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DESCRIPTION OF THE PRIMITIVE FAMILY
DIPLOMYSTIDAE (SILURIFORMES, TELEOSTEI, PISCES):
MORPHOLOGY, TAXONOMY AND
PHYLOGENETIC IMPLICATIONS

by
G. Arratia



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I. INTRODUCTION

Siluroid fishes are divided into about 32 families, 13 of them endemic to South America. The family Diplomystidae has been generally considered monogeneric. *Diplomystes*, with two species, *D. chilensis* (Molina, 1782) and *D. viedmensis* Mac Donagh, 1931, the latter with three subspecies, *D. viedmensis viedmensis* Mac Donagh, 1931, *D. viedmensis cayanus* Ringuet, 1965, and *D. viedmensis mesembrinus* Ringuet, 1982.

These fishes are restricted to southern South America. Older references cited it as widely distributed in central and southern Chile, and from San Juan to Patagonia in Argentina. At the beginning of this century, specimens of Diplomystidae were sold on the markets of Santiago de Chile (Eigenmann 1927) and of Buenos Aires (Berg 1901, Mac Donagh 1931). In contrast, today diplomystids are rarely found in rivers and lakes of Chile and Argentina. *D. chilensis* has disappeared from most of the cited localities as has *Nematogenys inermis*, another endemic southern South American catfish. Reasons for the extirpation of diplomystids (Arratia 1983 a: 218) all relate to their intolerance of changed environments.

Information about diplomystids is currently based upon very few specimens. Some body proportions and counts of rays are given in Valenciennes (1840), Günther (1864), Philippi (1866), Mac Donagh (1931), Ringuet (1965, 1982) and Ringuet et al. (1967). That information is partly contradictory because few specimens were studied and intraspecific variation was not considered (see Arratia et al. 1978, Arratia & Menu Marque 1981, 1984, Arratia 1983 b, for discussion of individual variability of catfishes). Descriptions of the palatine-maxillary mechanism have been given by Alexander (1965) and Gosline (1975); descriptions of the Weberian apparatus by Alexander (1965), Chardon (1968) and Fink & Fink (1981); of the pelvic girdle by Shelden (1937), Arratia et al. (1978) and Fink & Fink (1981); and of the caudal skeleton by Gosline (1961), Lundberg & Baskin (1969) and Arratia (1982 a).

The Diplomystidae is considered the most primitive living family of the suborder Siluroidei. Our knowledge of this family is mainly based on the Chilean *Diplomystes chilensis*. Characters regarded as primitive are: 1) maxilla not reduced in size, being narrow proximally, broad distally, and bearing a large medial process (Alexander 1965, Fink & Fink 1981), 2) maxilla toothed along most of its ventral border (Eigenmann 1927, Alexander 1965, Gosline 1975, Fink & Fink 1981), 3) "lagenar otolith equal in size to or larger than utricular otolith", 4) principal caudal fin-rays count 9/9 (Lundberg & Baskin 1969, Arratia 1982 a), and 5) maxillary barbels only. Characters 1, 2 and 3 were considered by Fink & Fink (1981) as features shared with primitive teleosts, and 4 and 5 as primitive features within siluroids.

When I finished the review of diplomystids from southern Chile, I received specimens of *Diplomystes chilensis* from "rivers from Santiago" collected by R. Philippi at the end of the last century, on loan from the Museum of Comparative Zoology, Harvard. To my surprise, these fishes are different from diplomystids now inhabiting the rivers

south of Santiago. Today *Diplomystes chilensis* does not occur in rivers of the Aconcagua and Maipo basins (Valparaíso and Santiago, respectively) (Duarte et al. 1971, Dazarola 1972, Arratia 1981 a). I tried therefore to get on loan specimens collected in the last century or at the beginning of this century in those regions. I was able to gather seventy-seven specimens from different localities in Chile, including those from "Santiago market", and a few specimens (nine) from Argentina.

This paper is a detailed description of the family Diplomystidae; a description of the Argentinean diplomystids and a comparison with the Chilean forms is presented for the first time. The family is exhaustively described, as basis for future work on interrelationships of catfishes.

II. MATERIAL AND METHODS

Eighty-six specimens of diplomystids were studied. Meristic and morphometric data were obtained for most specimens. Osteological observations were made on cleared and stained specimens and on radiographs of most specimens. Some of them were cleared and double-stained following a modification of the technique of Dingerkus & Uhler (1977) to permit examination of both cartilage and bone.

Illustrations were prepared by the author with the use of a Wild M-5 stereodissecting microscope equipped with a camera lucida. Details were checked with Leitz and Olympus compound microscopes with high resolution power and phase contrast; ligaments were also checked with polarized light; preparations of the skin were studied with a Stereoscan (SEM) Mark IIA (Cambridge).

The diplomystid specimens belong to:

Laboratorio de Biología, Universidad de Chile, Santiago-Sur (LBUCH);

Instituto de Zoología, Universidad Austral, Chile (IZUA);

Colección Ictiológica, Museo La Plata, Argentina (CIMLP);

Museum of Natural History, Lawrence, Kansas, USA (KU);

Museum of Comparative Zoology, Harvard, USA (MCZ);

Museum of Zoology, Ann Arbor, Michigan, USA (UMNZ);

California Academy of Sciences, San Francisco, California, USA (catalog numbers reading CAS (IUM) formerly of Indiana University, and CAS (SU) formerly of Stanford University);

Muséum national d'histoire Naturelle, Ichtyologie générale et appliquée, Paris, France (MNHN);

British Museum of Natural History, London, England (BMNH);

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK);

Natur-Museum und Forschungs-Institut "Senckenberg", Frankfurt am Main, Germany (SMF);

Museo Zoologico de "La Specola", Firenze, Italy (MZUF);

private collection of Dr. Atila Gosztonyi, Argentina (AG); and private collection of the author (PC).

Material examined is listed in the account of each species.

Numerous cleared and stained (cl & st) siluroid were used for comparison. Most specimens belong to the Division of Ichthyology, University of Kansas (KU), Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences, San Francisco, California (CAS), National Museum of Natural History, Washington D.C. (NMNH), Zoologisches Institut und Zoologisches Museum, Hamburg (ZMH), and private collection (PC); catalog numbers are mentioned in the text and figures.

Measurements

The methods employed to obtain most of the measurements are those described by Hubbs & Lagler (1947). Measurements were obtained with a vernier calliper reading to 0.1 mm, on the left side of each specimen. The maximum depth of the body was taken in front of the base of the first dorsal spine. The depth of the adipose fin was taken at the highest point of the fin. The length of the premaxilla and maxilla was taken from tip to tip of each bone, following their curvature; the length of the sphenotic, from the anterior extreme of the anterolateral process to the posterior margin of the bone; and that of the pterotic, from the anterior margin to the end of the sharp posterior process. The length of the dorsal spines and dorsal fin-rays was taken from the base to the distal end of each spine and ray.

Symmetry was not assumed, it was checked for every feature.

Counts

Counts of rays, vertebrae, teeth, spines, serrae of spines, etc., were made in most specimens under a Wild M-5 stereodissecting microscope; in the smallest specimens, by the use of compound Olimpus and Leitz microscopes.

Vertebral counts include the four vertebrae of the Weberian apparatus (the complex vertebra is counted as formed by three centra), and preural centrum 1 (ural centra are not considered). The fin-rays count of dorsal and anal fins follows Hubbs & Lagler (1947). The caudal fin-rays count follows Lundberg & Baskin (1969); besides the standard counts of simple and principal caudal rays, the number of the segmented and unbranched rays of both dorsal and ventral lobes is established for every species. The count of the principal caudal fin-rays of dorsal and ventral lobes is indicated by a slash (/). The count of the pectoral axillary glands considered both sides of the body as indicated by a slash (/).

Explanation of descriptions

The diagnosis and description of the type-species *Diplomystes chilensis* is followed by the diagnoses and descriptions of the other species of *Diplomystes* and the new genus; the last descriptions contrast those species only with *D. chilensis*; the description of *D.*

camposensis n. sp. gives information on ontogenetic changes of some structures. The description of *Diplomystes chilensis* is based on specimens measuring 163 to 230 mm, that of *D. nahuelbutaensis* n. sp. on 120 to 261 mm specimens, that of *D. camposensis* n. sp. on a series of growth of specimens of about 20 to 205 mm, and that of *Olivaichthys viedmensis* is based on about 28 to 206 mm standard length specimens.

The name of each species is followed by a list of figures, synonyms, common names, studied material, type-locality, etymology, diagnosis and description. The list of synonyms pretends to be complete. When the material has not been reexamined and doubt exists about its identity, an interrogation mark (?) precedes the reference. The list of material is that used for the descriptions. Each description presents a general review of the measurements and external morphology; most of the description is based on anatomical features as bones, sensory canals, and skin, as the most relevant structures within diplomystids.

Primitive and derived state of characters

In the present study three criteria are used to determine the primitive state of characters following the phylogenetic method (Hennig 1966, Wiley 1981, Ax 1985): comparison with other ostariophysans as outgroup (Roberts 1973, Fink & Fink 1981, present paper), widespread occurrence of a character within siluriforms, and ontogenetic appearance. Characters which are limited to subgroups within siluriforms are derived (advanced) characters at different levels.

Key-symbols of state of characters

The following symbols are used in the diagnoses to identify the states of characters in diplomystids:

- * = derived feature of Diplomystidae shared with other Siluroidei.
- *1 = unique derived character for the family Diplomystidae within Siluroidei.
- *2 = unique derived character of a genus or species within the family Diplomystidae.
- # unique primitive character to Diplomystidae within Siluroidei.

III. HISTORICAL REVIEW OF THE SPECIES OF DIPLOMYSTIDAE

Numerous authors have briefly described diplomystids under different generic names: e. g., *Silurus*, *Pimelodus*, *Arius*, *Diplomyste*, *Diplomystes*, *Diplomystax* (see synonyms, p. 12). It is not possible to check each specific description against the fishes since most of the type-specimens are lost. Most of the species were described from one or a few specimens.

Molina (1782) gave the first description of the diplomystid species, "*silurus Chilensis*" (no type-specimen mentioned). Gmelin (1806: 830) redescribed *Silurus chilensis* from

Chile, but he confused the two large Chilean freshwater catfishes, *Diplomystes* and *Nematogenys* (see Eigenmann 1927: 37). He mentioned a lanceolate caudal fin which characterizes *Nematogenys*. Valenciennes (1840) considered his *Arius papillosus* as the type-species of *Arius* (= *Diplomystes*). The material he used, deposited at the Muséum national d'histoire Naturelle, Paris, is reconsidered in this paper. Blunt palatine teeth (read vomerine teeth) ("dent mousses et comme gresues") were cited by Valenciennes (1840) as characteristic of the species; the type-locality was broadly designated as Valparaíso and Río de San Yago (= Santiago) (= Aconcagua and Maipo basins, respectively). Guichenot (1848) redescribed and illustrated *Arius papillosus* (= *Diplomystes papillosus*). Differences to Valenciennes' (1840) and Guichenot's (1848) descriptions were discussed by Philippi (1866) who had never seen any *Arius* (= *Diplomystes*) with blunt teeth as described by Valenciennes (1840).

Several additional species were described under the generic name *Arius* (= *Diplomystes*) (one by Leybold 1859, and five by Philippi 1866). The type-locality (Maipo basin) is known for "*Arius Carcharioides*" Leybold and for "*Arius Squalus*" Philippi. Unfortunately the localities of the other three species described by Philippi are unknown. Most diplomystid species previously identified as *Arius* were separated from each other using length and depth of the adipose fin, head length, and coloration.

From 1856 on, the names *Diplomyste* Duméril (1856) or *Diplomystes* Bleeker (1858) have been used for the above mentioned species. *Diplomyste*, (= one pair of barbels), was latinized as *Diplomystes* by Bleeker (1858) and as *Diplomystax* by Günther (1864). The name is not a Greek, or a Latinized Greek, or a strictly vernacular French name. The latinized version, *Diplomystes*, is the one actually accepted (see Gosline 1975: 4, Meyers 1960: 247). "*Diplomyste* per se is not a Greek name or even a Latinized Greek name. The prefix (*diplo*) is in order, but the transliteration *myste* has no meaning. Duméril (1856: 487) literally spells out, in both Greek and Roman alphabets, the derivation of the name, i. e. *diplo* = 'double', and *mystax* = 'poils de la levre superior'. Thus, as Günther (1864) noted, the correct name should be *Diplomystax*. However, the first 'Latinized' version of the French name had already been published (i. e. 'Latinized' by Bleeker as *Diplomystes* in 1858). It is unfortunate that Bleeker chose this variant and not, as Duméril had indicated, *Diplomystax*, since *mystes* means priest" (P. H. Greenwood in litteris).

The best description of *Diplomystes chilensis* is that by Eigenmann (1927). This author (1927: 36, 37) considered as synonyms all previously described species but he did not give arguments for his decision. My studies of Eigenmann's material plus other collections demonstrate me that he was in error.

Eigenmann (1927: 37) wrote that he was informed that the fishes from Santiago market were from Valdivia. That they actually were seems unlikely because of the distance involved and problems of transportation at that time. Most freshwater fishes sold in that market are from the Maipo basin. In addition, the features of Eigenmann's material are similar to those of diplomystids labeled as Santiago or Santiago province (Maipo basin).

Mac Donagh (1931, 1938) described *Diplomystes viedmensis* from Río Negro, Viedma, Mendoza, and San Juan, Argentina by using three specimens. Later, Ringuélet (1965) distinguished two subspecies or "geographic races" based on the same three specimens studied by Mac Donagh (and an additional one): *D. viedmensis cuyanus* from Yaucha, Vilucó, in Mendoza, and probably in San Juan, and *D. viedmensis viedmensis* from Río Negro and Río Aluminé, in Neuquén, Argentina. Ringuélet (1982) erected another "geographic race", *D. viedmensis mesembrinus* from Río Senguer, in Chubut (the southernmost locality known for the family). The description of each Argentinean subspecies considered one or two specimens only, and they are differentiated from each other on some body proportions, aspect of the skin, and coloration; other characters are unknown.

IV. SYSTEMATICS

The family Diplomystidae and their species

The family name **Diplomystidae** (order Siluriformes, suborder Siluroidei) derives from the name of the type-genus *Diplomystes*. Eigenmann (1890: 14) created the family on the basis of one feature (dentate maxilla). Eigenmann & Eigenmann (1890: 9, 25; 1891: 7, 9), Regan (1911: 557), Berg (1940: 447), Bertin & Arambourg (1958: 2305), de Buen (1958: 149) and Ringuélet et al. (1967: 263) define it more extensively. Each diagnosis has had the problem of being based on a combination of features, all being primitive. The emended diagnosis presented below is based on a combination of advanced and primitive characters; features apparently unique, and/or advanced to diplomystids within Siluroidei are discussed below.

D i a g n o s i s (emended): Catfishes with elongate body, more or less compressed caudal peduncle. Relatively large eye, not covered by skin. One pair of (maxillary) barbel. Nasal capsule bounded by mesethmoid, lateral ethmoid, cartilage of vomer, palatine, maxilla and antorbital (*). Pelvic fins broadly separated from each other (*). With (1) pectoral and (2) dorsal spines (*). Most of the dorsal fin base placed in the anterior half of the body. Adipose fin present. Caudal fin forked or slightly emarginated, lobes frequently asymmetric. Anus and urogenital pore narrowly separated. Skin of whole body covered with enormous simple or lobulate papillae embedded in a coloid-like substance (*1).

Extensive invasion of adductor mandibulae over cranial bones (frontal, pterotic, sphenotic, extrascapular and supraoccipital) (*). Sphenotic longer than pterotic (*). Sphenotic spine absent (*). Moderately large extrascapular roofing a small posttemporal fossa. Large lagena (**). Sagitta the largest otolith (*1). Pterosphenoid lacking a suture with the parasphenoid (*1). Parasphenoid lacking lateral wings (*). Large, broad rhomboidal vomer (*1). Dorsal margin of hyomandibula extending onto pterotic, prootic, sphenoid and pterosphenoid (*1). Circumorbital series comprises antorbital

and six to eight tube-like or half-cylinder infraorbitals (*). Long dentate maxilla, broad posteriorly and with long medial process (**). Maxilla with more than one row of functional teeth (*1). Large coronomeckelian bone, in adult stage (*1). Palatine with two articular facets anteriorly articulating with two facets of maxilla (*1). Hyomandibula and metapterygoid united by a "lap" joint (*1). Dorsal and ventral hypohyals present. Four ossified pharyngobranchials of similar length (**). Uncinate process only on epibranchial 3 (*). Pseudobranch present. Ossified supraneurals 3-4 present (**). Complex vertebra 2-4 not fused with vertebra 5. Separate second ural centrum present in young, lost in adults (*1). 9/9 principal caudal rays (**).

C o n t e n t : Two genera and five species:

1. Type-genus: *Diplomystes* Duméril:

Diplomystes chilensis (Molina, 1782)

Diplomystes nahuelbutaensis n. sp.

Diplomystes camposensis n. sp.

Diplomystes sp.

2. *Olivaichthys* n. gen.

Olivaichthys viedmensis (Mac Donagh, 1931).

G e o g r a p h i c a l d i s t r i b u t i o n : Freshwater, rivers and lakes, of Chile and Argentina, southern South America.

R e m a r k : No fossil diplomystids known.

Genus *Diplomystes* Duméril, 1856

S y n o n y m s :

Diplomyste: Duméril, A. M. (1856): Ichthyol, Analyt.: 487. — Eigenmann, C. (1927): Mem. Nat. Acad. Sci. 22: 36. — Gosline, W. (1945): Bol. Mus. Nac. (Rio de Janeiro), n. s., Zool. (33): 6. — de Buen, F. (1958): Inv. Zool. Chilenas 5: 150.

Diplomystes: Bleeker, P. (1858): Archipelagi Indici Prodomus I: 56. — Eigenmann, C., & R. Eigenmann (1890): Occas. Papers Calif. Acad. Sci., I: 26. — (1891): Proc. United States Nat. Mus., XIV: 13. — Berg, C. (1901): Com. Mus. Nac. Buenos Aires, t. 1 (9): 293. — (?)Ringuelet et al. (1967): Los Peces Argentinos de Agua Dulce: 263. — Arratia, G. (1981 a): Bull. Mus. Nac. Hist. Natur., Chile, Publ. Ocas. 34: 44.

