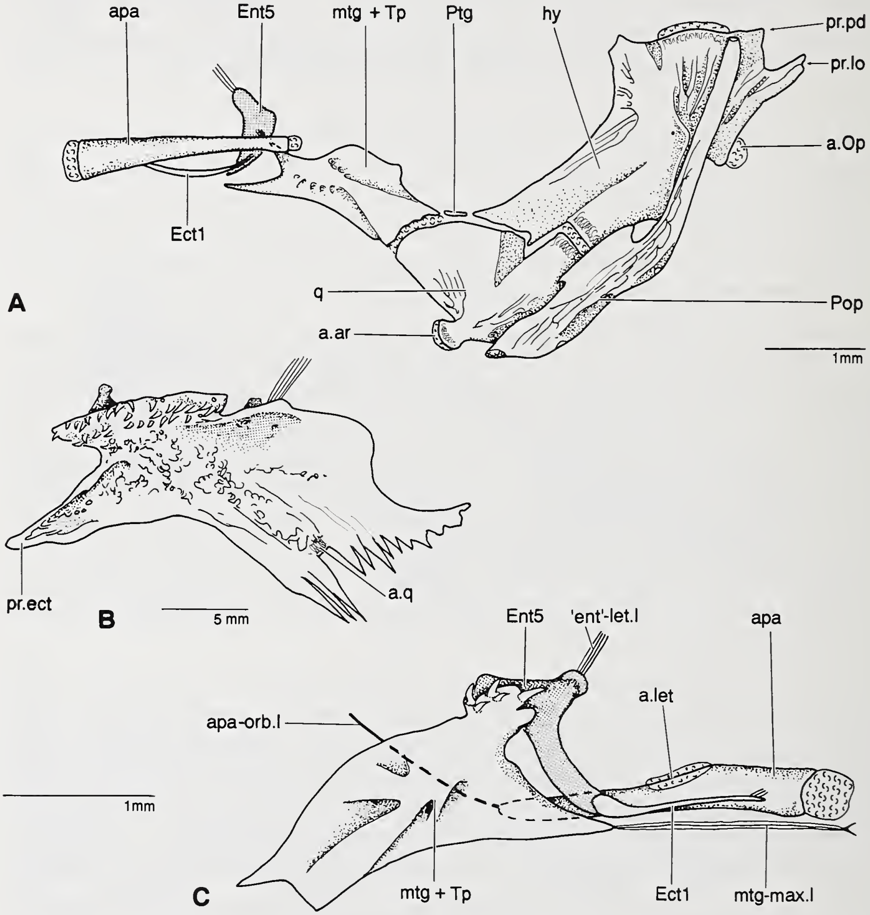

Fig.35: Suspensorium of *Parapimelodus valenciennesi.* — A: Suspensorium and preopercle, lateral view (41.6 mm standard length; ZMH 6669); B: Dermo+metapterygoid, medial view (190 mm standard length; KU 21084); C: Anterior part of the suspensorium, medial view (74.8 mm standard length; KU 21084).
a.ar: articular facet for articular; a.let: articulation for lateral ethmoid; a.Op: articular facet for opercle; apa: autopalatine; apa-orb.l: autopalatine-orbitosphenoid ligament; a.q: articular facet for quadrate; Ect1: 'ectopterygoid' type 1; Ent5: 'entopterygoid' type 5; 'ent'-let.l: 'entopterygoid'- lateral ethmoid ligament; hy: hyomandibula; mtg+Tp: dermo+metapterygoid; mtg-max.l: metapterygoid-maxillary ligament; Pop: preopercle; pr.ect: processus ectopterygoideus; pr.pd: processus posterodorsalis; pr.lo: processus levator operculi; Ptg: pterygoid type 1; q: quadrate.

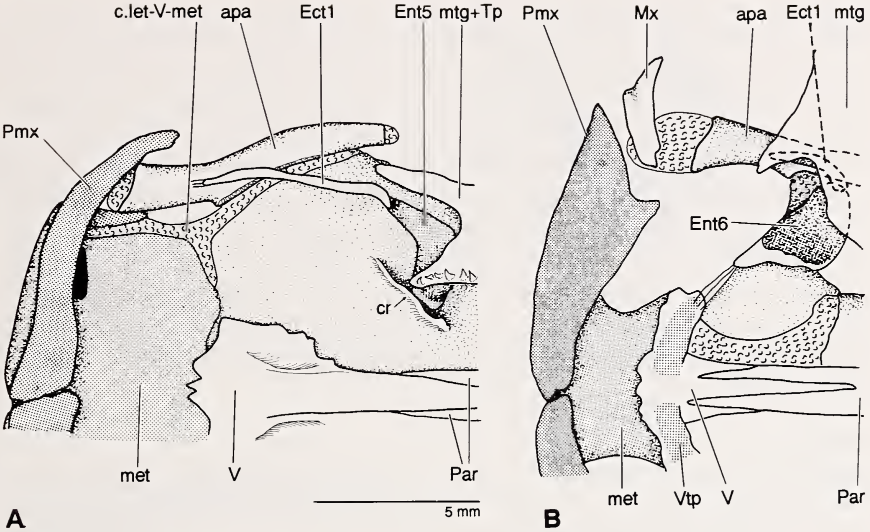

Fig.36: Autopalatine and surrounding bones, ventral view. — A: *Parapimelodus valenciennesi* (175 mm standard length; KU 21804); B: *Bagre marinus* (78.6 mm standard length; KU 3053). A,B same scale.
apa: autopalatine; c.let-V-met: cartilage joining lateral ethmoid, vomer, and mesethmoid; cr: crest; Ect1: 'ectopterygoid' type 1; Ent5-6: 'entopterygoid' types 5-6; met: mesethmoid; mtg: metapterygoid; mtg+Tp: dermo+metapterygoid; Mx: maxilla; Par: parasphenoid; Pmx: premaxilla; V: vomer; Vtp: vomerine toothplate.

In both small and large specimens, an elongate 'ectopterygoid' type 1 (Figs. 35A—C, 36A) lies ventral to the autopalatine. It is sharp anteriorly and curves posteromedially. Its posterior end is ligamentously attached to 'entopterygoid' type 5.

Anteriorly, the elongate autopalatine has a large nodule of fibrocartilage in adults. The small articular facets of the maxilla articulate with this fibrocartilage, which also abuts a cavity in the dorsal aspect of the premaxilla. Medially, the autopalatine articulates via cartilage with the lateral ethmoid. This cartilage reaches the mesethmoid but not the vomer in large individuals (Fig. 36A).

The 'ectopterygoid' type 1 is joined anteriorly by a short ligament to the autopalatine, and posteriorly to the 'entopterygoid' type 5. The 'entopterygoid' type 5 is also connected by short ligaments to the 'ectopterygoid' type 1, the dermo+metapterygoid, and lateral ethmoid. There is no ligament between the autopalatine and dermo+metapterygoid. A strong ligament extends from the ectopterygoid process of the metapterygoid to the maxilla, but a ligamentous link between metapterygoid and vomer is absent. A ligament extends from the posterior part of the autopalatine to the posterior part of the orbitosphenoid. There is no link between the metapterygoid-maxillary ligament and the ligamentum primordiale that extends from the coronoid cartilage of the lower jaw to the premaxilla. The autopalatine is attached by ligaments to the lateral ethmoid and antorbital. The antorbital is also attached to the premaxilla and nasal.

Regan (1911: 572) arranged some of the genera of pimelodids into subfamilies, according to the presence or absence of the 'ectopterygoid' type 1 and features of the 'entopterygoid' type 5 (shape and attachment and/or articulation with the lateral ethmoid and metapterygoid). Gosline (1975) considered the two dermal ossifications as (fractures of the) entopterygoid, but my observations of the early ontogeny of 'pimelodids' do not support such an hypothesis. *Parapimelodus* has the same 'ectopterygoid' type 1 as described in *Callophysus, Pimelodus, Piramutana*, and *Sciades* (Regan 1911), but it has teeth on the dermo + metapterygoid which are not described for other pimelodids.

Recently, Lundberg et al. (1991) characterized the subfamily Rhamdiinae by five synapomorphies, two of which are characters of the suspensorium. These are the process for insertion of the levator operculi muscle greatly expanded and adjacent to the pterotic, and quadrate with a free dorsal margin and a bifid shape. Both features are homoplastic; they are found in certain other 'pimelodids' and in other catfishes like certain 'bagrids'.

'Bagrids'

My interpretation of the pterygoid series is somewhat different from those of Tilak (1965), Jayaram (1966), and Mo (1991). According to Tilak (1965), the entopterygoid is absent in *Mystus, Rita*, and *Horabagrus*; however, the small, bent and rod-shaped bone that he identified as the ectopterygoid is joined by a ligament to the metapterygoid (Tilak 1965: Figs. 14, 15, 17), a role of the 'entopterygoid' in other catfishes.

The complex metapterygoid in 'bagrids' may or may not contact the hyomandibula. A small metapterygoid that has no contact with the hyomandibula is present in *Mystus (Mystus)* (Tilak 1965: Figs. 15, 16) and *Rita rita* (Mo 1991: Fig. 47); this is a specialization of these 'bagrids' compared to other catfishes (Joseph 1960). This condition, however, is also present in the 'pimelodids' *Heptapterus, Rhamdia*, and *Parapimelodus*. A sutural contact is found in 'bagrids' such as *Horabagrus* and *Mystus (Osteobagrus)* (Tilak 1965: Figs. 14, 17).

Schilbeids

My interpretation of the pterygoid series is somewhat different from those of Tilak (1961) and Gosline (1975) for *Eutropiichthys vacha*. A large bone synchondrally and suturally articulates with the quadrate. Based on its ontogenetic origin, this bone must be the metapterygoid (Fig. 37A), which dorsally occupies the position of the entopterygoid in other teleosts (excluding siluroids). A long, dentate bone identified as the ectopterygoid by Tilak (1961) and as a tooth plate by Gosline (1975) lies ventrolateral to the complex quadrate and metapterygoid. This bone broadens anteriorly and broadly extends below the small autopalatine. It partially occupies the position of ectopterygoid and dermopalatine in primitive teleosts, and therefore could be interpreted as ectopterygoid + dermopalatine (Fig. 37A, B). However, another interpretation could be that this bone is just a long dentate ectopterygoid; a third interpretation could be that this bone is a new formation. This third interpretation is the most reasonable approach if we study the distribution of this feature among siluriforms. Based on its position and comparison with other siluriforms, I identify it as a lateral toothplate; another additional element of the suspensorium of catfishes.

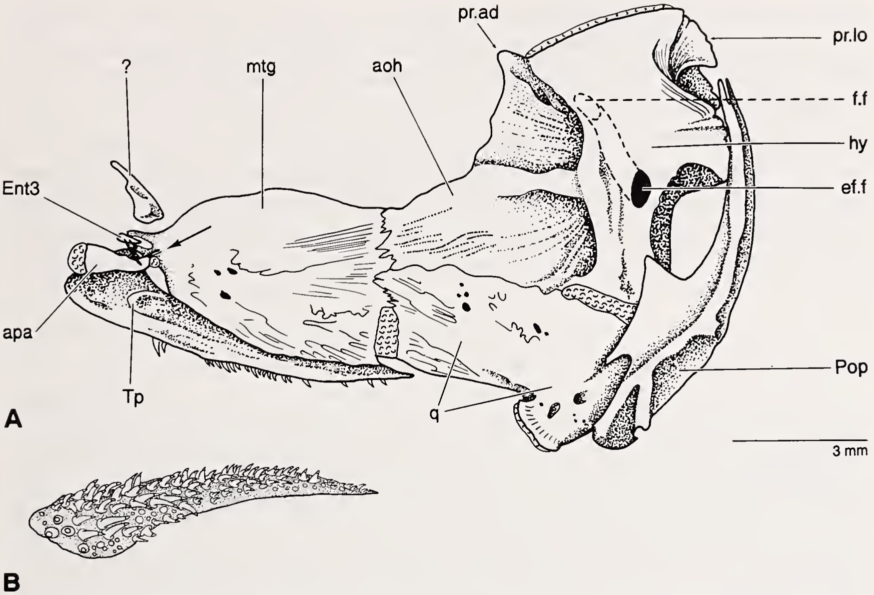

Fig.37: Suspensorium and preopercle of *Eutropiichthys vacha* (109 mm standard length; KU 12169). — A: Lateral view; arrow points to the autopalatine-metapterygoid ligament; B: Lateral toothplate, ventral view. Scale applies to both figures.
aoh: membranous outgrowth; apa: autopalatine; ef.f: exit foramen of the facial nerve; Ent3: 'entopterygoid' type 3; f.f: foramen for the passage of facial nerve; hy: hyomandibula; mtg: metapterygoid; Pop: preopercle; pr.ad: processus anterodorsalis; pr.lo: proccesus levator operculi; q: quadrate; Tp: lateral toothplate; ?: additional pterygoid?

The autopalatine is a small rod-like bone, that has cartilage both anteriorly and posteriorly. The small maxilla articulates through two small facets with the anterior autopalatinal cartilage. The anterior cartilage also rests on the posterior margin of the premaxilla. In *Ailia coilia* the autopalatine articulates with both the maxilla and the antorbital. In *Eutropiichthys*, the antorbital articulates with the lateral ethmoid (but not the maxilla) and is attached by ligaments to the autopalatine, premaxilla, and to the base of the nasal barbel.

Anteriorly, the metapterygoid produces two small projections. An 'entopterygoid' type 3 is located between the projections. The large metapterygoid is laterally sutured to the lateral tooth plate, and posterodorsally sutured to the hyomandibula and quadrate. In addition, a synchondral articulation is present between the lateral part of the metapterygoid and the pterygoid process of the quadrate.

In the specimen studied here, there is an additional small, flat bone present. It is medial to the metapterygoid and was not mentioned by Tilak (1961), and its presence is probably variable. This bone is free; I could detect no ligamentous, or other connection joining it to any surrounding bones.

The quadrate is a large bone, almost rectangular; with an elongate chondral pterygoid process that dorsally bears a membranous outgrowth. This membranous outgrowth is sutured to the metapterygoid and hyomandibula. In addition, the quadrate articulates with the hyomandibula through the symplectic cartilage. Posteriorly, the quadrate shares a suture with the preopercle. The preopercle also shares a short suture with the hyomandibula.

Short ligaments extend between the 'entopterygoid' type 3 and the metapterygoid, autopalatine, and lateral ethmoid. In addition, strong ligaments extend from the medial face of the metapterygoid to the lateral ethmoid and orbitosphenoid. I was unable to find a ligamentous connection between the autopalatine and orbitosphenoid; therefore, the most posterior ligament of the autopalatine is the autopalatine-metapterygoid ligament.

Tilak (1961) described a metapterygoid, a toothed ectopterygoid, and a small entopterygoid in *Eutropiichthys vacha*. Gosline (1975: 7) stated that in catfishes there is often a tooth-bearing plate on the oral surface of the metapterygoid-vomer ligament and that such a plate has frequently been identified as an ectopterygoid. Such an identification is questionable. "Sometimes part or all of such tooth plate becomes firmly attached to the metapterygoid as in the schilbeid *Eutropiichthys* (Tilak 1961: Figs. 7, 8)" (Gosline 1975: 7). I disagree with this interpretation of Tilak's figures because the specimen studied here (KU 12169) does not have a metapterygoid-vomer ligament. Instead it has a metapterygoid-lateral ethmoid ligament. Furthermore, this metapterygoid cannot be readily compared to the so-called ectopterygoid of Tilak (1961), or to that described by other authors. The bone identified as the entopterygoid by Tilak (1961) is considered here (by comparison with other ostariophysans) to be an 'entopterygoid' type 3.

Trichomycterids

A detailed description of the suspensorium of trichomycterids and of related literature is found in Arratia (1990a).

COMPARISON AMONG CERTAIN SILURIFORMS

The origin of the metapterygoid from the hyo-symplectic-pterygoquadrate plate takes place in two unique ways. This separates the siluroids into two groups:

(1) Siluroids with a small pars quadrata, where the metapterygoid arises as a perichondral ossification of an anterior cartilaginous projection — the pterygoid process — dorsal to the quadrate region of the hyo-symplectic-pterygoquadrate plate. Examples include diplomystids (Fig. 16A, B; Arratia 1987a: Fig. 25B), *Ictalurus* and *Pylodictis* (Figs. 24C, 25A), nematogenyids (Fig. 28A; Arratia 1990a: Fig. 12A, B), loricariids (Arratia 1990a: Fig. 13A—C), and callichthyids (Arratia 1990a).

(2) Siluroids with a complex quadrate, where the metapterygoid arises as a perichondral ossification of the anterior projection — the pterygoid process — of the large pars quadrata, and articulates both synchondrally and suturally with the anterior part of the chondral and membranous projection of the quadrate. Examples include *Heptapterus* (Fig. 34A), *Parapimelodus* (Fig. 35A), and Trichomycteridae (Arratia 1990a: Figs. 3A—D, 5A, B).

The first pattern is exhibited by the primitive diplomystids and within the loricarioids, by the nematogenyids and advanced loricariids. The second pattern is also exhibited by primitive and advanced siluroids. Both patterns may even be found in a single family; for example, both *Ictalurus* and *Pylodictis* have a simple quadrate, whereas *Noturus* has a complex quadrate (which represents the advanced condition among the Ictaluridae). The quadrate exhibits several evolutionary transformations among loricarioids. For example, *Nematogenys* has a short, broad quadrate similar to that of diplomystids and representative of the primitive condition. Loricariids have a simple, deep, narrow quadrate. Among loricarioids, a complex quadrate is found in the Trichomycteridae and Astroblepidae; however, the ontogenetic origin of the pterygoid process differs between them (Arratia 1990a).

Autopalatine

The length of the autopalatine in siluroids differs from group to group. The autopalatine is long early in ontogeny and stays long throughout growth, retaining large cartilaginous regions anteriorly and posteriorly, in *Diplomystes camposensis* within the Diplomystidae (Fig. 17A, B). In contrast, it is short in *Diplomystes chilensis* (Fig. 17C). The autopalatine is very small in *Eutropiichthys* (Fig. 37A) and *Ailia*; and it has atrophied to articulate posteriorly with the maxilla and lateral ethmoid in *Euchilichthys guentheri* (Starks 1926: Fig. 15); it is a small hoof-shaped nodular element in Siluridae (Howes & Ayanomiya Fumihito 1991: Fig. 13).

A rod-shaped autopalatine (Fig. 26A, B) seems to be most common in siluroids. However, young diplomystids and juvenile diplomystids have an anteriorly broad autopalatine (Figs. 16A—C, 17A, B) that is forked into two long maxillary processes. This is unique to the Diplomystidae. Grande (1987) noted that Tilak (1964) figured the autopalatine of *Ailia coila* with an anterior fork; however, it is not forked in the cleared and stained specimen KU 12156. Grande (1987) refers to a distinct notch in the anterior part of the autopalatine of Diplomystoidei based on Fink & Fink (1981: Fig. 11) and his examination of a single specimen of *Olivaichthys viedmensis*. Specimen MCZ 8290 figured in Fink & Fink (1981: Fig. 11) and in Arratia (1987a: Fig. 6A) does not have a notch. In both *Diplomystes chilensis* and *Olivaichthys viedmensis* both of the anterior elongate processes of the autopalatine fuse during ontogeny to leave only a foramen (Fig. 17C); whereas in *Diplomystes nahuelbutaensis* and *D. camposensis* both processes stay separate (as in early ontogeny) and therefore a deep notch is observed (Arratia 1987a: Figs. 14B, 24B, 25A—D). The autopalatine is broader anteriorly than posteriorly in †*Hypsidoris* and *Nematogenys*, but *Nematogenys* lacks the two maxillary processes. It is unknown if †*Hypsidoris* has two anterior maxillary processes in early ontogeny. The autopalatine is more or less triangular in *Trichomycterus*, although it may have an enormous anterior extent in some trichomycterids (Arratia 1990a: Fig. 11A).

In most catfishes, the antorbital is ligamentously attached to the autopalatine anteriorly (Fig. 38A—G), whereas these bones articulate in *Ailia*. The autopalatine does not articulate nor is it connected to infraorbital bones in some siluroids (including *Hypostomus* and *Callichthys* [Arratia 1987a, 1990a]).

The autopalatine is linked to the premaxilla in as many as six different ways:

(1) directly through the anterior nodule of cartilage of the autopalatine that laterally abuts against a cavity or the dorsal surface of the premaxilla (e.g., Siluroidea sensu Grande 1987);
(2) directly through a small ligament or short length of connective tissue that extends between the medial side of the anterior nodule of cartilage of the autopalatine and the premaxilla (e.g., *Olivaichthys* and *Nematogenys*);
(3) directly through the anterior nodule of cartilage that during ontogeny medially produces an articulation with the premaxilla (e.g., *Trichomycterus, Bullockia*, and *Eremophilus*);
(4) an indirect link through the antorbital, that is joined by ligaments to the autopalatine and premaxilla (e.g., *Parapimelodus, Eutropiichthys*, and a few specimens of *Noturus*);
(5) an indirect link through the maxilla, that articulates with the autopalatine and is joined to the premaxilla by a ligament (e.g., *Trichomycterus*);
(6) no link at all (e.g., *Diplomystes camposensis*).

The autopalatine articulates medially with cranial bones such as the lateral ethmoid and vomer in primitive catfishes. Diplomystids seem to be unique in that the articular facet with the vomer is also connected by a small amount of cartilage to the mesethmoid, lateral ethmoid, and orbitosphenoid. A similar joint is found in *Nematogenys, Rhamdia*, and *Heptapterus*, but a connection with the orbitosphenoid is missing. A direct articulation between autopalatine, lateral ethmoid, and vomer is present in trichomycterines. In adult *Parapimelodus* and ictalurids there is no direct or indirect articulation between autopalatine and vomer.

Burne (1909) found that the autopalatine impinged on the wall of the nasal cavity in *Clarias* and *Malapterurus*; he suggested that movements of the autopalatine would alter the volume of the nasal cavity as well as the movement of the barbels (nasal and maxillary). The autopalatine partially frames the wall of the nasal cavity in most catfishes including the diplomystids (Arratia 1987a) and it is attached to the antorbital (which also frames the nasal cavity). The antorbital may also be connected to the posterior nostril (Fig. 38A, B), or to the nasal bone (Fig. 38C—E), or to the base of the nasal barbel (Fig. 38F), or to the cartilaginous support of the nasal barbel (Fig. 38G). The antorbital has a dorsal projection that extends between both nostrils and is attached to the nasal bone in *Arius.*

The relationships of the anterior part of the autopalatine have to be extensively studied in many other catfishes. Only in this way will we learn about the distribution and evolutionary relationships among the seven patterns of articulation and linkage (Fig. 38A—G) presented here (other patterns may also be added by studying other catfishes).

The posterior part of the autopalatine may occupy the following positions in adult specimens of different catfish groups:

1. The posterior cartilage of the autopalatine borders 'entopterygoid' type 2 and the metapterygoid. These three bones are in the same plane (unlike other catfishes) and the short ectopterygoid process of the metapterygoid is lateral to the autopalatine.

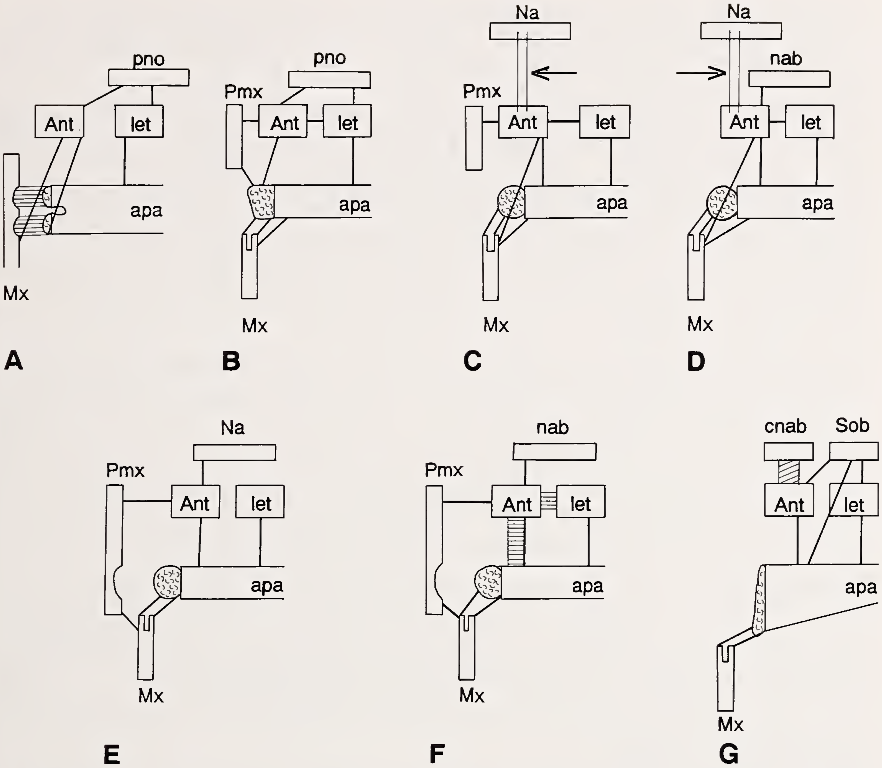

Fig.38: Attachments of the anterior part of the autopalatine to the surrounding bones, posterior nostril, and base of the nasal barbel in certain siluriforms. Arrow points to the intersection of the infraorbital and supraorbital sensory canals. A bar with horizontal lines represents an articulation. A bar with oblique lines represents a close attachment between the antorbital and cartilaginous support plate of the nasal barbel. — A: *Diplomystes* and *Olivaichthys*; B: *Nematogenys*; C,D: *Noturus*; E: *Parapimelodus*; F: *Ailia*; G: *Trichomycterus*.
Ant: antorbital; apa: autopalatine; cnab: cartilaginous plate supporting the nasal barbel; let: lateral ethmoid; Mx: maxilla; Na: nasal bone; nab: nasal barbel; Pmx: premaxilla; pno: posterior nostril; Sob: 'supraorbital'.

This state is known only in Nematogenyidae (Fig. 28B; Arratia 1990a).

2. The posterior cartilage of the autopalatine borders the entopterygoid (when present) and is dorsal to 'entopterygoid' type 1 (when present). The long ectopterygoid process of the metapterygoid is lateral to the autopalatine. This state is only known in Diplomystidae (Figs. 16A, C, 19A—D).
3. The posterior part of the autopalatine is dorsal to the metapterygoid and is not in contact with any dermal pterygoid. This state is observed in many catfishes, e.g., trichomycterines (Arratia 1990a: Figs. 7, 8), *Noturus* (Figs. 32C, 33), *Parapimelodus* (Figs. 35A, 36A), and *Eutropiichthys* (Fig. 37A).
4. The posterior part of the autopalatine extends dorsal or dorsolateral to the 'entopterygoid', not the metapterygoid. This pattern is found in ictalurids such as *Ameiurus melas, Ictalurus furcatus, I. punctatus*, and *Pylodictis* (Fig. 27A—D).