Diplomystax: Günther, A. (1864): Cat. Fishes Brit. Mus., v. V: 180.

G e o g r a p h i c a l d i s t r i b u t i o n : Central and southern Chile, South America.

D i a g n o s i s : Sphenotic more than 150 % of pterotic length (*2). Sphenotic with long anterolateral process (*2). Maxilla with two functional rows of teeth anteriorly, one row of teeth posteriorly, few maxillary teeth in adult (8-19). Three or none pectoral distal radials (*2). Loss of a separate pelvic radial (*2).

T y p e - s p e c i e s : *Diplomystes chilensis* (Molina, 1782).

Diplomystes chilensis (Molina, 1782)

(Figs. 1A—C; 2A—D; 3A; 4A—B; 5A—B; 6A—C; 7A—D; 8A; 9A—C; 10A; 38; Tables 1—3)

S y n o n y m s :

Silurus chilensis: Molina, J. I. (1782): Saggio sulla storia naturale del Chili, lib. 4: 225. — Bonnaterre (1788): Tableau Encyclop. Ichthyologie: 152. — (?) Gmelin, J. F. (1789): Systema Naturae Linn., pt. 1: 1359. — Bloch, M. E., & J. S. Schneider (1801): Systema Ichthyologiae: 378. — Molina, J. I. (1808): Geogr. Nat. Civil Hist. Chile (Irving's translation), n. 1: 153.

Pimelodus chilensis: Lacépède, B. G. (1803): Hist. Nat. Poiss., v. V: 114; 1840: 118 (Valparaíso, Santiago).

Arius papillosus: Valenciennes, A. (1840): Hist. Nat. Poiss., v. 15: 118 (Valparaíso, Santiago, Chile). — Guichenot, A. (1848): Hist. Chile, Zool., v. II: 305 (Chile), atlas, 1854, pl. 5 bis, fig. 1. — Philippi, R. (1866): Mber. Akad. Wiss. Berlin: 710.

Diplomyste papillosus: Duméril, A. M. (1856): Ichthyol. Analyt.: 487. — Eigenmann, C. (1909): Reports Princeton Univ. Exped. Patagonia III: 252. — Gosline, W. (1945): Bol. Mus. Nac., Zool., Rio de Janeiro: 33.

Diplomystes papillosus: Bleeker, P. (1858): Archipelagi Indici Prodomus I: 56; (1863): Nederl. Tijdschr. Dierk. I: 92. — Eigenmann, C., & R. Eigenmann (1888): Proc. Calif. Acad. Sci., 2d, ser. I: 149; (1890): Occas. Papers Calif. Acad. Sci., I: 26; (?) Lundberg, J., & J. Baskin (1969): Amer. Mus. Novitates (2398): 11, 18, 34—36. — Fink, S., & W. Fink (1981): J. Zool. Linn. Soc. 72 (4): 308—341.

Arius carcharioides: Leybold, F. (1859): An. Univers. Chile, v. XVI: 1083 (Río Seco, Colina, Province of Santiago).

Diplomystax papillosus: Günther, A. (1864): Cat. Fishes Brit. Mus., v. V: 180 (Chile).

Arius squalus: Philippi, R. (1866): Mber. Akad. Wiss. Berlin: 714 (Paine, province of Santiago). — Delfin, F. (1899): Rev. Chilena Hist. Nat. 3 (10—11): 156.

Arius carcharias: Philippi, R. (1866): Mber. Akad. Wiss. Berlin: 711 (Chile).

Arius villosus: Philippi, R. (1866): Mber. Akad. Wiss. Berlin: 713.

Arius micropterus: Philippi, R. (1866): Mber. Akad. Wiss. Berlin: 713. — Delfin, F. (1899): Rev. Chilena Hist. Natur. 3 (10—11): 156.

Arius synodon: Philippi, R. (1866): Mber. Akad. Wiss. Berlin: 714. — Delfin, F. (1899): Rev. Chilena Hist. Natur. 3 (10—11): 156. Eigenmann (1927) considers this species as synonym of *D. chilensis* although the head length is 5.9 in total length according to Philippi (1866); such proportion was not found in any of the specimens studied here; unfortunately the type-specimen — supposedly at the Museo Nacional de Historia Natural, Chile — could not be located.

Diplomyste chilensis: Eigenmann, C. (1927): Mem. Nat. Acad. Sci. 22: 13, 15, 20, 36, 37, in part. — (?) Fowler, H. W. (1951): Rev. Chilena Hist. Natur. (1947—1949): 281. — Mann, G. (1954): La vida de los peces en aguas chilenas; Santiago: 158 (in part). — (?) de Buen, F. (1958): Inv. Zool. Chilenas 5: 150—151.

Diplomystes chilensis: (?) Campos, H. (1972): Mus. Nac. Hist. Natur., Chile, Not. Mensual (198—199): 9—11.

Common names: "tollo", "tollo de agua dulce", "bagre".

Studied material:

Syntypes: MNHN B. 584: 1 specimen; Santiago (Chile); coll. C. Gay; 1832. — MNHN B. 585: 4 specimens; Santiago; coll. C. Gay; 1832.

Additional specimens: MNHN 1212: 1 specimen; Santiago; coll. C. Gay; 1832. — MNHN A. 9028: 1 specimen; Santiago; coll. C. Gay; 1832. — MCZ 8290: 2 specimens (alcohol) and 3 specimens (cl & st); rivers of Santiago; Leyboldt-Thayer expedition. — MCZ 36195: 1 specimen; Santiago; coll. R. Philippi. — CAS 13706: 8 specimens; Santiago market; coll. C. Eigenmann; 1919. — CAS 27839 (IUM 15550): 1 specimen; Santiago market; coll. C. Eigenmann; 1919. — CAS 45718: 1 specimen; Chile; coll. C. Eigenmann; 1919. — CAS 55427: 2 specimens; Santiago market; coll. C. Eigenmann; 1919. — CAS (SU) 23936: 1 specimen; coll. C. Eigenmann; 1919.

Type-locality: Rivers from near Valparaíso and Santiago, Chile, South America (apparently now extinct).

Diagnosis: Catfish with all fins having extremely fleshy bases. Head short, 24 to 27 % of standard length. Origin of pelvic fin anteriorly to the halflength of standard length (*2). Eye small, its diameter 31 to 44 % (\bar{x} = 35.2) in preorbital length. Nostrils surrounded by a fleshy fold; narial bridge (skin fold) partially obscuring posterior nostril. Few maxillary teeth (8—13, commonly 9). Anterior processes of the palatine fused (*2). Palatine short, its facets for lateral ethmoid, and cartilage joining with mesethmoid, vomer, lateral ethmoid and orbitoshenoid about half length of bone. Foramen for facial (on hyomandibula) hidden by a well developed arcus palatini crest. Few dorsal (14—18) and ventral (14—17) procurrent caudal rays (*2); 2/2 segmented unbranched caudal rays (*2). Numerous long basal papillae bearing seven to ten small projections or buds on skin around base barbel (*2). Numerous long lobulated or simple papillae covering the whole trunk (*2). Maxillary barbel and roof of mouth with many long papillae and elongate skin folds having taste buds; many long papillae on floor of mouth. One to three pectoral axillary glands (commonly two).

Coloration: Body enterly covered by grey "hairs" becoming slightly brownish toward the caudal region; white on ventral region (fresh material, according to Leybold 1859). Brown in the flanks, a little greenish, with or without spots; dorsum brown, flanks green, with brownish spots on dorsum and flanks, greyish ventrally (according to Valenciennes 1840, and Guichenot 1848).

Description: Elongate diplomystids (Fig. 1A) of about 210 mm total length; maximum length known 230 mm (MNHN B. 548). Origin of the dorsal fin closer to

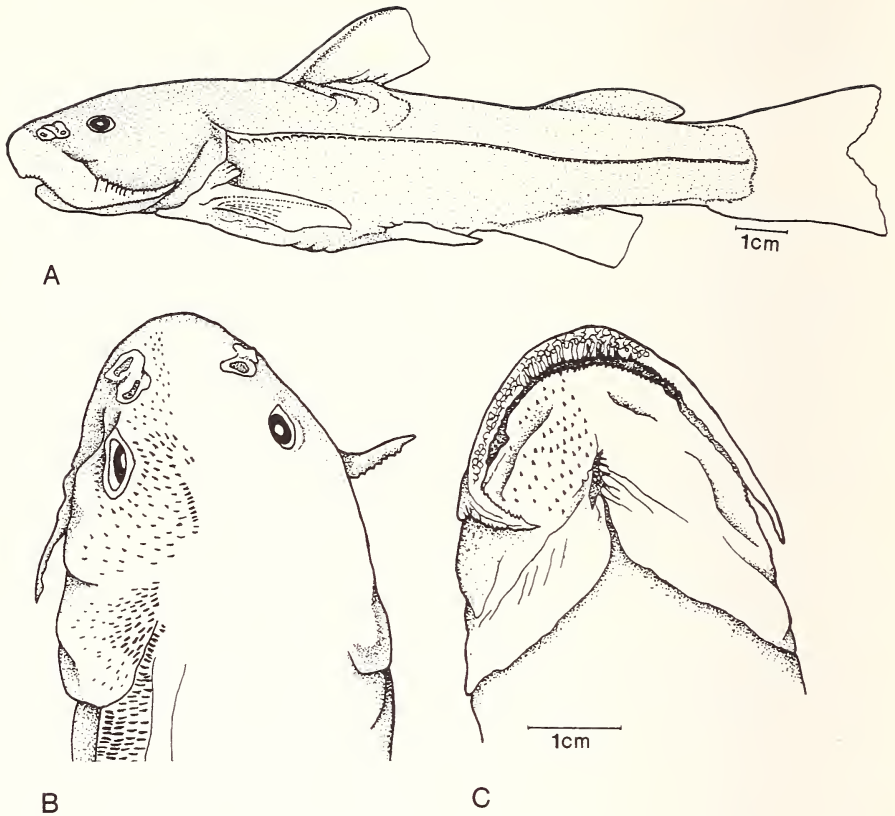


Fig. 1: *Diplomystes chilensis* (MCZ 8290). — A: Lateral view; B: Head, dorsal view; C: Head, ventral view. B—C illustrate (on left side) length of papillae.

snout than to base of tail (predorsal length 33 to 38 % of standard length); snout short, preorbital length 28 to 39 % of head length. Dorsal fin base shorter than deep. Dorsal spine shorter than the longest ray (73 to 93 % of the longest ray). Depth of adipose fin 20 to 32 % of its length (one specimen with a low adipose fin, 17 % of its length). Depth of adipose fin variable (16 to 32 % of its length, commonly 23 to 29 % of its length). For other body proportions see Table 1; for number of teeth, vertebrae and rays, Table 2.

Snout (Fig. 1B, C) pointed in young, slightly pointed or rounded in larger specimens. Subterminal mouth. Extremely fleshy snout and lips and base of maxillary barbel. Barbel length variable (shorter in MCZ 8290 and 36195; 39 to 44 % of head length), dorsal margin of barbel with numerous fleshy folds. Eye relatively small (Table 1) and placed dorsolaterally.

Table 1: Body proportions of species of *Diplomystes*. — max: maximum value; min: minimum value; N: number of specimens; \bar{x} : average; *: exceptional values found in one specimen.

	<i>Diplomystes chilensis</i>			<i>Diplomystes nahuelbutaensis</i>			<i>Diplomystes camposensis</i>		
	min	\bar{x}	max	min	\bar{x}	max	min	\bar{x}	max
N		13			13			20	
Total length / head length	4.5	(4.8)	5.1	4.0	(4.4)	4.7	3.9	(4.3)	4.8
Standard length / head length	3.7	(4.0)	4.3	3.3	(3.7)	4.0	3.1	(3.5)	4.1
Head length / standard length (%)	23	(24.9)	27	25	(26.7)	30	24	(28.8)	31
Predorsal length / standard length (%)	31	(34.7)	38	33	(35.9)	39	35	(37.5)	40
Preadipose fin length / standard length (%)	63	(65.9)	70	62	(67.5)	73	61	(67.8)	73
Prepelvic length / standard length (%)	44	(46.7)	49	48	(50.0)	54	49	(51.8)	57
Precanal length / standard length (%)	60	(63.7)	67	63	(66.3)	70	60	(65.4)	79
Adipose fin length / standard length (%)	20	(21.8)	24	16	(19.8)	24	18	(20.0)	22
Barbel length / head length (%)	39	(43.8)	44 (61)*	32	(43.8)	51	48	(52.5)	65 (39)*
Preorbital length / head length (%)	29	(34.2)	39	25	(29.1)	35	31	(35.2)	41
Preorbital length / standard length (%)	7	(8.5)	10	7	(7.7)	9	9	(9.8)	14
Head depth / standard length (%)	11	(12.9)	14	12	(13.4)	15	13	(15.6)	18
Head depth / head length (%)	48	(51.0)	55	46	(50.3)	57	46	(56.7)	79
Adipose fin depth / adipose fin length (%)	17	(25.0)	32	16	(18.7)	25	22	(26.3)	31
Peduncle depth / standard length (%)	9	(10.1)	11	7	(9.6)	11	9	(10.9)	15
Head width / head length (%)	62	(70.0)	72 (84)*	66	(74.6)	85	64	(76.7)	96
Mouth width / head width (%)	53	(62.7)	70	54	(63.8)	82	44	(55.4)	76
Mouth width / head length (%)	36	(44.1)	57	41	(48.7)	59	30	(43.6)	56
Interorbital width / head length (%)	26	(31.7)	38	29	(33.1)	42	28	(34.8)	42
Interorbital width / head width (%)	36	(43.5)	50	34	(42.5)	55	37	(41.6)	49
Eye diameter / head length (%)	7	(11.2)	14	11	(14.8)	19	11	(14.7)	17
Eye diameter / preorbital length (%)	31	(35.8)	44	40	(51.1)	65	34	(42.9)	64

Table 2: Teeth, vertebrae and rays of *Diplomystes*. — Count of maxillary teeth and pectoral serrae only in large specimens. (sp: splint; Roman numbers: spines; \bar{x} : average; *: according to Eigenmann & Eigenmann 1890, Eigenmann 1927).

	<i>Diplomystes chilensis</i>	<i>Diplomystes nahuelbutaensis</i>	<i>Diplomystes camposensis</i>
Maxillary teeth	8 (\bar{x} : 9) 13	11 (\bar{x} : 10.5) 13	12 (\bar{x} : 14.6) 19
Branchiostegal rays	8–9 (7)*	9–10	9–10
Vertebrae	41–43	39–41	40–44
Precaudal vertebrae	14–17	15–17	15–17
Caudal vertebrae	23–27	23–26	26–27
Ribs	10–12	11–13	11–13
Pectoral rays	I+9–10	I+9	I+9
Pectoral serrae	12	8–9	9–12
Pelvic rays	sp+6	sp+6	sp+6
Dorsal rays	II+7 (I+7–8)*	II+7	II+7
Dorsal pterygiophores	8	8	8
Anal rays	12–15 (9–12)*	14–15	11–15
Principal anal rays	9–11	10–11	8–11
Anal pterygiophores	10–12	11–13	12
Caudal rays	47 (\bar{x} : 48.9) 53	47 (\bar{x} : 49.6) 52	52 (\bar{x} : 52.7) 56
Dorsal procurrent caudal rays	14 (\bar{x} : 15.3) 18	15 (\bar{x} : 16.3) 18	17 (\bar{x} : 17.6) 19
Ventral procurrent caudal rays	14 (\bar{x} : 14.9) 17	14 (\bar{x} : 15.8) 18	17 (\bar{x} : 18.0) 19
Rays of dorsal caudal lobe	23 (\bar{x} : 24.3) 27	24 (\bar{x} : 25.3) 27	26 (\bar{x} : 26.5) 28
Rays of ventral caudal lobe	23 (\bar{x} : 22.9) 26	23 (\bar{x} : 24.8) 27	25 (\bar{x} : 26.1) 28

Branchiostegal membranes weakly joined to isthmus, widely joined to each other (usually they are folded in preserved material) and extending broadly posterior to opercle (Fig. 1C).

A thick layer of adipose tissue lies beneath the skin of the head and over the roof of the cranium, extending broadly over and in front of the mesethmoid. The adductor mandibulae originates on the roof of the frontal, sphenotic, pterotic, supraoccipital and extrascapular; its stronger areas of attachment are on the pterotic, the strongest being on the transverse crest on the supraoccipital which extends onto the frontal. Dorsally, the adductor mandibulae muscles are separated from each other by only a short distance and they are partially covered by the layer of adipose tissue. There are bad differentiated divisions of the adductor mandibulae; the lower part inserts musculously entirely on the medial part of the posterodorsal border of the angulo-articular (not on the dentary); the dorsal and inner parts of the muscle insert tendinously on the coronoid cartilage, and on the large coronomeckelian bone.

The liver is lobulated; the longest lobe is placed on the left side of the body; enormous blood vessels irrigate the mesenterium and the liver. The kidneys occupy most of the dorsal region of the pleuroperitoneal cavity; they become broader anteriorly and partially surround the gasbladder laterally. The testes are deeply incised producing larger lobes anteriorly and many elongate fine lobes distally. Only one large ovaric sac is present; it does not show an external division; the wall of this ovaric sac is thick and encloses many small oocytes.



Fig. 2: *Diplomystes chilensis* (MNHN B. 585). — SEM of skin (colloid-like substance removed). A: Papillae and buds of the skin of the dorsoposterior region of the maxillary barbel (SEM 52x); B: Enlargement of the papillae and buds illustrated in A (SEM 152x); C: Papillae and taste bud of the roof of the mouth (SEM 470x); D: Large pit organ and papillae of the skin of the dorsal part of the trunk just posterior to the head (SEM 43x).

Numerous long (1 to 2 mm) lobulated or simple papillae (2A, D) all over the body, including fins and mouth. The papillae (and cephalic sensory tubules and tubules of the lateral line) all over the skin of the body are embedded in a coloid-like substance of unknown chemical composition which makes the skin look smooth. Only the distal tips of the papillae (and the sensory pores) are exposed, otherwise the coloid-like substance,

fills all spaces between papillae (and the sensory tubules). Each papilla of the barbel, and area closer to the barbel, usually bears on its tip one to ten small projections (Fig. 2A, B) of similar shape as the basal papilla. Underside of upper lip, maxillary barbel (Fig. 1C, 2A, B, 3A) and roof of mouth have a characteristic configuration of extremely elongate skin folds, deep grooves and papillae. Taste buds (Fig. 2C) of roof of the mouth, are placed in long, sharp papillae, usually each papilla has two taste buds on the distal tip; the papillae of the mouth are ordered in rows. Other taste buds are placed on longitudinal skin folds extending along median and lateral regions of the roof of mouth. Floor of mouth has many long papillae in syntypes, fewer papillae in other specimens. Ventral region of head and branchiostegal membranes are covered by many sharp or rounded papillae, especially elongate in MNHN B. 584, B. 585, 1212 and A. 9082. Papillae are longest in dorsolateral region, immediately behind opercle and dorsal to pectoral fin (Fig. 1B). The examination with SEM shows that papillae of dorsal region of trunk are elongate, they lack the eight to ten projections present on papillae around barbels (compare Figs. 2A, B, D). Pit organs (Fig. 2D) are easily confused with the papillae; they are elongate and they may be lobulated or simple, as the papillae. Papillae are slightly shorter on dorsal part of opercle and between orbits.

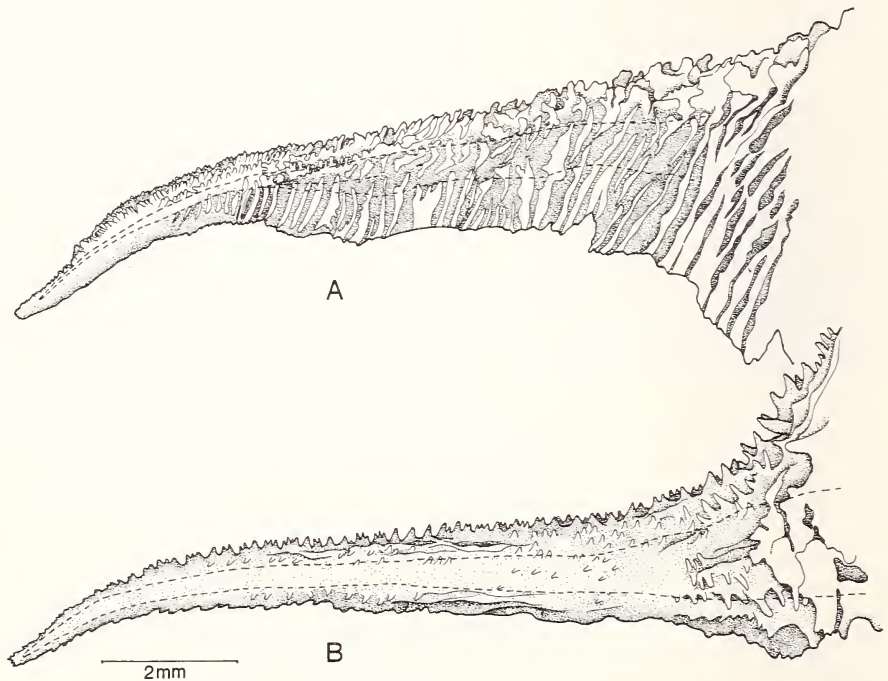


Fig. 3: Papillae and skin folds of the maxillary barbel in median view. — A: *Diplomystes chilensis* (MCZ 8290); B: *Diplomystes camposensis* n. sp. (KU 19209).

Pectoral axillary glands opening through skin just below cleithral process, in deep cleft where the pectoral spine rests. Opening rounded or elongate; some glands contain a large yellow ball, resembling condensed mucus. Most specimens have 2/2 pectoral axillary glands, two specimens with 1/1.

Anus and urogenital pore narrowly separate, the latter piercing a rounded or triangular urogenital papilla. Anus and urogenital pore placed between pelvic fins but not covered by fin-rays.

Lateral line enclosed along flank by ossicles of irregular shape and length; lateral line complete (to base of principal caudal rays) or nearly so; end of lateral line curves dorsally or in some few specimens, ventrally.

All specimens studied here were discolored. According to Molina (1782) the catfish is "brown upon the sides and whitish under the belly". According to Valenciennes (1840) the color is greyish, a little greenish on the back and without any spots as the figure shows; according to Guichenot (in Gay 1848) it is brownish with green spots on the back, however his figure shows that the whole animal is marbled with brownish spots, the back brown, the flank green, the belly greyish and all colors change continuously into each other" (in Philippi 1866). The most interesting description is that of Leybold (1859: 1084) based on fresh material ("the upper and lower lips are covered by white papillae; the body is entirely covered by soft grey 'hairs', becoming slightly brownish towards the caudal region and white on the ventral region").

Several osteological features of diplomystids have been used by former authors to justify the primitiveness of the family; all of them based on one or two specimens. Here follows a detailed description of anatomy of taxonomic and phylogenetic value.

Cranium

The dorsal surface of the cranium is gently inclined, producing a slightly curved profile anteriorly. The mesethmoid (Fig. 4A, 5A, B) is laterally compressed for most of its length and projects ventrolaterally into the anteroventral processes which articulate with the dorsal surface of the premaxillae. Dorsoposteriorly, the mesethmoid joins by simple "lap" joint with the frontals; laterally with the lateral ethmoid and ventrally with the vomer through a synchondral joint. A median unossified space (filled with cartilage) lies between the mesethmoid, lateral ethmoid and vomer.

Each lateral ethmoid forms a lateral wing extending posterolateral to the mesethmoid and ventrolateral to the frontal. Each lateral ethmoid is widely overlapped by the frontal (Fig. 4A). Each long tube-like nasal bone lies anteriorly adjacent to the lateral ethmoid.

The dorsal surface of the cranium is mainly roofed by the frontals (Fig. 4A), which are widest at the level of the lateral ethmoid. Two long fontanelles separate the frontals; both fontanelles are of similar length, the posterior one prolonged into the supraoccipital while the anterior one extends into the mesethmoid. The region between the fon-

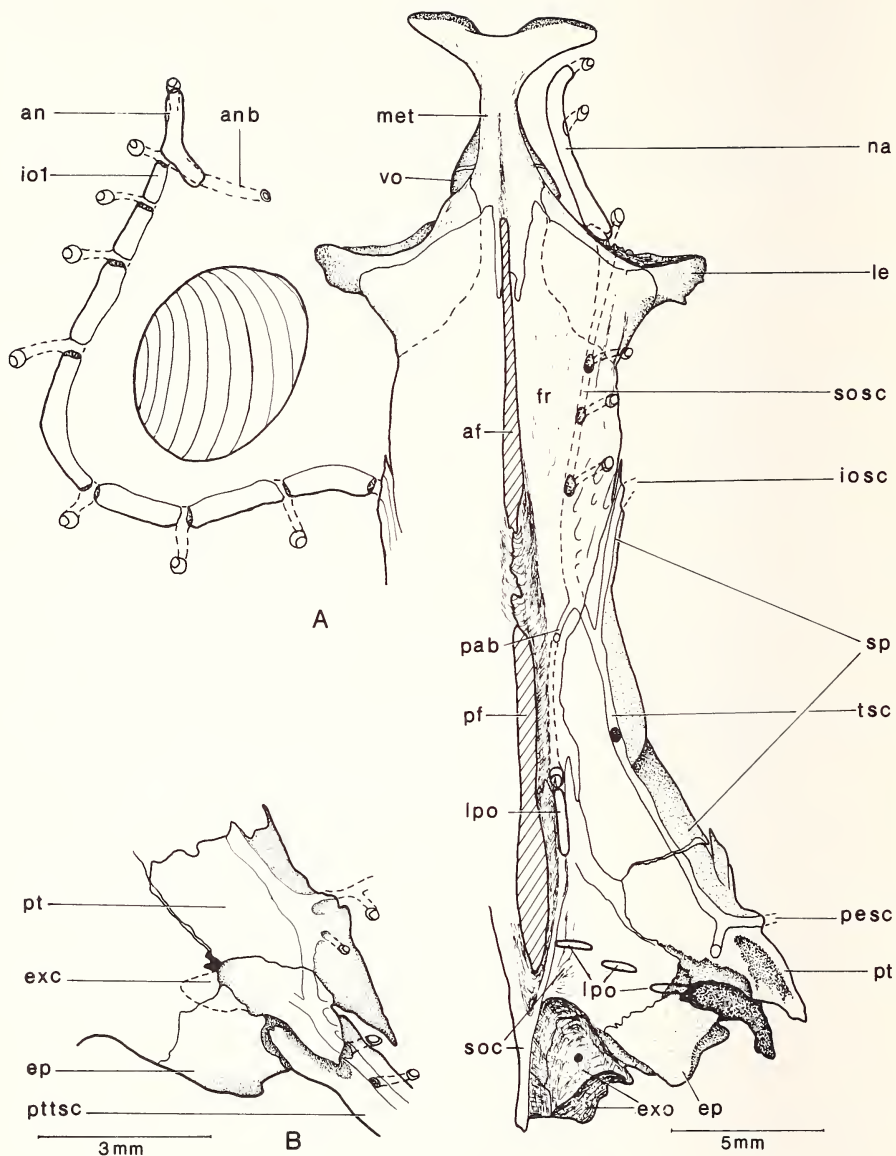


Fig. 4: *Diplomystes chilensis* (MCZ 8290, MNHN B. 585). — A: Cranium in dorsal view (extrascapular removed), and circumorbital series; large pit organs figured on the right side; B: Posterior part of cranium in dorsal view illustrating relationships of the extrascapular with cranial and uppermost pectoral girdle bones.

af: anterior frontal fontanelle; an: antorbital; anb: antorbital branch of infraorbital sensory canal;

tanelles and along the lateral margin of the posterior fontanelle is raised for the origin of muscles (adductor mandibulae).

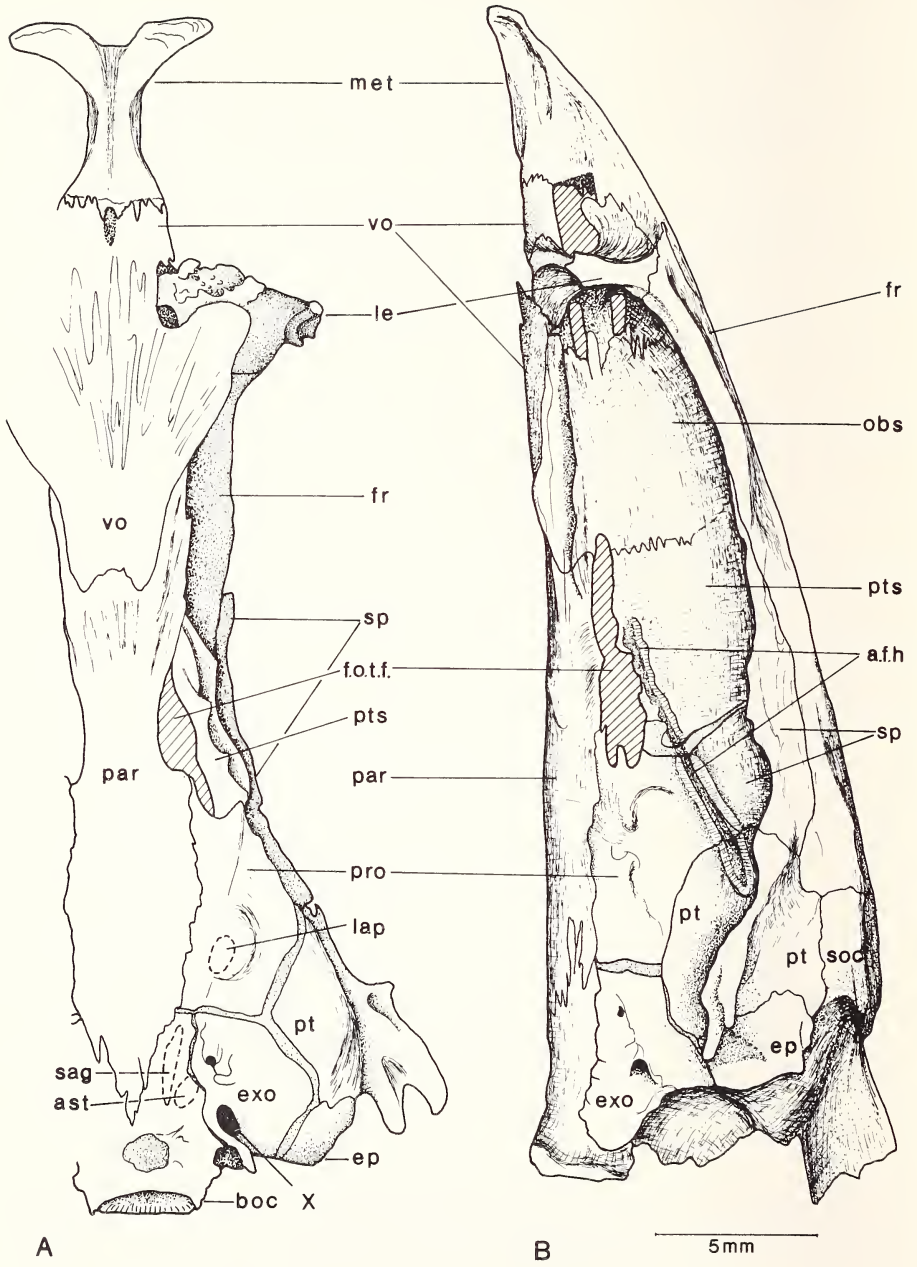
The sphenotic is elongate, longer than the pterotic; externally it is narrow anteriorly, and it lacks a sphenotic spine (= postorbital process of McMurrich 1884 a). The pterotic is posteroventrally angular; anteriorly it forms an external sharp projection. The pterotic, epioccipital and supraoccipital enclose a posttemporal fossa (Fig. 4A) (= temporal fossa of Alexander 1965) which is roofed by the extrascapular (Fig. 4B).

A small flat, thin extrascapular (Fig. 4B) lies on the pterotic and the dorsal limb of the posttemporosupracleithrum; the bone lies partially below the supraoccipital and epioccipital, and is strongly sutured to the cranium in large specimens. The boomerang-shaped extrascapular carries a short section of the main lateral canal on its external lateral surface; apparently the main lateral canal does not give off a supratemporal commissure.

The supraoccipital crest is small, only slightly elevated, and its dorsal surface smooth and narrow. The intercalar is absent. The exoccipitals (Fig. 5A, B) are comparatively large bones forming the posteroventral walls of the neurocranium; each is slightly inflated ventrally and bears a large oval foramen for the vagus nerve and a small one for the glossopharyngeal nerve. Each exoccipital sutures dorsally with the supraoccipital, joins synchondrally with the pterotic and epioccipital dorsally and the prootic ventrally, and sutures with the basioccipital ventrally. No space separates the basi- and exoccipitals.

The short basioccipital (Fig. 5A, B) sutures anteriorly with the parasphenoid, which extends posteriorly partially covering the basioccipital. Each prootic is slightly inflated ventrolaterally and opens anteriorly in a large trigeminofacial foramen for the optic, facial and trigeminal nerves; the foramen is bounded by the parasphenoid, prootic, pterosphenoid, and orbitosphenoid. The prootic sutures ventrally with the parasphenoid and joins synchondrally with the exoccipital posteriorly, pterotic and sphenotic dorsally and pterosphenoid anteriorly. The hyomandibular articulation includes a small region of the pterotic, runs along the sphenotic-prootic joint, and continues extensively in a narrow groove in the pterosphenoid in adults, whereas it articulates mainly with sphenotic and prootic in young. The hyomandibular articulation has a dorsal position in the pterotic, then inclines abruptly ventrally along the sphenotic-prootic joint ending in the pterosphenoid close to the optic, facial and trigeminal foramen. The pterosphenoid is a rather large bone forming the dorsal boundary of this foramen and therefore does not suture with the parasphenoid as in other catfishes.

ep: epioccipital; exc: extrascapular; exo: exoccipital; fr: frontal; iol: first infraorbital; iosc: infraorbital sensory canal; le: lateral ethmoid; lpo: large pit organs; met: mesethmoid; na: nasal; pab: parietal branch of supraorbital sensory canal; pesc: preopercular sensory canal; pf: posterior frontal fontanelle; pt: pterotic; ptts: posttemporosupracleithrum; soc: supraoccipital; sosc: supraorbital sensory canal; sp: sphenotic; tsc: temporal sensory canal; vo: vomer.



A basiptyergoid process is lacking. The parasphenoid (Fig. 5A, B) is broad and covered anteriorly by the posterior part of the vomer. The parasphenoid extends broadly below the basioccipital, lacks a lateral wing articulating with the prootic, or the wing is rudimentary. The large rhomboidal shaped vomer joins with the parasphenoid, orbitosphenoid, lateral ethmoid and mesethmoid. There are two elongate foramina between the lateral ethmoid and orbitosphenoid (Fig. 5A), placed mainly in the posterior part of the lateral ethmoids.

Two (occasionally one) autogenous tooth plates lie on the ventral face of the vomer; each tooth plate bears conic teeth larger and broader (but not longer) than those of the external row of both the premaxilla and dentary.

Circumorbital series

The circumorbital series (Fig. 4A) consists of antorbital and seven (occasionally six) bony tubes enclosing the infraorbital sensory canal, which ends dorsally to antorbital. The antorbital is a thin, slightly comma-shaped bone which relates to the maxilla by a ligament. Supraorbital and sclerotic bones are absent.

Palato-quadrate and mandibular apparatus

The premaxilla is shorter than the maxilla (it is more than 60 % of maxillary length). The premaxillae seem to be fused in the midline in specimens MNHN 1212 and 9028 (208.4 and 202.1 mm in total length, respectively). Six to eight irregular rows of tall teeth cover the ventral surface of the premaxilla. The largest are in the two external rows and are spatulate or incisiform; the teeth of internal rows are gradually smaller and may be conic or slightly incisiform.