5. The posterior part of the autopalatine articulates with the lateral ethmoid and is dorsal to the metapterygoid. This pattern is found in *Loricaria, Loricarichthys* (Arratia 1990a: Fig. 13A, B), and *Callichthys.*

The posterior end of the autopalatine in catfishes may or may not have a large nodule of cartilage, or fibrocartilage in adults. A posterior cartilage is present in siluriforms such as the Diplomystidae, Ictaluridae, *Parapimelodus*, and *Eutropiichthys*; this cartilage is absent in the Trichomycteridae and Loricariidae (Arratia 1990a). Although the posterior cartilage is present in a variety of catfishes, only it forms an articular surface for the entopterygoid in the Diplomystidae and for 'entopterygoid' type 2 in the Nematogenyidae. In other siluroids, the posterior cartilage does not articulate with the sesamoid 'entopterygoids'.

The posterior part of the autopalatine may or may not be connected to the orbitosphenoid or pterosphenoid by a ligament (e.g., to the orbitosphenoid in Diplomystidae and *Parapimelodus*; to the pterosphenoid in *Trichomycterus*). The lack of a direct ligamentous link between the autopalatine and orbitosphenoid or pterosphenoid is characteristic of siluroids such as *Ictalurus, Pylodictis, Noturus, Eutropiichthys*, and *Nematogenys*. However, an indirect link between the autopalatine and orbitosphenoid is achieved through a 'entopterygoid' in *Ameiurus, Ictalurus*, and *Pylodictis.*

The autopalatine is directly connected to the metapterygoid by one (ligament 17 of Ghiot 1978, Ghiot et al. 1984) or two ligaments or connective tissue (e.g., diplomystids, nematogenyids, and ictalurids) or indirectly by ligamentous connections through a sesamoid 'entopterygoid' (e.g., *Bagre, Galeichthys*, and *Parapimelodus*).

Subautopalatine toothplate

Ostariophysans do not have a dermopalatine (Fink & Fink 1981: 315); however, dentate elements associated with the autopalatine are present in some catfishes; recently, Howes & Ayanomiya Fumihito (1991) considered that the posterior extension of the autopalatine of siluroids is probably the dermopalatine. The development of the catfishes studied herein does not support such a hypothesis. Large individuals of the diplomystid *Olivaichthys* have a tooth patch attached by a ligament to the autopalatine; this element was identified as the dermopalatine by Arratia (1987a), who considered the presence of a dermopalatine appearing late in ontogeny to be an autapomorphy of *Olivaichthys.* In contrast, in *Amia* and primitive teleosts, the dermopalatine ossifies before the autopalatine (Arratia & Schultze 1991: Table 1).

Starks (1926: Fig. 12) figured a large 'dermopalatine' closely associated with the medial face of the vomerine toothplate and posterior to a parasphenoid toothplate in an adult 'pimelodid', *Sciadeichthys troscheli.* Recently Bailey & Stewart (1984: Figs. 2B, 5a—c) labelled a bagrid toothplate as the dermopalatine; this element is partially ventral to the autopalatine. Skelton et al. (1984) named a similar toothplate in 'bagrids' as the subpalatine. Grande (1987) however, named two plates present in †*Hypsidoris* as accessory ectopterygoid toothplates. One toothplate is ventral to the autopalatine (as in *Olivaichthys*) and the other toothplate is between the vomerine toothplate and the autopalatine (Fig. 22C). Unfortunately, this position has no connection with any ec-

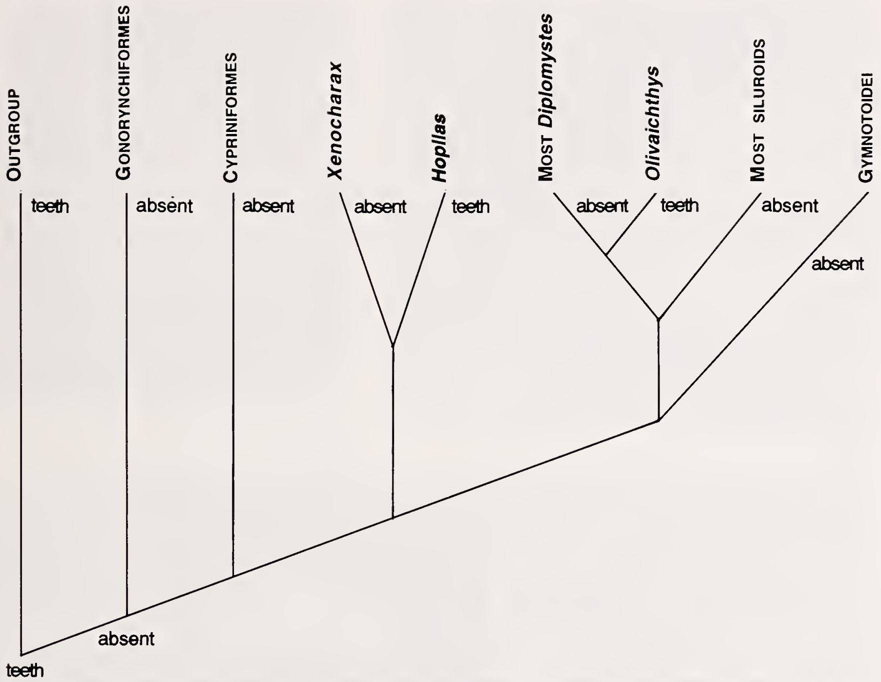

Fig.39: Distribution of autopalatal toothplate in ostariophysans (hypothesis of relationships after Fink & Fink 1981). — absent: absence of toothplate; teeth: toothplate attached or fused to autopalatine.

topterygoid (even if this were present) and therefore the name accessory ectopterygoid toothplate is inappropriate in the absence of any convincing evidential support. While information on the ontogeny of the suspensorium is unavailable for some groups, it is not possible to judge whether the toothplate originates ventral to the autopalatine, or whether it is a displaced vomerine toothplate. I will therefore consider the dentate plate ventral to the autopalatine as a subautopalatine toothplate.

The distribution of the character — absence of dermopalatine (Fig. 39) — in ostariophysans, leads to the conclusion that the subautopalatine toothplate present in *Hoplias*, in some diplomystids, †hypsidorids, 'pimelodids', and 'bagrids' is a new formation. Because ontogenetic studies of most siluroids are lacking, as are detailed studies of larger individuals, it is uncertain how widespread the presence of the subautapalatine toothplate is among 'pimelodids', ariids, and 'bagrids'. A subautopalatine toothplate has not been observed in large ictalurids.

Antorbital

Although the antorbital is not part of the suspensorium, I will discuss here its connection with the suspensorium. The antorbital — highly modified in shape and size (Arratia 1987a) — connects by ligaments to the autopalatine, maxilla, and lateral ethmoid in most of the catfishes studied here (Fig. 38A—G). It may also be connected with the premaxilla (e.g., *Nematogenys, Ailia, Parapimelodus*, and some specimens of *Noturus*). The antorbital is connected with the 'supraorbital' (united by a ligament with the frontal) in *Trichomycterus* (Fig. 38G) as well as in other trichomycterids. There is no doubt that the antorbital has a sensory function because it carries the anterior part of the infraorbital sensory canal. In addition, it also participates in the movement of the maxillary barbel through its ligamentous connections to the autopalatine, maxilla, lateral ethmoid, and other bones (Fig. 38A—G). These facts characterize the siluroid antorbital (a synapomorphy of siluroids?). (A dermal antorbital that is attached by connective tissue to the lateral ethmoid, autopalatine, and maxilla is found in primitive characiforms.) The articulation of the antorbital with the autopalatine (Fig. 38F) present in some siluroids, is considered here to be an advanced condition present only in a few groups such as the schilbeids.

Metapterygoid

According to my studies, the only pterygoid bone consistently present in siluroids is the metapterygoid. Although it is a chondral bone, its appearance varies within catfishes. It is mainly formed as a perichondral ossification of pars metapterygoidea in diplomystids. The perichondral ossification is restricted to a small area in *Parapimelodus, Noturus, Eutropiichthys*, and all other siluroids studied here. Enlargement of the bone is achieved mainly by membranous outgrowths.

The metapterygoid in catfishes commonly occupies the position of both the ectopterygoid and entopterygoid in other teleosts. According to Boulenger (1904) and Hashmi (1957) the metapterygoid is absent in Siluridae. Starks (1926) identified the bone anterior to the quadrate as the ectopterygoid. Starks (1926: 324—325) based his identification on the fact that he "knows of no case where the pterygoid (ectopterygoid) if present is separated from the quadrate", "the metapterygoid, if represented at all, may be incorporated with the pterygoid; but it may be as well incorporated with the hyomandibular". The last interpretation has also been followed by Hoedeman (1960), Arratia & Menu Marque (1981, 1984), Arratia et al. (1978), Howes (1985), and Howes & Teugels (1989). However, Arratia (1990a) showed that the hyomandibula and metapterygoid are independent bones in loricarioids. Recently, Howes & Teugels (1989) interpreted the metapterygoid of some siluroids as a compound bone which in addition to the metapterygoid itself may include the ectopterygoid and entopterygoid. Since these authors did not offer evidence supporting such an interpretation and my observation on ontogenetic series does not support them, I will not discuss Howes & Teugels interpretation further.

In catfishes the metapterygoid (Lundberg 1982, Howes 1985, Arratia 1987a) commonly overlaps the anterior membranous outgrowth of the hyomandibula, similar to the position of the palatoquadrate cartilage in early ontogeny of other teleosts. Exceptions where the bones do not overlap, include siluroids such as the 'pimelodids' *Heptapterus, Rhamdia*, and *Parapimelodus* (Figs. 34A, B, 35A), and the 'bagrids' *Pseudeutropius atherinoides* (Tilak 1964: Fig. 20) and *Bagrus bayard* (Skelton et al. 1984: Fig. 15A). A very narrow overlap is present in *Nematogenys* (Fig. 28D).

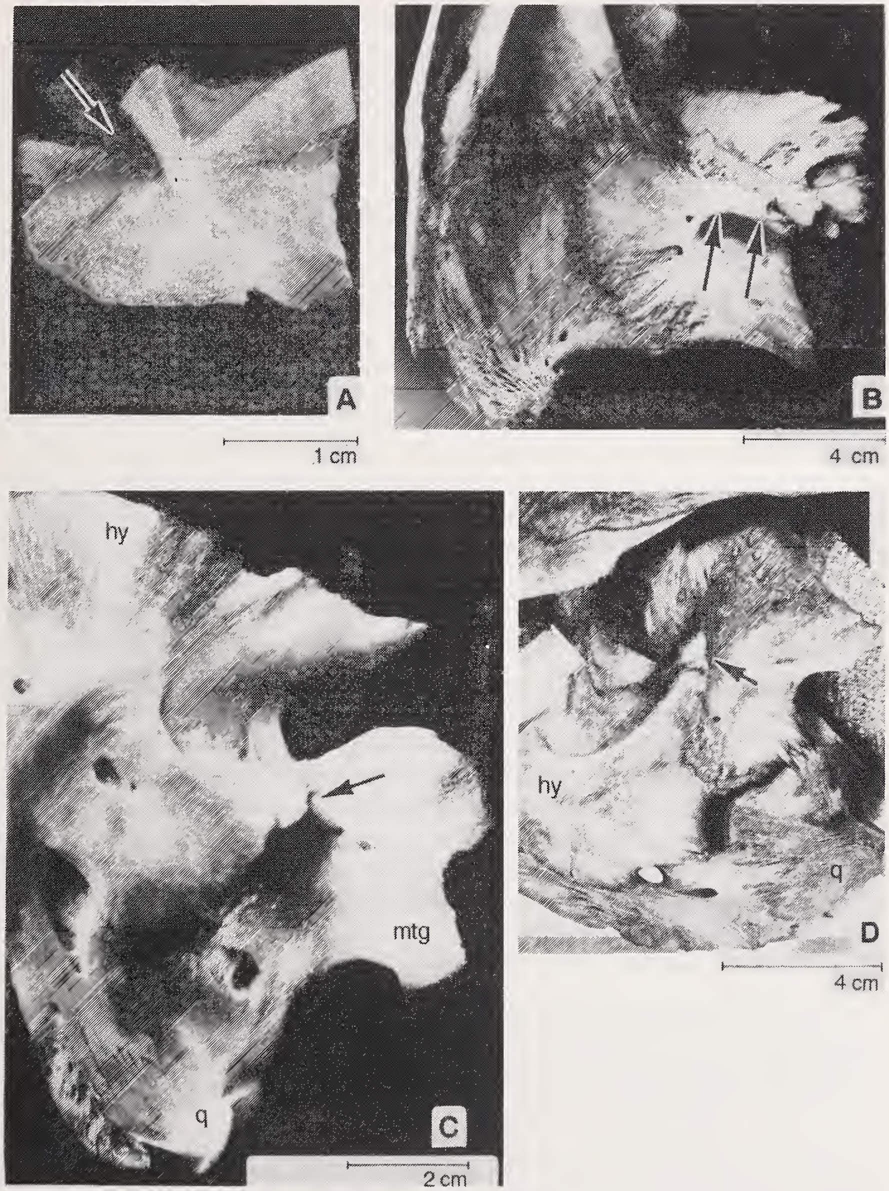

Fig.40: Metapterygoid, lateral views. — A: *Amia calva* (disarticulated specimen; KU uncat.); arrow points to a notch; B: *Pylodictis olivaris* (neurocranium of 360 mm in length; KU 13122); C: *Ictalurus furcatus* (neurocranium of about 270 mm in length; KU 15866); D: *Ictalurus furcatus* (neurocranium of about 280 mm in length; KU 11343). B—D, Arrows point to the 'lateral process' of metapterygoid.
hy: hyomandibula; q: quadrate.

An enormous metapterygoid (which forms much of the palatal region) is characteristic of *Eutropiichthys* (Fig. 37A), whereas a rudimentary metapterygoid is present in advanced trichomycterids such as tridentines and vandellines (Arratia 1990a: Figs. 11A—C). In the trichomycterid *Ochmacanthus* the autopalatine enlarges to form most of the palate. These are examples of the widely divergent patterns of construction of the palatal region in catfishes.

The metapterygoid in catfishes such as diplomystids (Figs. 17A, 18C), †*Hypsidoris* (Fig. 22D), and *Parapimelodus* (Fig. 35A), has a dorsal notch separating the processus basalis and the posterodorsal part of the metapterygoid as in *Amia* and primitive teleosts (Fig. 40A; Arratia & Schultze 1991: Figs. 1D, 15B, 20A, 23, 24). The processus basalis is small or absent in advanced siluroids (e.g., *Trichomycterus, Eutropiichthys*).

A well-developed 'lateral process' is consistently present on the lateral surface of the metapterygoid in ictalurids such as *Pylodictis olivaris* (Fig. 40B; Lundberg 1982: Fig. 25C) and in large *Ictalurus furcatus* (Fig. 40C—D). Based on the distribution of this character among ostariophysans, the 'lateral process' present in *Pylodictis* is nonhomologous with the processus metapterygoideus lateralis present in *Amia* and primitive teleosts (Arratia & Schultze 1991: Figs. 20A, 23, 24), because it is missing in more primitive catfishes as well as in other primitive ostariophysans. Instead it is a specialization of primitive ictalurids in which the process serves as attachment for the anteriormost section of the levator arcus palatini muscle.

The ventrolateral or anterolateral projection of the metapterygoid is named here the ectopterygoid process because it occupies the position of the ectopterygoid in other teleosts. There is no ontogenetic evidence that would cause us to consider the process as a fused ectopterygoid, as proposed by Howes & Teugels (1989). The ectopterygoid process is variable in extent in primitive catfishes and may be a well-developed sharp projection (Figs. 17A—C, 18C, 35A, B), or a moderately long, slightly expanded projection (Figs. 28B, 32) or a rudimentary projection (Fig. 26C). Large *Ictalurus furcatus* may not have the process at all. Advanced catfishes such as the trichomycterids lack the basal, lateral metapterygoid, and ectopterygoid processes; this combination of features is an advanced one within catfishes.

The joint between the posteroventral part of the metapterygoid and the anterior or anterodorsal part of the quadrate is a unique feature of siluroids within the teleosts. In other teleosts, the ventral or anteroventral part of the metapterygoid articulates with the posterior, posterodorsal or anterodorsal part of the quadrate. Within siluroids, the joint between the ventral part of the metapterygoid and anterodorsal part of the quadrate is interpreted as the primitive condition, retained in diplomystids and nematogenyids. The joint between the posteroventral part of the metapterygoid and anterior projection of the quadrate is shared by several siluroids including ictalurids, trichomycterids, pimelodids, and schilbeids. The joint between the metapterygoid and symplectic cartilage in diplomystids and nematogenyids is interpreted as a derived feature within siluroids. This state is not homologous to the situation found in the clupeomorph *Denticeps* (Arratia & Schultze 1991: Figs. 28A, B), cypriniforms (Fig. 8A, B) or characiforms (Fig. 10A), because the development of the metapterygoid differs between siluroids and other ostariophysans.

The posterodorsal part of the metapterygoid is commonly sutured (sutura serrata or dentata) with the anteroventral part of the anterior membranous outgrowth of hyomandibula in catfishes. A lap joint or sutura limbata is unique to the diplomystids and a sutura harmonica may be found in the trichomycterids. There is no sutural contact between the hyomandibula and metapterygoid in some catfishes such as *Heptapterus, Rhamdia*, and *Parapimelodus* (Figs. 34A, B, 35A), *Loricaria* (Arratia 1990a), and *Pseudeutropius* (Tilak 1964: Fig. 20). In the sisorid *Glyptosternum* (Tilak 1963: Fig. 45), there is a short suture and a ligament between the metapterygoid and hyomandibula, an uncommon condition within siluroids.

The medial part of the metapterygoid may be connected through ligaments to bones of the cranium. For instance: the ligamentous connection between the metapterygoid and parasphenoid, and metapterygoid and posterior part of the vomer is unique to diplomystids (Fig. 19D). The metapterygoid is ligamentously connected to the orbitosphenoid in catfishes such as *Ameiurus* (Fig. 27A) and tachysurids (Tilak 1965: 157). A strong ligament between the metapterygoid and vomer is present in *Galeichthys* and *Bagre marinus.*

Dermo + metapterygoid

The metapterygoid itself does not bear dermal toothplates in teleosts (Jollie 1986); however, the metapterygoid of *Parapimelodus* (Fig. 35B, C) bears a few teeth anteromedially as it does in the 'bagrid' *Chrysichthys brachynemas* (Skelton et al. 1984: Fig. 14A). This bone is therefore not the metapterygoid alone, but the metapterygoid fused with a dermal toothplate. This compound bone is unusual in teleosts, even though Daget (1964) has mentioned it for some. A dermo + metapterygoid is unknown in other 'pimelodids'.

A dermal toothplate is medial to the metapterygoid in the tachysurids *Tachysurus gagora* (Tilak 1965: Fig. 14), *T. serratus*, and *T. thalasinus*. The toothplate is attached by ligaments to the autopalatine and lateral ethmoid according to Tilak (1965: 157), but unfortunately he did not mention whether there is an attachment between the metapterygoid and the toothplate. According to my interpretation, the metapterygoid toothplate — not present in diplomystids, most catfishes or other ostariophysans — is a neoformation as suggested by Tilak (1965). Whether the metapterygoid toothplate is an autapomorphy of *Tachysurus* or a synapomorphy of Tachysuridae has to be demonstrated.

Quadrate-metapterygoid-maxillary ligament

In most catfishes a ligament extends from the quadrate to the metapterygoid and maxilla (e.g., *Noturus*), or the ligament extends only between the quadrate and maxilla (e.g., *Diplomystes*), or the ligament extends only between metapterygoid and maxilla (ligament 5 of Ghiot 1978; e.g., *Pimelodus clarias*), or the ligament is absent (e.g., *Sorubin lima*; Ghiot 1978). A ligament only links the metapterygoid and the maxilla in *Para-*

pimelodus, Bagre, and *Galeichthys* (also *Pimelodus* and *Bagrus* according to Alexander [1965: 106]). The quadrate-metapterygoid-maxillary ligament, or quadrate-maxillary ligament (sometimes quadrate-autopalatine-maxillary ligament), or metapterygoid-maxillary ligament anteriorly bifurcates and each branch inserts on a separate, short articulatory process on the maxilla. I was unable to find a ligament between the maxilla and metapterygoid, or the maxilla and quadrate in *Loricaria*, but there is a ligament between the metapterygoid and premaxilla.

The ligamentum primordiale extends from the lower jaw to the medial side of the maxilla and is usually independent of the metapterygoid-maxillary ligament or the quadrate-metapterygoid-maxillary ligament in siluroids. However, these ligaments may be united such that the ligamentum primordiale in diplomystids inserts on the maxilla, premaxilla, and sometimes on the autopalatine (Arratia 1987a: 25—26, Fig. 7D).

At present, I am unable to evaluate the evolutionary transformations of this ligament that connects the maxilla with the suspensorium, because the information is lacking for most catfishes.

A noteworthy feature of *Galeichthys felis* is an elongate structure, that stains with alcian-blue. It is similar to the central rod within the maxillary barbel; it is attached to the lateral face of the angular (at the coronoid process) and the medial side of the maxilla. This rod lies beside the ligamentum primordiale. I have not seen any similar structures in other catfishes; this structure is anteriorly bifurcate, but it is not attached to the articular processes of the maxilla.

Quadrate and symplectic

In general, two types of quadrate (Fig. 15A, B) are found in catfishes:

1) a simple quadrate that may be present as a small, triangular-shaped bone mainly bearing articular facets (typical of diplomystids); and
2) a complex quadrate that is peculiarly shaped and has an anterior projection that may be of chondral (e.g., *Trichomycterus*; Arratia 1990a) or membranous origin (e.g., *Astroblepus*; Arratia 1990a).

Ontogenetic studies reveal that the enlargement of the complex quadrate and its peculiar shape are acquired through growth.

Catfishes lack the posterior or posteroventral membranous process of the quadrate found in other teleosts. In adults of some ictalurids such as *Ictalurus*, the quadrate (Fig. 41A, B) has a chondral posterior expansion (occupying the position of the membranous posterior process of other teleosts) that sutures to the preopercle.

The presence or absence of a symplectic is open to interpretation. I interpret the cartilage between the hyomandibula and quadrate as the remnant of the symplectic cartilage present early in ontogeny; an ossified symplectic is absent in siluroids. The cartilage has been considered as a remnant of the symplectic or a symplectic cartilage by McMurrich (1884a), Herrick (1901), Kindred (1929), Bhimachar (1933), Skelton (1981), Howes (1983a), and the present paper. This cartilage forms a bridge between the hyomandibula and quadrate. In other teleosts (Arratia & Schultze 1991) the hyomandibula articulates with the symplectic, not the quadrate.

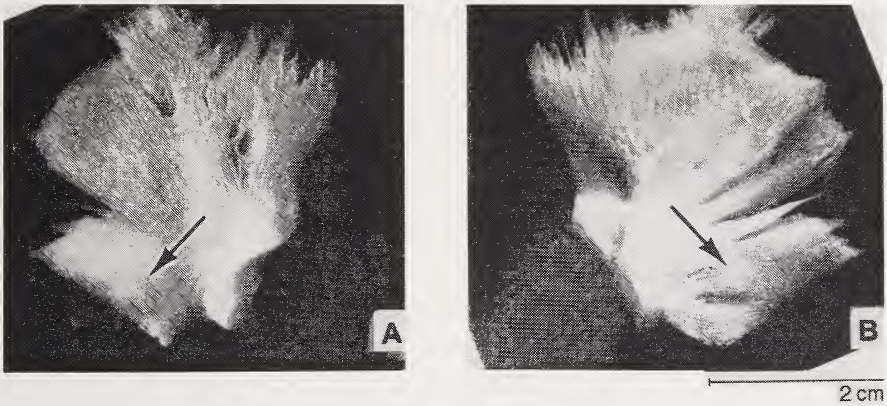

Fig.41: Quadrate of *Ictalurus punctatus* (815 mm standard length; KU 15342). — A: Lateral view; B: Medial view. The chondral posteroventral process of the quadrate is indicated by an arrow.

Ontogenetic studies do not support the loss or fusion of bones (e.g., quadrate and symplectic), but my interpretation has support in the presence of a large cartilaginous symplectic in some diplomystids (Fig. 14A, B) and in *Hypophthalmus* (Howes 1983a: Fig. 23), and in the fusion of the hyo-sympletic and pterygoquadrate early in the ontogeny of siluroids. This fusion produces a special alignment of the hyomandibula and quadrate that is unique to siluroids (Ryder 1887, Kindred 1929, de Beer 1937, Srinivasachar 1956, 1957, 1958a, b, Arratia 1988, 1990a).

An ossified, separate 'symplectic' is present in *Malapterurus* according to Howes (1985: Fig. 13); but this bone occupies a different position and has a unique relationship with the hyomandibula. It is not part of the suspensorium itself, but an ossification lateral to the hyomandibula and quadrate and should not be considered a symplectic.

Hyomandibula

Some of the most interesting features of the hyomandibula include the following features.

1) The presence of a well-developed anterior membranous outgrowth that enlarges during growth. This is an advanced condition within siluroids shared by many catfishes; diplomystids and nematogenyids have a small anterior membranous outgrowth in comparison with siluriforms such as schilbeids and trichomycterids (compare Figs. 17A, 28D, 37A). The anterior membranous outgrowth is rudimentary in 'pimelodids' such as *Heptapterus, Pimelodus, Rhamdia*, and *Parapimelodus* (Figs. 34B, 35A), and in certain 'bagrids' (e.g., *Mystus* and *Rita*; Tilak 1965).
2) The anterior membranous outgrowth of the hyomandibula and the metapterygoid support the eye in some siluroids, including *Eutropiichthys* and *Loricaria*. The eye lies only on the hyomandibula in *Hypostomus*. In primitive catfishes such as diplomystids and nematogenyids, the eye lies on the metapterygoid.
3) A posterior process (Fig. 42B, C) placed between the processus posterodorsalis and opercularis at the posterior margin of the hyomandibula is present in some cat-

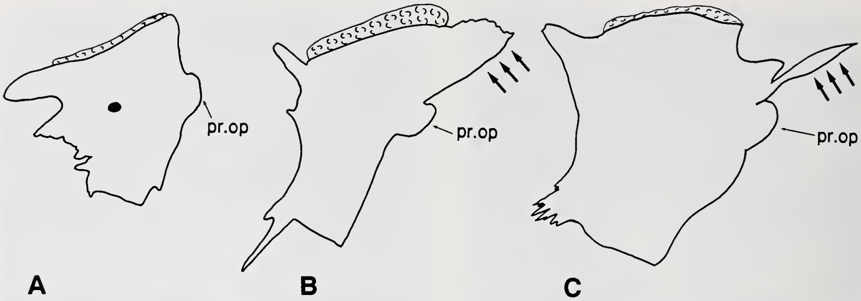

Fig.42: Diagram of hyomandibula. — A: *Diplomystes camposensis*; B: *Rhamdia sapo*; C: *Bagre marinus*. Arrows point to the processus levator operculi.
pr.op: processus opercularis.

fishes. I identify it as the processus levator operculi because it serves as origin site of the levator operculi muscle. It is absent in diplomystids (Figs. 14A, B, 16A—C, 42A), †*Hypsidoris*, and ictalurids, whereas it is broad and ends in a sharp projection in *Nematogenys* (Fig. 28D). It is long in *Heptapterus* and *Rhamdia* (Figs. 34B, 35A, 42B), in *Bagre* (Fig. 42C), and *Arius* (Rao & Lakshmi 1984). In *Nematogenys*, the levator operculi originates on the processus levator operculi of the hyomandibula and on the pterotic; it inserts on the lateral surface of the opercle (Fig. 43B), a unique condition of the family Nematogenyidae according to Howes (1983b). A similar lateral insertion on the opercle is present in *Heptapterus* (Fig. 43C); this condition is autapomorphic to Nematogenyidae and *Heptapterus*. In *Rhamdia* (Fig. 43D) and *Parapimelodus*, the levator operculi originates on the medial aspect of the elongate processus levator operculi of the hyomandibula and inserts on the dorsal and dorsoposterior margin of the medial aspect of the opercle. In diplomystids, the lateral fibers of the levator operculi originate on the dorsoposterior margin of hyomandibula, the pterotic (mainly), and the posttemporo-supracleithrum (Fig. 43A); the insertion of the muscle is as in *Rhamdia*.

4) The position of the opening for the hyoideomandibular nerve trunk has a variety of patterns in adult catfishes and is a feature that needs more attention. The nerve pierces the hyomandibula and then runs lateral to it (Fig. 21A, B) in diplomystids, unlike any other extant siluroid or ostariophysan, where the nerve runs inside the bone. I consider the pattern in diplomystids to be an autapomorphy.
5) The presence or absence of the levator arcus palatini crest and process (that are well-developed in most diplomystids and ictalurids) is another interesting feature that needs attention. This is because it results in change of the insertion of the levator arcus palatini muscle. The muscle has two sections in *Diplomystes camposensis* (Fig. 21C) and *Ictalurus punctatus* (Fig. 26C), whereas it has three sections in *Diplomystes chilensis* (Fig. 21D). The muscle (Fig. 28C) is divided into three sections, almost independent slips, in *Nematogenys*, whereas only one large muscle is present in *Parapimelodus*. The division of the levator arcus palatini muscle was mentioned first by McMurrich (1884b) and later by Winterbottom (1974) for ictalurids. In all of the taxa mentioned above, the insertion of the levator arcus palatini muscle is on

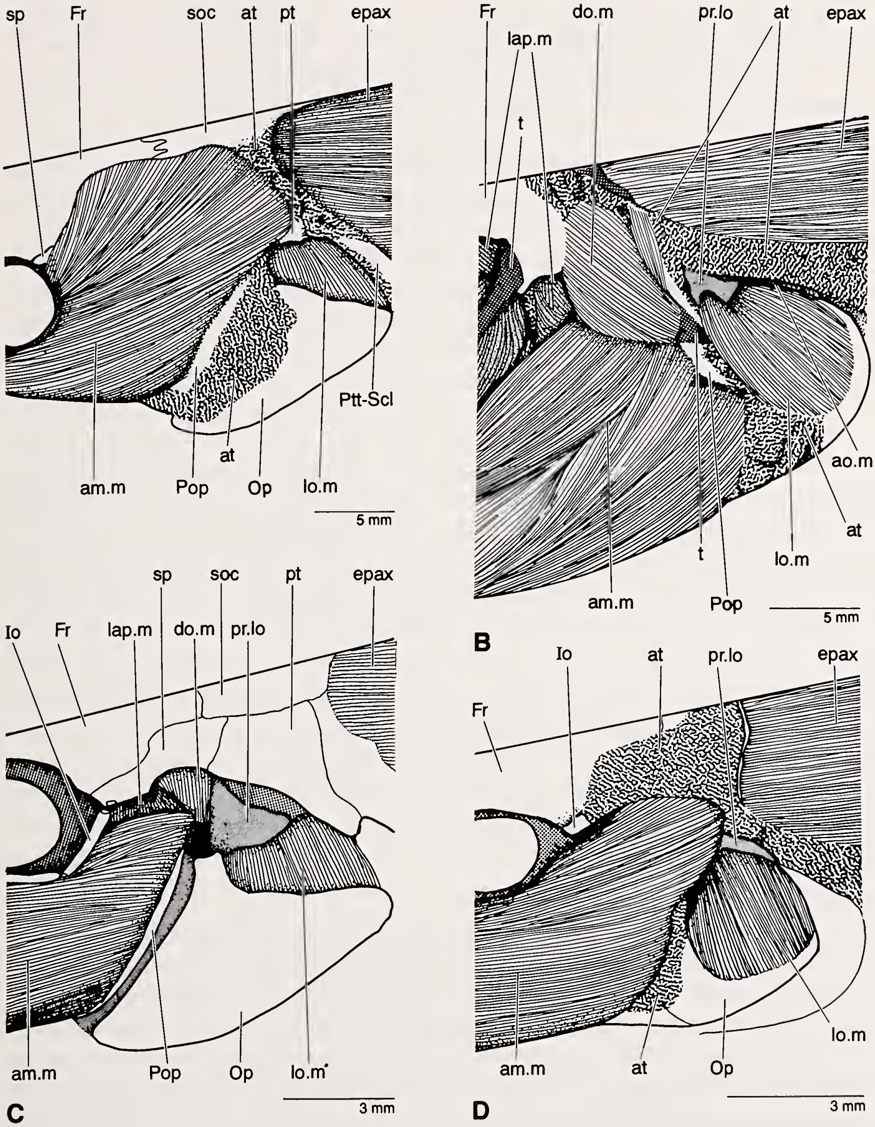

Fig.43: Levator operculi and its relationships in certain catfishes; dorsolateral view of posterior part of head. — A: *Diplomystes camposensis* (PC 220189); B: *Nematogenys inermis* (PC uncat.); C: *Rhamdia sapo* (PC 100285); D: *Heptapterus mustelinus* (PC 147).

at: adipose tissue; am. m: adductor mandibulae; ao. m: adductor operculi; do. m: dilator operculi; epax: epaxialis; Exc: extrascapular; Fr: frontal; Io: infraorbital; lap. m: levator arcus palatini; lo. m: levator operculi; Op: opercle; Pop: preopercle; pr.lo: processus levator operculi; pt: pterotic; Ptt-Scl: posttemporo-supracleithrum; soc: supraoccipital; sp: sphenotic; t: tendon.

the frontal and sphenotic. Although the muscle originates close to the lateral ethmoid in diplomystids, I have not seen the muscle originating on this bone. In *Nematogenys*, the muscle originates at the posterior orbital portion of the frontal and sphenotic; in *Parapimelodus*, the muscle originates mainly or only on the sphenotic.

6) The joint between the hyomandibula and preopercle is variable. Catfishes do not have a preopercular process on the hyomandibula, but the preopercle articulates with the posteroventral margin of the hyomandibula through a harmonic suture (e.g., diplomystids: Fig. 17A), or through a dentate or serrate suture with the posteroventral margin of the hyomandibula (e.g., large ictalurids: Fig. 26C). In some catfishes there is a harmonic suture joining both bones, but dorsally a space remains between them, as in *Eutropiichthys* (Fig. 37A).
7) The cranial bones framing the hyomandibular fossa or facet for the hyomandibula are important to consider (Table 1). The diplomystids are unique in that the processus anterodorsalis of the hyomandibula articulates bone-to-bone with the pterosphenoid and the pterosphenoid forms most the articulation throughout growth. In cypriniforms and gymnotoids only a small section of the pterosphenoid articulates with the hyomandibula, and in this case, through cartilage. In some ictalurids, such as *Ictalurus*, the processus anterodorsalis articulates bone-to-bone with the frontal. In catfishes the autosphenotic and pterotic frame the hyomandibular fossa and this is the common condition (Table 1).

   The inclusion of the prootic in the hyomandibular fossa is characteristic of primitive siluroids (Diplomystidae) and some more advanced siluroids (Nematogenyidae and Trichomycteridae) (Table 1). However, in Trichomycteridae the sphenotic is fused with the prootic to form a single element and this element is part of the hyomandibular fossa. In trichomycterids, the pterosphenoid also forms part of the fusion, but is not included in the hyomandibular fossa.

Dermal pterygoids

The reduction in size and number of pterygoids has been considered a specialization of siluroids by McMurrich (1884a), Starks (1926), Nawar (1954), Srinivasachar (1958b), Joseph (1960), and Gosline (1975). As Regan (1911) and Alexander (1965) noted, the ectopterygoid is commonly absent in catfishes, as is the entopterygoid. Pterygoid bones in most catfishes are highly specialized sesamoid elements, connected by ligaments to cranial bones or other bones of the suspensorium; including the metapterygoid and/or autopalatine, or additional bones whose function is unclear (e.g., additional pterygoid in *Parapimelodus*; Fig. 36A).

The bone described here as a dermal ectopterygoid — homologous with that of primitive ostariophysans — is found in some individuals within the Diplomystidae, on one or both sides of the palatal region (Figs. 16A—C, 17A, 19A—D). This small element is ventral to the autopalatine and both bones are attached by connective tissue. It does not articulate with either the entopterygoid or the quadrate, as is generally found in other ostariophysans and teleosts.

Sesamoid 'entopterygoids'

'Entopterygoid' types 1—7 have well-defined ligamentous connections with surrounding bones. For instance, it is common for the catfishes I studied to have a ligament between the metapterygoid and 'entopterygoid' types 1—7 (Fig. 2A—G). In addition, 'entopterygoid' types 1—7 may be joined only to the vomer (types 1—2), or only to the lateral ethmoid (types 3, 5) or to both bones (types 4, 6, 7). It is the common condition of 'entopterygoid' types 2—7 to be linked simultaneously to autopalatine, metapterygoid, and one or more cranial bones (e.g., lateral ethmoid, vomer). A ligamentous connection between the sesamoid 'entopterygoid' and the vomer is not unique to the Diplomystidae as was stated by Alexander (1965), because it is present in other catfishes, including the Nematogenyidae and Ictaluridae. A ligamentous connection between 'entopterygoid' type 1 and the posterior part of the vomer is unique to diplomystids, because in other catfishes the connection is achieved through the anterior part of the vomer (lateral wing) (compare Figs. 19D, 27A—C, 28A, 33).

'Entopterygoid' types 2—7 have a consistent link between the autopalatine and metapterygoid (Fig. 2B—G). The ligamentous connection may be direct, that is from the autopalatine to the 'entopterygoid' and then to the metapterygoid (Fig. 2B—D, G), or it may involve an 'ectopterygoid' type 1 (that appears early in ontogeny as a calcification in the autopalatine-metapterygoid ligament) between the autopalatine and the 'entopterygoid' types 5—6 (e.g., *Bagre*, *Parapimelodus*; Figs. 2E, F, 36A, C). The link is absent in diplomystids.

These data may not appear to be useful when examined separately, but the study of the bones *in situ*, and their relationships with the surrounding bones, reveals the presence of well-defined patterns of suspensoria in catfishes. Fig. 13C shows that diplomystids have a unique pattern of position and relationship of the autopalatine, ectopterygoid, entopterygoid and 'entopterygoid' type 1 (when present). Even though there is intraspecific variation within the family, the absence of the three pterygoids again produces a pattern not found in any other siluroid.

Comparison between 'entopterygoid' types 1—7 described here with those in the literature is difficult, because ligamentous connections have not been commonly mentioned. Nevertheless, I would like to discuss some of the sesamoid 'entopterygoids' described by Tilak (his ectopterygoid). A long, L-shaped entopterygoid ventral to the autopalatine anteriorly and in close contact with the hyomandibula posteriorly, is present in the amblycipitid *Amblyceps mangois* (Tilak 1967: 64, Fig. 2). This 'entopterygoid' occupies a position and has a relationship that differs from entopterygoids types 1—7 (see Terminology); but without knowing its precise ligamentous connections, it is not possible to further define it within the scheme presented here. Gosline (1975: 17) suggested that there was a remote resemblance of this amblycipitid entopterygoid to the bone in sisorids labelled AB in Tilak (1963a: Fig. 42). Bone AB of Tilak does not posteriorly contact the hyomandibula and it may be an additional pterygoid. Moreover, the entopterygoid in *Amblyceps* is dorsally joined by a ligament to the hyomandibula, unlike the catfishes studied here.

The 'entopterygoid' generally does not bear teeth in catfishes; nevertheless, a small, toothed 'entopterygoid' with a ligamentous connection to the metapterygoid is present in the tachysurid *Bactrachocephalus mino* (Tilak 1965: Fig. 13). A large toothed bone anterior to the metapterygoid was figured for *Tachysurus malabaricus* (Tilak 1965: Fig. 12). A large toothed bone with a posterior projection extending close to the quadrate is present in *Osteogeniosus militaris* (Tilak 1965: Fig. 9); and although Tilak (1965) named this bone the ectopterygoid, he recognized (p. 156) that the homology of this bone was not clear and that it could be a displaced autogenous toothed element.

Gosline (1975: 1) concluded that the palatine-maxillary mechanism is represented in modern catfishes by two basal types: that of *Diplomystes* with a toothed maxillary, and that of the 'Bagridae', Ariidae, and several other families in which the 'entopterygoid' forms a movable link between the autopalatine and the posterior part of the suspensorium. The present study reveals that a movable 'entopterygoid' is the most common condition in siluroids and is represented by several patterns, types 2—7 (Fig. 2B—G). In addition to the movable pattern is the immovable type found in large adult ictalurids and 'pimelodids' (e.g., *Rhamdia*), where the 'entopterygoid' becomes sutured to the metapterygoid or to the metapterygoid plus the vomer. The highly specialized pattern of *Trichomycterus* may also be immovable in adults. The determination of the homology of the sesamoid 'entopterygoid' and the dermal entopterygoid is difficult because of the intraspecific variation among the Diplomystidae. I consider the occasional 'entopterygoid' type 1 in *Olivaichthys* to be a new formation not present in other ostariophysans; however, it needs to be confirmed in more individuals before to accept it as an 'entopterygoid'. If this element is a true 'entopterygoid', then, the sesamoid 'entopterygoid' type 1 and the dermal entopterygoid are non-homologous because both pterygoids are present in the same individual. In contrast, 'entopterygoid' types 2—7 are found alone in catfishes without the dermal entopterygoid. According to the distribution of the entopterygoid and 'entopterygoid' (2—7) in ostariophysans, both elements are homologous, because an 'entopterygoid' is present in diplomystids as well as in all probable ancestors of siluroids. I interpret the sesamoid 'entopterygoid' as an evolutionary transformation of the dermal endopterygoid following Ax (1987).

Sesamoid 'ectopterygoid'

A tendon bone ectopterygoid or 'ectopterygoid' type 1 is connected by ligaments to the 'entopterygoid' and to the autopalatine (Figs. 2E, F, 34A, B, 35A, C, 36A) in some 'pimelodids', including *Pimelodus, Parapimelodus, Microglanis, Callophysus, Piramutana*, and *Sciades* (Regan 1911, present paper), in ariids (Regan 1911, Starks 1926, present paper), and in 'bagrids' (Regan 1911, Starks 1926, Jayaram 1966, present paper). A tendon bone 'ectopterygoid' is absent in some 'pimelodids' such as *Rhamdia, Pimelodella, Heptapterus, Hemisorubim, Sorubim*, and *Luciopimelodus* (Regan 1911, Starks 1926, Azpelicueta et al. 1981, present paper).

The tendon bone 'ectopterygoid' type 1 (a calcification within the autopalatine-metapterygoid ligament), which is a sesamoid bone because of its ligamentous connections and function is not homologous with the dermal ectopterygoid present in diplomystids because a tendon bone 'ectopterygoid' is absent in nematogenyids and ictalurids (see below), and probably in †hypsidorids; therefore, the presence of the 'ectopterygoid' type 1 is a neoformation found in some 'pimelodids', 'bagrids', and ariids.

Opercle and preopercle

I will comment here on the opercular bones, because of their relationship to the suspensorium.

The opercle in trichomycterines has two articulations: the dorsal one with the hyomandibula, and a ventral articulation, where an opercular process or knob fits in a concave articular surface of the preopercle (Arratia 1990b: Fig. 2B). This feature is interesting, because this is a semimovable articulation produced between two dermal bones. This

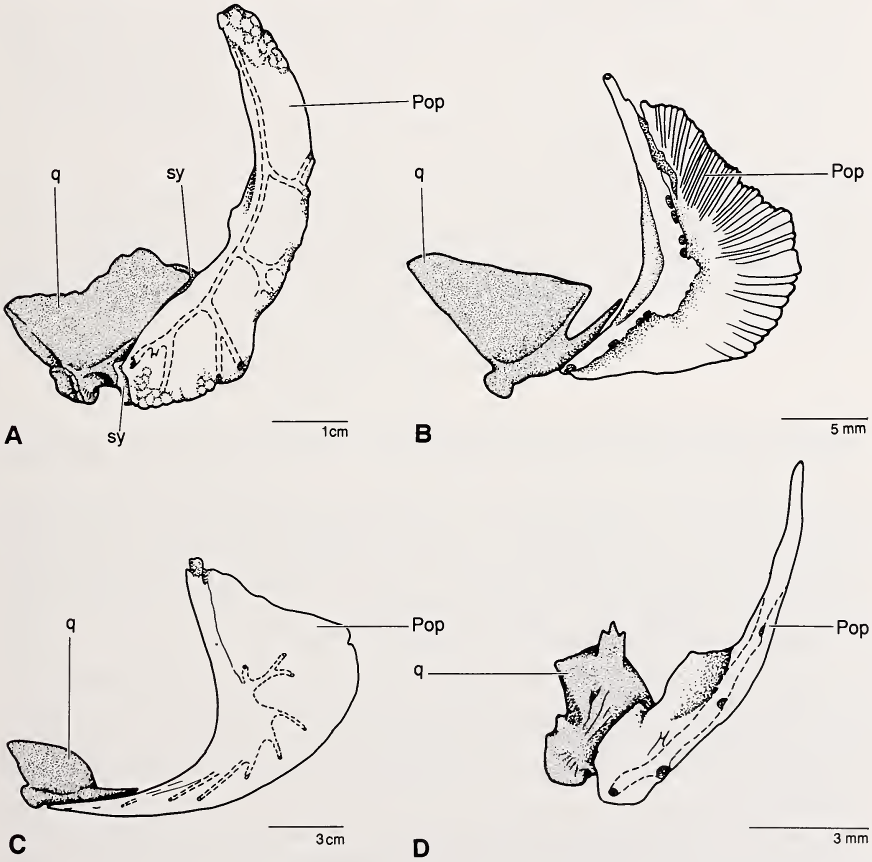

Fig.44: Preopercle and quadrate, lateral view. — A: *Amia calva* (disarticulated specimen; KU 21338); B: *Elops saurus* (225 mm standard length; KU 3053); C: *Chanos chanos* (neurocranium 148 mm in length; CAS-SU 35075); D: *Diplomystes nahuelbutaensis* (disarticulated specimen; BMNH 1867-10-2:22).
Pop: preopercle; q: quadrate; sy: symplectic.

implies a modification in the appearance of the dermal bone to produce two articular facets; in some specimens I have even found a small cartilage between the two articular facets. The question is: where is the cartilage derived from? I have not found evidence in young specimens that this cartilage originated in the hyo-symplectic; the only other possible hypothesis is that it is formed during growth from the transformation of connective tissue from the surrounding area.

The preopercle in most siluroids is commonly an elongate dorsoventral structure, mainly carrying the preopercular sensory canal. It has been proposed that catfishes (unlike other teleosts) lack a horizontal limb of the preopercle (Fink & Fink 1981: 321). My comparative studies reveal that the preopercle of primitive catfishes has both the dorsal and ventral limbs and carries the sensory canal just like it does in *Amia* and in other teleosts (Fig. 44A—D). The preopercle of most siluroids has a short ventral limb; in addition, it lacks the posterior or posteroventral outgrowth present in most other teleosts (Fig. 44B, C). In some siluroids, including *Loricaria* and *Ochmacanthus*, it has a short dorsal arm and it does not reach the opercular process of the hyomandibula. It is longer in *Parapimelodus* and *Eutropiichthys* (Figs. 35A, 37A). The ventral part of the siluroids preopercle sutures to the posteroventral articular facet of the simple quadrate or quadrate complex.

The dorsal part of the preopercle may fit in a weakly-defined articular surface in the posteroventral part of the hyomandibula, or both bones may be so closely sutured that it is difficult to separate them in adult catfishes (because of fine bony trabeculae). The sutural relationship between the preopercle and the hyomandibula, symplectic cartilage, and quadrate is a synapomorphy of the catfishes.

COMPARISON AMONG OSTARIOPHYSANS AND THEIR RELATIONSHIPS

The suspensorium of ostariophysans has undergone many evolutionary transformations that provide useful characters at different hierarchic levels. Fink & Fink (1981: 315—321) described 67 synapomorphies amongst the higher levels of ostariophysan relationships. In addition to these, there are several other features of the suspensorium that characterize ostariophysans and are analyzed below.

A combined outgroup that includes elopomorphs, clupeomorphs, and escoids have been used here as an outgroup to polarize characters. The numbers of the characters shown in the cladograms in Fig. 45A and B and Appendix 1 correspond to those below. Characters 39 to 131 are from Fink & Fink (1981) and correspond to characters outside the suspensorium.

Character 1. The cartilaginous palatoquadrate visible early in ontogeny is lateral to the dorsal portion of the hyoid arch (hyo-symplectic) in ostariophysans and other teleosts except for the catfishes and gymnotoids (Arratia 1988, 1990a, present paper, Arratia & Schultze 1991). In catfishes the posterior part of the palatoquadrate is fused with the hyoid arch, whereas in gymnotoids the posterior part of the palatoquadrate is medial to the dorsal limb of the hyoid arch. Although I have coded these conditions as 1 and 2 (Appendix 1), their polarity is unknown; e.g., it is unclear whether the placement of the palatoquadrate medial to the hyo-symplectic is more primitive than the fused elements in catfishes, or whether both conditions have evolved directly from the primitive stage. Character 1[1] might be a synapomorphy of gymnotoids, or possibly of siluriforms, whereas character 1[2] is a synapomorphy of catfishes.

1) Palatoquadrate:
   0: lateral to hyo-symplectic cartilage
   1: medial to hyo-symplectic cartilage
   2: fused with hyo-symplectic cartilage

Character 2. A single, elongate palatoquadrate (Figs. 3, 4A, B, 8A) is characteristic of ostariophysans and other actinopterygians except for catfishes. In catfishes, the palatoquadrate has a separate pars autopalatina (Figs. 24A—D, 46A—C; Arratia 1988, 1990a, Arratia & Schultze 1991).

2) Palatoquadrate:
   0: as a single unit
   1: pars autopalatina separate from the pars pterygoquadrata

Character 3. In ostariophysans as well as in other actinopterygians, the posterior part of the palatoquadrate is not fused to the dorsal part of the hyoid arch. In catfishes both parts are fused, forming the hyo-symplectic-pterygoquadrate plate (Figs. 24A—D, 46A—C; de Beer 1937, Srinivasachar 1956, 1957, 1958a, b, Arratia 1988, 1990a, Arratia & Schultze 1991).

3) Posterior part of palatoquadrate:
   0: not fused with hyo-symplectic cartilage
   1: fused with hyo-symplectic cartilage

Character 4 and 5. The posterodorsal part of the palatoquadrate is simple in primitive ostariophysans as well as in other teleosts; however, it is bifid in cypriniforms and characiforms. Within the ostariophysans, cypriniforms and characiforms share a posteriorly bifurcate pterygoquadrate early in ontogeny; this feature may be or may not be retained in adults (Figs. 8A—B, 10A; Arratia & Schultze 1991: Fig. 28A—E). According to Fink & Fink (1981: their characters 26 and 30) "in otophysans the endochondral portion of the metapterygoid is an axe-shaped bone, either double headed (most cypriniforms and characiforms), or single headed, with the posterior half of the bone absent (siluriforms)." I have not found ontogenetic evidence to support this character — that the posterior part of the metapterygoid is absent in Siluriformes, sensu Fink & Fink (1981). The metapterygoid of diplomystids and other primitive catfishes has the same notch separating the processus basalis from the posterior part of the early metapterygoid (similar to the metapterygoid early in ontogeny of other primitive ostariophysans and other teleosts and *Amia*; see Arratia & Schultze 1991). The metapterygoid of gymnotoids, however, is a small triangular bone lacking the processus basalis, the notch, and the posterior part that joins the hyomandibula and cartilage between hyomandibula and symplectic. I therefore consider that this character is not a synapomorphy of gymnotoids and catfishes, but a gymnotoid autapomorphy.

Fink & Fink (1981) also state that "In siluriforms the endochondral portion of the metapterygoid is triangular and appears to be equivalent to the anterior half of the metapterygoid in primitive otophysans" (their character 31). I am unable to find support for this character because the ontogeny of the fishes do not support it. The metapterygoid of diplomystids not only has a triangular-shaped endochondral portion; in addition, the triangular endochondral portion in gymnotoids is just the opposite (it extends posteriorly) of that illustrated for *Diplomystes* by Fink & Fink (1981: compare Figs. 11, 12) and herein (Figs. 12A, B, 17A, 18C).

4) Posterodorsal portion of the palatoquadrate (in young individuals and some adults):
  0: smooth
  1: bifid
  2: fused to the hyoid arch

When this character is run in the PAUP program as unordered, the result is that character-state 1 appears in parallel in Cypriniformes and Characiformes; when the character is ordered, the program interprets it as an otophysan synapomorphy, that has a reversal (4[0]) in gymnotoids. When character-state 2 is replaced by "?", the PAUP program interprets 4[0] as a synapomorphy of siluriforms.