The maxilla lies ventrolateral to the premaxilla; its articular process is long; lateral to the articular process, the maxilla curves abruptly backward, ending in a broad truncate or slightly truncate posterior margin. About two-thirds of its ventral margin carries tall, spatulate or slightly incisiform teeth; near the articular process they are ordered in two rows and posteriorly in one row. Eight to thirteen teeth may be found in each adult maxilla, the most common count is nine; the teeth of the external row are of similar length along the maxilla. The maxilla articulates with the palatine through two facets; posterolaterally it supports the (?)cartilaginous base of the maxillary barbel.

Fig. 5: *Diplomystes chilensis* (MCZ 8290). — A: Cranium in ventral view (vomerine tooth plates removed); B: Cranium in lateral view.

a.f.h.: articular facet for hyomandibula; ast: asteriscus; boc: basioccipital; ep: epioccipital; exo: exoccipital; f.o.t.f.: foramen for optic, trigeminal and facial nerves; fr: frontal; lap: lapillus; le: lateral ethmoid; met: mesethmoid; obs: orbitosphenoid; par: parasphenoid; pro: prootic; pt: pterotic; pts: pterosphphenoid; sag: sagitta; soc: supraoccipital; sp: sphenotic; vo: vomer; X: foramen for vagus nerve.

The palatine has both anterior processes fused (Fig. 6A) (specimens MNHN B. 585, MCZ 8290, CAS 13706; Fink & Fink 1981: 11). The posterior part of the palatine is short. Palatine teeth are absent with one exception (MNHN 1212) where only one palatine bears a tooth plate with six conic teeth. The palatine anteriorly forms a narrow double surface articulating with the maxilla; dorsally it has two articular facets, the inner one for a cartilage joining with the mesethmoid, vomer (mainly), lateral ethmoid and the orbitosphenoid, the external one for the lateral ethmoid; both facets are near the midlength of the palatine.

The palatine extends posteriorly beyond its articulation with the lateral ethmoid, forming a slightly broad projection directed medially. A small thin bone lies behind the posterior extremity of the palatine (bone 4 of McMurrich 1884 a: 284; mesopterygoid or endopterygoid of other authors) in some specimens (MNHN B. 585, MCZ 8290). Bone 4 encloses partially the cartilage of the posterior extremity of the palatine.

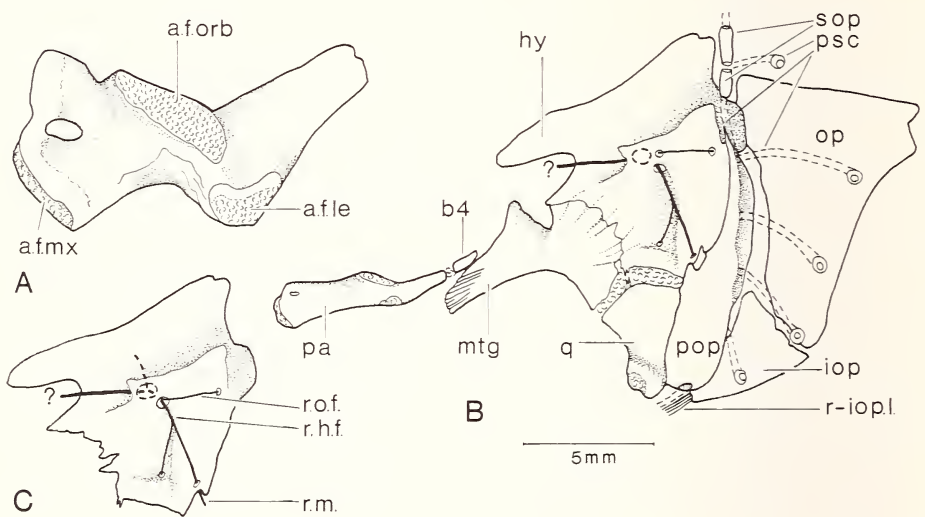


Fig. 6: *Diplomystes chilensis* (MCZ 8290, MNHN B. 585). — Suspensorium and opercular apparatus.

A: Palatine, dorsal view; B: Palatine, quadrate, hyomandibula, metapterygoid and opercular apparatus (preopercular sensory canal illustrated), lateral view; C: Hyomandibula and facial nerve, lateral view.

a.f.le: articular facet for lateral ethmoid; a.f.mx: articular facet for maxilla; a.f.orb: articular facet for cartilage joining with mesethmoid, vomer (mainly), lateral ethmoid and orbitosphenoid; b4: bone 4 of McMurrich; hy: hyomandibula; iop: interopercle; mtg: metapterygoid; op: opercle; pa: palatine; pop: preopercle; psc: preopercular sensory canal; q: quadrate; r.h.f.: ramus hyomandibular of facial nerve; r-iop.l.: ligamentum mandibularis interoperculare; r.m.: ramus mandibularis; r.o.f.: ramus opercularis facialis; sop: suprapreopercles; ?: unknown ramus.

According to my studies on *Diplomystes chilensis*, two pterygoid bones may be present: the metapterygoid and occasionally an additional pterygoid (ectopterygoid of other authors). When an additional pterygoid is present, it is a small oval bone lying ventral to the posterior end of the palatine and of bone 4 of McMurrich. A short ligament extends between the palatine and the additional pterygoid, when it is present. No cartilage joins both bones. The bone 4 of McMurrich arises as an ossification around the posterior cartilage of the palatine. The upper posterior border of the metapterygoid is somewhat concave; the medial ridge of most of the anterodorsal flange of the bone is attached by ligaments to the vomer and to the parasphenoid (MNHN B. 585), to the lateral ethmoid, to the vomer and to the parasphenoid in other specimen (CAS 13706) (to the lateral ethmoid according to Regan 1911; only to vomer, according to Alexander 1965). The metapterygoid (Fig. 6B) is anterodorsal to the quadrate and forms part of the ventral region of the suspensorium; it partially occupies the place in which the ectopterygoid is situated in other teleosts. A small articular cartilage is in the joint between the quadrate and metapterygoid and between the quadrate and hyomandibula; a part of the posterior margin of the metapterygoid connects with the hyomandibula by a "lap" joint which in some larger specimens appears as a smooth suture.

The small, triangular quadrate (Fig. 6B) is thicker ventroposteriorly and it lacks a posteroventral process, in adults; its posteroventral margin joins the preopercle.

The lower jaw of adult specimens comprises the dentary, the angular, articular and the retroarticular partially fused (partial joints between the three bones may be seen), a coronomeckelian bone and Meckel's cartilage.

The dentary is the largest bone of the mandible; the bone is very shallow but becomes a little broader anteriorly, close to the symphysis, to accommodate the teeth. A ventral bony flange, posteriorly directed, is small or absent in the anteroventral part of the dentary. Each dentary is grooved on the inner surface to receive Meckel's cartilage, the angular component of the posterior part of the mandible, and part of the coronomeckelian bone. The dorsal tip of the dentary externally overlaps the dorsal tip of the angular. The dentary bears six or more irregular rows of tall teeth near the symphysis. Teeth have spatulate tips in the external rows and conic tips in the inner rows.

The ventrolateral surface of the posterior part of the mandible is formed by the angular. The articular extends posteromedially producing a broad surface for the quadrate; the articular is large medially, posteriorly joins with the retroarticular; the latter is medial to the angular. A short ligament extends between the posterodorsal part of the articular and the quadrate (ligamentum quadratomandibularis laterale, terminology of Liem 1970); two strong ligaments (Fig. 7A—C) sit on the retroarticular and posterior part of the articular; the external one extends between the lower jaw and the interopercle (ligamentum mandibulo — interoperculare); the medial one (larger), between the lower jaw and epi- and interhyal (ligamentum mandibulo — hyoid). The medial region (Fig. 7A—C), extending from the dorsal tip of the angular and the coronomeckelian bone, is covered by a hard coronoid cartilage (remains of the large Meckel's cartilage of early ontogeny). A ligament (ligamentum primordiale) extends between the dorsal tip of the

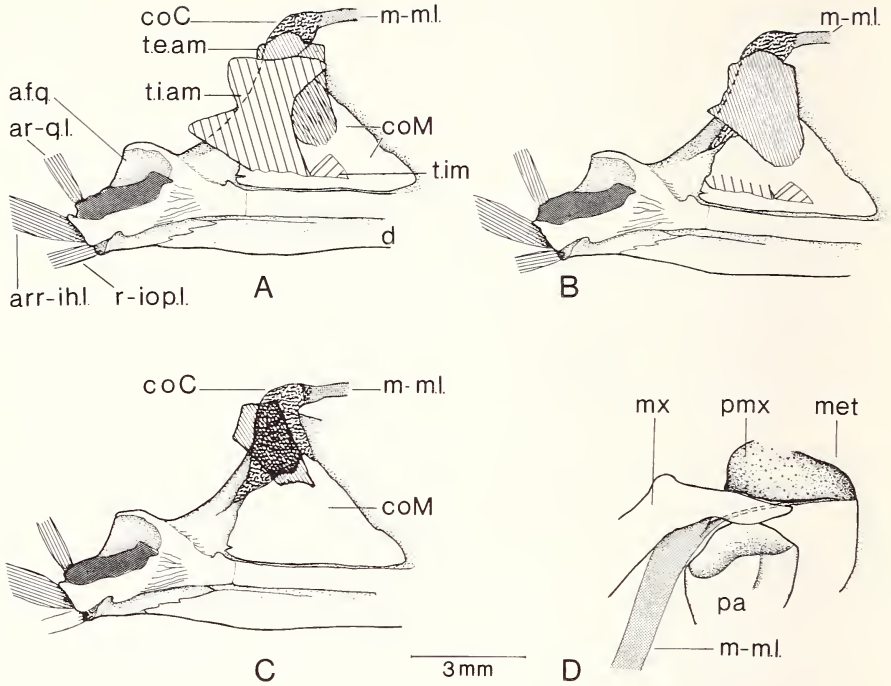


Fig. 7: Lower jaw (medial view), tendons and ligamentum primordiale of diplomystids. — A, B, C: Sequence of medial views (medial to lateral showing the presence of tendons and coronoid cartilage); D: Relationships of the ligamentum primordiale with the articular process of maxilla (slightly moved from its normal position) and premaxilla.

a.f.q.: articular facet for quadrate; ar-q.l.: ligamentum quadratomandibularis laterale; arr-ih.l.: ligamentum mandibulo-hyoid; coC: coronoid cartilage; coM: coronomeckelian bone; d: dentary; met: mesethmoid; m-m.l.: ligamentum primordiale; mx: maxilla; pa: palatine; pmx: premaxilla; r-iop.l.: ligamentum mandibulo-interoperculare; t.e.am.: tendon of external section of adductor mandibulae; t.i.am.: tendon of the inner section of adductor mandibulae; t.im.: tendon of intramandibularis portion of adductor mandibulae.

coronoid cartilage and the anteroventral margin of the articular process of the maxilla; a narrow section of this ligament extends to the premaxilla (Fig. 7D); an additional section extends to the palatine on one side of only one specimen. The posterior margin of the coronoid cartilage serves as an attachment for a large tendon which extends on the dorsal part of the coronomeckelian bone; this tendon (Fig. 7B, C) is connected with the dorsal section of the adductor mandibulae. An elongate groove in the middle region of the coronomeckelian bone serves as an attachment for another tendon (Fig. 7A) connected with an inner section of the adductor mandibulae; an anterior small section of this tendon (Fig. 7A) connects the muscle (intramandibularis portion of the adductor mandibulae) covering the medial region of the dentary.

The postarticular process is rudimentary; the articular facet for the quadrate comprises mainly the articular and a small contribution of angular. The mandibular sensory canal opens dorsoposterior to the angular, posteriorly adjacent to the articular facet.

One or two ossicles enclose the sensory canal between the mandible and the preopercle. They may be asymmetric in number and size on the opposite sides of the head.

Hyomandibula, hyoid and opercular apparatus

The hyomandibula (Fig. 6B, C) is a large bone whose straight dorsal margin is oriented oblique to the cranium. Its anterior end lies in a groove in the pterosphenoid. Most of the dorsal margin articulates in a narrow groove corresponding to the synchondral joint between the sphenotic and prootic. About two-thirds of the posterior margin of the hyomandibula articulates with the dorsal arm of the preopercle; the posterior margin produces a somewhat ovoid projection, the articular facet of the opercle. Part of the anterior margin has a "lap" joint with the metapterygoid; the "lap" joint may appear as a suture in large specimens; the ventroanterior margin joins to the quadrate through a cartilage and a weak, small suture.

There is a well developed horizontal levator arcus palatini crest. Five or six distinct foramina are present on the external face of the hyomandibula; the facial nerve penetrates the anterior part of the horizontal levator arcus palatini crest, and exists laterally by two or three foramina (Fig. 6B). In some specimens, the facial nerve radiates in three rami which emerge by three foramina through the wall of the horizontal arcus palatini crest; a small branch of the facial, the ramus opercularis facialis, runs shortly over the bone and penetrates another small foramen; the lower branch is the hyomandibular branch of the facial nerve which bifurcates (hyomandibular and mandibular rami) close to the ventral margin of the bone and a thick ramus (of unknown name)

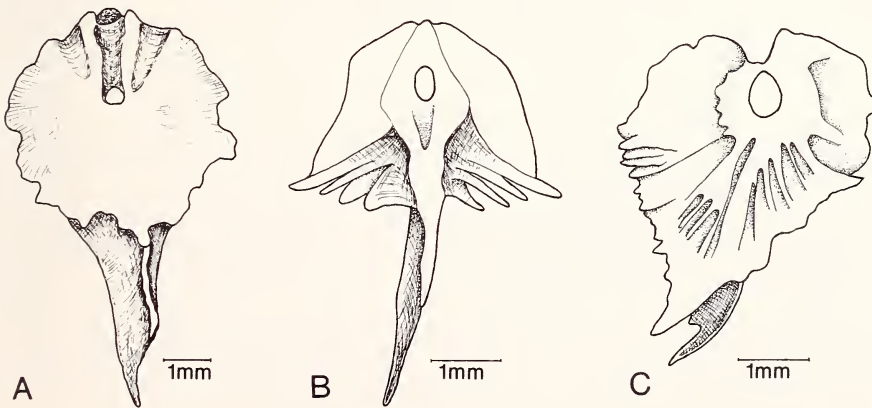


Fig. 8: Urohyal, ventral view. — A: *Diplomystes chilensis* (MCZ 8290); B: *Diplomystes nahuelbutensis* n. sp. (CAS 55425); C: *Diplomystes camposensis* n. sp. (PC 110276).

is directed anteriorly (in some specimens, this ramus innervates the area surrounding the posterior part of the orbit; in other specimens the ventral region of the orbit and extends anteriorly). In some specimens, the facial nerve bifurcates leaving the foramen, and only two foramina are present in the wall of the arcus palatini crest.

The elements of the hyoid arch were partially disarticulated in the cleared and stained specimens I studied. With the exception of the urohyal, I have not found any significant difference between *Diplomystes chilensis* and *D. camposensis* n. sp. (see page 56, Fig. 27A, C.). There are eight or nine branchiostegal rays; I have not found any specimen with seven rays as stated by Eigenmann & Eigenmann (1890). The urohyal (Fig. 8A) is a small, rather narrow bone; ventroanteriorly, it produces a rounded area pierced by a small oval foramen and it has a slender posterior extension.

Opercular series

Suprapreopercles (two or three), preopercle, opercle and interopercle (Fig. 6B) are present; all are toothless. The suprapreopercles are elongate bony tubes carrying the preopercular canal; the number of suprapreopercles varies between individuals and also between sides of a specimen. The preopercle ends dorsally in a narrow tip; its ventral arm lacks an anterior projection; the preopercle is tightly bound to the hyomandibula and quadrate. The dorsal margin of the opercle is straight; the dorsal part of the posterior margin forms two blunt projections; the bone is loosely articulated with hyomandibula and interopercle. The interopercle is a small bone attached to the posterior part of retroarticular and articular through a strong ligament (ligamentum mandibulo — interoperculare).

Branchial apparatus

The elements of the branchial apparatus were disarticulated in all available cleared and stained specimens; I do not find any important difference between the branchial apparatus of this species and *Diplomystes nahuelbutaensis* n. sp. (see description in page 41, Fig. 17A, B).

Cephalic sensory canals

The supraorbital canal is enclosed within the nasal, frontal and sphenotic bones; it gives off seven or eight elongate tubules (Fig. 4A), each one opening in a pore. Three pores are on the nasal, two or three on the frontal and one on the supraoccipital, commonly; the supraorbital canal bifurcates into the orbital and parietal branches on the frontal. The parietal branch is short and enclosed by bone in the frontal; it runs posteriorly opening in a pore close to the frontal-supraoccipital suture or over the anterior part of the supraoccipital. Just posteriorly, adjacent to the pore of the parietal branch, there is a pit organ (?anterior pit-line) (Fig. 4A) which externally looks like an elongate compact structure, slightly clearer than the surrounding skin.

Supra-, infraorbital and temporal canals join each other in the sphenotic. The infraorbital canal gives off eight or nine (occasionally seven) elongate tubules, each ending in

a pore (Fig. 4A). The infraorbital canal produces two branches on the antorbital. The lower branch is very short; the dorsal, or antorbital branch, extends dorsally to the dorsal margin of the bone, opening in a pore which is hidden by the skin fold surrounding the posterior nostril.

The temporal canal does not give off any tubule on the sphenotic; one branch is given off on the pterotic, and continues into the preopercular canal. (A short posterior branch, opening in a pore on the pterotic, is present in some specimens.) Immediately posterior to the extrascapular, the main lateral canal gives off another short tubule opening in a pore.

The preopercular canal (Fig. 6B) passes through the suprapreopercles and preopercle; it gives off five tubules, four of them on the opercle and interopercle. The mandibular canal gives off five tubules; the first pore is distant from the symphysis. The canal running between the last mandibular pore and the posteroventral opening of the preopercular canal is enclosed by one or two ossicles, and it gives off one tubule and pore.

A series of six large pit organs (Fig. 4A) according to definition by Herrick (1901) or pore-tube commissures (according to Lekander 1949) (?middle pit-line) crosses the skin between the extrascapulars; these pit organs are especially obvious in specimen MNHN 9082 (the largest specimen I have seen); every large pit organ is innervated by several fine nerves which are difficult to observe in the dissected specimens. The most lateral pit organ is placed on the extrascapular. The skin covering the mesethmoid has two large pit organs in the position of the rostral commissure; another large pit organ is placed in front of the anterior nostril. I have seen large pit organs (irregularly located) on the skin of the trunk of specimen MNHN 9082 (Fig. 2D).