5) Small, triangular chondral metapterygoid lacking notch and processus basalis:
  0: absent
  1: present

Character 6. Fink & Fink (1981) state that "In gonorynchiforms the suspensorium is elongate in a parasagittal plane in the region between the articular condyle for the quadrate and the hyomandibula" (their character 29). (This is however, not the articular condyle for the quadrate; it is for the lower jaw.) Although this character was considered by them to be an autapomorphy of the gonorynchiforms, a parasagittal elongation of suspensorium between the articular condyle of the quadrate and hyomandibula is not unique to gonorynchiforms among the ostariophysans. This is because parasagittal elongation is also present in the primitive *Xenocharax*. However, in these two cases, each is independently derived (compare Figs. 4D, 10A). In gonorynchiforms the parasagittal elongation is due to the separation between the quadrate and symplectic, whereas in *Xenocharax* the elongate symplectic is almost parallel to the long axis of the body and is medial to the quadrate. I propose to modify this character as follows:

6) Parasagittal elongation of suspensorium due to separation between the quadrate and symplectic:
  0: absent
  1: present

This character is only present in gonorynchiforms, among ostariophysans, and it is not found in other primitive teleosts — therefore it is a gonorynchiform autapomorphy.

Character 7. A bony autopalatine is present in ostariophysans, but not in gymnotoids (compare Figs. 4D, 8B, 10A, 12A, B, 17A). In the latter, the pars autopalatina is still present in most adult gymnotoids; however, some gymnotoids exhibit chondroidal osteogenesis in the pars autopalatina and therefore only a chondroidal autopalatine is formed (Fig. 12B—D).

7) Bony autopalatine:
0: present
1: absent

Character 8. A dermopalatine is absent in ostariophysans. Toothplate(s) associated with the autopalatine are found in certain catfishes (see below).

8) Dermopalatine:
0: present
1: absent

Character 9. In ostariophysans as well as other teleosts, the autopalatine articulates with one or more cranial elements; however, a cranial articulation — either direct or indirect via cartilage — is missing in gymnotoids, even in those forms with a chondroidal autopalatine.

9) Autopalatine articulates with neurocranium through cartilage or directly:
0: present
1: absent

Character 10. The anterior cartilage of the autopalatine contacts the mesethmoidal-vomerine region throughout an intermediate cartilaginous, fibrocartilaginous, or chondroidal element in ostariophysans, with the exception of the catfishes and the gymnotoids.

10) Anterior cartilage of autopalatine, or pars autopalatina, or chondroidal autopalatine has a direct or indirect contact with neurocranium:
0: present
1: absent

Character 11. The autopalatine may articulate indirectly with the vomer as it does in ostariophysans. The autopalatine and vomer articulate indirectly through cartilage or fibrocartilage in primitive gonorynchiforms, characiforms, and catfishes. In diplomystids there is a large surface that articulates with the cartilage contacting the vomer (mainly), and also the lateral ethmoid, mesethmoid, and orbitosphenoid (Figs. 16B, C, 19B, C). A chondroidal element connects the autopalatine and vomer in adult cypriniforms. No articulation is present in gymnotoids.

11) Autopalatine and vomer:
0: articulate indirectly through cartilage or fibrocartilage
1: articulate indirectly through a chondroidal element between the mesethmoid and vomer (character 4 by Fink & Fink 1981)
2: do not articulate with each other

Character 12. The location of the articulation between the autopalatine and vomer differs among ostariophysans. The anterior cartilage or fibrocartilage of the autopalatine (Fig. 6A—D) articulates either directly or indirectly with the vomer in ostariophysans, with the exception of catfishes and gymnotoids. However, the condition differs in both groups. In catfishes, the articulation between the autopalatine and vomer is near the midpoint of the length of the autopalatine; in gymnotoids, there is no articulation between the pars autopalatina or the chondroidal autopalatine and vomer.

12) Vomerine articular surface on autopalatine:
0: placed anteriorly
1: placed at midlength of the autopalatine
2: no articulation present

When this character is run unordered, the PAUP program interprets 12[1] as a synapomorphy of catfishes and 12[2] as a synapomorphy of gymnotoids. When the character is ordered, the PAUP interprets 12[1] as a synapomorphy of siluriforms. When character-state 2 is replaced by "?", the PAUP program interprets 12[1] as a synapomorphy of siluriforms.

Character 13 and 14. The autopalatine articulates with the lateral ethmoid in cypriniforms, characiforms, and catfishes. Neither the pars autopalatina or the chondroidal autopalatine articulates with the lateral ethmoid in gymnotoids. Gonorynchiforms resemble primitive teleosts such as elopomorphs (Arratia & Schultze 1991: Fig. 35D, E) and osteoglossomorphs (without autopalatine; Arratia & Schultze 1991: Fig. 20A, B) in the lack of this articulation. However, part of the outgroup — the clupeomorphs and the esocoids — present the articulation. Considering that the closer outgroup has the articulation, I consider its presence as the primitive condition. Therefore, I interpret the absence of the articulation between autopalatine and lateral ethmoid as an autapomorphy of the gonorynchiforms. There are also differences in the location of the articular facet for the lateral ethmoid on the autopalatine (Fig. 6B—D). For instance, it is on the posterior cartilage of the autopalatine in *Xenocharax*, but on the medial surface of the small autopalatine in *Hoplias* (Fig. 11). It is closer to the posterior cartilage of the autopalatine than to the midlength in cypriniforms. It is at about the midlength of the bone or slightly anterior to it in catfishes.

13) Autopalatal articulation with lateral ethmoid:
0: present
1: absent
2: neither pars autopalatina or chondroidal autopalatine articulate with lateral ethmoid

There is no difference when the character is run ordered or unordered in the PAUP program. Character 13[1] is a gonorynchiform synapomorphy and 13[2] a gymnotoid synapomorphy. When character-state 2 is replaced by "?", the PAUP program interprets 13[1] as a gonorynchiform synapomorphy.

14) Articulation between the autopalatine and lateral ethmoid near the midlength of the autopalatine:
0: absent
1: present

This character is a synapomorphy of catfishes at the primitive level; several advanced catfishes lack this feature (e.g., Taverne & Aloulou-Triki 1974, Arratia 1990a).

Character 15. A single articular facet for the autopalatine or for a maxillary-autopalatal cartilage is present on the maxilla of ostariophysans, with the exception of catfishes. In primitive catfishes, two large articular facets on the maxilla articulate with the anterior cartilage(s) of the autopalatine (Figs. 18A, B, 19A—C).

15) Maxilla with two articular facets for autopalatine:
0: absent
1: present

Character 16. Fink & Fink (1981) state that "In siluriforms, a ligament extends between the maxilla adjacent to its articulation with the palatine and the dorsal tip of the lower jaw" (their character 45). The ligamentum primordiale in diplomystids extends between the maxilla (premaxilla and/or autopalatine, occasionally) (Arratia 1987a: Fig. 7A—C) and the coronoid cartilage of the lower jaw, not on the angular portion of the angulo-articulo-retroarticular. The gymnotoids examined here do not have a coronoid cartilage in the lower jaw and the insertion is between the maxilla and the bony dorsal tip of the coronoid process of the lower jaw.

16) Ligamentum primordiale connects the dorsal tip of the lower jaw with the maxilla:
0: absent
1: present

Character 17. Fink & Fink (1981) state that, "In cypriniforms the anterior portion of the palatine has a dorsomedial process which abuts against the mesethmoid" (their character 21). The processus dorsomedialis mainly abuts the lateral portions of the vomer in primitive cypriniforms and a short ligament connects this process and the mesethmoid. I therefore modify the character by Fink & Fink (1981) as follows:

17) Processus dorsomedialis of autopalatine ligamentously attached to mesethmoid:
0: absent
1: present

Character 18. Fink & Fink (1981), following previous researchers state that "In cypriniforms the palatine articulates posteriorly in a concave facet on the mesopterygoid." (Swinnerton 1902, Starks 1926, Ramaswami 1955a, 1955b, 1957, Roberts 1973, Gosline 1975, Fink & Fink 1981: their character 22). The posterior cartilage of the autopalatine articulates with the entopterygoid in the Diplomystidae and with the 'entopterygoid' type 2 in the Nematogenyidae. This differs from the cypriniforms in the mobility of the bones. In cypriniforms the articulation is semimovable, and the autopalatine is able to move in relation to the concave articular facet of the entopterygoid, and both bones are linked by a short ligament. In primitive catfishes, the entopterygoid or 'entopterygoid' type 2 are closely attached to the autopalatine and both bones are not able to move in relation to each other.

18) Semimovable articulation between the posterior cartilage of the autopalatine and a concave facet of the entopterygoid:
0: absent
1: present

Character 19. Fink & Fink (1981) state that, "In cypriniforms, the ectopterygoid does not overlap the palatine anteriorly, permitting mobility of the palatine relative to the rest of the suspensorium" (their character 25). It is true that the ectopterygoid does not reach the autopalatine in cypriniforms; instead, a ligament links both bones, and the autopalatine is mobile. However, in the characiform *Xenocharax* (CAS-SU 15639), there is a loose connection between the ectopterygoid and autopalatine, and the latter is mobile relative to the rest of the suspensorium; a situation not observed in *Hoplias* and other characiforms studied herein (not in *Xenocharax* specimens studied by S. Fink, in litteris). At this time, I therefore suggest changing this character as follows:

19) The ectopterygoid does not extend ventrally to the autopalatine nor does it suture with the autopalatine:
0: absent
1: present

Character 20. Fink & Fink (1981) state that, "In siluriforms the ectopterygoid is greatly reduced posteriorly (siluroids) or absent (gymnotoids)" (their character 26). This character is correct in part; I would like to point out that it is true only for diplomystids among the siluroids, which may have a small ectopterygoid or lack the ectopterygoid entirely. In most catfishes the ectopterygoid is absent. A few catfishes present an 'ectopterygoid'.

20) Ectopterygoid:
0: well developed
1: rudimentary or absent

Character 21. Fink & Fink (1981) state the following, "In siluroids the mesopterygoid is reduced to a small plate of bone posteromedial to the posterior tip of the palatine and is not in contact with the posterior portion of the suspensorium" (their character 27). This statement is, maybe, only true for diplomystids among the catfishes; an 'entopterygoid' is present in the other catfishes studied here. In other ostariophysans, as well as in other teleosts, the entopterygoid is a moderately large plate of bone articulating with the autopalatine, metapterygoid, and quadrate posteriorly (Figs. 4D, 8B, 10A).

21) Entopterygoid small, reduced to a small cup-like bone near the posterior cartilage of the autopalatine:
0: absent
1: present

Character 22. Fink & Fink (1981) also say that, "In gymnotoids the mesopterygoid has a vertical strut which usually articulates with the orbitosphenoid" (their character 28). The dorsomedial (Fig. 12A, B) process of the entopterygoid of gymnotoids may articulate with the orbitosphenoid as well as the cartilage between the orbitosphenoid and lateral ethmoid, or with all three elements together (e.g., adult *Gymnotus carapo*). The dorsomedial process of the entopterygoid is not present in other teleosts.

22) Entopterygoid with a vertical dorsomedial process:
0: absent
1: present

Character 23. The entopterygoid is the sole or the main support of the eye in most teleosts (Arratia & Schultze 1991); however the condition differs in catfishes, where the metapterygoid, the metapterygoid and the hyomandibula, or the hyomandibula alone may support the eye.

23) Entopterygoid is the main support of the eye:
 0: present
 1: absent

Character 24. Fink & Fink (1981) state that "In siluroids the metapterygoid is situated anterodorsal to the quadrate and forms part of the ventral border of the suspensorium (Fig. 11). In other ostariophysans and primitive teleosts, the metapterygoid is posterodorsal to the quadrate" (their character 32).

24) Metapterygoid anterodorsal to quadrate and forms part of the ventrolateral border of the suspensorium:
 0: absent
 1: present

Character 25 and 26. In the Gymnotoidei the metapterygoid (Fig. 12A, B) is at least medial to (in some species) and partially overlapped by the hyo-symplectic, a position which is retained in adults (e.g., *Sternopygus* in Fink & Fink 1981, Mago-Lecía et al. 1985: Fig. 3; and personal observation for *Gymnotus* and *Hypopomus*). This condition found in gymnotoids appears to be a unique feature of the group within the ostariophysans. In gymnotoids a ligament extends between the metapterygoid and posterior ceratohyal. A similar ligament is not found in other primitive ostariophysans and primitive teleosts.

25) Metapterygoid-posterior ceratohyal ligament:
 0: absent
 1: present

26) Posterior margin of the metapterygoid medial to hyomandibula:
 0: absent
 1: present

Character 27. In primitive siluroids the posterior margin of the metapterygoid is both sutured (dentata and/or serrata) and synchondrally articulates with the hyomandibula and quadrate (Figs. 17A, 22D). In most ostariophysans the posterior margin of the metapterygoid only articulates with the anteroventral part of the hyomandibula and the cartilage between the hyomandibula and symplectic (Figs. 4D, 8B, 10A); often the metapterygoid overlaps the hyomandibula producing a lap joint.

27) Posterior margin of metapterygoid sutured to hyomandibula and quadrate:
 0: absent
 1: present

Character 28. A membranous posteroventral process of the quadrate is present in most teleosts; this process is absent in siluroids.

28) Posteroventral process of quadrate:
 0: present
 1: absent

Character 29. In most teleosts the quadrate and hyomandibula are attached by connective tissue to the preopercle, whereas they are sutured in siluroids. Quadrate and hyomandibula are sutured to preopercle by a sutura harmonica in diplomystids (Fig. 17A) and nematogenyids (Fig. 28D), however sutura dentata and serrata are found in other catfishes (Figs. 22D, 26C, 33C, 34B). A combination of both sutura harmonica and sutura serrata is present in certain catfishes (e.g., *Synodontis*: Taverne & Aloulou-Triki 1974: Fig. 39).

29) Quadrate and hyomandibula are sutured to preopercle:
0: absent
1: present

Character 30. A metapterygoid-quadrate fenestra (Fig. 8B) is present in primitive cypriniforms such as *Opsariichthys* and *Zacco* and most characiforms. A quadrate-metapterygoid fenestra is absent in other ostariophysans.

30) Metapterygoid-quadrate fenestra:
0: absent
1: present

A metapterygoid-quadrate fenestra is shared by cypriniforms (at least in the primitive members) and characiforms; nevertheless the clupeomorph *Brevoortia* has also this fenestra (Gosline 1973) and also, a posteriorly bifurcated pterygoquadrate early in ontogeny. Gosline (1973) considered the metapterygoid-quadrate fenestra to be independently acquired in cypriniforms and characiforms by citing its presence in *Brevoortia*. Fink & Fink (1981: 320) considered the fenestra to be an otophysan character.

Character 31. A well-ossified, slightly triangular symplectic bone is present in ostariophysans and other teleosts except siluroids.

31) Symplectic bone:
0: present
1: absent

Character 32. The hyomandibula may articulate through one or two articular facets with the neurocranium (see Table 1).

32) Hyomandibula articulates with neurocranium through:
0: a double articular facet
1: a single articular facet

Character 33. The hyomandibula does not articulate with the pterosphenoid in most ostariophysans except the catfishes and gymnotoids (Table 1). However, the pterosphenoid and anterior part of the hyomandibula articulate bone-to-bone in diplomystids (an autapomorphy of Diplomystidae according to Arratia 1987) and a synchondral articulation between both bones is present in gymnotoids.

33) Pterosphenoid:
0: not articulating with hyomandibula
1: articulates bone-to-bone with hyomandibula
2: synchondrally articulates with hyomandibula

When the character is unordered, the PAUP program interprets 33[1] as a siluroid synapomorphy and 33[2] as a gymnotoid synapomorphy. When the character is ordered, 33[1] is interpreted as a siluriform synapomorphy.

Character 34. In most ostariophysans and other primitive teleosts the interhyal articulates with the cartilaginous region between the hyomandibula and symplectic. A small interhyal is present in certain catfishes such as diplomystids and nematogenyids, but it is absent in others (Arratia 1990a). However, in primitive siluroids the proximal part of the small interhyal does not articulate with the dorsal part of the hyoid arch and a ligament extends between the posterior ceratohyal and the hyomandibula (Arratia 1990a). A ligament connects both bones in catfishes without an interhyal.

34) Interhyal:
0: articulating proximally with the cartilaginous region between hyomandibula and symplectic
1: proximal articulation lost; a ligament joins the posterior ceratohyal and hyomandibula

Character 35. In gymnotoids the quadrate articulates with both the articular and the retroarticular when the mouth is closed; in other ostariophysans the retroarticular is not included in the articular facet. The retroarticular excluded from the quadrate-mandibular joint is a character present in most clupeocephalans; however, among the combined outgroup, the retroarticular is included in the quadrate-mandibular joint in elopomorphs and osteoglossomorphs (Nelson 1973, Patterson & Rosen 1977, Arratia 1987b). I consider the absence of the retroarticular from this joint as the primitive condition by comparison to the clupeocephalans.

35) Quadrate articulates with articular and retroarticular when mouth closed:
0: absent
1: present

Character 36. The retroarticular is a separate bone in the lower jaw of ostariophysans (Figs. 8C, 10C, D, 12E, F). However in catfishes the retroarticular is fused early in ontogeny to a well-developed articular and a small angular producing a compound element, the angulo-articulo-retroarticular (Fig. 20A, B). The retroarticular is partially fused to the angulo-articular in a large specimen of *Chanos chanos* examined here (CAS-SU 35075).

36) Retroarticular as separate ossification in adult individuals:
0: present
1: absent

Character 37. The Meckelian cartilage is an elongate cartilage — tube-like — in most teleosts. However it projects dorsally in siluroids, forming the coronoid process of the Meckelian cartilage, which is medial to the dorsal projections of the dentary and angular. A well-developed coronoid cartilage is present in the early ontogeny of catfishes and it is retained in adult primitive siluroids such as diplomystids (Figs. 20A, B; Arratia 1987a: Figs. 7A—C, 26A, B, F).

37) A well developed dorsal projection — coronoid process — of the Meckelian cartilage:
0: absent
1: present

Characters 38 to 130 correspond to characters taken from Fink & Fink (1981). When a character is modified, it is explained in the text.

Character 38. Kinethmoid bone attached by ligaments to the anterodorsal margin of the mesethmoid and to the premaxillary ascending process (Fig. 5B; Arratia & Schultze 1991: Fig. 30A):
0: absent
1: present

Character 39. Vomer articulated anteriorly with mesethmoid (Fink & Fink 1981: Fig. 4):
0: absent
1: present

Character 40. Anteroventral processes of the mesethmoid articulated directly with premaxillae (Figs. 5A—C, 19A—C; Fink & Fink 1981: Fig. 3C—F):
0: absent
1: present

Character 41. Compressed dorsal portion of the mesethmoid that appears slender from dorsal aspect:
0: absent
1: present

Character 42. Bone and cartilage of interorbital septum greatly reduced:
0: absent
1: present

Character 43. Basisphenoid:
0: present
1: absent

Character 44. Sacculi and lagenae situated more posteriorly and nearer the midline than in other primitive teleosts (Rosen & Greenwood 1970):
0: absent
1: present

Character 45. Foramen on the ventral face of the prootic through which the utricular otolith is visible (Weitzman 1962: Fig. 4):
0: absent
1: present

Character 46. Separate ossifications of the parietals are present from early ontogeny in the outgroup. However, separate parietals are absent in adult siluroids; a single bone occupies the position of parietals plus supraoccipital in other teleosts. This character is modified from the original description by Fink & Fink (1981).

46) Parietals as separate ossifications from early in ontogeny:
0: present
1: absent

Character 47. Dorsomedial opening into posttemporal fossa (Fink & Fink 1981: Fig. 5C):
0: absent
1: present

Character 48. Intercalar:
0: present
1: absent

Character 49. An exoccipital or exoccipital and supraoccipital with a prominent posterodorsal cartilaginous margin framing the foramen magnum is present in young primitive gonorynchiforms; the cartilaginous margin is comparatively smaller in large individuals.

49) Exoccipitals or exoccipitals and supraoccipital with a prominent posterodorsal cartilaginous margin framing the foramen magnum:
0: absent
1: present

Character 50. Large, globular lagenar capsule projecting well lateral to the cranial condyle:
0: absent
1: present

Character 51. Sclerotic bones:
0: present
1: absent

Character 52. In primitive catfishes and gymnotoids the infraorbital series is mainly formed by the infraorbital canal-bearing portions of the bones. In certain advanced siluriforms, the infraorbital may be slightly expanded.

52) Primitively, infraorbital series formed largely or entirely of canal-bearing portions of bones:
0: absent
1: present

Character 53. A dermal supraorbital bone is present in most members of the outgroup and in primitive ostariophysans. A dermal supraorbital bone is absent in siluriforms. In certain advanced catfishes such as trichomycterids, a tendon bone supraorbital forms early in ontogeny as an ossification of the ligament connecting the frontal with infraorbital bones. This element is not homologous with the dermal supraorbital, and it is considered herein as a new formation. The character by Fink & Fink (1981) is modified as follows:

53) A dermal supraorbital bone:
0: absent
1: present

Character 54. Subopercle:
0: absent
1: present

Character 55. An opercle approximately triangular-shaped is present in primitive catfishes and in numerous advanced ones. In contrast, the shape of the opercle is highly modified in certain catfishes such as the trichomycterids.

55) Primitively, opercle approximately triangular in shape rather than approximately rectangular:
0: absent
1: present

Character 56. Premaxillae extend furthest dorsally adjacent to the midline (Fig. 5B; Fink & Fink 1981: Fig 3B):
0: absent
1: present

Character 57. Very thin, flat premaxilla:
0: absent
1: present

Character 58. Maxilla posterolateral to lateral processes of mesethmoid and not articulating directly with mesethmoid (Figs. 5C, D, 19A—C; Fink & Fink 1981: Fig. 3C—F):
0: absent
1: present

Character 59. As Fink & Fink (1981) noted, the maxillary barbel in primitive cypriniforms is at the rictus of the mouth and may or may not be closely associated with the tip of the maxilla. All siluroids have a maxillary barbel that has a central rod of a substance that stains with alcian blue, but whose structure and composition are still unclear and vary among catfish groups (see Arratia 1987a, for literature on the subject). The maxillary central rod is proximally expanded and forms a support plate that is medial to the maxilla. The barbels of cypriniforms and siluroids are interpreted to have evolved independently.

59) Maxillary barbel:
0: absent
1: present

Character 60. Supramaxilla:
0: present
1: absent

Character 61. Teeth in the jaws:
0: present
1: absent

Character 62. Replacement teeth for outer row dentary teeth and some premaxillary teeth formed in trench or crypts in the bone:
0: absent
1: present

Character 63. "Epibranchial organ":
0: absent
1: present

Character 64. Teeth on the second and third pharyngobranchial and basihyal are present in primitive teleosts and in characiforms among ostariophysans. A basihyal is absent in catfishes, therefore the character by Fink & Fink (1981) is modified as follows:

64) Teeth from second and third pharyngobranchials and basihyal, when the last is present:
0: present
1: absent

Character 65. Two posterior pharyngobranchial toothplates:
0: present
1: absent

Character 66. Teeth on the fifth ceratobranchial:
0: present
1: absent

Character 67. Toothplates associated with basibranchials 1—3:
0: present
1: absent

Character 68. One pharyngobranchial toothplate:
0: absent
1: present

Character 69. Fifth ceratobranchial enlarged, extending much dorsally than the other ceratobranchials:
0: absent
1: present

Character 70. Teeth on the fifth ceratobranchial ankylosed to the bone:
0: absent
1: present

Character 71. Gasbladder divided into a smaller anterior and larger posterior chamber, with the ductus pneumaticus near the constriction (Rosen & Greenwood 1970):
0: absent
1: present

Character 72. Anterior chamber of gasbladder partially or completely covered by a silvery peritoneal tunic:
0: absent
1: present

Character 73. Peritoneal tunic of anterior chamber of the gasbladder attached to the anteriormost two pleural ribs (Rosen & Greenwood 1970):
0: absent
1: present

Character 74. Dorsal mesentery suspending the gasbladder heavily thickened anterodorsally near its attachment to the vertebral column and with many transverse fibers:

0: absent
1: present

Character 75. Expanded dorsomedial portions of anterior neural arches that abut against each other and the posterior margin of the exoccipital, forming a roof over the neural canal:
0: absent
1: present

Character 76. Neural arch anterior to the arch of the first vertebral centrum:
0: present
1: absent

Character 77. Anterior neural arch especially enlarged and with an extensive, tight joint with the exoccipital or exoccipital and supraoccipital:
0: absent
1: present

Character 78. Scaphium as a modification of the first neural arch:
0: absent
1: present

Character 79. Ossified claustrum:
0: absent
1: present

Character 80. The scaphium extends well anterior to the border of centrum 1:
0: absent
1: present

Character 81. Second neural arch modified to form the intercalarium:
0: absent
1: present

Character 82. Third neural arch with an elongate anterodorsal process which projects lateral to the ascending process of the intercalarium:
0: absent
1: present

Character 83. Anterior margin of the third neural arch approaches closely the posterior border of the neurocranium:
0: absent
1: present

Character 84. Dorsal part of the third neural arch with a distinct, short anterior margin which is vertical in orientation:
0: absent
1: present

Character 85. Anteroventral process of the third neural arch articulated or fused to a dorsal prominence on the second centrum:
0: absent
1: present

Character 86. Third and fourth neural arches fused together and to the complex centrum:

0: absent
1: present

Character 87. Fifth neural arch fused to its centrum:

0: absent
1: present

Character 88. Three anterior vertebrae foreshortened, with the anterior centrum being especially foreshortened, the second less so, and the third slightly less again:

0: absent
1: present

Character 89. Centra 2—4 fuse into a complex centrum in primitive catfishes (diplomystids); the fifth or more posterior centra are added to the fusion in other catfishes.

89) Centra 2—4 fused into a complex centrum:

0: absent
1: present

Character 90. The anteriormost parapophyses may be present in the outgroup or absent; when they are present, they are autogenous.

90) Anteriormost two parapophyses, when present, fused to the centra:

0: absent
1: present

Character 91. Parapophysis, fused or autogenous, on the anterior centrum:

0: present
1: absent

Character 92. Parapophysis of the second centrum:

0: present
1: absent

Character 93. Elongate lateral process of the second centrum that projects well into the somatic musculature:

0: absent
1: present

Character 94. Rib and parapophysis of third centrum anteriorly elongate proximally, rib truncate distally, and a thin curved transformator process attached to gasbladder:

0: absent
1: present

Character 95. The tripus fuses to the centrum by a thin, flexible lamellae as can be seen in early ontogeny in diplomystids, ictalurids, nematogenyids, trichomicterids, and other catfishes; however, as results of the growth of the surrounding bones and the movement of the tripus, the lamellae are commonly fragmented from early in ontogeny.