Vertebrae and Weberian apparatus

The Weberian apparatus of large specimens of *D. chilensis* has been figured by Fink & Fink (1981). My results, also in larger specimens, do not show any significant differences but I include here some additional information. The claustrum (Fig. 9A) may or may not have an elongate sharp ascending process; the claustrum articulates anteriorly with the exoccipital. Apparently no ligament joins the claustrum and scaphium. The ascending process of the intercalarium lacks an articular facet; it is easily displaced. A compound ligament connects the scaphium, horizontal process of intercalarium, and tripus; the latter (Fig. 9C) is a very thin, delicate bone. The os suspensoria do not meet each other in the midline. Three blood vessels run ventral to the complex centrum, the aortic artery medially and the posterior cardinal veins laterally. Each vein is partly shielded by the os suspensorium; no superficial ossifications cover the veins.

A broad supraneural bone (Fig. 9A) (result of the early fusion of a large supraneural 3 and a small supraneural 4, ventroposteriorly) is found in most specimens. Supraneurals 3 and 4 are separate bones (Fig. 9B) in specimen MNHN B. 584. A strong ligament extends between the posterior margin of the supraneural 4 and the neural arch of the complex vertebra. A thick cartilage covered by both claustra and articulated with

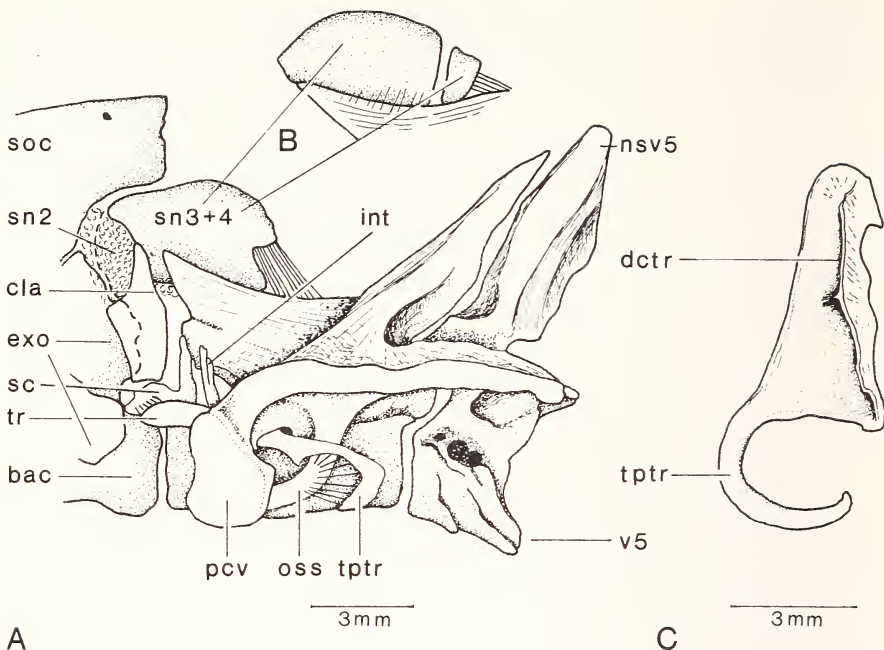


Fig. 9: *Diplomystes chilensis* (MCZ 8290, MNHN B. 584, 585). — A: Weberian apparatus and its relationships, and supraneurals, lateral view; B: Supraneurals 3 and 4; C: Tripus, dorsal view. bac: basioccipital; cla: claustrum; dctr: dorsal crest of tripus; exo: exoccipital; int: ascending process of intercalarium; nsv5: neural spine of vertebra 5; oss: os suspensorium; pcv: parapophysis of complex vertebra; sc: scaphium; sn2–4: supraneurals 2–4; soc: supraoccipital; tr: tripus; tptr: transformator process of tripus; v5: vertebra 5.

supra- and exoccipitals, is ventroanterior to the supraneural 3 + 4; probably it represents the second (unossified supraneural, Fig. 9A). A separate fifth supraneural bone has been observed in the radiographs of *D. chilensis* (at least MCZ 8290, 36195, CAS 13706).

The vertebrae are similar in shape to those of *Diplomystes camposensis* n. sp. (Fig. 29B–C) but lack the large foramina present in the abdominal vertebrae of *Diplomystes camposensis* n. sp. *Diplomystes chilensis* has 41–43 ($\bar{x} = 42$) vertebrae (Table 2). There are 16–19 abdominal and 23–27 caudal vertebrae. There are 10 to 12 pairs of ribs, the first pair is situated on the sixth or seventh vertebra.

Epineural and epipleural bones are absent.

Pectoral girdle and fin

The suspensorium of the pectoral girdle consists of a large bone, the posttemporoprosupracleithrum. The posttemporal part of this complex bears a short dorsal limb

which articulates with the pterotic, extrascapular and epioccipital. Ventromedially, the bone produces another limb (transcapular of Kindred 1929; ossified Baudelot's ligament of Fink & Fink 1981) which extends medially and is bound by ligaments to the cranium and also to the anterior part of the parapophysis of the complex vertebra. Frequently this limb is bifurcated close to the basioccipital or divides into several bony splints. A short ligament (Baudelot's ligament) connects this limb to the basioccipital in adults. (The pectoral girdle is similar among diplomystids; therefore see Fig. 30A—C, based on several specimens.)

The largest element of the girdle is the cleithrum which articulates with a small scapulo-coracoid; the coracoid part of the complex has an anteroventral projection joined at its end to the cleithrum. The latter has a dorsal limb ending in several bony splints which articulate in a ring formed by the joint of the posttemporosupracleithrum and the parapophysis of the complex vertebra. The posterior margin of the cleithrum bears a sharp posteriorly directed cleithral process. The straight symphysis between the two girdles is narrow and formed by the cleithra plus the anteroventral tip of the coracoid part of the scapulo-coracoids.

Three proximal radials are ordered in a single row. I have not found distal radials in the specimens examined.

The pectoral fin has one spine and nine or ten soft rays; the spine is shorter than the adjacent two pectoral rays. It is serrated on its posterior margin only; the number of serrae increases with age. The growth of the spine is similar to that described for some catfishes by Reed (1924).

Pelvic girdle and fin

The pelvic girdle and fin were figured by Fink & Fink (1981: Fig. 21E). The adult girdle presents two anterior elongate processes. The posterior process is short, and the articular facet for the lepidotrichia is somewhat laterally placed; the fins are inserted obliquely and are widely separated medially in adults; no proximal or distal radials were found in adult specimens.

There are six soft rays and one small bony splint.

Dorsal fin

The dorsal fin is similar among the diplomystids, therefore see the description of *Diplomystes camposensis* n. sp. based on many young and adult specimens (page 63, Fig. 29A). The dorsal fin has two spines and seven soft rays in all specimens studied (I have not found any specimen with only one spine and seven or eight soft rays as stated by Eigenmann 1927).

Anal fin

The total number of anal rays varies from 12 to 15, very often 13. There are frequently nine principal anal rays, occasionally ten or eleven. The most common formula is four

procurent rays plus nine principal rays. Ten anal pterygiophores are present, occasionally 11 or 12. The first pterygiophore is shorter than the second one.

Caudal fin

The description is based on juvenile and adult specimens. The support of the caudal fin is given by the last six or seven vertebrae, commonly seven. The compound centrum (Fig. 10A) is mainly formed by preural centrum 1 and the contribution of the ural centrum 1 seems to be poor; the posterior part of the compound centrum has a deep indentation to receive the base of hypurals 3 and 4. The compound centrum is shorter and smaller than the ten preceding caudal vertebrae. Dorsally, the neural arch of the compound centrum is open in each specimen I examined; the long epural is bifurcated at

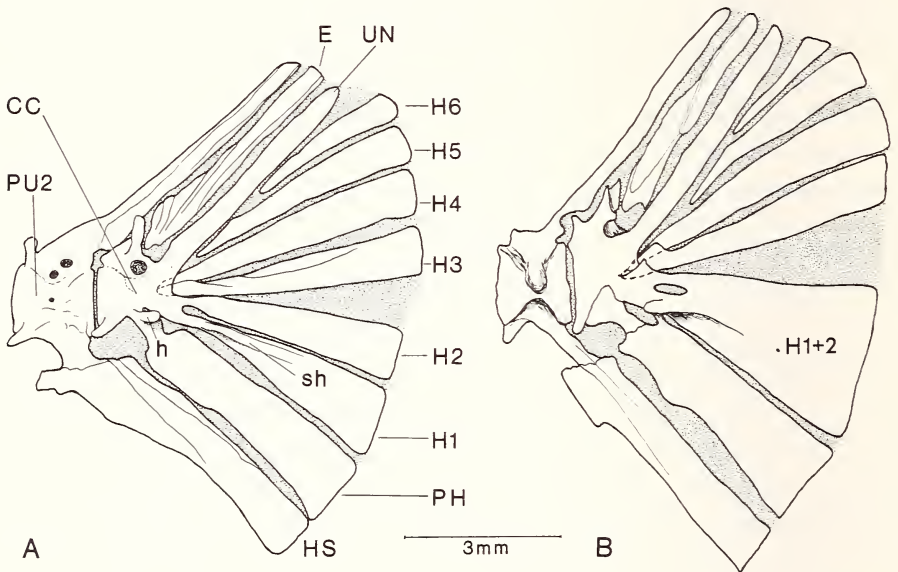


Fig. 10: Caudal skeleton, lateral view (caudal fin-rays removed). — A: *Diplomystes chilensis* (MCZ 8290); B: *Diplomystes nahuelbutaensis* n. sp. (CAS 55425).

CC: compound centrum; E: epural; H 1–6: hypural 1–6; h: hypurapophysis; HS: haemal spine 2; PH: parhypural; PU2: preural centrum 2; sh: secondary hypurapophysis; UN: uroneural.

its ventral extremity; it seems that the epural arises as a fracture of the dorsal part of neural arch 1 (plus its neural spine) as shown by the young specimens. The uroneural is fused with the dorsoposterior portion of the compound centrum; the uroneurals are separate from each other in the midline. The haemal arch of the parhypural is narrow; the parhypural and the base of hypurals 1 and 2 fuse to the compound centrum. There are six hypurals. In most specimens hypurals 1 and 2 are separated but they are partially

fused in two specimens and totally fused in five specimens. Hypurapophysis and secondary hypurapophysis are developed on the parhypural and hypural 1.

There are 47—53 caudal rays ($\bar{x} = 48.9$), and 9/9 principal caudal rays. There are 2 (one specimen with 1) segmented, unbranched rays in the upper lobe and 2 (one specimen with 3) in the lower lobe and 14 to 16 dorsal procurrent rays and 14 to 17 ventral procurrent rays. The upper lobe may have the same number of rays, or more rays than the lower lobe (see Table 2 for number of rays).

The caudal fin is slightly forked; the lobes are frequently asymmetric in shape and length; in some specimens the upper lobe is larger than the lower one, and vice versa.

Diplomystes nahuelbutaensis n. sp.

(Figs. 8B; 10B; 11A—C; 12A—B; 13; 14A—B; 15A—C; 16; 17A—B; 18A; 38; Tables 1—3)

S y n o n y m s :

Diplomyste chilensis: Eigenmann, C. (1927): Mem. Nat. Acad. Sci. 22: 13, 15, 20, 36—37 (in part: specimens from Lautaro).

Diplomystes papillosus: Shelden, F. F. (1937): Ann. New York Acad. Sci. v. 37, art. 1: 40—41.

Diplomystes papillosus: Oliver, C. (1949): Bol. Soc. Biol. Concepción (24): 55.

S t u d i e d m a t e r i a l :

Holotype: CAS(IUM) 55423, specimen of 222 mm standard length; Río Cautín, Lautaro, Chile; coll. C. Eigenmann; February 13, 1919.

Paratypes: CAS 55424, 6 specimens and CAS 55425, 1 specimen (cl & st); Río Cautín, Lautaro; coll. C. Eigenmann; February 13, 1919. — CAS 55426, 1 specimen; Río Loncomilla, San Javier, Chile; coll. C. Eigenmann; March 23, 1919. — CAS 30875, 2 specimens; Estero Nonguén, Concepción, Chile; coll. C. Eigenmann; March 20, 1919. — MCZ 61245, 2 specimens; Los Altos del Río Bío-Bío; coll. V. H. Ruiz & H. Oyarzo; March 30, 1984. — BMNH 1876-10-2: 22, 1 skeleton.

Additional material: UMMZ 212177, 1 specimen; Río Bío-Bío near Marimenuco, Malleco, Chile; coll. G. F. Edmunds; December 1, 1963.

C o m m o n n a m e s : "tollo", "bagre".

T y p e - l o c a l i t y : Río Cautín, in Lautaro, Bío-Bío basin, and Río Loncomilla; Chile; South America.

E t y m o l o g y : The specific name refers to Cordillera de Nahuelbuta, an especial geological and ecological region of the Cordillera de la Costa in Chile, where the holotype and most paratype specimens were collected.

D i a g n o s i s : Moderately elongate fish (Fig. 11A); bases of fins scarcely fleshy. Eye relatively small, 40 to 65 % of preorbital length. Snout short, preorbital length 7 to 9 % of standard length (*2). Origin of pelvic fin slightly posterior to the half length of standard length. Low adipose fin, depth 16 to 25 % of its length. Nostrils surrounded by a small skin fold, posterior nostril widely exposed (*2) (Fig. 11B). Palatine with two separate anterior processes (*2). Palatine short, its facets for lateral ethmoid, and cartilage joining with mesethmoid, vomer, lateral ethmoid and orbitosphenoid about half-length of bone. Foramen for facial (on hyomandibula) hidden by a well developed horizontal levator arcus palatine crest. One vomerine tooth plate (*2). Dentary with a ventral bone flange close to symphysis (*2) (Fig. 15C). Teeth on mandibles and branchial apparatus needle-like (*2), with spatulate or conic tips; vomerine teeth short, broad and conic. Skin smooth with short papillae over the body, barbel, roof and floor of mouth. Buds as "rose" structure, forming a geometric figure, on skin of base of barbel (*2). Two or three pectoral axillary glands (commonly 3/3).

C o l o r a t i o n : Dorsum of head and trunk dark violet or blackish. Ventral part

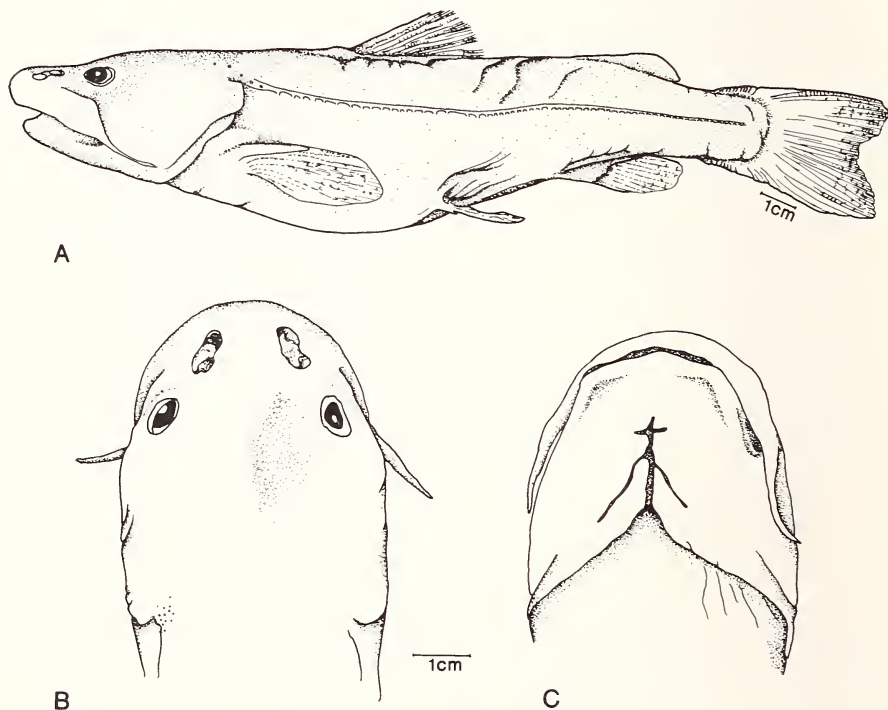


Fig. 11: *Diplomystes nahuelbutaensis* n. sp. (CAS [IUM] 55423). — A: Lateral view; B: Head, dorsal view; C: Head, ventral view.

of head, flanks and ventral part of trunk somewhat orange; tips of pectoral, dorsal, anal and caudal fins darker.

Description: *Diplomystes* of about 260 mm in total length as adult; maximum length known about 300 mm. (The type specimen [CAS 55423] is actually 261 mm in total length and 222 mm in standard length. Eigenmann [1927] gives 255 mm in standard length for the specimen. I attribute the difference to shrinkage while in preservation for about sixty-five years [1919–1984]; in life the fish probably reached about 300 mm in total length, as reported to me by older residents of the area between Concepción to Cautín, Chile. They state without exception that diplomystids over 300 mm in total length were commonly found in deep zones of rivers and lakes.) Body proportions variable, more or less overlapping those of other *Diplomystes* (Table 1). Eye diameter 40 to 65 % (\bar{x} = 52 %) of preorbital length. Low adipose fin, its depth is 16 to 25 % (\bar{x} = 18.7 %) of its length. Snout slightly rounded (Fig. 11B, C). Number of vertebrae and fin-rays in Table 2.

The following description of the coloration is based on MCZ 61245 (in alcohol), two specimens recently collected. Dorsum of head and trunk is dark violet or blackish. Ventral part of head, flanks and ventral part of trunk is orangish in one specimen; in the other flanks are slightly violet to blackish; tips of pectoral, dorsal, anal and caudal fins are darker (Table 3).