95) Parapophysis of tripus fused to the centrum (early in ontogeny) by a thin, flexible bony lamella which projects posterodorsally from the centrum:
0: absent
1: present

Character 96. Transformator processes of the tripus separated posteriorly by the width of the complex centrum:
0: absent
1: present

Character 97. Shortened pleural rib of the fourth centrum, and rib and parapophysis fused to each other, and having a median process, the os suspensorium, which is attached both to the mesentery suspending the gasbladder and gasbladder itself:
0: absent
1: present

Character 98. 'Transverse process' of the fourth vertebra with an ovoid, anterolateral face which approaches the suspensorium of the pectoral fin:
0: absent
1: present

Character 99. 'Transverse process' of the fourth vertebra expanded in a horizontal plane and the ovoid anterior face articulates with the suspensorium of the pectoral fin:
0: absent
1: present

Character 100. 'Transverse process' of the fourth vertebra fused to the complex centrum:
0: absent
1: present

Character 101. Os suspensorium with an elongate anterior horizontal process which is closely applied to surface of vertebral centra 2—4:
0: absent
1: present

Character 102. Os suspensorium without posteromedial process:
0: absent
1: present

Character 103. All pleural rib elements, particularly the fourth pleural rib and tripus, project from the centra at an angle close to the horizontal:
0: absent
1: present

Character 104. Single ossified element that comprises supracleithrum, ossified Baudelot's ligament, and perhaps also the posttemporal:
0: absent
1: present

Character 105. Reduction of number of postcleithra to one or none:
0: absent
1: present

Character 106. Baudelot's ligament attached to the skull in the region of the cranial condyle or the lagenar capsula:
0: absent
1: present

Character 107. Thick Baudelot's ligament bifurcated distally:
0: absent
1: present

Character 108. Anterior and posterior parts of Baudelot's ligament attached to the cleithrum:
0: absent
1: present

Character 109. More posterior pectoral fin-rays offset posteriorly from the anterior ray:
0: absent
1: present

Character 110. Flanges for muscle attachment proximally on the ventral pectoral ray halves about equal in size to those on the dorsal pectoral ray halves:
0: absent
1: present

Character 111. Pelvic girdle and fin:
0: present
1: absent

Character 112. Dorsal fin:
0: present
1: absent

Character 113. Anal fin elongate, extending along nearly the entire ventral margin of the body, from the region of the pectoral-fin origin anteriorly to the caudal fin or caudal filament posteriorly:
0: absent
1: present

Character 114. Middle radial ossification along the entire length of both dorsal and anal fin pterygiophores:
0: present
1: absent

Character 115. Anal fin-rays articulate directly with the proximal radials and distal radials are reduced:
0: absent
1: present

Character 116. Principal caudal fin-ray count is 9/9 or less:
0: absent
1: present

Character 117. Caudal support skeleton consolidated into a single element and caudal fin greatly reduced in size or absent:

0: absent
1: present

Character 118. Haemal arches anterior to that of second preural centrum are laterally unfused in part of the outgroup (e.g., elopomorphs; Schultze & Arratia 1988), whereas they are laterally fused in other part of the outgroup (e.g., osteoglossomorphs, clupeomorphs, salmonids; Schultze & Arratia 1988, 1989, Arratia 1991, Arratia & Schultze in press). However, there are significant differences in the time that the fusion occurs between the perichondral ossification of the haemal arch and the autocentrum. I modify this character as follows:

118) Haemal arches anterior to that of second preural centrum perichondrally fused to the autocentrum from early ontogeny:

0: absent
1: present

Character 119. According to Fink & Fink (1981), the haemal spine of preural centrum 1, the parhypural and hypural 1 are fused to the compound centrum at some stage of development. This is not completely correct because the parhypural and the hypural do not fuse to a 'compound centrum'. According to my studies on the development, histology, and macromorphology of the caudal skeleton I modify this character as follows:

119) Cartilaginous or ossified arcocentra of preural centrum 1 and that at the base of hypural 1 are fused to the 'compound centrum' in some stage of development:

0: absent
1: present

Character 120. Hypural 1 separated from the 'compound centrum' by a hiatus in adult stage:

0: absent
1: present

Character 121. Hypural 2 fused to a 'compound centrum':

0: absent
1: present

Character 122. Epurals:

0: three
1: two or fewer

Character 123. Dorsal and pectoral fin spines:

0: present
1: absent

Character 124. A unique alarm substance is present in the epidermis of the skin in most ostariophysans. It is unknown if diplomystids produce the alarm substance. Gymnotoids lack the substance (Pfeiffer 1977).

124) Unique alarm substance in the epidermis:
0: absent
1: present

Character 125. Ostariophysans have nuptial tubercles with a well developed keratinous cap (Wiley & Collette 1970). I have never seen nuptial tubercles with or without a keratinous cap in diplomystids. Keratinous skins are known in some siluroids (Wiley & Collette 1970, Arratia 1987a); apparently keratinous tubercles are not associated with breeding behaviour in siluroids.

125) Nuptial tubercles with a well developed keratinous cap:
0: absent
1: present

Character 126. Electrogenic condition:
0: absent
1: present

Character 127. Anus located well anterior on the body, ventral or anterior to the pectoral-fin origin:
0: absent
1: present

Character 128. Scales on body:
0: present
1: absent

Character 129. Adipose fin:
0: absent
1: present

Character 130. Posteromedial extension of the perilymph system of the ear, sinus impar, communicates to the ear vibrations transmitted from the gasbladder by modified skeletal structures of the anterior vertebrae:
0: absent
1: present

First cladistic analysis

When the 37 characters of the suspensorium (1—37) presented above and in Appendix 1 are analyzed using the PAUP 3 program, only three trees are generated (consistency index = 0.956; tree length = 45). The consensus tree differs in the arrangement of the gonorynchiforms, cypriniforms, and characiforms from that of Fink & Fink (1981: Fig. 1) and in Otophysi not being monophyletic (compare Figs. 45A & 45B).

The scheme of relationships generated with the 37 characters from the suspensorium is represented in figure 45B. Node A corresponds to the trichotomy among Gonorynchiformes, [Cypriniformes + Characiformes], and [Siluroidei + Gymnotoidei]. Node B corresponds to the branching of cypriniforms and characiforms, and is supported by two synapomorphies. Among the studied ostariophysans, the suspensorium of characiforms is the most generalized; it is characterized by one homoplasy; cypriniforms share

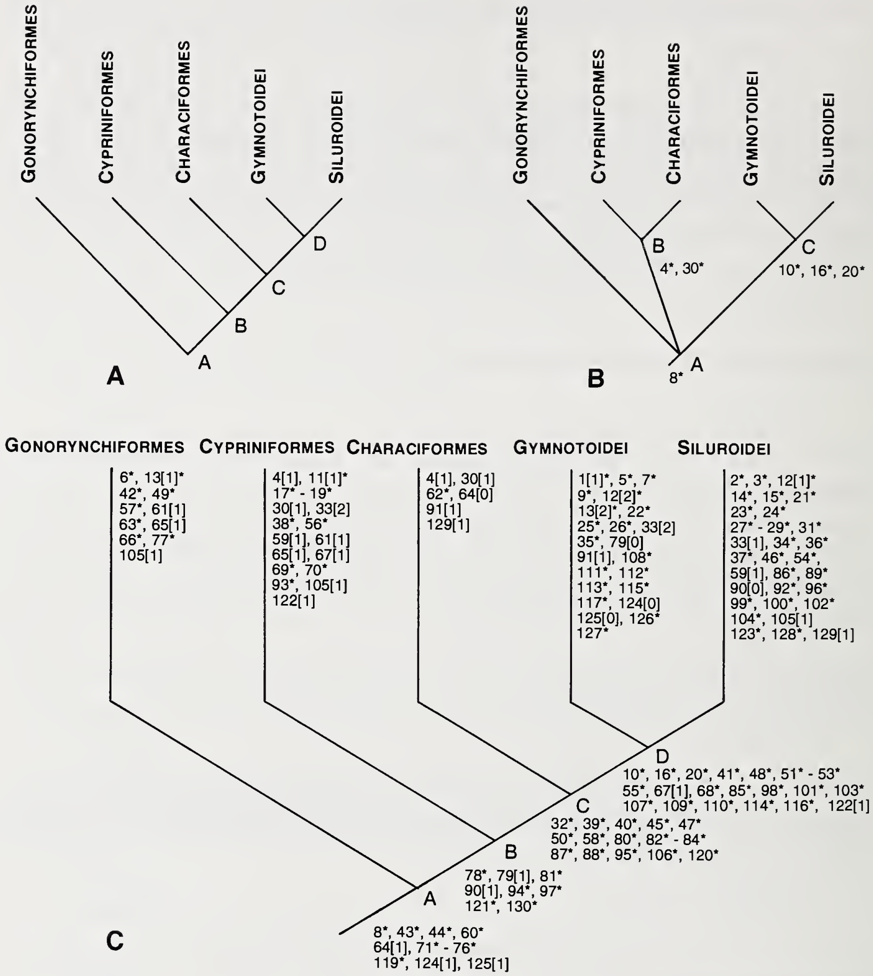

Fig.45: Hypothesis of phylogenetic relationships of ostariophysans. — A: According to Fink & Fink (1981); B: Based on 37 characters of the suspensorium (consistency index 0.956). Only the unique derived characters (*) are presented. For explanation of characters and character states see text and Appendix 1; C: Based on 130 morphological characters (consistency index 0.888). Homoplasies are presented by their character states, but an asterisk represents a unique derived character.

three unambiguous synapomorphies and one homoplasy. Node C corresponds to the branching of Siluroidei and Gymnotoidei and is supported by three synapomorphies.

The results of this study — based only on the suspensorium — partially support the schemes of relationships proposed by Rosen & Greenwood (1970), Roberts (1973), and Fink & Fink (1981) at the level of [Cypriniformes + Characiformes] and [Siluroidei + Gymnotoidei]. The sister-group relationship between catfishes and gymnotoids proposed by Fink & Fink (1981) is supported by additional characters of the suspensorium.

Second cladistic analysis

When the 37 characters of the suspensorium (1—37) plus 93 characters outside the suspensorium (from Fink & Fink 1981) presented above and in Appendix 1 are analysed using the PAUP 3 program, only one tree is generated (consistency index 0.888; tree length = 152). This tree has the same arrangement from that of Fink & Fink (1981) (compare Figs. 45A & 45C). There are no differences in the topology of the tree when the 130 characters are considered as ordered or unordered, but a slight difference in the consistency indices (0.888 and 0.871, respectively). There are no differences in the topology of the trees when all non-applicable conditions are coded as "2" (e.g., characters 1, 4, 11, 12, 12, and 13) or as "?", but a slight difference in the consistency indeces (0.888 and 0.885, respectively).

The suspensorium of ostariophysans provides a few synapomorphies at the higher levels. For example, one synapomorphy shared by ostariophysans (characters 8[1]): absence of a dermopalatine (see Fink & Fink 1981, Arratia & Schultze 1991). One synapomorphy (character 32[1]) shared by the characiphysans: hyomandibula articulates with the neurocranium through a single articular facet (Table 1). Three synapomorphies (characters 10[1], 16[1], and 20[1]) are shared by the siluriforms: anterior cartilage of autopalatine does not have contact with neurocranium; ligamentum primordiale inserts on the dorsal tip of the lower jaw; and ectopterygoid rudimentary or absent.

The suspensorium provides a few characters supporting the gonorynchiforms (characters 6[1] and 13[1]); the cypriniforms (characters 4[1], 11[1], 17[1], 18[1], 19[1], 30[1], and 33[1]); and the characiforms (characters 4[1] and 30[1]). In contrast, the suspensorium provides numerous synapomorphies for gymnotoids (characters 1[1], 5[1], 7[1], 9[1], 12[2], 13[2], 22[1], 25[1], 26[1], 33[2], and 35[1]), and siluroids (characters 2[1], 3[1], 12[1], 14[1], 15[1], 21[1], 23[1], 24[1], 27[1], 28[1], 29[1], 31[1], 33[1], 34[1], 36[1], and 37[1]). Character-states 1[2] and 4[2] are similar states to 3[1], therefore only the last one is counted as a siluroid synapomorphy. Character-states 11[2] and 13[2] are similar, therefore only 12[2] is counted as a gymnotoid synapomorphy.

Although I have modified several characters by Fink & Fink as shown above, eliminate a few of them from this analysis because of variation in the outgroup and/or ingroup, and added new ones, my results confirm the scheme of relationships of the ostariophysans published by Fink & Fink (1981: Fig. 1).

For characters supporting the different nodes see figure 45C, Appendix 1, and description of characters presented above.

RELATIONSHIPS AMONG PRIMITIVE CATFISHES

First cladistic analysis

The relationships among a few primitive catfishes are evaluated on the basis of the 75 characters listed below; the gymnotoids (first outgroup) and the characiforms (second outgroup) are considered as a combined outgroup, following the results by Fink & Fink (1981) and of the present study.

Diplomystids exhibit variability in some characters; all variable taxa present in Appendix 2 are considered in the analyses (Figs. 46A—C, 47A—E) as bearing only the derived states. For example, characters 16[1] and 44[1] in *Diplomystes camposensis*; characters 16[1] and 66[3] in *D. chilensis*; characters 16[1], 21[1], 24[1], 42[1], and 66[3] in *Olivaichthys viedmensis*. See Appendix 2 for the matrix of character states. Characters are explained below.

Character 1. A dentate maxilla (Figs. 16A, 18B, 19B, 22A, C) is present in primitive catfishes including the Diplomystidae (e.g., Eigenmann 1927, Alexander 1965, Gosline 1975, Arratia 1987a), and †Hypsidoridae (Grande 1987). The presence of maxillary teeth has been interpreted as the primitive condition by most authors; however, McAllister (1968) considered it a secondarily derived condition. The presence of maxillary teeth in primitive catfishes may have different interpretations depending on the outgroups. Most ostariophysans do not have maxillary teeth, with the exception of the characiforms and primitive siluroids (i.e., Diplomystidae and †Hypsidoridae). The distribution of this character (Fig. 48) among extant ostariophysans, indicates that the presence of maxillary teeth has two possible interpretations: it may be a reversal from the condition present in primitive teleosts such as primitive clupeomorphs, osteoglossomorphs, and elopomorphs, or it may be a new formation because it is not present

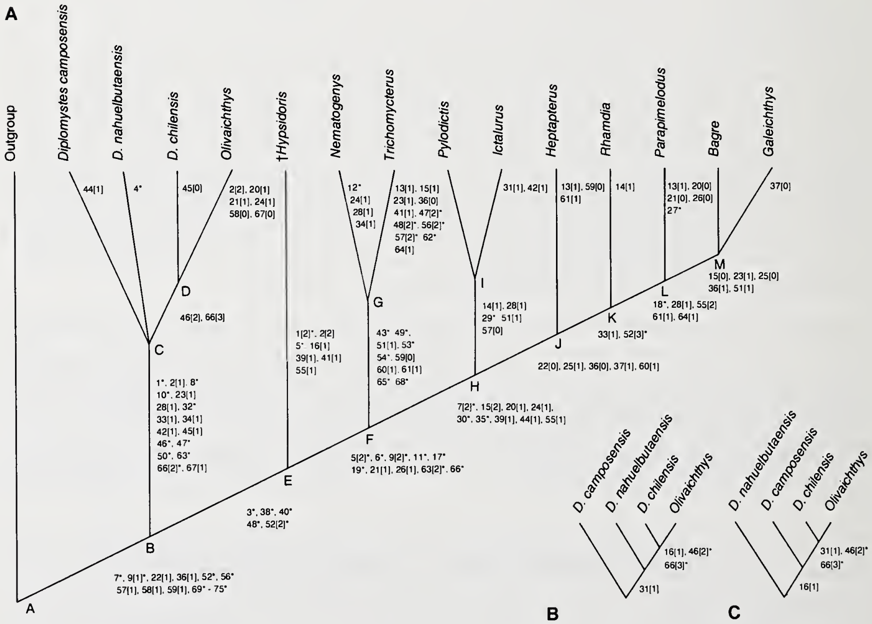

Fig.46: Hypotheses of phylogenetic relationships of certain primitive catfishes based on 75 morphological characters. All characters are ordered with the exception of characters 1, 5, 7, 9, 47, 63, and 66. Characters are explained in the text; for character states see Appendix 2. Homoplasies are presented by their character states, but an asterisk represents a unique derived character. — A: Consensus tree of two equally parsimonious trees (consensus index 0.672); B—C: Topologies showing probable phylogenetic relationships among diplomystids.

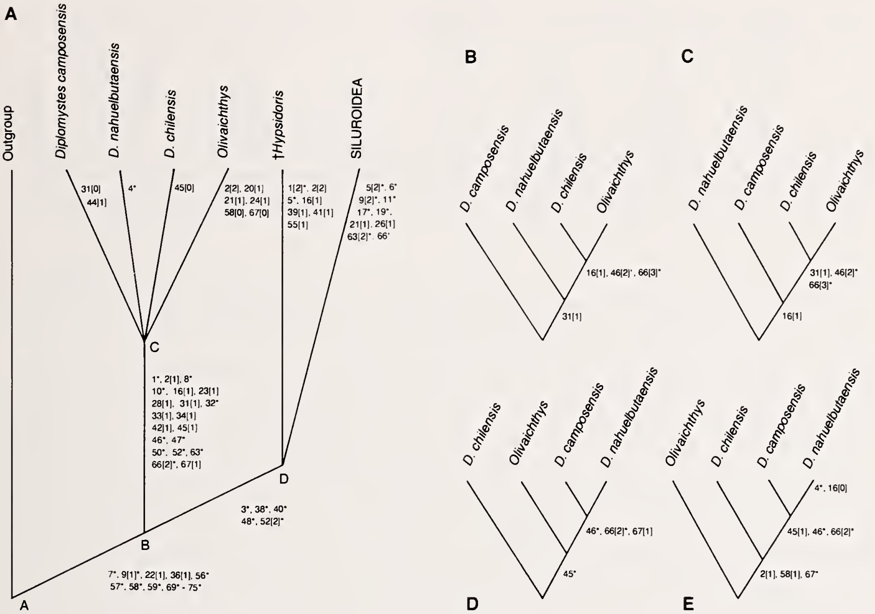

Fig.47: Hypotheses of phylogenetic relationships of certain primitive catfishes based on 75 morphological characters. All characters are unordered. Characters are explained in the text; for character states see Appendix 1. Homoplasies are presented by their character states, but an asterisk represents a unique derived character. — A: Consensus tree of four equally parsimonious trees (consistency index 0.672)'; B—E: Topologies showing probable phylogenetic relationships among diplomystids.

in any of the possible ancestors of characiforms and siluriforms. By comparison with the combined outgroup and with most ostariophysans, I consider the absence of maxillary teeth as the primitive condition (see Appendix 2).

The absence of maxillary teeth is a synapomorphy of Siluroidea according to Grande (1987). However, I consider the presence of teeth along most of the oral margin as a synapomorphy of diplomystids, and the teeth anteriorly placed on the maxilla as an autapomorphy of †*Hypsidoris.*

Teeth along most of the oral margin of maxilla (Figs. 11, 19B) are present in parallel in *Hoplias* and diplomystids, however in *Xenocharax* there are only a few teeth in a single row close to the articular process of the maxilla. In †*Hypsidoris*, the teeth are also concentrated anteriorly, close to the articular process (Fig. 22C). Most catfishes do not have maxillary teeth; however, the presence of teeth placed anteriorly in the maxilla is an autapomorphy of †*Hypsidoris.*

1) Maxilla with:
    0: no teeth
    1: teeth along most of the oral margin
    2: teeth anteriorly placed

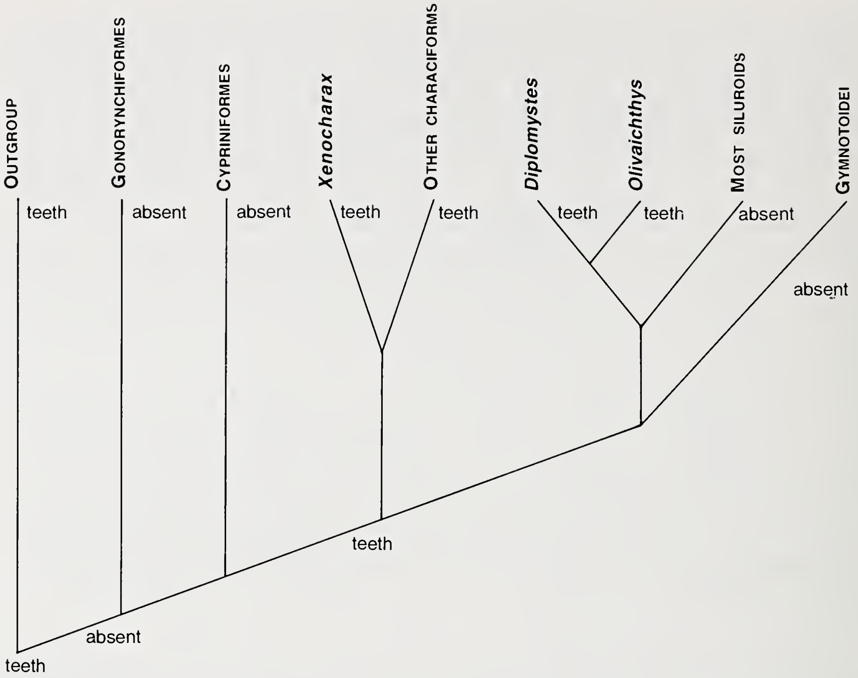

Fig.48: Distribution of maxillary teeth in ostariophysans (hypothesis of interrelationships after Fink & Fink 1981 and present paper).

Character 2. A maxilla with several rows of teeth occurs in parallel in †*Hypsidoris* and the diplomystid *Olivaichthys*. The presence of one or two rows of teeth in the maxilla is the common condition found in *Diplomystes*.

2) Maxilla:
- 0: without teeth
- 1: with one or two rows of teeth
- 2: several rows of teeth

Character 3 and 4. A single elongate anterior process of the maxilla bearing one articular facet for the pars autopalatina or the autopalatine is present in gymnotoids and characiforms respectively; in the Diplomystidae the process carries two facets for the articulation with the autopalatine. These facets are parallel to each other and they may be close to each other as in *Diplomystes camposensis* (Fig. 19A) or they may be broadly separate as in *D. nahuelbutaensis* (Fig. 18B). The facets may be seen as slight concavities (e.g., *D. camposensis*), or as short, broad projecting processes (e.g., *D. nahuelbutaensis*). In most siluroids, the anterior articular region of the maxilla is rudimentary and modified into two rudimentary processes, each of which articulate with the autopalatine. This feature is a synapomorphy of †*Hypsidoris* plus Siluroidea (=Siluroidei sensu Grande 1987).

3) Maxilla that has two small articular facets for the autopalatine, both on two rudimentary processes:
   0: absent
   1: present

4) Maxilla that has two large articular facets for autopalatine broadly separated from each other, both on two rudimentary processes at the elongate anterior maxillary process (Fig. 18B):
   0: absent
   1: present

This feature is an autapomorphy of *Diplomystes nahuelbutaensis*; this new character should be added to the diagnosis given by Arratia (1987a).

Character 5. The most common condition in siluriforms is the presence of two autopalatal processes on the maxilla that articulate with the anterior cartilage of the autopalatine. These two autopalatal processes are well developed in †*Hypsidoris*; but they are small in most catfishes. In the Diplomystidae, there is only one maxillary anterior process, but with two articulations, that separates the premaxilla and autopalatine (Fig. 19A—C); however, in young diplomystids the anterior cartilage of the autopalatine touches the premaxilla. The condition present in adult Diplomystidae is unique among the siluriforms. In †*Hypsidoris*, the two well-developed autopalatal processes extend between the autopalatine and premaxilla; probably the processes separated both bones completely.

The loss of the single elongate anterior process of the maxilla was considered a synapomorphy of the Siluroidea by Grande (1987: character 6); this character is confirmed herein. The presence of two well-developed anterior processes (character 5[1]) is an autapomorphy of †*Hypsidoris*.

5) Maxilla:
   0: with one long anterior process separating the autopalatine (when present) from the premaxilla or with slight contact betwen the autopalatine and premaxilla
   1: with two well-developed anterior processes that separate the autopalatine and premaxilla
   2: without the long anterior process

Character 6. The maxilla of most catfishes is small, therefore the enlarged premaxillae form most of the upper oral margin. The size and shape of the maxilla differs among catfishes; it is longest and most distally expanded in diplomystids (Figs. 19A, 20A—C). In †*Hypsidoris* it is comparatively shorter than in diplomystids and slightly expanded distally (Fig. 22A, C). In most siluroids it is reduced to just the anterior portion. The loss or reduction of the distal portion of the maxilla is a synapomorphy of the Siluroidea according to Grande (1987: character 5); this character is confirmed herein.

6) Maxilla:
   0: with elongate or slightly elongate body expanded distally
   1: rudimentary

Character 7. The autopalatine of characiforms is shorter than that of catfishes; it largely corresponds to the anterior part of the catfish autopalatine (Fig. 6C—D). A rod-like autopalatine (Figs. 26A, B, 27A—D, 32, 34A, B, 35A, C) is the common condition for catfishes; however, an autopalatine that is broad anteriorly, and elongate and narrow posteriorly, is true of a few catfishes such as the diplomystids, †hypsidorids, and nematogenyids (Figs. 18A, 22D, 28D). In trichomycterines, the autopalatine is broad anteriorly but the posterior part becomes narrower gradually, therefore the posterior part is not as elongate and slender as in diplomystids (Arratia 1990a).

The presence of a extremely small or rod-shaped autopalatine is a synapomorphy of the Siluroidea according to Grande (1987); however, the Nematogenyidae and Trichomycteridae have well-developed autopalatines, expanded anteriorly (Figs. 28D, 29A, B; Arratia 1987a, 1990a, Arratia & Menu Marque 1984). The presence of a rod-shaped autopalatine is a synapomorphy of the Ictaluridae and most advanced catfishes (Fig. 46A). The presence of an autopalatine that is broad anteriorly, and elongate posteriorly, is a synapomorphy of the primitive catfishes (= Siluroidei sensu Fink & Fink 1981; Siluriformes sensu Grande 1987).