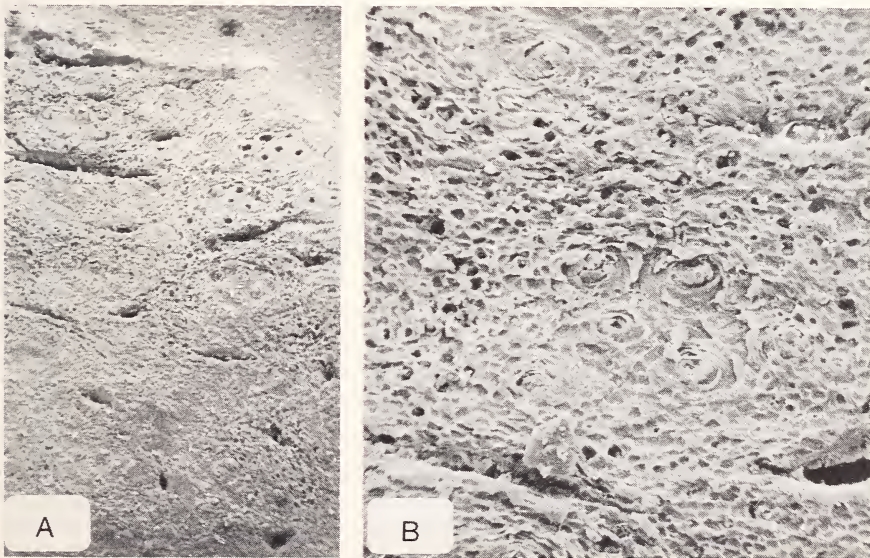


Fig. 12: *Diplomystes nahuelbutaensis* n. sp. (MCZ 61245). — Skin of the dorsoposterior region of the maxillary barbel. A: Papillae and buds (SEM 52x); B: Enlargement of a section of the skin showing the buds (SEM 132x).

Table 3: Some features of diplomystids species.

Feature	<i>Diplomystes chilensis</i>	<i>Diplomystes nahuelbutaensis</i>	<i>Diplomystes camposensis</i>	<i>Olivaiichthys viedmensis</i>
Lateral ethmoid . . .	broad and short	slender and long	broad and short	slender and long
Broad extension of lateral ethmoid below frontal	yes	no	no	no
Anterolateral process of sphenotic . . .	long	long	long	short
Sphenotic length more than 150 % of pterotic length	yes	yes	yes	no
Narrow joint between pterosphenoïd and parasphenoid	no	no	in some specimens	no
Two foramina for optical, facial and trigeminal nerves	no	no	in some specimens	no
Nasal as . . . (in adult)	bony-tube	bony-tube	half-cylinder or bony-tube	bony-tube
Infraorbitals as . . . (in adult)	bony-tubes	bony-tubes	half-cylinders or bony-tubes	bony-tubes
Infraorbitals	6 or 7	8	8 or 9	8 or 9
Anterior processes of palatine . . .	fused	separated	separated	separated
Articular facets on palatine for lateral ethmoid . . .	half of length of palatine	half of length of palatine	first third of length of palatine	half of length of palatine
Palatine tooth plate (in adult)	no	no	no	yes
Vomerine tooth plates (in adult)	2	1	2	2
Foramina on external face of hyomandibula . . .	5 or 6	5 or 6	3 or 4	5 or 6
Rami of facial nerve on external surface of hyomandibula . . .	4	3	3	3
Rows of maxillary teeth on anterior part of maxilla (adult)	2	2	2	3 or more
Rows of maxillary teeth on posterior part of maxilla (adult)	1	1	1	2 or more
Teeth on dentary (in adult)	moderately long	longest	moderately long	comparatively shortest
Bony flange on dentary	no	yes	no	no

T-shaped urohyal (in adult)	no	no	no	yes
Suprapreopercles	bony-tubes	bony-tubes	bony-tubes or half-cylinders	bony-tubes
Pores of cephalic sensory canal	distinctive	inconspicuous	distinctive	distinctive
Tubules of infraorbital canal	8 or 9 (occasionally)	9	9 or 10	10 or 11
Pectoral distal radials	none	none	3 (occasionally 0)	5 or 6
Free pelvic radial (in young)	no	no	no	yes
Arch of parhypural (in adult)	slender	slender	broad	slightly broad
Nostrils surrounded by large skin folds	yes	no	yes	yes
Posterior nostril completely covered by skin fold	partially	widely exposed	yes	partially
Length of papillae on body	long	shorter	shorter	shorter
Epidermal papillae on barbel	elongate	slightly conic	round	slightly conic
Papillae on skin of mouth	many and long	few and long	few and short	few and short
Pelvic fin origin posterior to the half of standard length	no	yes	yes	yes
Coloration (fresh specimens)	Grey body becoming brownish toward caudal region	?	Uniform dark brown or dark purple on dorsum and flanks or with irregular spots on a brown or purple ground	Pale purple and with abundant spots on dorsum and flanks. Uniform dark or pale brown on dorsum and flanks
	White in ventral region		Whitish, yellowish or orangish in ventral region	
Coloration (preserved material)	Brown in dorsum and flanks; or brownish or greyish, a little greenish; or with or without green or brownish spots on dorsum	Dark violet or blackish on dorsum and flanks	Similar to above described, but color becomes slightly pale	Many black spots on purple, greyish ground
	Whitish in ventral part of body	Orangish in ventral part of body	Yellowish, orangish or whitish in ventral part of body	Whitish, greyish or yellowish in ventral part of body

The whole skin appears smoother and with fewer small rounded or conic papillae than that of *Diplomystes chilensis* with a stereo microscope, nevertheless the SEM reveals that the elongate buds may be placed in papillae or not (Fig. 12A, B). The elongate buds are together in groups of five or six; around each bud is a curious distribution of skin folds and grooves (Fig. 12B) which form a "rose" shape structure. The surface of the skin of head and trunk has grooves and pores and a few papillae.

The lateral ethmoid (Fig. 13) projects ventrolaterally; it is comparatively smaller than that of *Diplomystes chilensis* (compare Figs. 4A & 13). The extension of the bone below the frontal is smaller than in *D. chilensis* (Table 3), therefore the joints with the frontal and mesethmoid are correspondingly shorter. The frontal overlaps the mesethmoid; both bones meet in a broad "lap" joint. The roughly rectangular sphenotic has a lateral, elongate anterior process which carries a section of the infraorbital sensory

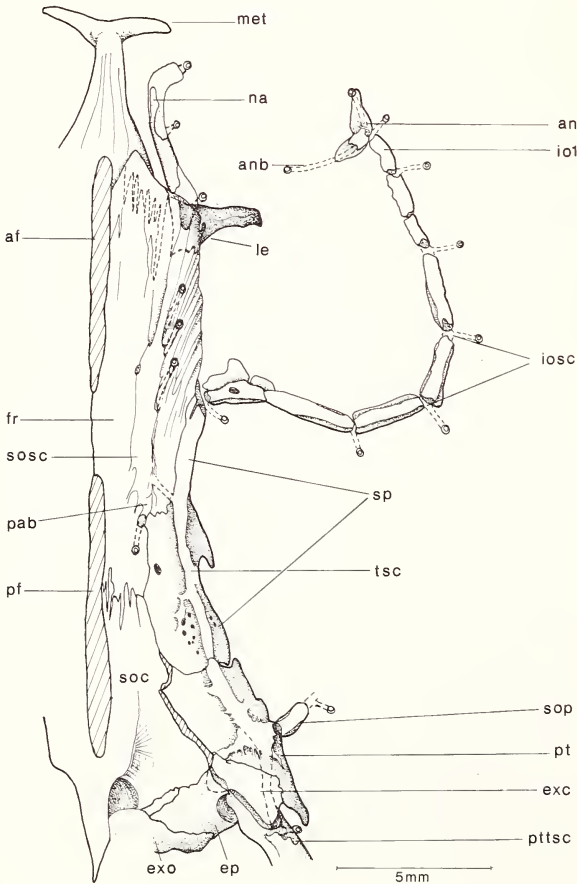


Fig. 13: *Diplomystes nahuelbutaensis* n. sp. (CAS 55425). — Cranium in dorsal view, circumorbital series, and part of the posttemporosupracleithrum.

af: anterior frontal fontanelle; an: antorbital; anb: antorbital branch of infraorbital sensory canal; ep: epioccipital; exc: extrascapular; exo: exoccipital; fr: frontal; io1: first infraorbital; iosc: infraorbital sensory canal; le: lateral ethmoid; met: mesethmoid; na: nasal; pab: parietal branch of supraorbital sensory canal; pf: posterior frontal fontanelle; pt: pterotic; ptsc: posttemporosupracleithrum; soc: supraoccipital; sop: suprapreopercle; sosc: supraorbital sensory canal; sp: sphenotic; tsc: temporal sensory canal.

canal. A narrow elongate space separates the supraoccipital, sphenotic and pterotic, in some large specimens.

The extrascapular differs in shape from that of *Diplomystes chilensis* (compare Figs. 4B & 13).

One (occasionally two incompletely fused to each other) tooth plate (Fig. 14B) lies ventral to the vomer. The vomerine tooth plate is heart-shaped and is covered by short conic teeth.

The circumorbital series (Fig. 13) has eight infraorbitals (more bones than in *D. chilensis*; Table 3) as bony tubes; the antorbital is slightly comma-shaped; the last infraorbital bears thin bony plates (not seen in *D. chilensis*) and may partially overlap the anterior part of the sphenotic.

The premaxillary, maxillary (Fig. 14A, B) and dentary teeth (Fig. 15C) are longer than those of *D. chilensis* and *D. camposensis* n. sp., they are needle-like (shape not found in other *Diplomystes*). Eleven to thirteen teeth may be found in each adult maxilla (Table 2). Palatine tooth plates are absent.

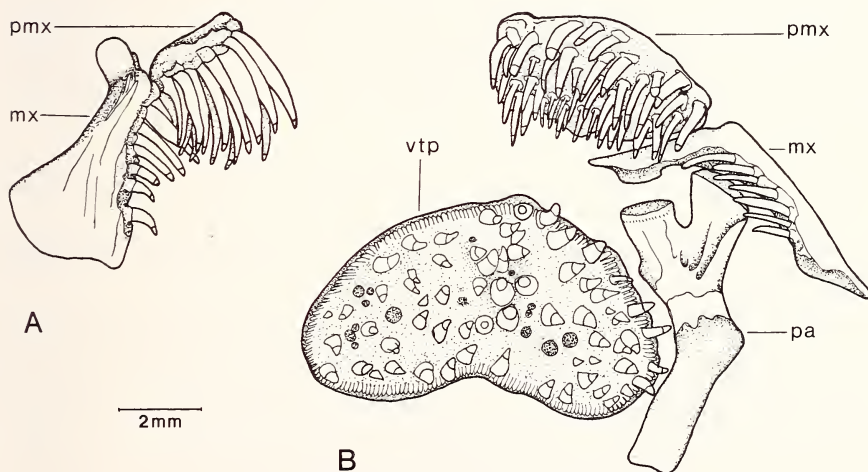


Fig. 14: *Diplomystes nahuelbutaensis* n. sp. (CAS 55425). — A: Premaxilla and maxilla, lateral view; B: Premaxilla, maxilla, vomerine tooth plate and palatine, ventral view.

mx: maxilla; pa: palatine; pmx: premaxilla; vtp: vomerine tooth plate.

The postarticular process of the lower jaw is rudimentary and the opening of the mandibular canal (Fig. 15A) is dorsolaterally placed in the posterior part of the jaw. The anterior part of the dentary (Fig. 15B) becomes broader close to the symphysis, providing support to the longer teeth placed in many rows; the dentary bears a shallow bony flange anteroventrally (Fig. 15B) which is not present in the other diplomystids.

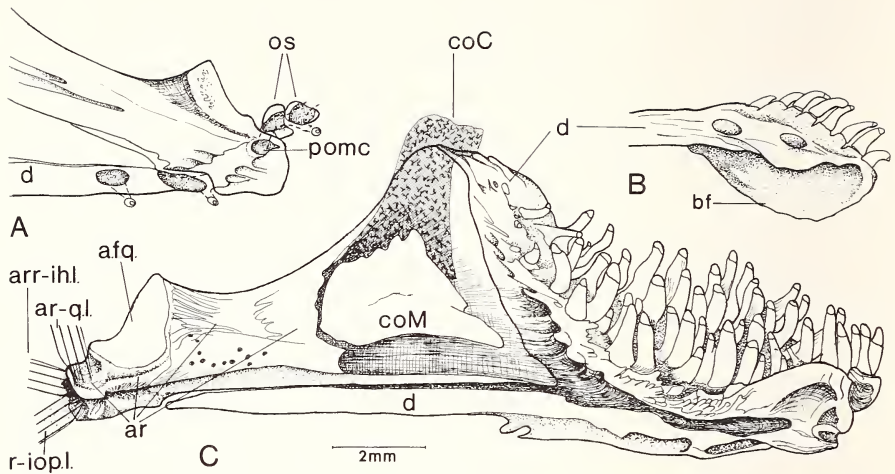


Fig. 15: *Diplomystes nahuelbutaensis* n. sp. (CAS 55425, BMNH 1876-10-2:22). — Lower jaw. — A: Posterior part in lateral view; B: Anterior part of dentary, ventral view; C: Medial view. a.f.q: articular facet for quadrate; ar: articular bone; ar-q.l.: ligamentum quadratomandibularis laterale; arr-ih.l.: ligamentum mandibulo-hyoid; bf: bony flange; coC: coronoid cartilage; coM: coronomeckelian bone; d: dentary; os: ossicles placed between the posterior part of lower jaw and preopercle; pomc: posterior opening of mandibular sensory canal; r-iopl.l.: ligamentum mandibularis-interoperculare.

The articular and coronomeckelian bone (Fig. 15C) are well developed; the latter enlarges greatly during growth.

A well developed horizontal crest for the attachment of the levator arcus palatini muscle is present on the lateral face of the hyomandibula. In the articular region (Fig. 16) between hyomandibula and metapterygoid, another small plate like bone exists in specimen CAS 55425; this plate like bone could be a result of a fracture affecting the articular region between both bones, or it could represent a separate bone, at the moment identified as (?)metapterygoid, that I have found in specimens of *D. camposensis* n. sp. (Fig. 25A, C, D).

The hyoid arch is similar to that of *Diplomystes camposensis* n. sp., see description in page 56, based on several specimens. The urohyal (Fig. 8B) is widest ventroanteriorly; it produces several projections lateroposteriorly, and extends posteriorly into an elongate process.

Each of the first three branchial arches has a suspensory pharyngeal or modified pharyngobranchials 1–3, each one without tooth plates (Fig. 17A, B). The well ossified elongate pharyngobranchials 1–2 are placed parallel and dorsal to epibranchials 1–2, while pharyngobranchial 3 (ossified) lies over the dorsal end of the epibranchials 1–2

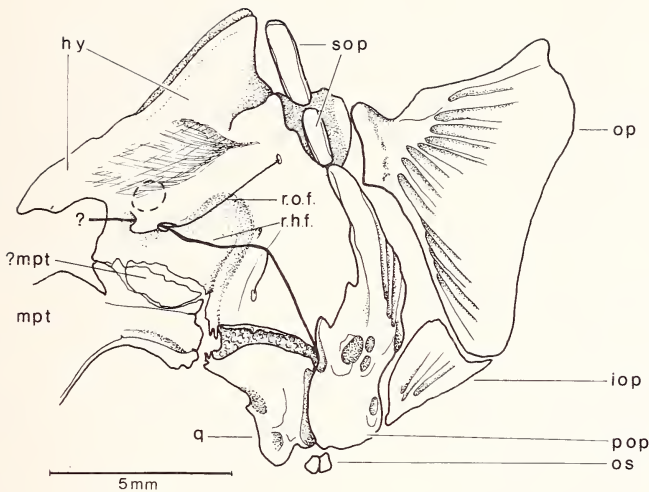


Fig. 16: *Diplomystes nahuelbutaensis* n. sp. (MCZ 61245, CAS 55425). — Pterygoid bones, hyomandibula, quadrate and opercular apparatus, lateral view.

hy: hyomandibula; iop: interopercle; mpt: metapterygoid; ?mpt: ?piece of the metapterygoid; op: opercle; os: ossicles; pop: preopercle; q: quadrate; r.h.f.: ramus hyomandibular of facial nerve; r.o.f.: ramus opercularis facialis; sop: suprapreopercles; ?: unknown ramus.

and pharyngobranchials 1–2. Pharyngobranchial 4 is ossified, forming a small elongate bone, and is attached ventrally to a tooth plate with long slender conic teeth.

Epibranchials 1–2 are longer than epibranchials 3–4; a fifth small cartilaginous epibranchial is present; only epibranchial 3 bears an uncinuate process. Epibranchial 4 is slightly broad and has a short lateral projection which I do not consider an uncinuate process. Each epibranchial bears few gill rakers. Each epibranchial is widely separated from its ceratobranchial (cartilage is filling the space between both bones).

The ceratobranchials are elongate and lack a notch on their margins. Ceratobranchial 5 (Fig. 17B) is somewhat broad, with a narrow dorsal end; the inner surface of the bone is covered by many tall conic teeth (needle-like), with the exception of the region close to the medial margin which is covered by several rows of small conic teeth. Both margins of ceratobranchials 1–4 bear few gill rakers irregularly distributed. Ceratobranchial 5 bears only one row of five gill rakers. Ceratobranchials 1–2 articulate with short hypobranchials 1–2; an ossified hypobranchial 3 is absent. Basibranchial 1 is absent; basibranchial 2, located adjacent to hypobranchials 1–2, is a slightly elongate bone followed by a slightly smaller basibranchial 3. Pharyngobranchial 4 and ceratobranchial 5 are the only toothed elements of the branchial skeleton.

A small free pseudobranch with lamellae set along an axis holds from the first pharyngobranchial to the medial face of the hyomandibula. An overgrowth of connective tissue is close to the pseudobranch.