7) Autopalatine, when present:
  0: short, slightly broad anteriorly
  1: broad anteriorly, narrow and elongate posteriorly
  2: rod-like

Character 8. The autopalatine abutting a cavity on the dorsal aspect of the premaxilla is the common condition in characiforms and most catfishes (Figs. 29A, B, 33, 34B, 36A). In diplomystids, however, the autopalatine does not abut the dorsal surface of the premaxilla and this is therefore a synapomorphy of the Diplomystidae. The anterior cartilage of the autopalatine is not preserved in the material available of †*Hypsidoris*. Due to the breadth and size of the anterior part of the autopalatine in †*Hypsidoris* (Fig. 22B), I suspect that the situation was similar to that in the Diplomystidae. However, I prefer to code this character as unknown (?) (see Appendix 2). In most catfishes, the anterior cartilage or fibrocartilage of the autopalatine retains its position with respect to the dorsal aspect of the premaxilla through the action of connective tissue and ligaments. In trichomycterines however, a synchondral articulation is formed during growth between the anteromedial portion of the cartilage of the autopalatine and the premaxilla.

8) Autopalatine, when present, that abuts the dorsal surface of the premaxilla:
  0: present
  1: absent

Character 9. In most teleosts the maxilla and autopalatine are joined by a single articulation; however, a double, anteroventral articulation is a synapomorphy of the catfishes. The double articulation is anteroventrally oriented in diplomystids and †hypsidorids (my interpretation of Grande's 1987 figures) but is lateroventrally oriented in other catfishes. The presence of a double anteroventral articulation is therefore a synapomorphy of the Siluroidei sensu Fink & Fink (1981) = Siluriformes sensu Grande (1987), and the presence of a lateroventral articulation between the autopalatine and maxilla is a synapomorphy of the Siluroidea.

9) Articulation between autopalatine, when present, and maxilla that is:
0: single, laterally oriented
1: double, anteroventrally oriented
2: double, lateroventrally oriented

Character 10. A hinge joint between the autopalatine and maxilla is the common condition among characiforms and catfishes; the presence of this joint permits an enormous mobility of the maxilla and autopalatine in both young and juvenile individuals. With increased growth, the autopalatine loses this mobility (e.g., *Nematogenys, Parapimelodus*). In diplomystids, the anterior process of the maxilla articulates via two articular facets in the same plane as the autopalatine; however, the maxilla is not displaced along the body axis as in other catfishes.

10) Hinge joint between the maxilla and autopalatine, when present:
0: absent
1: present

Character 11. The absence of the autopalatine extension dorsal to the dermal entopterygoid is a synapomorphy of the Siluroidea. The condition is variable in *Diplomystes* because many specimens lack the entopterygoid.

11) Posterior part of the autopalatine, when present, extending dorsally to reach the dermal entopterygoid:
0: present
1: absent

Character 12. The presence of the posterior cartilage of the autopalatine, 'entopterygoid', and metapterygoid (Fig. 28D) in the same plane is an autapomorphy of the Nematogenyidae (Arratia 1990a).

12) Posterior cartilage of the autopalatine, when present, 'entopterygoid', and metapterygoid in the same plane:
0: absent
1: present

Character 13. The presence of the posterior part of the autopalatine extension dorsal to the metapterygoid alone, is a homoplastic feature that characterizes trichomycterines (Arratia & Menu Marque 1984, Arratia 1990a), *Heptapterus*, and *Parapimelodus* (Fig. 34B) among the studied catfishes.

13) Posterior part of autopalatine, when present, extends dorsally to reach only the metapterygoid:
0: absent
1: present

Character 14. The posterior part of the autopalatine is dorsal or dorsolateral to the 'entopterygoid' alone in *Ameiurus, Ictalurus*, and *Pylodictis* (Fig. 27A—D) among the studied catfishes.

14) Posterior part of autopalatine dorsal or dorsolateral to only the 'entopterygoid':
0: absent
1: present

Character 15. A large cartilage is present between the mesethmoid, vomer, lateral ethmoid, and orbitosphenoid in diplomystids. A bony contact between the autopalatine and vomer is therefore missing and these bones articulate with each other through this cartilage. In more advanced catfishes the area of cartilage is small and lies between only the mesethmoid, vomer, and lateral ethmoid (e.g., *Nematogenys*) so that the autopalatine and vomer articulate directly. An articulation between the autopalatine and vomer is entirely missing in other catfishes (e.g., *Ictalurus*). I would predict that a direct articulation between the autopalatine and vomer is a synapomorphy of the Siluroidei. The absence of an articulation between the autopalatine and vomer is a homoplastic feature characteristic of ictalurids, *Heptapterus, Rhamdia*, and *Parapimelodus.*

15) Pars autopalatina or autopalatine articulates with vomer:
    0: through cartilage
    1: directly
    2: no articulation is present between these bones

Character 16. The absence of a subautopalatine tooth plate is the widespread condition in the outgroup; however, *Hoplias* — among the studied characiforms — bears a subautopalatine toothplate. The presence of a subautopalatine toothplate is considered herein to be independently derived in *Hoplias* (Fig. 11), *Diplomystes chilensis, Olivaichthys* (Fig. 19D), and †*Hypsidoris* (Fig. 22C).

16) Subautopalatine toothplate that attaches to the autopalatine:
    0: absent
    1: present

Character 17. The absence of a dermal ectopterygoid is hypothesized here as a synapomorphy of the Siluroidea. The condition is variable in *Diplomystes* because many specimens lack an ectopterygoid.

17) Dermal ectopterygoid that is present ventral or partially ventral to the autopalatine:
    0: present
    1: absent

Character 18. The presence of a sesamoid ectopterygoid joining the autopalatine and 'entopterygoid' is a synapomorphy of a clade including *Parapimelodus, Bagre*, and *Galeichthys.*

18) Sesamoid ectopterygoid that joins the autopalatine and 'entopterygoid':
    0: absent
    1: present

Character 19. The absence of a dermal entopterygoid is hypothesized here to be a synapomorphy of the Siluroidea. The small entopterygoid is absent in some diplomystids.

19) Dermal entopterygoid:
    0: present
    1: absent

Character 20. The attachment by ligaments and/or connective tissue between the 'entopterygoid' and the lateral ethmoid is a derived condition of catfishes above the level of [*Nematogenys* + *Trichomycterus*] in figure 46A. This character is coded with a question mark for *Trichomycterus* because this taxon lacks the 'entopterygoid'.

The presence of a ligament and/or connective tissue extending between the entopterygoid and the lateral ethmoid is a homoplastic character that occurs above the level of the ictalurids (Fig. 46A) and occasionally in *Olivaichthys*. A reversal is found in *Parapimelodus*.

20) A ligament and/or connective tissue attaches the 'entopterygoid' to the lateral ethmoid:
0: absent
1: present

Character 21. The presence of a link between the 'entopterygoid' and vomer is predicted as a synapomorphy of the Siluroidea.

21) A ligament and/or connective tissue attaches the 'entopterygoid' and the vomer:
0: absent
1: present

This is a homoplastic character that is not found in *Trichomycterus* (without 'entopterygoid') and that has a reversal in *Parapimelodus*.

Character 22. A short ligamentous connection between the autopalatine and metapterygoid is present in catfishes, including diplomystids, nematogenyids, and trichomycterines. In *Ictalurus, Pylodictis*, and *Noturus*, a short, dense link of connective tissue is present. The presence of a link between these bones is a synapomorphy of the catfishes; however, this feature is lost in more advanced catfishes. A link between these bones is absent in the 'pimelodids' such as *Heptapterus, Rhamdia, Cetopsorhamdia, Pimelodella, Pimelodus*, and *Parapimelodus*, and also in *Galeichthys* and *Bagre marinus*; this secondary loss or reversal characterizes catfishes more advanced than ictalurids in figure 46A.

22) Autopalatine and metapterygoid that are linked by a ligament or connective tissue:
0: absent
1: present

Character 23. The metapterygoid-vomer ligament arises in parallel in Diplomystidae, *Trichomycterus*, and [*Bagre* + *Galeichthys*] (Fig. 46A).

23) Metapterygoid-vomer ligament:
0: absent
1: present

Character 24. The presence of a metapterygoid-'entopterygoid' ligament characterizes the clade that includes ictalurids and more advanced catfishes (Fig. 46A). A ligament also occurs in *Nematogenys* and in a few individuals of *Olivaichthys*. It is most parsimonious to interpret the 'entopterygoid' and its ligament present in *Olivaichthys* as a new formation, because the 'entopterygoid' type 1 in *Olivaichthys* is present together with a dermal entopterygoid. Therefore, it is not possible to consider this bone homologous with a dermal entopterygoid or 'entopterygoid' present in advanced catfishes.

24) Metapterygoid-'entopterygoid' ligament:
0: absent
1: present

Character 25. The common condition among catfishes is the presence of a metapterygoid and hyomandibula that are sutured to each other. The metapterygoid and hyomandibula do not articulate with each other in *Heptapterus, Rhamdia*, and *Parapimelodus* as well as in certain 'bagrids'; this character that appears to be a 'pimelodid' synapomorphy is, in the context of all the other data, interpreted by the PAUP analysis as a derived condition of [*Heptapterus* + [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]]] (Fig. 46A). Note, however, that the last two genera are characterized by the presence of a suture between the metapterygoid and hyomandibula.

25) Metapterygoid and hyomandibula:
0: synchondrally articulating and/or sutured to each other
1: separate from each other (no articulation present)

Character 26. The presence of a notch separating the processus basalis and the posterodorsal part of the metapterygoid is the primitive condition in teleosts (Arratia & Schultze 1991). The loss of this notch is a synapomorphy of the Siluroidea (homoplastic character).

26) Metapterygoid with a notch separating the processus basalis from the posterodorsal part of the bone:
0: present
1: absent

Character 27. Dermo+metapterygoid:
0: absent
1: present

Character 28. The presence of a well-developed anteroventral process of the metapterygoid, the ectopterygoid process (Figs. 16A—C, 17A, 28D), is a homoplastic character present at least in diplomystids, nematogenyids, and the clade including [*Parapimelodus* + [*Bagre* + *Galeichthys*]]. It is not, however, present in all; for example, the ectopterygoid process is absent in ictalurids and trichomycterids.

28) Ectopterygoid process of metapterygoid:
0: absent
1: present

Character 29. A well-developed lateral process of the metapterygoid is present in ictalurids such as *Pylodictis* and a few species of *Ictalurus* (Fig. 40B—D). The presence of this process is a unique derived condition. In addition, there is another character associated with the presence of this process: the anterior development of the levator arcus palatini muscle that inserts on the lateral process of the metapterygoid (unlike any other catfish studied here).

29) Well-developed lateral process on the lateral surface of the metapterygoid for insertion of the levator arcus palatini muscle:
0: absent
1: present

Character 30. The presence of a bone-to-bone articulation between the hyomandibula and pterosphenoid is an autapomorphy of the Diplomystidae. This articulation develops throughout ontogeny in diplomystids. The hyomandibula that articulates with autosphenotic only is a synapomorphy of the clade that includes ictalurids plus more advanced catfishes (Fig. 46A).

30) Hyomandibula that articulates with autosphenotic and pterotic only:
0: absent
1: present

Character 31. A levator arcus palatini crest is present on the lateral surface of the hyomandibula for the attachment of the levator arcus palatini muscle. In diplomystids (Fig. 21A—D) — except *Diplomystes camposensis* (Figs. 16B, C, 17A) — and *Ictalurus* (Fig. 26C) the crest is well-developed and mainly horizontal to the dorsal margin of the hyomandibula. In other catfishes the crest may be vertically placed and is not well-developed (e.g., *Nematogenys*; Fig. 28C). There are however some exceptions such as *Clarias.*

The presence of a well-developed horizontal levator arcus palatini crest is a derived feature of *Diplomystes nahuelbutaensis, D. chilensis, Olivaichthys*, and *Ictalurus*. In contrast, Bornbusch (1991) interpreted the presence of a prominent crest as the primitive state for Siluroidea. The difference in our interpretations of this character is based on his interpretation of the presence of a prominent crest in †*Hypsidoris* (in my opinion, it is not well-developed as in certain diplomystids and ictalurids; PU 20570 a; Fig. 23).

31) Horizontal levator arcus palatini crest on the lateral surface of the hyomandibula:
0: rudimentary or absent
1: well developed

Character 32. The hyoideomandibularis nerve trunk runs in a canal inside the bone in ostariophysans excluding diplomystids, where the nerve runs on the lateral aspect of the hyomandibula (Fig. 21A, B; Arratia 1987a). The lateral course of the hyoideomandibularis nerve trunk is an autapomorphy of the Diplomystidae.

32) Hyoideomandibularis nerve trunk lateral to the hyomandibula:
0: absent
1: present

Character 33. A small elongate bone (Fig. 49) uniting epibranchial 1 and the hyomandibula is absent in primitive characiforms and gymnotids as well as in most catfishes; however, this element is present in diplomystids and a few other catfishes (e.g., *Rhamdia*). The small bone present in diplomystids was identified as pharyngobranchial 1 by Arratia (1987a: Fig. 27C); however, this bone has a unique location and relationships unlike pharyngobranchial 1 of other primitive teleosts. The presence of pharyngobranchial 1 however, must be considered homoplastic because it is present in Diplomystidae and also in the clade formed by [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]] (Fig. 46A).

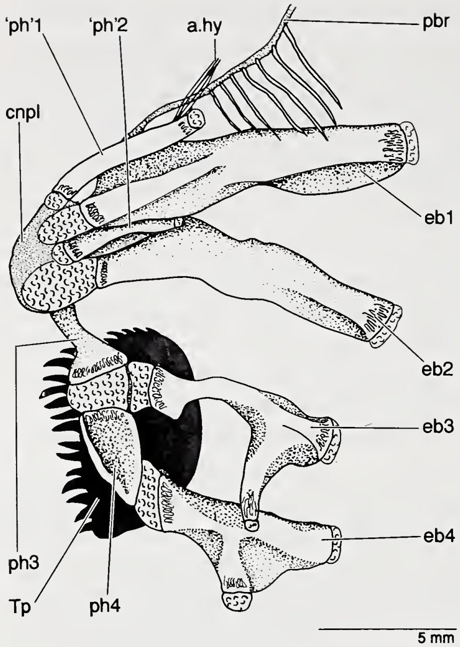

Fig.49: Upper section and branchial arches of *Diplomystes camposensis*, right side, dorsal view (PC 110276).
a.hy: attachment to hyomandibula; cnpl: plate of connective tissue; eb 1-4: epibranchial 1-4; ph 1-2: pharyngobranchial 1-2; ph 3-4: pharyngobranchial 3-4; pbr: pseudobranch; Tp: toothplate.

33) Small, elongate pharyngobranchial that is attached to epibranchial 1 and the medial aspect of hyomandibula:
0: absent
1: present

Character 34. A small pseudobranch (Fig. 49) is present in primitive catfishes such as diplomystids (Arratia 1987a) and nematogenyids. It is absent in most catfishes, as well as *Xenocharax* and *Hoplias* and gymnotoids. The pseudobranch is long in diplomystids and has a variable number of lamellae (9—15), whereas it is short in Nematogenyidae with 2 or 3 lamellae.

34) Pseudobranch that is imbedded in connective tissue to the medial aspect of the hyomandibula:
0: absent
1: present

Character 35. The hyomandibular fossa is commonly formed by the sphenotic and pterotic; however, the prootic may also form part of the fossa (Table 1). The absence of the prootic in the hyomandibular fossa is a synapomorphy of catfishes above the level of [*Nematogenys* + *Trichomycterus*] (Fig. 46A).

35) Prootic participating in the framing of the hyomandibular fossa:
0: present
1: absent

Character 36. The metapterygoid functioning as the main support of the eye is a synapomorphy of the primitive catfishes; however, this character has undergone several evolutionary transformations among siluroids (Arratia 1990a).

36) Metapterygoid functioning as the main support of the eye:
0: absent
1: present

Character 37. The quadrate partially supporting the eye is unusual in teleosts; however, this condition is present in some catfishes such as *Heptapterus, Rhamdia, Parapimelodus*, and *Bagre*.

37) Quadrate functioning as one of the elements supporting the eye:
0: absent
1: present

Characters 38 to 41 are from Grande (1987); they were proposed as synapomorphies of the Siluroidei sensu Grande (38 to 40 herein) and of †Hypsidoroidea (41 herein).

Character 38. The character proposed by Grande (1987) as a synapomorphy of the Siluroidei is "17 or fewer principal caudal rays (vs. 18 or more in *Diplomystes* and other primitive teleosts)." Most primitive extant teleosts have 19 principal caudal rays (Schultze & Arratia 1989), this however was not coded in this analysis because it is found outside of this taxonomic problem. The presence of 18 rays is an independently derived character of a few primitive extant teleosts such as the clupeomorph *Denticeps*, and of the siluriforms Diplomystidae and certain gymnotoids. Nematogenyidae are unique in that the procurrent rays become segmented during growth and all caudal rays are segmented in large adult individuals (Arratia 1982, 1983). An increase in the segmentation also has been observed in *Noturus* species (Schultze & Arratia 1989).

The presence of 17 caudal rays is a synapomorphy at the primitive level of Siluroidei (sensu Grande 1987); reduction in the number of principal caudal rays characterizes a number of different clades among the siluroids (Lundberg & Baskin 1969, Arratia 1982, 1983).

38) Caudal fin with:
0: 18 or more principal caudal rays
1: 17 or fewer principal caudal rays

Character 39. A membranous bony extension on the ventral surface of the fifth centrum is absent in catfishes such as diplomystids, nematogenyids, and trichomycterids (Arratia 1987: Fig. 28A, Arratia & Menu Marque 1984: Fig. 3B). The presence of this membranous bony extension was considered as a synapomorphy of the Siluroidei by Grande (1987: character 2); however, it is interpreted herein as a homoplastic feature occurring in parallel in †*Hypsidoris* and the clade above the [*Nematogenys* + *Trichomycterus*] (Fig. 46A).

39) Membranous bony extension over the ventral surface of the fifth centrum:
0: absent
1: present

Character 40. The fifth centrum closely joined to the complex centrum is a synapomorphy of the †*Hypsidoris* + Siluroidea according to Grande (1987: character 3). I am uncertain of the meaning of "joined closely" as stated by Grande (1987), because centra 4 and 5 become ankylosed or fused during growth in extant catfishes, except the Diplomystidae and *Trogoglanis* (Lundberg 1982); I have therefore modified this character to read "ankylosed or fused."

40) Fifth centrum that is ankylosed or fused to the complex centrum:
0: absent
1: present

Character 41. This character was proposed as the sole autapomorphy of the †Hypsidoroidea by Grande (1987); however, a well-developed coronoid process of the dentary (and also the angular) is present in trichomycterines (e.g., *Trichomycterus roigi*; Arratia & Menu Marque 1984: Fig. 7A—D). The presence of this character in both groups is interpreted here as independently derived.

41) Unusually high and narrow coronoid process of the dentary and angular:
0: absent
1: present

Characters 42 to 68 are from Arratia (1987a).

Character 42. In most catfishes the autosphenotic is smaller than or of similar length to the pterotic; however, an autosphenotic larger than the pterotic is present in catfishes such as diplomystids, except for a few individuals of *Olivaichthys* (Arratia 1987a: Figs. 4A, 13, 22A), and ictalurids (Lundberg 1982: Figs. 8A, 11A, B, 12A, B).

42) Sphenotic of similar length to or smaller than pterotic:
0: present
1: absent

Character 43. An extrascapular (Arratia 1987a: Figs. 4A, 13, 22A, 41A—C) is present in primitive catfishes; it is absent in catfishes such as loricarioids (e.g., Nematogenyidae, Trichomycteridae, and Loricariidae) and *Clarias*.

43) Extrascapular:
0: present
1: absent

Character 44. A suture between the pterosphenoid and parasphenoid is a synapomorphy of ictalurids and more advanced catfishes as shown in figure 46A. In juvenile *Bagre marinus* these bones almost contact each other; however, I am uncertain whether there is a suture between them in larger specimens. This character is variable in *Diplomystes camposensis*; only some specimens have the suture between the pterosphenoid and parasphenoid (Arratia 1987a: Fig. 23A).

44) Suture between the pterosphenoid and parasphenoid:
0: absent
1: present

Character 45. The presence of a long posterior part of the autopalatine, more than the half of the length of the bone (Figs. 17A, B, 18A) is a synapomorphy of *Diplo-*

mystes that it is lost in *Diplomystes chilensis* which has a very short autopalatine posteriorly (Fig. 17C).

45) Posterior portion of the autopalatine that is long, more than half of the length of the bone:
0: absent
1: present

Character 46. The most common condition in teleosts is the presence of an undivided autopalatine anteriorly (Figs. 4D, 6A—C). An anteriorly bifurcate autopalatine (Figs. 6D, 16A—C, 17A, B, 18A) is a synapomorphy of the Diplomystidae. The anterior fusion of both maxillary processes of the autopalatine (Fig. 17C) later in the ontogeny of certain individuals of *Diplomystes chilensis* and *Olivaichthys viedmensis* is a synapomorphy shared by these species.

46) Anterior part of autopalatine:
0: undivided
1: divided into two elongate processes which remain separate in adults
2: divided into two elongate processes which fuse anteriorly later in ontogeny

Character 47. The presence of a coronomeckelian is common in teleosts; however, the coronomeckelian is absent in *Trichomycterus* as well as in other advanced loricarioids. The presence of a coronomeckelian bone that increases its size considerably during ontogeny is an autapomorphy of the Diplomystidae (Fig. 20B; Arratia 1987a).

47) Coronomeckelian:
0: small, enlarging moderately during ontogeny
1: large, enlarging greatly during ontogeny
2: absent

Character 48. Dorsal and ventral hypohyals are about equal in size and shape in diplomystids (Arratia 1987a: Fig. 27B; Arratia & Schultze 1990: Fig. 4A). In most catfishes however, the ventral hypohyal is larger than the dorsal one (Arratia & Schultze 1990: Figs. 4B—D, 8A). The dorsal hypohyal is absent in catfishes such as trichomycterids and loricariids (Arratia & Menu Marque 1984: Fig. 8A; Arratia & Schultze 1990: Figs. 5A, 6A). The presence of both dorsal and ventral hypohyals of different sizes is hypothesized herein as a synapomorphy of †*Hypsidoris* + Siluroidea.

48) Dorsal and ventral hypohyals:
0: similar in size
1: unequal in size
2: dorsal hypohyals absent

Character 49. The prootic and autosphenotic are fused in adult *Nematogenys* and *Trichomycterus*. In *Trichomycterus*, however, the pterosphenoid is also included in this fusion. The fusion of bones occurs early in ontogeny in trichomycterids, whereas fusion occurs during later growth in *Nematogenys*.

49) Prootic and autosphenotic fusion:
0: absent
1: present

Character 50. Vomer: A T-shaped or arrow-shaped bone is the generalized condition present in catfishes and this fact was established by Howes (1983b). The presence of an almost rhomboid vomer is an autapomorphy of the Diplomystidae (Arratia 1987a: Figs. 5A, 23A).

50) T-shaped or arrow-shaped anterior portion of the vomer:
  0: present
  1: absent

Character 51. A separate first abdominal centrum is not unique for diplomystids among catfishes; a well-separated centrum also is present in †*Hypsidoris* (Grande 1987) and in some adult catfishes such as *Heptapterus, Rhamdia*, and *Parapimelodus*. Although this is a homoplastic character, the absence of a separate first centrum (due to loss or fusion) can be considered a synapomorphy of [*Nematogenys* + *Trichomycterus*] and of [*Bagre* + *Galeichthys*].

51) First centrum of the Weberian complex that is present as a separate element:
  0: present
  1: absent

Character 52. The presence of a complex Weberian centrum formed by the fusion of centra 2—4 is a synapomorphy of the catfishes. The fusion of abdominal centra 2—5 is a synapomorphy of †*Hypsidoris* plus primitive members of Siluroidea. The addition of more posterior centra is a synapomorphy of [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]] (Fig. 46A).

52) Weberian apparatus includes:
  0: no fusion of centra
  1: fusion of abdominal centra 2—4
  2: fusion of abdominal centra 2—5
  3: fusion of abdominal centra 2—6 or more

Character 53. The presence of a swimbladder divided into a pair of lateral vesicles is a synapomorphy of [*Nematogenys* + *Trichomycterus*] (Fig. 46A). This is not a unique condition because a swimbladder separated into two vesicles is also present in some other catfishes (Chardon 1968).

53) Swimbladder that is divided into a pair of completely separated lateral vesicles:
  0: absent
  1: present

Character 54. Bony capsules around the swimbladder vesicles that only open laterally is a synapomorphy of [*Nematogenys* + *Trichomycterus*] (Fig. 46A), but not unique to these forms. Encapsulated swimbladder vesicles are also present in other catfishes such as loricariids, astroblepids, and perhaps callichthyids. However, it has not yet been demonstrated that the bony capsules are formed in the same way in all of these fishes.

54) Parapophyses of vertebrae 3—4 or 3—5 that form a bony capsule around the swimbladder vesicles that open only laterally:
  0: absent
  1: present

Character 55. The presence of blood vessels running in a groove surrounded by lamellar walls in the ventral part of the Weberian apparatus occurs in parallel in †*Hypsidoris* and the clade including ictalurids plus more advanced catfishes (Fig. 46A). Blood vessels running in a tube-like lamellar formation ventral to the Weberian apparatus is a synapomorphy of [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]] (Fig. 46A).

55) Blood vessels:
    0: ventral to the centra of the Weberian apparatus
    1: in a groove partially surrounded by lamellar walls in the ventral part of the Weberian apparatus
    2: enclosed in a tube-like lamellar formation ventral to the Weberian apparatus

Character 56. The presence of four proximal pectoral radials is the primitive condition for teleosts; in contrast, three proximal pectoral radials are present in diplomystids (Arratia 1987a: Figs. 30A, D) and most other catfishes. When three proximal radials are present, the first radial is a large mass of cartilage that may ossify late in ontogeny, in addition to the two other elongate radials (Arratia 1987a: Fig. 30A). Three fully ossified, elongate proximal radials are present in *Nematogenys*. Two ossified radials or one ossified and one cartilaginous radial are present in trichomycterines. The presence of three proximal pectoral radials is a synapomorphy of primitive catfishes. The presence of three elongate well-ossified radials is an autapomorphy of the Nematogenyidae.

56) Pectoral fin with:
    0: four proximal pectoral radials
    1: three proximal pectoral radials
    2: two or fewer proximal radials

Character 57. Characiforms such as *Xenocharax* and *Hoplias* have a higher number of pelvic fin-rays (10 and 8, respectively) than most catfishes. Exceptions include *Ictalurus* (8) and *Pylodictis* (9). The presence of six pelvic fin-rays is a synapomorphy of catfishes. The high number of rays found in *Ictalurus* and *Pylodictis* is a secondarily derived condition.