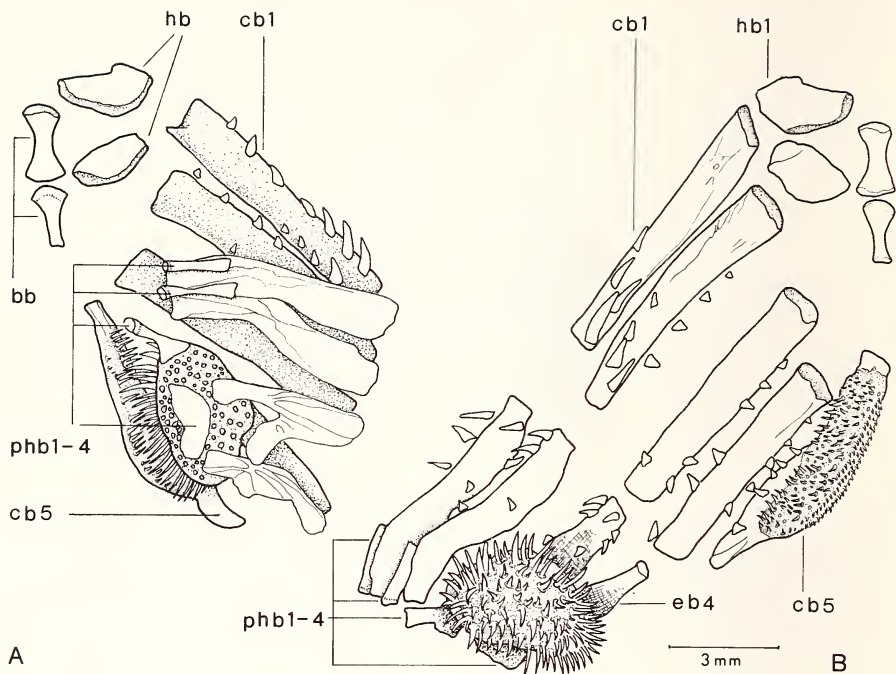


Fig. 17: *Diplomystes nahuelbutaensis* n. sp. (CAS 55425). — Branchial apparatus. — A: Dorsal view; B: Branchial bones, inner view.

bb: basibranchial; cb1–5: ceratobranchial 1–5; eb1–4: epibranchials 1–4; hb: hypobranchials; phb1–4: pharyngobranchials 1–4.

The cephalic sensory canals differ in minor ways from those of *D. chilensis* (compare Figs. 4A & 13; Table 3): e. g., the pores of *D. nahuelbutaensis* n. sp. are very small and difficult to see, and the sensory tubules are slightly shorter; the short parietal branch ends on the frontal; it runs posteriorly opening in a pore over the frontal; large pit organs as those present in other species of *Diplomystes*, were not found in the specimens I examined.

Fins

Pectoral girdle does not have any significant difference to those above described (page 30) for *Diplomystes chilensis*. The pectoral spine acquires more serrae during growth (in large specimens has eight or nine serrae); the distal tip of the spine (Fig. 18A) consists of separate segments which becomes smaller distally. The segments have a characteristic shape and each becomes part of the ossified spine during growth. The pelvic girdle has three separate anterior processes.

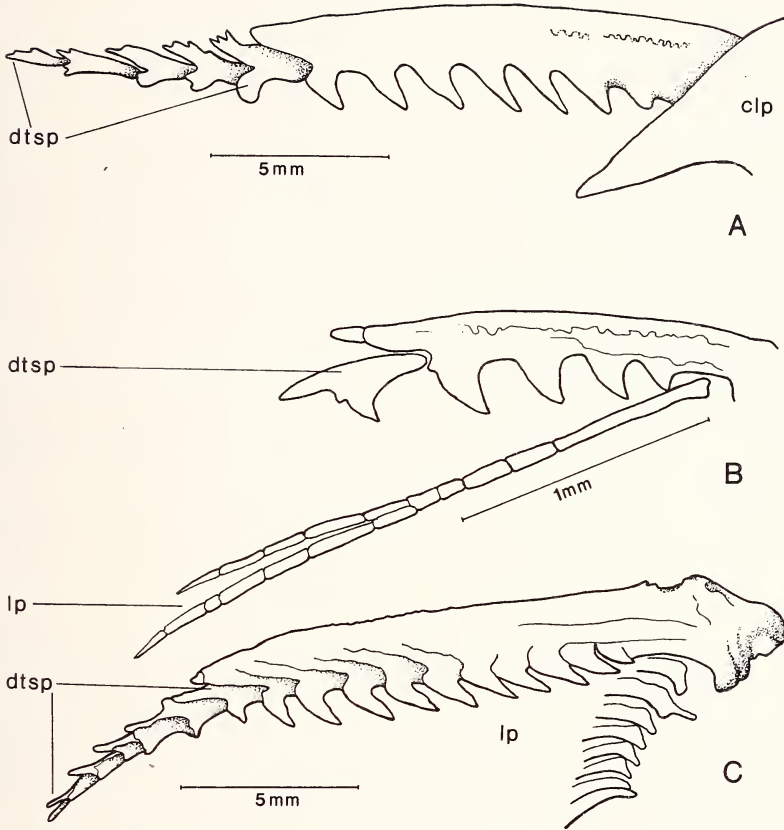


Fig. 18: Pectoral spine and serrae. — A: *Diplomystes nahuelbutaensis* n. sp. (CAS 55425); B: Spine and first pectoral ray of a young specimen of *Diplomystes camposensis* n. sp. (PC 110276); C: *Diplomystes camposensis* (PC 110276).

clp: cleithral process; dtsp: distal tip of the spine; lp: lepidotrichium.

The anal fin has 14 or 15 rays (excepting one specimen with 12); usually 10 or 11 principal anal rays and 11 or 13 anal pterygiophores are present. The first ossified pterygiophore is shorter (only one specimen has a moderately long pterygiophore) than the second one.

Seven vertebrae support the caudal skeleton, without exception. Hypurals 1 and 2 are separate from each other in most specimens but fused in two (Fig. 10B). There are 47 to 53 caudal rays (see Table 2 for numbers of rays); two or three segmented, unbranched rays in the dorsal lobe, and three or four segmented, unbranched rays in the ventral lobe.

Diplomystes camposensis n. sp.

(Figs. 3B; 8C; 19A–C; 20A–B; 21A–B; 22A–B; 23A–B; 24A–B; 25A–D; 26A–F; 27A–C; 28A–C; 29A–C; 30A–D; 31; 32A; 33A; 38; Tables 1–3)

S y n o n y m s :

Diplomyste chilensis: Eigenmann C. (1927): Mem. Nat. Acad. Sci. 22: 13, 15, 20, 36–37 (in part: specimens from Lago Riñihue).

Diplomyste papillosus: Chardon, M. (1968): Mus. Roy. Afrique Centrale, sér. 8, Sci. Zool.: 29–35.

Diplomystes chilensis: (?)Campos, H. (1972): Mus. Nac. Hist. Natur., Chile, Not. Mensual (198–199): 9–11. — Arratia et al. (1978): Studies Neotropical Fauna & Env. 13: 188–189. — Arratia, G. (1981): Bull. Mus. Nac. Hist. Natur., Chile, Publ. Ocas. 34: 44 (in part: rivers of Valdivia). — (1982): Bol. Mus. Nac. Hist. Nat., Chile, 39: 54–55, cuadro 1,2. — (1983): Studies Neotropical Fauna & Env. 18 (4): 218, 225, 227, 232. — Arratia et al. (1985): Deserta 7 (1): 64, 72, 86, 102, 103 (in part: specimens from Valdivia region).

C o m m o n n a m e : "tollo", "bagre".

S t u d i e d m a t e r i a l :

Holotype: IZUA 3302: 1 specimen 169.6 mm in standard length; Lago Riñihue, Chile; coll. A. Arriagada & A. Klink; October 2, 1983.

Paratypes: IZUA 3303: 2 specimens; Lago Riñihue; November 4, 1975. — IZUA 2807: 1 specimen; Lago Riñihue. — SMF 7579: 1 specimen; Río Valdivia; coll. H. Campos; December 11, 1964. — MCZ 54388: 1 specimen; Río San Pedro, Los Lagos; Chile; coll. G. Arratia; March 22, 1979. — CAS 55428: 2 specimens, Lago Riñihue; coll. C. Eigenmann; March 16, 1919. — KU 19210: 1 specimen (cl & st), Río San Pedro, Purey, Chile; coll. G. Arratia & H. Diaz; February 19, 1967. — KU 19209: 3 specimens; Río San Pedro, Los Lagos; coll. G. Arratia & H. Diaz; February, 1976. — KU 19257: 1 specimen; Río Curalelfú, Los Lagos; coll. G. Arratia & H. Diaz; February, 1976. — PC 110276: 2 specimens (cl & st), PC 120276: 1 specimen (cl & st), PC 130276: 1 specimen (cl & st), PC 140276: 1 specimen (cl & st), all collected in Río San Pedro, Los Lagos, by G. Arratia. — PC 111285: 1 specimen; Río San Pedro close to Río Chinchilca; coll. K. Busse; December 11, 1985. — PC 011986 a: 2 specimens; desagüe Lago Riñihue; coll. K. Busse; January, 1986. — PC 011986 b: 3 specimens (cl & st); desagüe Lago Riñihue; coll. K. Busse; January, 1986. — MZUF 5546: 1 specimen; Los Lagos; coll. A. Chang & G. Arratia; 1976. — ZFMK 14800: 1 specimen; Río San Pedro, close to Taco 3; coll. K. Busse; December 14, 1985. — ZFMK 14801–14805: 5 specimens; desagüe Lago Riñihue; coll. K. Busse; January 1986.

T y p e - l o c a l i t y : Valdivia basin, Lago Riñihue; Valdivia region, southern Chile; South America.

E t y m o l o g y : The specific name refers to Dr. Hugo Campos, Chilean ichthyologist, who has encouraged me to make this research.

D i a g n o s i s : Nasal and suprapreopercles as tube-like or half-cylinder bones. Infraorbital sensory canal enclosed by seven or eight tube-like or half-cylinder infraorbital bones. Premaxillary length less than 50 % of maxillary length; maxilla with 12 to 19 teeth (commonly 15). Elongate palatine, its articular facet for lateral ethmoid, and cartilage joining with mesethmoid, vomer, lateral ethmoid and orbitosphenoid at about the first third of bone length (*2). External surface of hyomandibula with three or four foramina. Foramen for facial nerve (in hyomandibula) exposed; levator arcus palatini crest poorly developed (*2). More than 52 caudal fin-rays. Nostrils surrounded by large skin folds; a skin fold covering completely posterior nostril (Fig. 19A). Numerous short round papillae all over body including lips and branchiostegal membranes (Fig. 19C), slightly acute on maxillary barbel (Fig. 3B). Buds distributed along an axis in the papilla (*2). Short papillae having taste buds on roof and floor of mouth. Without pectoral axillary glands (occasionally one gland on one side of body) (*2).

C o l o r a t i o n : Uniform dark brown or dark purple on dorsum and flanks or with irregular spots on brown or purple ground; yellowish, orangish or whitish ventrally in fresh specimens. Slightly paler than those described above, in preserved specimens.

D e s c r i p t i o n : An elongate diplomystid (Fig. 19A) of about 250 mm total length as adult; maximum length known 249 mm; IZUA 3302 (Campos in litt.). Body proportions in Table 1. Snout well developed and pointed in young, slightly pointed or rounded in adults (Fig. 19B, C). Origin of dorsal fin closer to halflength of the body than to the snout, therefore dorsal fin is more posteriorly placed than in *D. chilensis* and *D. nahuelbutaensis* n. sp. The origin of the pelvic fin is posterior to the half of the standard length, therefore the pelvic girdle is more posteriorly placed than in *D. chilensis*. Adipose fin depth 22 to 31 % (\bar{x} = 26 %) of its length. Pectoral fins are longer in young than in adult specimens; they reach pelvic fins in young; the distal tip of the pectoral fin becomes distant from origin of pelvic fins during growth. Tip of pelvic fin reaches origin of anal fin in young, it becomes separated during growth. Both pelvic fins closer to each other in young than in adult specimens. All fins markedly fleshy. Number of teeth, vertebrae and rays in Table 2.

The following description of the gasbladder is based on fresh material: Slightly rounded physoclistous gasbladder (Fig. 20A) represented only by the anterior chamber of the ostariophysan gasbladder and covered by dense silvery peritoneum. Gasbladder located ventral to vertebral column and firmly attached to tripus and os suspensorium by dense hard peritoneal tunic which forms a half-cylinder attached to the complex vertebral centrum and produces lateral triangular wings. Each wing forms a flat "facet" (Fig. 20A) attached to the transformator process of the tripus. Dorsally the gasbladder has a groove down the midline. Internally, the gasbladder is incompletely divided into two chambers (Fig. 20B) by a thick hard septum. Transversely, a thin transparent layer of epithelium incompletely divides these two chambers; a retia mirabilia-glandular system

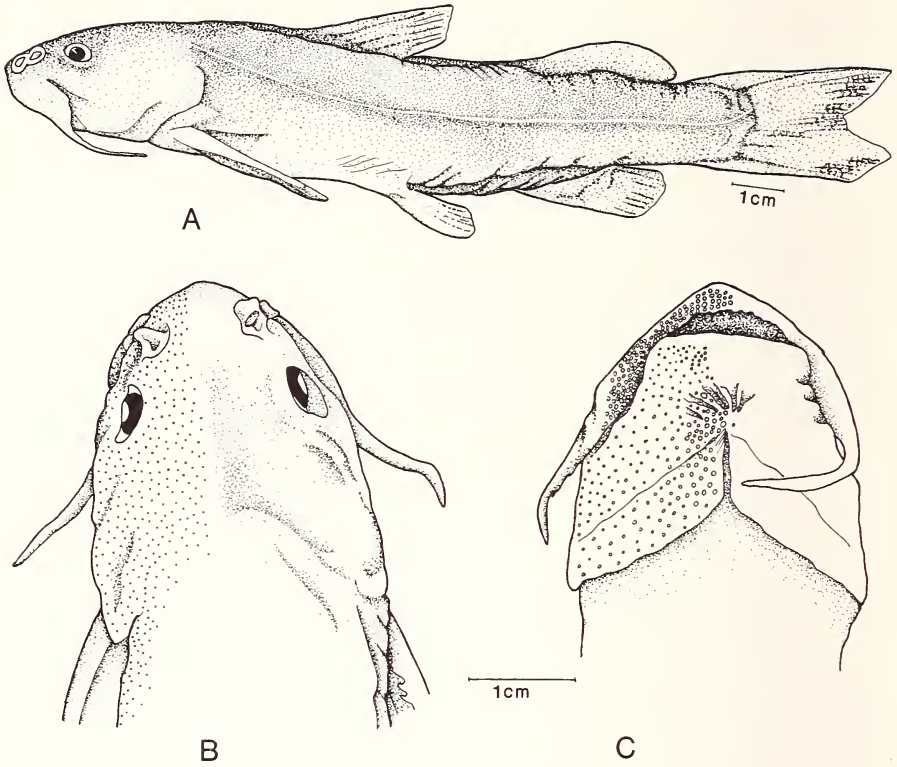


Fig. 19: *Diplomystes camposensis* n. sp. (KU 19209). — A: Lateral view; B: Head, dorsal view (distribution of papillae illustrated on left side); C: Head, ventral view (distribution of papillae illustrated on left side).

is close to the septum and lies on the epithelium as small glands or a wider area of gland tissue.

There are scarce and slightly pointed papillae on the skin of head of young specimens; some few papillae are on the trunk of juvenile specimens. The papillae of the head are similar to those of *D. chilensis* but shorter. Many short rounded verrucose papillae cover all the body in larger specimens; large and rounded papillae are around the mouth (Fig. 19C); sharp and short papillae and longitudinal skin folds are found in the roof of the mouth; round and conic papillae and skin folds cover the maxillary barbel (Fig. 3B). The ventral region of the head (Fig. 19C) is covered by round (or conic, sometimes) papillae. Each papillae of the base of the barbel or close to lips, has six or more elongate buds (Fig. 21A, B) which are surrounded by many skin folds, these buds are

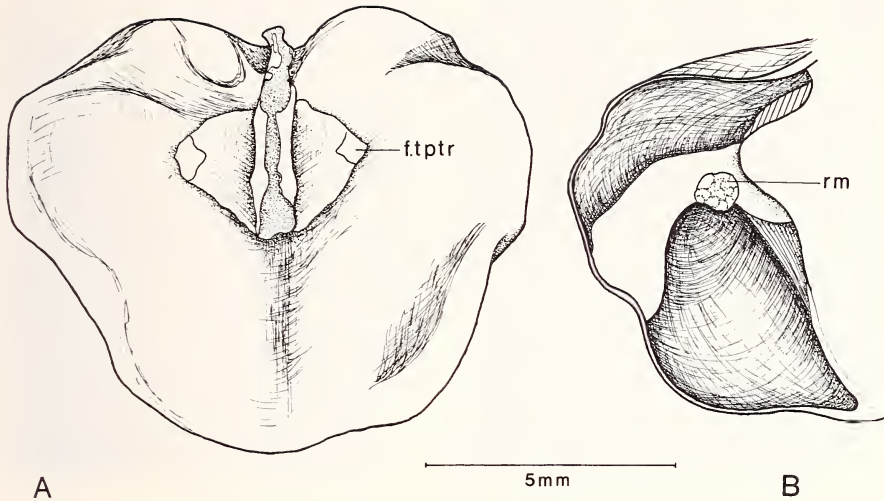


Fig. 20: *Diplomystes camposensis* n. sp. (IZUA 3303). — Gasbladder. — A: Dorsal view; B: Section of the gasbladder illustrating the inner camarae.

ftptr: facet for the transformator process of the tripus; rm: retia mirabilia — glandular system.

ordered along a longitudinal axis in each papilla. Sensory pores are easily confused with the elongate buds; the studies with SEM reveal that each pore (Fig. 21C) looks as the taste buds found in other species of siluroids, in having a crater-like shape. The skin of the trunk (Fig. 21D) has many short buds which may be simple or lobulated.

Coloration variable with age and different from locality to locality. Juvenile specimens are pale, varying from pale yellowish or greyish to brownish. Adult specimens are uniform dark brown on dorsum and flanks, or dark purple on dorsum and flanks, or with irregular spots on a brown or purple ground color. Yellowish, orangish or whitish in ventral region. (Specimens preserved in alcohol show a similar coloration; but slightly paler than fresh specimens as described above [Table 3]).