57) Pelvic fin, when present, with:
    0: more than six rays
    1: six rays
    2: less than six rays

Character 58. Cartilaginous pelvic radials are usually absent in catfishes; however, a small cartilaginous pelvic radial has been observed in *Olivaichthys viedmensis* (Arratia 1987a: Fig. 37A) and *Noturus exilis*. The absence of a cartilaginous pelvic radial is a synapomorphy of catfishes. The presence of a cartilaginous pelvic radial in early ontogeny of *Olivaichthys viedmensis* is a reversal to the primitive condition, and therefore an autapomorphy of this species.

58) Pelvic fin with cartilaginous radial:
    0: present
    1: absent

Character 59. The presence of spines in the dorsal fin is a synapomorphy of catfishes. However, some catfishes lack spines (e.g., *Nematogenys* and *Trichomycterus*).

59) Dorsal fin spines:
0: absent
1: present

Character 60. A caudal fin with less than six hypurals occurs in parallel in [*Nematogenys* + *Trichomycterus*] and in the clade above the ictalurids in figure 46A.

60) Caudal fin skeleton with six or more hypurals:
0: present
1: absent

Character 61. The fusion of hypurals 1 and 2 is a homoplastic character occurring in [*Nematogenys* + *Trichomycterus*], *Heptapterus*, and [*Parapimelodus* + [*Bagre* + *Galeichthys*]].

61) Hypurals 1 and 2:
0: not fused to each other
1: fused to each other

Character 62. Hypural 1 fused to the parhypural represents the derived condition of *Trichomycterus*, but is not unique to trichomycterines (Lundberg & Baskin 1969).

62) Hypural 1:
0: not fused to the parhypural
1: fused to the parhypural

Character 63. The PAUP program interprets the presence of three or four pairs of barbels as a synapomorphy of the Siluroidea (however, it could be a synapomorphy of *Hypsidoris* [unknown condition] + Siluroidea) and the presence of one pair of barbels as an autapomorphy of Diplomystidae. The same result was obtained when the character was unordered.

63) Barbels:
0: absent
1: present as only maxillary barbel
2: present as more than one pair of barbels

Character 64. The sensory canals in teleosts may be simple, branched, or reduced (Webb 1989). These three conditions are present in catfishes, however the most generalized condition is the presence of simple sensory canals. Branching of the canals is observed during growth in some catfishes; this condition is a synapomorphy of [*Parapimelodus* + [*Bagre* + *Galeichthys*]] (Fig. 46A). A reduction in sections of the cephalic sensory canals is characteristic of some catfishes such as trichomycterids, in which complete sections of the lateral line system are lost (e.g., preopercular, mandibular, and supraorbital canals [Baskin 1973, Pinna 1988, Arratia 1990b]).

64) Cephalic sensory canals:
0: simple
1: branched

Character 65. The presence of integumentary teeth on the outside surface of the body is a synapomorphy of [*Nematogenys* + *Trichomycterus*] (Fig. 46A). This character is not unique to these forms, but a synapomorphy of the loricarioids (Baskin 1973, Howes 1983b).

65) Integumentary teeth on the outside surface of the body:
0: absent
1: present

Character 66. The common condition among catfishes is the absence of supraneural bones. The Diplomystidae have a supraneural; however different conditions are observed in diplomystids: character 66[2] is found in some individuals of *Olivaichthys viedmensis*, and in all studied individuals of *Diplomystes camposensis* and *D. nahuelbutaensis*. Character 66[3] is observed in most studied specimens of *Olivaichthys* and also in *Diplomystes chilensis*.

The presence of a single small, ossified supraneural is an autapomorphy of Diplomystidae. The presence of a compound element or of two separate elements in *Diplomystes chilensis* and *Olivaichthys viedmensis* is a synapomorphy shared by these two species. The absence of the bone is a synapomorphy of the Siluroidea.

66) Supraneural above the Weberian apparatus in adults:
0: present as one single, large element
1: absent
2: present as one single, small element
3: present as one element with two ossification centers or two separate elements

Character 67. A supraneural that articulates with the claustrum is the primitive condition present in characiforms (Weitzman 1962, Fink & Fink 1981) and in *Olivaichthys viedmensis*. In the latter, the supraneural and claustrum contact and articulate during growth. In addition, the increased growth of the claustrum dorsally in *Olivaichthys viedmensis* separates the supraneural from the cranial occipital region.

The presence of a supraneural that does not articulate with the claustrum is a synapomorphy of the Diplomystidae, whereas the articulation between these bones present in *Olivaichthys* is an autapomorphy of this genus.

67) Supraneural:
0: articulates with claustrum
1: does not articulate with claustrum

Character 68. A short (e.g., *Nematogenys*) or a rudimentary lateral line in trichomycterines (Arratia & Menu Marque 1984, Arratia 1987a) is a synapomorphy of [*Nematogenys* + *Trichomycterus*].

68) Lateral line:
0: complete
1: short or reduced

Characters 69 to 75 are synapomorphous features of catfishes according to the previous analysis (pp. 86—107).

Character 69. Palatoquadrate that is separated into the pars autopalatina and pars

pterygoquadrata:
0: absent
1: present

Character 70. Pterygoquadrate fused with the cartilaginous hyo-symplectic:
0: absent
1: present

Character 71. Articulation between the autopalatine and lateral ethmoid at about the midlength of the autopalatine:
0: absent
1: present

Character 72. Metapterygoid anterodorsal to the quadrate and forming part of the ventrolateral border of the suspensorium:
0: absent
1: present

Character 73. Posteroventral process of quadrate:
0: present
1: absent

Character 74. Quadrate and hyomandibula that are sutured to the preopercle:
0: absent
1: present

Character 75. Bony symplectic:
0: present
1: absent

Results

Two analyses were performed using the 75 characters listed above and their character states listed in Appendix 2. The first analysis was done with all characters as ordered, except for characters 1, 5, 7, 9, 47, 63, and 66 (Fig. 46A—C). The second analysis considered all characters as unordered (Fig. 47A—E). Both analyses are identical in the phylogenetic position of the taxa; the differences are due to the unresolved relationships among diplomystids (compare Figs. 46A, 47A).

Figure 46A corresponds to the consensus of two equally parsimonious trees (consistency index = 0.672) at 137 evolutionary steps. The consensus shows the sequence from characiforms + gymnotoids (outgroup) at the base, to *Bagre* and *Galeichthys*.

Node B corresponds to the branching between the diplomystids and the [†*Hypsidoris* + Siluroidea]: This node is supported by 16 characters: 11 characters are uniquely derived, whereas five characters are homoplastic (Fig. 46A). Node C corresponds to the trichotomy among diplomystid species. This node is supported by nine uniquely derived characters and eight homoplastic ones (Fig. 46A). Node D corresponds to the branching between *Diplomystes chilensis* and *Olivaichthys*. This node is supported by two homoplastic characters (46[2] and 66[3]). *Diplomystes camposensis* and *D. nahuelbutaensis* are characterized by one autapomorphy (44[1] and 4[1]), respectively. *D. chilensis* is characterized by one homoplastic character (45[0]). *Olivaichthys viedmensis* is characterized by six homoplastic characters (2[2], 20[1], 21[1], 24[1], 58[1], and 67[0]) (Fig. 46A). The polytomy among diplomystids in this analysis is due to the unresolved position of *Diplomystes camposensis* as the plesiomorphic sister group of the remaining diplomystids (Fig. 46B) or *D. nahuelbutaensis* as the plesiomorphic one (Fig. 46C).

Node E corresponds to the branching between †*Hypsidoris* and Siluroidea. Node E is supported by five uniquely derived characters. †*Hypsidoris* is characterized by two derived characters (1[2] and 5[1]) and five homoplasies (2[2], 16[1], 39[1], 41[1], and 55[1]).

Node F corresponds to the branching of [*Nematogenys* + *Trichomycterus*] and more derived catfishes. Node F is supported by eight uniquely derived characters and two homoplastic ones.

Node G corresponding to the branching of *Nematogenys* and *Trichomycterus*: This node is supported by six uniquely derived characters (Fig. 46A). *Nematogenys* is characterized by one autapomorphy (12[1]) and three homoplastic characters (24[1], 28[1], and 34[1]). *Trichomycterus* is characterized by four unique derived characters (47[2], 48[2], 56[2], and 62[1]) and seven homoplastic characters (13[1], 15[1], 23[1], 36[0], 41[1], 57[2], and 64[1]). All of these features are characters of trichomycterines or trichomycterids. No derived character is known for the genus *Trichomycterus* (Arratia 1990b).

Node H corresponds to the branching between ictalurids and more advanced catfishes. It is supported by three derived characters and six homoplasies (Fig. 46A). Node I corresponds to the branching between *Pylodictis* and *Ictalurus*: Node I is supported by one uniquely derived character and four homoplastic ones. *Ictalurus* is characterized by two homoplastic characters (30[1] and 42[1]).

Node J corresponds to the branching between *Heptapterus* and [*Rhamdia* + [*Parapimelodus* + [*Bagre* + *Galeichthys*]]]: Node J is supported by five homoplastic characters (Fig. 46A). *Heptapterus* is characterized by three homoplastic features (13[1], 59[0], and 61[1]).

Node K corresponds to the branching between *Rhamdia* and [*Parapimelodus* + [*Bagre* + *Galeichthys*]]. Node K is supported by one uniquely derived character and one homoplastic character (Fig. 46A). *Rhamdia* is characterized by one homoplastic character (14[1]).

Node L corresponds to the branching between *Parapimelodus* and [*Bagre* + *Galeichthys*]. Node L is supported by one uniquely derived character and four homoplastic ones.

Node M corresponds to the branching between *Bagre* and *Galeichthys*. Node M is supported by five homoplastic characters. *Galeichthys* is characterized by one reversal, character 37[0].

Second cladistic analysis

The relationships among primitive catfishes were evaluated on the basis of the 75 characters listed above and in Appendix 2. All variable characters of Diplomystidae are considered in this analysis as bearing only their primitive states. For example, characters 16[0] and 44[1] in *Diplomystes camposensis*; characters 16[0] and 66[2] in *D. chilensis*; characters 15[0], 21[0], 24[0], 42[0], and 66[2] in *Olivaichthys viedmensis.* All characters are ordered, except characters 1, 5, 7, 9, 47, 63, and 66.

Results

Figure 50A corresponds to the consensus tree of four equally parsimonious trees at 256 evolutionary steps (consistency index = 0.656). The topology of the consensus tree is identical to that in figure 46A, except for the arrangement of the taxa within Diplomystidae. Node C (Fig. 50A) shows the unresolved relationships among the diplomystids as represented by figures 50B—E.

Only one tree is generated when the 75 characters listed above and in Appendix 2 are run as unordered (consistency index = 0.695; tree length = 131). The tree has the same arrangement of taxa, except among diplomystids, where *Olivaichthys* appears as the plesiomorphic sister group of *Diplomystes chilensis* + [*D. camposensis* + *D. nahuelbutaensis*].

Overall Results

The comparison between both trees (Figs. 46A & 50A) reveals that variable characters are capable of modifying tree topology. In both trees, the differences are at the level of the Diplomystidae. In figure 46A the most primitive diplomystids are *Diplomystes camposensis* and *D. nahuelbutaensis*, whereas *Olivaichthys* is the most primitive diplomystid or it is a polytomy among diplomystids (Fig. 50A—D) when variable taxa are considered to only exhibit the primitive state. Variation may be crucial in the understanding of relationships of catfishes, because variation is known from many structures among catfishes (e.g., Regan 1911, Alexander 1965, Lundberg & Baskin 1969, Lundberg 1982, Arratia 1982, 1983, 1987a, Arratia & Menu Marque 1981, 1984, Arratia & Schultze 1990).

Both analyses (Figs. 46A, 50A) support Grande's (1987) arrangement of the higher categories of catfishes, his Siluriformes, Siluroidei, †Hypsidoroidea, and Siluroidea. The present study provides additional characters supporting them (see below).

Chardon (1968) proposed the suborder Bagroidei with nine superfamilies; among them, the superfamily Bagroidae includes Bagridae, Pimelodidae, Ictaluridae, Ariidae and Olyridae. Several characters proposed by Chardon (1968) as diagnostic for Bagroidae are primitive or homoplastic and in addition, the monophyly of the Bagroidae has not yet been demonstrated. According to the present study, Bagroidae is supported by nine synapomorphies (Fig. 46A: Node H). The synapomorphies are: the presence of a rodlike autopalatine (not unique to Bagroidae); no articulation present between autopalatine and vomer, the 'entopterygoid' attached by ligaments and/or connective tissue to the lateral ethmoid; metapterygoid-'entopterygoid' ligament present; hyomandibula articulating with autosphenotic and prootic; presence of the prootic as one of the bones framing the hyomandibular fossa; membranous bony extension over the ventral surface of the fifth centrum present; suture between pterosphenoid and parasphenoid present;

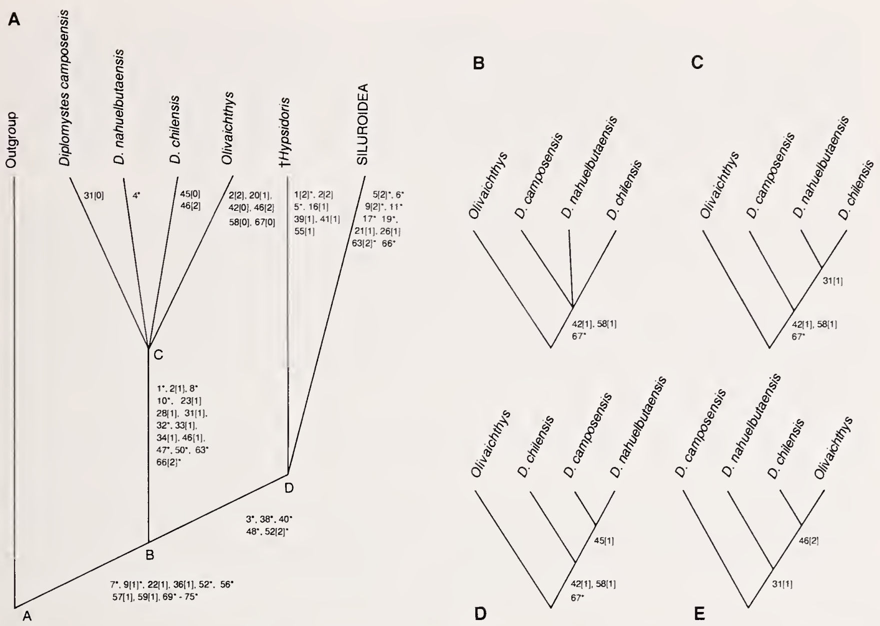

Fig.50: Hypothesis of phylogenetic relationships of certain primitive catfishes based on 75 morphological characters. All characters are ordered with exception of characters 1, 5, 7, 9, 47, 63, and 66. Characters are explained in the text; for character states see Appendix 2; however, character of Diplomystidae are considered as bearing only their primitive character states. Homoplasies are presented by their character states, but an asterisk represents a unique derived character. — A: Consensus tree of four equally parsimonious trees (consensus index 0.656); B—E: Topologies showing probable phylogenetic relationships among diplomystids.

and blood vessels partially surrounded by lamellar walls in the ventral part of the Weberian apparatus. Among the Bagroidae, the 'Pimelodidae' is not a monophyletic group, and the monophyly of the Bagridae has not been demonstrated yet. In addition, 'pimelodids', 'bagrids', and ariids are poorly known.

CONCLUSIONS

Early ontogeny

Dermal bones are the first to ossify in ostariophysans as well as in other teleosts (e.g., in 5.5 mm total length *Noturus hildebrandi* the cleithrum is ossified, and in a 6 mm specimen of *Trichomycterus areolatus* the cleithrum, premaxilla, dentary, and preopercle are visible) (Arratia & Schultze 1990). The only sure recognition of cartilage bones may be achieved using growth series; there is no way to distinguish between dermal and membrane bones. It is only by convention that a researcher accepts the definition of dermal and membrane bones by Patterson (1977).

The growth of bones from the palatoquadrate and hyo-symplectic cartilages results largely from perichondral ossifications in all of the teleosts that I have studied (see Arratia & Schultze 1991). However, in catfishes the bones mostly enlarge through the appearance and expansion of membranous outgrowths. Jollie (1986: 371) stated that the metapterygoid is essentially dermal with no apparent chondral process; this statement is surprising considering that the metapterygoid arises from the palatoquadrate cartilage.

The study of ontogenetic series is not only helpful in testing homologies or for determination of primitive states of characters as suggested by Nelson (1978, 1985) and Mabee (1987, 1989), but it also provides a set of characters useful in taxonomy and for evaluating phylogenetic relationships. For example, characters representing early ontogenetic conditions are synapomorphies of the catfishes (1—4) and Characiformes (5).

(1) Posterior part of the palatoquadrate, the pterygoquadrate, fused with the hyosymplectic cartilage;
(2) palatoquadrate divided into a pars autopalatina and a pars pterygoquadrata;
(3) posterior part of the autopalatine not contacting the pars pterygoquadrata through cartilage;
(4) the fusion of the pterygoquadrate and hyo-symplectic to produce a special alignment of the bones of the suspensorium during growth; and
(5) posterodorsal portion of the palatoquadrate bifid.

Some morphological characters may change during ontogeny. The sequence of the changes and/or the ontogenetic transformations are also useful characters. For example,

(1) a subautopalatine toothplate is absent early in the ontogeny of diplomystids; however, the toothplate appears later in the ontogeny in *Olivaichthys* and *Diplomystes chilensis* and
(2) the anterior part of the autopalatine is bifid early in the ontogeny of diplomystids; however, both processes become fused during the growth of *Olivaichthys* and *Diplomystes chilensis*, yet both processes remain independent of one another in *D. camposensis* and *D. nahuelbutaensis*.

Homology of chondral bones of the suspensorium

The changes in position and shape of the bones of the suspensorium may be associated to the movement of the maxillary and nasal barbels (when present), in addition to the compression or depression of the head observed in many catfishes. These changes affect all elements of the suspensorium. The chondral elements of the suspensorium of catfishes are highly modified both in shape and in position when compared with other teleosts. For example, the hyomandibula occupies the position of the metapterygoid of other teleosts, whereas the metapterygoid occupies the position of both the ectopterygoid and the entopterygoid, or of just the entopterygoid. Despite these differences, the autopalatine, metapterygoid, quadrate, and hyomandibula are homologous in teleosts.

There is no ontogenetic evidence, in any of the catfishes examined, that the hyomandibula and/or metapterygoid, and autopalatine are compound elements (contra Howes & Teugels 1989 and Howes & Ayanomiya Fumihito 1991, respectively).

Homology of entopterygoid and 'entopterygoid'

The entopterygoid is a small dermal bone that may or may not be present in diplomystids. The diplomystid dermal entopterygoid is homologous with that of other teleosts and non-teleostean fishes (Arratia & Schultze 1991). The 'entopterygoid' is a tendon bone by origin and a sesamoidal element connected by ligaments to other bones of the suspensorium and cranial elements, unlike the dermal entopterygoid.

'Entopterygoid' type 1, occasionally present in *Olivaichthys*, is a new formation. 'Entopterygoid' type 1 and a dermal entopterygoid are both present in a single individual, therefore the two elements are non-homologous.

According to the distribution of this character (Fig. 51) among catfishes, the 'entopterygoid' (except for 'entopterygoid' type 1) is homologous with the entopterygoid present in diplomystids. For such a scheme of homology to be true, I have had to assume that †*Hypsidoris* had either a entopterygoid or an 'entopterygoid', or that the loss of one or another bone in †*Hypsidoris* is an autapomorphy of this fish.

The 'entopterygoid' has a variety of ligamentous connections in catfishes (Fig. 2B—G); it is very probable that more patterns will be added to figure 2A—G as more catfishes are studied. The diversity of ligamentous connections of the 'entopterygoid' may be useful for taxonomic and phylogenetic purposes in catfishes.

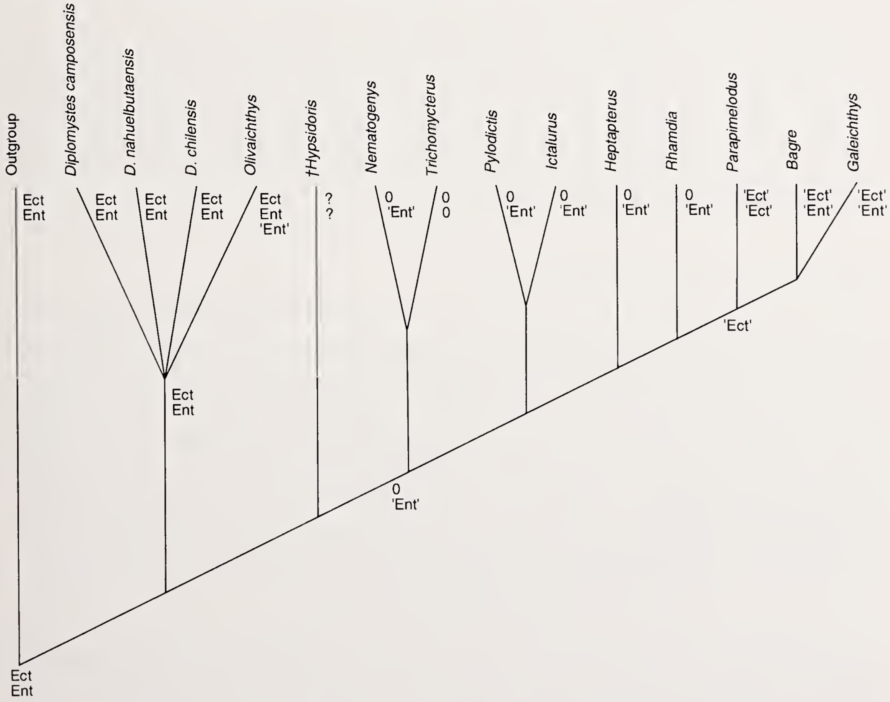

Fig.51: Distribution of certain palatal bones in catfishes. — Entopterygoid (Ent) and 'entopterygoid' ('Ent'); ectopterygoid (Ect) and 'ectopterygoid' ('Ect'). 0 = absence of the bone; ?: unknown condition.

Homology of ectopterygoid and ’ectopterygoid’

A dermal ectopterygoid is present only in diplomystids among the catfishes (Fig. 51). The diplomystid dermal ectopterygoid is homologous with that of other teleosts and non-teleostean fishes (Arratia & Schultze 1991). The presence of the ’ectopterygoid’ type 1 present in catfishes such as some ’pimelodids’, ’bagrids’, and ariids is interpreted here as a new formation because this tendon bone is absent in the ancestor of these groups.

Homology of certain ligaments

A ligament that extends between the ’entopterygoid’ and metapterygoid (Fig. 2B—G) is present in members of Siluroidea; according to the hypothesis of relationships presented herein, it is homologous among them. Within loricarioids, it is absent in trichomycterids as well as more advanced forms.

A ligament that extends between ’entopterygoid’ and lateral ethmoid (Fig. 2B—G) is present in Siluroidea, but it is absent in advanced members that lack the ’entopterygoid’.

A ligament that extends between ’entopterygoid’ and vomer is present in members of Siluroidea, but it is lost in several catfishes such as trichomycterids and more advanced loricarioids, *Parapimelodus*, and schilbeids (Fig. 2B—G).

The presence of the autopalatine-metapterygoid ligament is a synapomorphy of catfishes. I consider the appearance of the ’ectopterygoid’ within this ligament and its separation into two ligaments (Fig. 2E, F) as an evolutionary transformation of the autopalatine-metapterygoid ligament; therefore, the autopalatine-’ectopterygoid’ ligament and the ’ectopterygoid’-metapterygoid ligament are homologous with the autopalatine-metapterygoid ligament.

Diversity of bones of the suspensorium

The most primitive pattern of the suspensorium of catfishes is that of diplomystids, which in addition to the autopalatine, metapterygoid, quadrate, and hyomandibula, have both a small ectopterygoid and an entopterygoid. Although six elements may also be present in other catfishes, there is variation in the non-chondral elements. For example, six bones are present in the suspensorium of *Parapimelodus, Bagre*, and *Galeichthys*, however they do not have a dermal ectopterygoid; instead they have a specialized sesamoid ’ectopterygoid’. In addition, they lack a dermal entopterygoid, but they have a sesamoid ’entopterygoid’. Therefore, the same number of bones (six) present in the suspensorium of diplomystids and some ’pimelodids’, ’bagrids’, and ariids does not correspond to the same elements by ontogenetic origin.

A more specialized pattern within the suspensorium is present in ictalurids. Ictalurids (e.g., *Pylodictis, Ictalurus, Noturus*) have five bones. They have lost the dermal ectopterygoid and/or sesamoid ’ectopterygoid’; and instead of a dermal entopterygoid they have a sesamoid ’entopterygoid’. Another specialized pattern that represents an increased loss of elements is that present in trichomycterines. Trichomycterines have four bones in the suspensorium; they do not have a dermal or sesamoid ectopterygoid or entopterygoid.

The diversity of the suspensorium of catfishes affects not only the number of bones, but also the ligamentous links between the remaining bones. For example, ictalurids have five bones in the suspensorium, and at least two patterns of ligamentous connections are known. 'Entopterygoid' type 4 is found in *Noturus* (Fig. 2D) and 'entopterygoid' type 7 (Fig. 2G) is found in *Pylodictis* and a few species of *Ictalurus*. A more complex ligamentous pattern is present in *Ameiurus melas*. The study of the variation in the ligamentous connections of the sesamoid 'entopterygoid' and the 'ectopterygoid' in catfishes is necessary to our understanding of the evolutionary transformations of the suspensorium of siluriforms.

Variation

Variability in bones, muscles, and ligamentous connections is commonly present in the suspensorium of catfishes. The variation may be ontogenetic or may only affect adult individuals and varies both intraspecifically or interspecifically.

The high degree of variation present in the Diplomystidae (Arratia 1987a; present paper) is critical because the Diplomystidae are considered to be the most primitive family within the Siluriformes. The determination of the most plesiomorphic species of diplomystid varies according to whether the primitive or apomorphic states of certain characters are considered in cladistic analyses. Thus, *Olivaichthys viedmensis* is the most primitive diplomystid when only the plesiomorphic states of variable characters are considered (Arratia 1987a; present paper: Fig. 50B—D). The scheme of relationships among diplomystids changes when only the apomorphic states of variable characters are considered (Fig. 46A). Based on these results, I advocate the description and evaluation of the variation in other catfishes so that we may understand its role within species and among catfish subgroups.

The suspensorium of ostariophysans

Fink & Fink (1981) demonstrated that the major extant ostariophysan taxa are monophyletic; this is also confirmed by the present study (Fig. 45B, C). However, my results based on 37 characters of the suspensorium (Fig. 45B) show a different arrangement of the ostariophysans than that proposed by Fink & Fink (1981) and herein. The difference is the result of my having considered characters belonging to only one morphological system. The study of the suspensorium provides numerous characters supporting the monophyly of cypriniforms, gymnotoids, and catfishes. Because the last two groups are highly diverse in the evolutionary transformations of their suspensoria, however, they share only three synapomorphies (Fig. 45C).

Higher categories of Siluriformes

Grande (1987) proposed that the Siluriformes (= Siluroidei sensu Fink & Fink 1981) are divided in the suborders Diplomystoidei (sensu Chardon 1968) and Siluroidei. According to the present study, these taxa are characterized at the **primitive** level by the following synapomorphies listed for each category (see text and Figs. 45C, 46A, 50 for additional characters). The characters may be transformed in subgroups (e.g., pairs of barbels, maxillary processes, and maxillary teeth).

Siluriformes: Palatoquadrate separated into pars autopalatina and pterygoquadrata. Pterygoquadrate fused with hyo-symplectic cartilage. Autopalatine broad anteriorly, narrow and elongate posteriorly. Articulation between autopalatine and maxilla, double and anteroventrally placed. Autopalatine and metapterygoid linked by a ligament or connective tissue. Metapterygoid as main support of the eye. Metapterygoid anterodorsal to quadrate and forming part of the ventrolateral border of the suspensorium. Posteroventral process of quadrate absent. Quadrate and hyomandibula sutured with preopercle. Centra 2—4 forming the complex Weberian vertebra. Small, single supraneural above the Weberian apparatus. Pectoral fin with three proximal radials. Pelvic fin with six rays. Pelvic fin with cartilaginous radial absent. Dorsal spine present.

Diplomystoidei: Maxilla with teeth along most of oral margin. Maxilla with two large articular facets for autopalatine, both on the single, elongate anterior process. Anterior part of autopalatine divided into two processes early in ontogeny. Autopalatine not lying on the dorsolateral aspect of premaxilla. Hinge joint between maxilla and autopalatine absent. Hyomandibula articulates bone-to-bone with pterosphenoid. Hyoideomandibularis nerve trunk lateral to hyomandibula. Coronomeckelian bone large; usually increasing in size during growth. Ossified pharyngobranchials 1 and 2 attached to epibranchial 1 and to medial aspect of hyomandibula. Sphenotic of similar length or smaller than pterotic. Rhomboidal-shaped vomer. Single, small supraneural above Weberian apparatus in adult stage. Only maxillary barbel present. (For additional characters see Arratia 1987a, and above.)

Since Diplomystoidei comprises only the family Diplomystidae, the diagnoses of both are the same.

Siluroidei (sensu Grande 1987): Maxilla with two rudimentary processes bearing small facets for articulation with autopalatine. Dorsal and ventral hypohyals of different sizes. Fifth abdominal centrum ankylosed or fused with the Weberian complex vertebra. Weberian apparatus including fusion of abdominal centra 2—5. Caudal fin with 17 or fewer principal caudal fin rays.

The Siluroidei include the superfamilies †Hypsidoroidea and Siluroidea (Grande 1987) which are characterized by the following synapomorphies listed for these categories below.

†Hypsidoroidea: Two synapomorphies (maxillary teeth anteriorly located and maxilla with two well-developed processes that separate the autopalatine and premaxilla) and five homoplastic characters (numerous maxillary tooth rows; subautopalatine toothplate present; membranous bony extension over the ventral surface of the fifth abdominal centrum; extremely high coronoid process of dentary and angular; blood

vessels in a groove partially surrounded by lamellar walls in the ventral part of the Weberian apparatus) support this fossil clade.

†Hypsidoroidea comprises only the family †Hypsidoridae, known from the genus †*Hypsidoris.* The diagnoses of the three taxa are co-extensive.

Siluroidea: Maxilla without long anterior process. Maxilla rudimentary. Articulation between autopalatine and maxilla double and lateroventral. Dermal ectopterygoid and entopterygoid absent. 'Entopterygoid' and vomer linked by ligament and/or connective tissue. Metapterygoid without notch separating processus basalis and posterodorsal part of the bone. No supraneural above Weberian apparatus in adult stage.

Among the Siluroidea, the monotypic family Nematogenyidae can be diagnosed by: the presence of an 'entopterygoid' type 2; metapterygoid, 'entopterygoid' type 2, and autopalatine all located on the same level; the division of the levator arcus palatini muscle into three portions inserting on the posterior part of the frontal and autosphenotic; a well-developed levator operculi lateral to the opercle; and a minuscule pseudobranch medially attached to the hyomandibula.

ACKNOWLEDGEMENTS

This paper is dedicated to Frank Cross in his retirement as Professor and Curator of the University of Kansas (Lawrence, Kansas, USA) because of his continuous support to my research; for reading and commenting many of my long manuscripts over the years; and overall, for his deep knowledge about fishes that he generously shares with others.

The present paper has been possible through the help of numerous individuals and institutions which donated or loaned me material studied here. For gifts of specimens, I am indebted to my colleagues A. Manríquez and I. Vila (Universidad de Chile, Santiago, Chile), J. R. Casciotta and M. Azpelicueta (Museo de La Plata, Argentina), S. Menu Marque (Buenos Aires, Argentina), B. Burr (Southern Illinois University, Carbondale, Illinois, USA). For loan of specimens I would like to thank H. Campos (Universidad Austral de Chile, Valdivia, Chile), A. Gosztonyi (Chubut, Argentina), W. Saul (Academy of Natural Sciences of Philadelphia, Pennsylvania, USA), W. Eschmeyer, E. Anderson and D. Catania (California Academy of Sciences, San Francisco, USA), B. Chernoff (Field Museum of Natural History, Chicago, USA), K. Liem and K. Hartel (Harvard University, Cambridge, USA), M. L. Bauchot and G. Teugels (Muséum National d'Histoire Naturelle, Paris, France), M. Louette (Musée Royal de l'Afrique Centrale, Tervuren, Belgium), F. Cross and E. O. Wiley (Museum of Natural History, The University of Kansas, Lawrence, USA), G. Howes and P. H. Greenwood (Natural History Museum, London, Great Britain), R. Rosenblatt (Scripps Institution of Oceanography, University of California, La Jolla, USA), J. McEachran and M. Retzer (Texas A&M University, College Station, USA), W. L. Fink and D. Nelson (University of Michigan, Ann Arbor, USA), F. J. Schwartz (University of North Carolina, Morehead City, USA), K. Busse (Zoologisches Forschunginstitut und

Museum A. Koenig, Bonn, Germany), and H. Wilkens (Zoologisches Institut und Zoologisches Museum, Hamburg, Germany).

My sincerest thanks to Mercedes Azpelicueta, Sara Fink, and Scott Schaefer for valuable comments on the manuscript; to Lance Grande (Field Museum of Natural History, Chicago) for permission to reproduce the photographs of †*Hypsidoris*; to Frank Cross for his efforts gathering ontogenetic series of *Ictalurus*; to Daniel Goujet (Muséum National d'Histoire Naturelle, Paris) and Hans Bjerring (Naturhistoriska Riksmuseet, Stockholm) for their help in different ways; to Kathleen Shaw (The University of Kansas, Lawrence, USA) for her comments and criticism of style and grammar; and to Jan Elder and Judy Wiglesworth (Word Processing Center, The University of Kansas) for typing the manuscript.

This research was partially supported by the following institutions: Universidad de Chile, Servicio de Desarrollo Científico (grant Nr. 748-8034); Division of Fishes and Division of Vertebrate Paleontology, Museum of Natural History, The University of Kansas; California Academy of Sciences (a travel grant); Field Museum of Natural History, Chicago, Illinois, USA (research grant); Muséum National d'Histoire Naturelle, Paris, France; and Swedish Museum of Natural History, Stockholm, Sweden.

ABSTRACT

The suspensorium of ostariophysans as well as that of other teleosts is characterized by the presence of chondral elements (autopalatine, metapterygoid, and quadrate) and dermal elements (ectopterygoid and entopterygoid). The dermopalatine fused to the autopalatine present in primitive clupeocephalans is absent in ostariophysans. Tendon bone pterygoids and additional elements as toothplates may be found among catfishes. The suspensorium of cypriniforms, gymnotoids, and catfishes is highly specialized and several synapomorphies characterize each of these groups. Among the ostariophysans, gymnotoids and catfishes have very different and highly specialized suspensoria; still they share three synapomorphies — the anterior cartilage of the autopalatine or pars autopalatina does not articulate with the neurocranium, ligamentum primordiale inserts on the dorsal tip of the lower jaw, and the ectopterygoid is rudimentary or absent.

The suspensorium of catfishes is highly specialized from early in ontogeny. Differences in the palatoquadrate separate siluriforms from the other teleosts. For example, the palatoquadrate is divided into the pars autopalatina and the pars pterygoquadrata; the pars pterygoquadrata is fused to the dorsal limb of the hyoid arch to form the hyosymplectic-pterygoquadrate plate and this produces a special alignment of the suspensorium in catfishes. The bones commonly identified as the ectopterygoid and the entopterygoid in catfishes are tendon bones that are characterized by unique ligamentous connections with other bones of the suspensorium (e.g., metapterygoid) and/or cranial bones (e.g., vomer, lateral ethmoid, orbitosphenoid), and they are sesamoid elements. The sesamoid 'entopterygoid' (types 2—7) is an evolutionary transformation of the dermal entopterygoid; both bones are homologous. In contrast, the sesamoid 'ectopterygoid' present in some catfishes such as 'pimelodids', 'bagrids', and ariids is non-

homologous with the dermal ectopterygoid present in diplomystids. This is because both — a tendon bone 'ectopterygoid' and an ectopterygoid — are missing in the ancestor of 'pimelodids', 'bagrids', and ariids.

The ligamentous and/or connective tissue connections present between the 'entopterygoid' and vomer, 'entopterygoid' and lateral ethmoid, and 'entopterygoid' and metapterygoid are homologous among members of Siluroidea; one or another is lost in some advanced members of this clade. The presence of the autopalatine-metapterygoid ligament is a synapomorphy of catfishes; the division of this ligament into two due to the appearance of the calcification of the 'ectopterygoid' is considered as a derived condition. Because of their origin and distribution among catfishes, the autopalatine-'ectopterygoid' ligament and the 'ectopterygoid'-metapterygoid ligament are homologous with the autopalatine-metapterygoid ligament.

The study of the suspensorium reveals that it is difficult to understand the bony suspensorium of siluroids without ontogenetic investigations. In this way the sesamoid 'entopterygoid' and its ligamentous connections become a tool in systematic and phylogenetic interpretations. The presence of toothplates or other dermal elements should be investigated early in ontogeny to determine their early position and relationships, allowing more useful comparisons to be made.

A phylogenetic analysis based on 130 morphological characters confirms the scheme of phylogenetic relationships of ostariophysans proposed by Fink & Fink (1981). Phylogenetic analyses based on 75 morphological characters of certain primitive catfishes confirms Diplomystidae as the sistergroup of [†Hypsidoridae + Siluroidea]; among Siluroidea, nematogenyids are more primitive than ictalurids, 'pimelodids', and ariids. The characterization of the higher categories of Siluriformes sensu Grande (1987) such as the Diplomystoidei, Siluroidei, †Hypsidoroidea, and Siluroidea are analyzed and discussed. Additional diagnostic characters are provided for these clades.

ZUSAMMENFASSUNG

Das Suspensorium der Ostariophysi ist wie das anderer Teleosteer aus Knorpelelementen (Autopalatinum, Metapterygoid, und Quadratum) und dermalen Elementen (Ectopterygoid und Entopterygoid) aufgebaut. Ein mit dem Autopalatinum verschmolzenes Dermopalatinum, das primitive Clupeocephali besitzen, fehlt den Ostariophysi. Bei den Siluriformes können Pterygoide, die aus Sehnenknochen aufgebaut sind, und zusätzliche Elemente wie Zahnplatten auftreten. Das Suspensorium der Cypriniformes, Gymnotoidei und Siluroidei ist hoch spezialisiert; mehrere Synapomorphien charakterisieren jede dieser Gruppen. Innerhalb der Ostariophysi haben die Gymnotoidei und Siluroidei sehr verschiedene hoch spezialisierte Suspensoria; dennoch haben sie drei Synapomorphien gemeinsam: Der vordere Knorpel des Autopalatinums oder der Pars autopalatina artikuliert nicht mit dem Neurocranium, das primordiale Ligament inseriert an der dorsalen Spitze des Unterkiefers, und das Ectopterygoid fehlt oder ist rudimentär.

Das Suspensorium der Siluroidei ist bereits früh in der Ontogenie hoch spezialisiert.

Unterschiede im Palatoquadrat unterscheiden die Siluroidei von anderen Teleosteern. Zum Beispiel ist das Palatoquadrat unterteilt in Pars autopalatina und Pars pterygoquadrata. Die Pars pterygoquadrata ist mit dem dorsalen Arm des Hyoidbogens verschmolzen, so daß sie eine Symplectic-Pterygoquadratum-Platte bilden, wodurch das Suspensorium der Siluroidei eine besondere Anordnung erhält. Die Knochen, die gewöhnlich als Ectopterygoid und Entopterygoid der Siluroidei bezeichnet werden, sind Sehnenknochen, die durch einzigartige ligamentöse Verbindungen mit anderen Knochen des Suspensoriums gekennzeichnet sind (z.B. Metapterygoid) und/oder Kopfknochen (z.B.: Vomer, laterales Ethmoid, Orbitosphenoid); es handelt sich um Sesamknochen. Das sesamoide 'Entopterygoid' der Typen 2 bis 7 ist eine evolutive Umbildung des dermalen Entopterygoids; beide Knochen sind homolog. Im Gegensatz dazu ist das sesamoide 'Ectopterygoid', das in einigen Siluroidei wie den 'Pimelodidae', 'Bagridae' und Ariidae auftritt, nicht homolog mit dem dermalen Ectopterygoid der Diplomystidae. Dies ist aus dem Fehlen beider Knochen, des Sehnenknochen-'Ectopterygoids' und eines Ectopterygoids, bei den Vorfahren der 'Pimelodidae', 'Bagridae' und Ariidae abzuleiten.

Die ligamentösen und/oder bindegewebsartigen Verbindungen zwischen 'Entopterygoid' und Vomer, 'Entopterygoid' und lateralem Ethmoid und zwischen 'Entopterygoid' und Metapterygoid sind innerhalb der Siluroidea homolog; die eine oder andere Verbindung kann bei einigen Vertretern dieser monophyletischen Gruppe verloren gehen. Das Vorhandensein eines Ligaments zwischen Autopalatinum und Metapterygoid ist eine Synapomorphie der Siluroidei; die Aufteilung des Ligaments in zwei durch Verknöcherung des 'Ectopterygoids' ist als fortschrittliches Merkmal anzusehen. Aufgrund seines Ursprungs und der Verteilung innerhalb der Siluroidei, sind das Ligament zwischen Autopalatinum und 'Ectopterygoid' und das zwischen 'Ectopterygoid' und Metapterygoid als homolog mit dem Ligament zwischen Autopalatinum und Metapterygoid zu betrachten.

Das Studium des Suspensoriums zeigt, daß es schwierig ist, das knöcherne Suspensorium ohne ontogenetische Untersuchungen zu verstehen. In diesem Sinne ist das sesamoide 'Ectopterygoid' und seine ligamentösen Verbindungen ein Beispiel für systematische und phylogenetische Interpretation. Das Auftreten von Zahnplatten oder anderer dermaler Elemente sollte ebenfalls auf seine frühe ontogenetische Entwicklung hin untersucht werden, um die frühe Lage und die Beziehungen dieser Elemente zu bestimmen, so daß sinnvollere Vergleiche möglich werden.

Eine phylogenetische Analyse von 130 morphologischen Merkmalen bestätigt die stammesgeschichtlichen Beziehungen der Ostariophysi, wie sie von Fink & Fink (1981) vorgeschlagen wurden. Eine phylogenetische Analyse von 75 morphologischen Merkmalen gewisser primitiver Siluroidei bestätigt die Diplomystidae als Schwestergruppe von [†Hypsidoridae + Siluroidea]; innerhalb der Siluroidea, sind die Nematogenyidae primitiver als die Ictaluridae, 'Pimelodidae' und Ariidae. Die Merkmale der höheren Einheiten der Siluriformes in Sinne von Grande (1987) wie der Diplomystoidei, Siluroidei, †Hypsidoridae und Siluroidea werden analysiert und diskutiert. Zusätzliche diagnostische Merkmale für diese monophyletischen Gruppen werden aufgeführt.

RESUMEN

El suspensorio de los ostariofisos, al igual que el suspensorio de otros teleósteos, se caracteriza por la presencia de elementos condrales (autopalatino, metapterigoides y cuadrado) y dermales (ectopterigoides y entopterigoides). El dermopalatino, que se encuentra fusionado al autopalatino en clupeocéfalos primitivos, está ausente en ostariofisos. Huesos pterigoideos originados como calcificaciones de ligamentos (huesos de tendón) y elementos adicionales como placas dentadas se encuentran presente en ciertos bagres. El suspensorio de cipriniformes, gimnótidos y bagres es altamente especializado; varias sinapomorfías caracterizan a cada uno de estos grupos. Dentro de los ostariofisos, los bagrès y gimnótidos tienen los suspensorios mas diversificados. Gimnótidos y bagres comparten tres sinapomorfías: el cartílago anterior del autopalatino o pars autopalatina no está articulado al neurocráneo, el ligamentum primordiale inserta en el extremo dorsal de la mandíbula inferior y el ectopterigoides está ausente en la mayoría de ellos.

El suspensorio de los bagres es especializado desde estados tempranos de la ontogenia. Diferencias en el palatocuadrado (cartilaginoso) separan a los bagres de otros teleósteos. Por ejemplo: el palatocuadrado de los bagres está dividido en dos secciones que son la pars autopalatina y pars pterygoquadrata. La pars pterygoquadrata se fusiona al miembro dorsal del arco hioídeo formando el cartílago hio-simplectico-pterigocuadrado; esta fusión produce una orientación espacial especial del suspensorio de los bagres. Los huesos que comunmente se han identificado como el ectopterigoides o pterigoides y el entopterigoides o mesopterigoides en bagres son calcificaciones de ligamentos (huesos de tendón); estos huesos se caracterizan por sus relaciones ligamentosas con otros huesos del suspensorio como por ejemplo el metapterigoides y/o con huesos craneanos como por ejemplo el vomer, orbitoesfenoides y el etmoides lateral; debido a sus relaciones ligamentosas estos huesos son considerados como huesos sesamoídeos. El 'entopterigoides' o entopterigoides sesamoídeo, es interpretado como una transformación evolutiva del entopterigoides dermal; ambos huesos son homólogos entre si. El ectopterigoides sesamoídeo que se encuentra presente en ciertos bagres como 'pimelódidos', 'bágridos' y áridos no es homólogo con el ectopterigoides dermal presente en diplomystidos. Esta no-homología es debida a la ausencia de un 'ectopterigoides' o ectopterigoides en los posibles antecesores de 'pimelódidos', 'bágridos' y áridos.

Las conecciones ligamentosas y/o a través de tejidos conjuntivos presentes entre el 'entopterigoides' y vomer, 'entopterigoides' y etmoides lateral y 'entopterigoides' y metapterigoides son homólogas a través de miembros de Siluroidea; una u otra conección se pierde en algunos taxones avanzados de Siluroidea. La presencia del ligamento autopalatino-metapterigoides es una sinapomorfía de los bagres; la división de este ligamento en dos ligamentos debido a la aparición de la calcificación del 'ectopterigoides' es considerado como un caracter apomórfico. Debido a su origen (división del ligamento autopalatino-metapterigoides) y a su distribución en bagres, los ligamentos autopalatino-'ectopterigoides' y 'ectopterigoides'-metapterigoides son homólogos con el ligamento autopalatino-metapterigoides.

El estudio del suspensorio muestra que es difícil entender esta estructura en bagres en ausencia de investigaciones ontogenéticas. Estudios del desarrollo muestran que las conecciones ligamentosas del 'entopterigoides' pueden proporcionar caracteres útiles en interpretaciones taxonómicas y filogenéticas. La presencia de placas dentadas u otros elementos dermales que se encuentran en ciertos bagres, deben investigarse desde estados ontogenéticos tempranos para determinar su posición y relaciones con otros elementos y sus variaciones a través del crecimiento; esto permitirá hacer comparaciones mas útiles.

El analisis filogenético basado en 130 caracteres morfológicos confirma el esquema de relaciones filogenéticas de los ostariofisos propuesto por Fink & Fink (1981). Análisis filogenéticos basados en 75 caracteres morfológicos de ciertos bagres primitivos confirma a Diplomystidae como el grupo hermano de la clade [†Hypsidoridae + Siluroidea]; dentro de Siluroidea, nematogénidos son mas primitivos que ictalúridos, 'pimelódidos' y áridos.

Se presenta y se discute la caracterización de categorías superiores tales como Diplomystoidei, Siluroidei (sensu Grande 1987), †Hypsidoroidea y Siluroidea. Se proveen caracteres diagnósticos adicionales de estos taxones.

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Appendix 1: Character states of 130 characters of the suspensorium and other morphological structures in ostariophysans. For explanation see pp 86—107.

	Characters
	1111111111222222222233333333334444444444
	1234567890123456789012345678901234567890123456789
Outgroup	000000000?000000000000000000000000000000000000000
Gonorynchiformes	0000010100001000000000000000000000000000011100001
Cypriniformes	0001000100100000111000000000010020000100001100000
Characiformes	0001000100000000000000000000010100000011001110100
Siluroidei	2112000101010111000110110011101111011011101111110
Gynotoidei	1000101111222000000101001100000120100011101110110

	Characters
	55555555556666666666777777777788888888889999999999
	01234567890123456789012345678901234567890123456789
Outgroup	000000000000000000000000000000000000000?0000000000
Gonorynchiformes	00000001001101111000011111110000000000000000000000
Cypriniformes	00000010011100110101111111101101000000001001100100
Characiformes	10000000101010000000011111101111111001101100110100
Siluroidei	11111100111000100110011111101111111111110010111111
Gynotoidei	11110100101000100110011111101011111101101100110110

	Characters
	1111111111111111111111111111111
	0000000000111111111122222222223
	0123456789012345678901234567890
Outgroup	000000000000000000?0?0?00000000
Gonorynchiformes	0000010000000000001100001100000
Cypriniformes	0000010000000000001101101100001
Characiformes	0000001000000000001111001100011
Siluroidei	111111110110001010111111??00111
Gynotoidei	0101001111111111111111100011001

Appendix 2: Character states of 75 morphological characters in siluriforms. For explanation of characters see pp 108—126.

	Characters
	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5
Outgroup	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Bagre	0 0 1 0 2 1 2 0 2 0 1 0 0 0 0 0 1 1 1 1 1 0 1 1 0 1 0 1 0 1 0 0 1 0 1 1 1 1 1 1 0 0 0 ? 0 0 0 1 0 0 1 3 0 0 2 1 1 1 1 1 1 0 2 ? 0 1 ? 0 1 1 1 1 1 1 1
Diplomystes camposensis	1 1 0 0 0 0 1 1 1 1 0 0 0 0 0 1 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 1 1 1 0 1 0 0 0 0 0 1 0 1 1 1 1 0 0 1 0 1 0 0 0 1 1 1 1 0 0 0 1 0 0 2 1 0 1 1 1 1 1 1 1
Diplomystes chilensis	1 1 0 0 0 0 1 1 1 1 0 0 0 0 0 1 0 0 0 0 0 1 1 0 0 0 0 1 0 0 1 1 1 1 0 1 0 0 0 0 0 1 0 0 0 2 1 0 0 1 0 1 0 0 0 1 1 1 1 0 0 0 1 0 0 3 1 0 1 1 1 1 1 1 1
Diplomystes nahuelbutaensis	1 1 0 1 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 1 1 1 1 0 1 0 0 0 0 0 1 0 0 1 1 1 0 0 1 0 1 0 0 0 1 1 1 1 0 0 0 1 0 0 2 1 0 1 1 1 1 1 1 1
Galeichthys	0 0 1 0 2 1 2 0 2 0 1 0 0 0 0 0 1 1 1 1 1 0 1 1 0 1 0 1 0 1 0 0 1 0 1 1 0 1 1 1 0 0 0 1 0 0 0 1 0 0 1 3 0 0 2 1 1 1 1 1 1 0 2 1 0 1 ? 0 1 1 1 1 1 1 1
Heptapterus	0 0 1 0 2 1 2 0 2 0 1 0 1 0 2 0 1 0 1 1 1 0 0 1 1 1 0 0 0 1 0 0 0 0 1 0 1 1 1 1 0 0 0 1 0 0 0 1 0 0 0 2 0 0 1 1 1 1 0 1 1 0 2 0 0 1 ? 0 1 1 1 1 1 1 1
†Hypsidoris	2 2 1 0 1 0 1 ? 1 ? ? 0 ? ? ? 1 ? 0 ? ? ? ? ? ? 0 0 0 ? 0 ? 0 0 ? ? ? 1 0 1 1 1 1 0 0 ? ? ? 0 1 ? 0 0 2 ? 0 1 ? ? 1 1 0 0 0 ? ? 0 ? ? ? ? ? 1 1 1 1 1
Ictalurus	0 0 1 0 2 1 2 0 2 0 1 0 0 1 2 0 1 0 1 1 1 1 0 1 0 1 0 1 1 1 1 0 0 0 1 1 0 1 1 1 0 1 0 1 0 0 0 1 0 0 1 2 0 0 1 1 0 1 1 0 0 0 2 0 0 1 ? 0 1 1 1 1 1 1 1
Nematogenys	0 0 1 0 2 1 1 0 2 0 1 1 0 0 0 0 1 0 1 0 1 1 0 1 0 1 0 1 0 0 0 0 0 1 0 1 0 1 0 1 0 0 1 0 0 0 0 1 1 0 1 2 1 1 0 1 1 1 0 1 1 0 2 0 1 1 ? 1 1 1 1 1 1 1 1
Olivaichthys	1 2 0 0 0 0 1 1 1 1 0 0 0 0 0 1 0 0 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 0 1 0 0 0 0 0 1 0 0 1 2 1 0 0 1 0 1 0 0 0 1 1 0 1 0 0 0 1 0 0 3 0 0 1 1 1 1 1 1 1
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