Cranium

There are differences between the cranium of young and adult specimens. Young specimens (about 30 mm in standard length) have a shorter and relatively wider cranium than adults (of about 180 mm in standard length). The frontals are not separated anteriorly by an anterior fontanelle; the latter appears during growth and in juveniles and adults extensively separates the frontals anteriorly, and extends into the mesethmoid. In young specimens the posterior frontal fontanelle is wide, reaching far back into the supraoccipital; it is connected laterally with spaces separating the frontals, sphenotic, and supraoccipital. There is an unossified epiphyseal bar contacting both

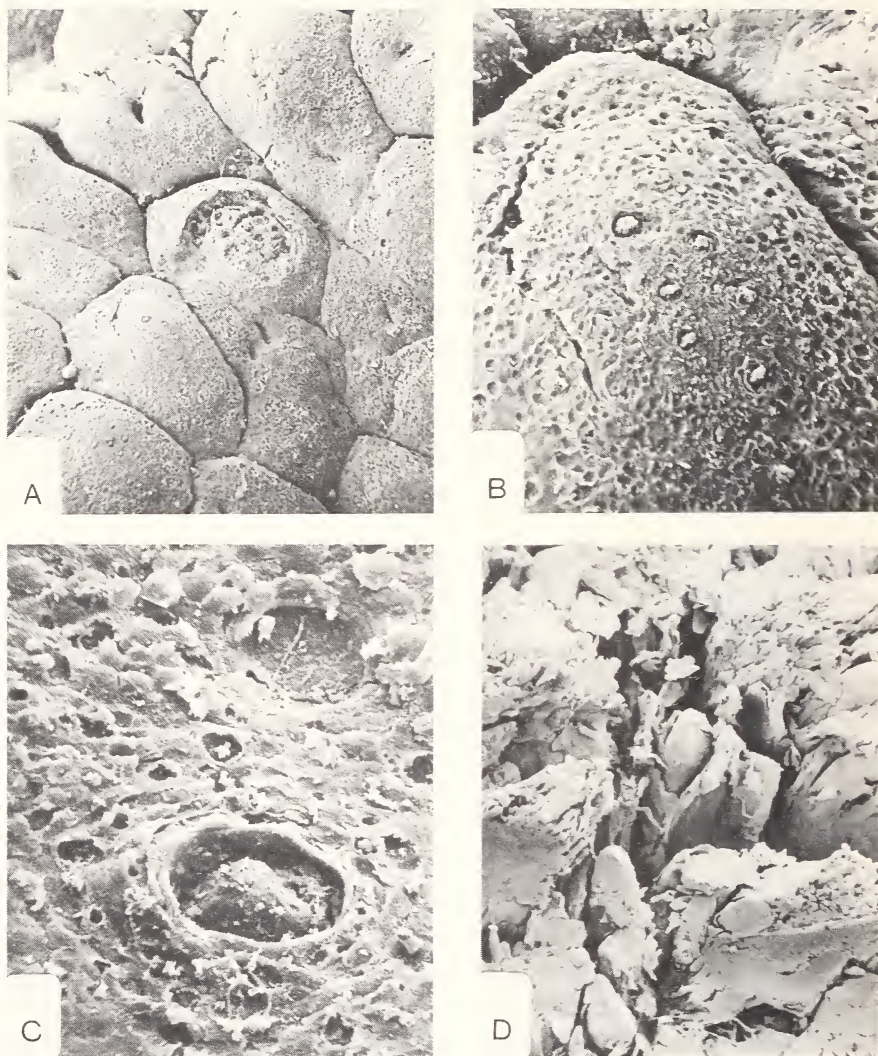


Fig. 21: *Diplomystes camposensis* n. sp. (SMF 7579). — SEM of the skin. — A: Papillae of the skin of the dorsoposterior region of the maxillary barbel (SEM 43x); B: Enlargement of the papillae, and buds (SEM 175x); C: Sensory pore of the supraorbital sensory canal, between orbits (SEM 420x); D: Skin of the dorsal region of the trunk just posterior to head (SEM 160x).

frontals. In the anterior part of the supraoccipital and laterally displaced is a small parietal on one side of the cranium of one specimen; both bones fuse, thus in adult specimens only one bone can be seen. In young specimens, the anterior part of the

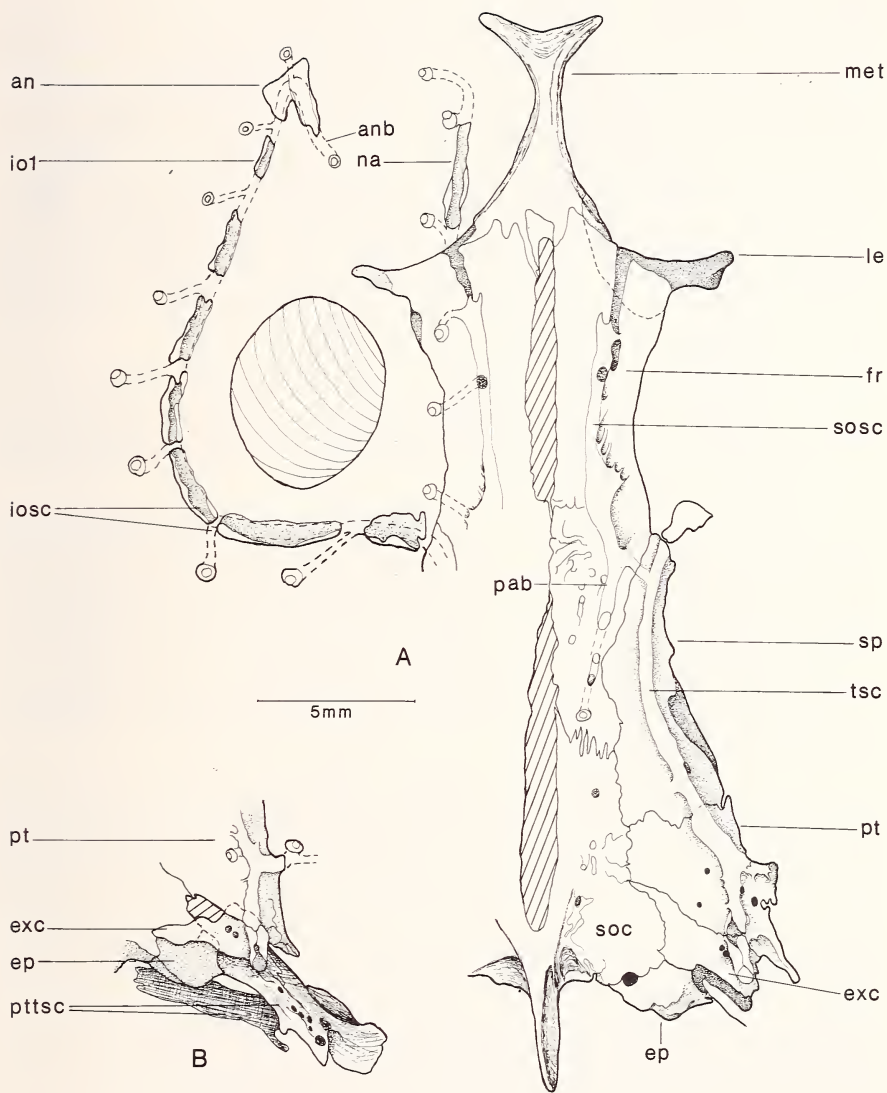


Fig. 22: *Diplomystes camposensis* n. sp. (PC 110276, 120276). — A: Cranium in dorsal view, and circumorbital series; B: Posterior part of the cranium in dorsal view illustrating the relationships of the extrascapular with cranial and uppermost pectoral girdle bones.

an: antorbital; anb: antorbital branch of infraorbital sensory canal; ep: epioccipital; exc: extrascapular; fr: frontal; iol: first infraorbital; iosc: infraorbital sensory canal; le: lateral ethmoid; met: mesethmoid; na: nasal; pab: parietal branch of supraorbital sensory canal; pt: pterotic; ptsc: posttemporosupracleithrum; soc: supraoccipital; sosc: supraorbital sensory canal; sp: sphenotic; tsc: temporal sensory canal.

supraorbital sensory canal runs laterally to the frontal, and the nasal bone is not ossified. During growth, the anterior part of the sensory canal is incorporated in the ossified frontal. The infra-, supraorbital and temporal canals are incompletely protected by bones in young specimens. The supraorbital and temporal canals are enclosed by bone in the frontal, sphenotic, and pterotic, but only partially enclosed by a half-cylinder of bone in the nasal and infraorbital bones of adult specimens (Fig. 22A).

The mesethmoid projects abruptly downwards anterior to the frontal (Fig. 23B) in adults. Mesethmoid and frontals widely overlap each other forming an irregular "flap" joint (Fig. 22A). In the largest specimens, the lateral walls of the mesethmoid (Fig. 23B) are mostly ossified; a small cartilaginous area is present close to the joint between the mesethmoid and lateral ethmoid. Each lateral ethmoid is overlapped by the frontal and forms a lateral spine-like wing which extends laterally.

Frequently, the lateral ethmoids are strongly asymmetric. The frontals are separated by two large fontanelles in the largest specimens; the anterior one may be divided into two fontanelles in some specimens. Anteriorly, the margin of each frontal produces a narrow deep notch which prolongs far back.

The extrascapular (Fig. 22A, B) is bounded to the pterotic, epioccipital, supraoccipital and posttemporosupracleithrum; it carries part of the main lateral canal on its external margin. The extrascapular is incorporated into the cranial roof in the largest specimens (Fig. 22A). A small narrow posttemporal fossa bounded by the pterotic, epioccipital, and exoccipital is roofed by the extrascapular; this fossa is filled with fatty tissue. The fossa is completely closed in large specimens. A sharp crest arises on one extrascapular in SMF 7579; it serves as the origin of fibers of the adductor mandibulae, anteriorly, and of the epaxialis, posteriorly.

The short basioccipital (Fig. 23A) is anteriorly sutured and synchondrally joined with the parasphenoid; laterally it is synchondrally joined with the prootic and partially with the exoccipital; an elongate narrow space is present between these bones in some specimens (Fig. 23B); posteriorly the basioccipital articulates with the first vertebral centrum. In some specimens, the sides of the basioccipital (Fig. 23B) project anteroventral to the joint between the exoccipital and prootic, but these external projections are missing in most specimens (Fig. 23A).

Each prootic opens anterolaterally in a large foramen for the passage of the facial, trigeminal and optic nerves. This foramen is bounded by the parasphenoid, prootic, pterosphenoid and orbitosphenoid. An additional elongate foramen occurs only in some specimens (Fig. 23A) of this species, in contrast to the above described *Diplomystes chilensis* and *D. nahuelbutaensis* n. sp. It serves for the passage of the optic nerve alone; the two foramina are separated from each other by a narrow bridge produced by the pterosphenoid which joins narrowly with the parasphenoid, a condition not seen in any other diplomystid studied.

Two large autogenous tooth plates lie on the lateroventral surface of the vomer of adult specimens; they bear large conic teeth, arranged in four to six irregular rows. In young

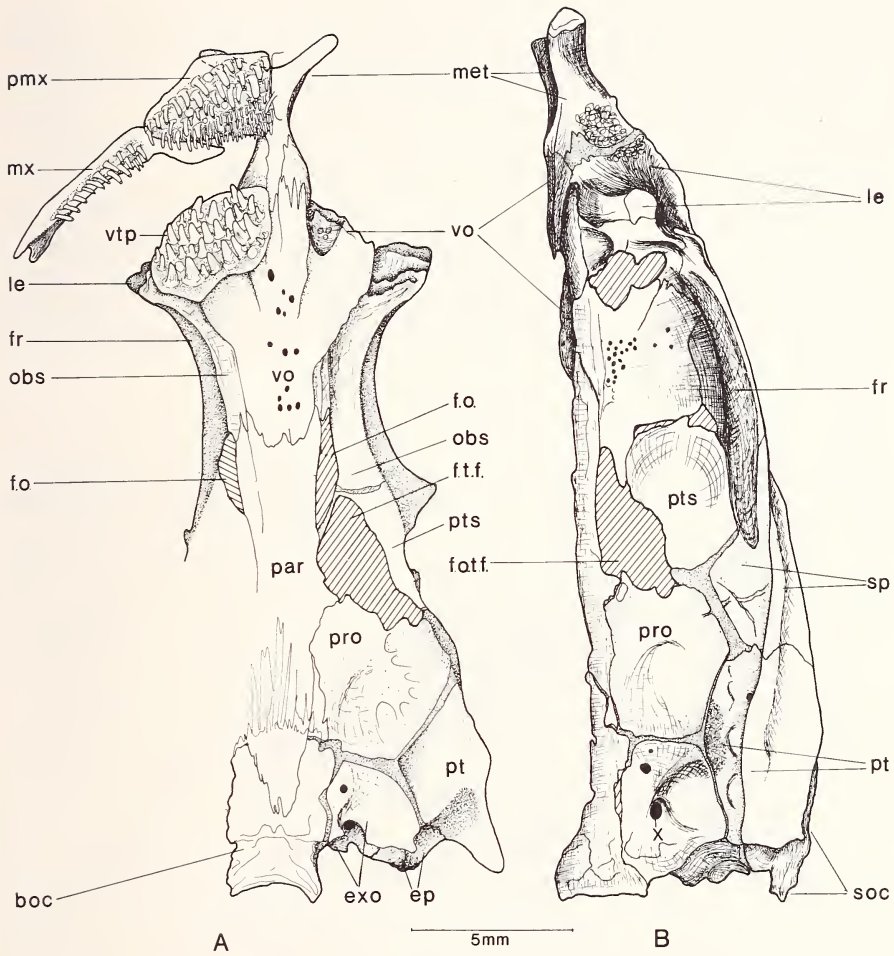


Fig. 23: *Diplomystes camposensis* n. sp. (PC 110276, 130276). — A: Cranium in ventral view (premaxilla, maxilla, vomerine tooth plate figured on one side); B: Cranium in lateral view. boc: basioccipital; ep: epioccipital; exo: exoccipital; f.o.: foramen for optic nerve; f.o.t.f.: foramen for optic, trigeminal and facial nerves; fr: frontal; f.t.f.: foramen for trigeminal and facial nerves; le: lateral ethmoid; met: mesethmoid; mx: maxilla; obs: orbitosphenoid; par: parasphenoid; pmx: premaxilla; pro: prootic; pt: pterotic; pts: pterosphenoid; soc: supraoccipital; sp: sphenotic; vo: vomer; vtp: vomerine tooth plate; X: foramen for vagus nerve.

specimens, each plate (Fig. 25A) develops independently of the vomer and from the palatine; during ontogeny it becomes larger and acquires more teeth and may fuse to the ventrolateral surface of the vomer.

Each pterosphenoid joins the sphenotic and prootic posteriorly, orbitosphenoid

anteroventrally, and frontal dorsally; occasionally it has a narrow joint with the parasphenoid. The large orbitosphenoid is separated from the lateral ethmoid by a large foramen and in some specimens narrow spaces separate the orbitosphenoid from pterosphenoid posteriorly.

Circumorbital series

There are nine or ten circumorbital bones (Fig. 22A); the antorbital is irregular in shape, or slightly comma-shaped in some specimens; the eight or nine infraorbitals are tube-like bones or half-cylinder bones open laterally, whereas they are tube-like bones in other *Diplomystes* (Table 3); the last bone has a more plate-like shape (Fig. 22A), similar to that of *D. nahuelbutaensis* n. sp.; the last two or three infraorbitals may be plate-like bones.

Palato-quadrate and mandibular apparatus

The premaxilla (Fig. 23A, 24A, B) is shorter than the maxilla. About six to eight irregular rows of conic teeth cover the ventral surface of the premaxilla; the largest teeth

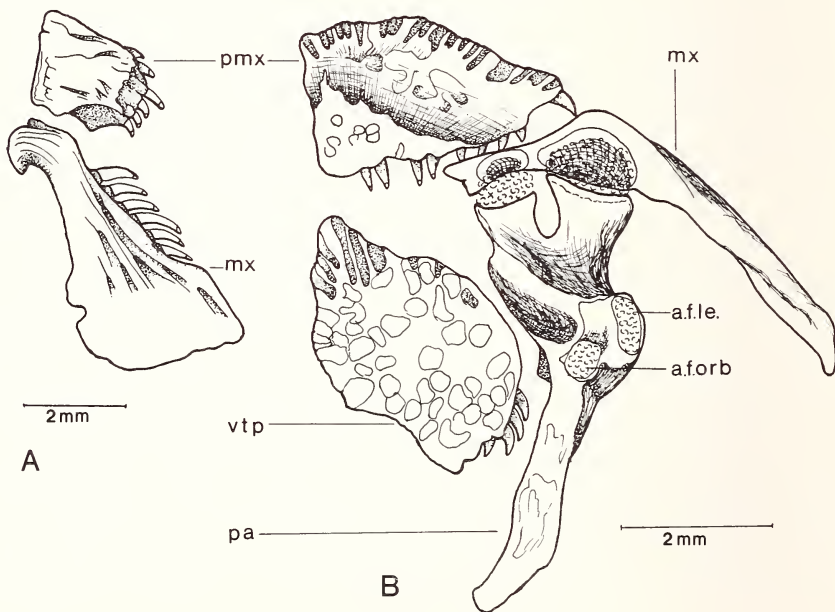


Fig. 24: *Diplomystes camposensis* n. sp. (PC 130276). — A: Premaxilla and maxilla, lateral view; B: Premaxilla, maxilla, palatine and vomerine tooth plate, dorsal view.

a.f.le.: articular facet for lateral ethmoid; a.f.orb: articular facet for a cartilage joining with mesethmoid, vomer (mainly), lateral ethmoid and orbitosphenoid; mx: maxilla; pa: palatine; pmx: premaxilla; vtp: vomerine tooth plate.

are those of the two external rows (Fig. 23A). The teeth are comparatively shorter than those of *Diplomystes nahuelbutaensis* n. sp. The lateral surface of the maxilla (Fig. 24A) shows several grooves in the bone. About two-thirds of the free ventral margin of the maxilla bears tall, slightly spatulate teeth; the teeth are ordered in two rows close to the articular process and in one row posteriorly, with the exception of SMF 7579, which has two rows covering most of the ventral margin of the bone; the maxilla has 12–19 teeth, commonly 15.

The palatine (Fig. 24B, 25A–D) is an elongate bone, with two processes anteriorly. The posterior part of the palatine does not articulate with the pterygoid bones (Fig. 25A–D), it does not relate through cartilage with them. The distal part of the palatine is best ossified. The palatine originates as cartilage, therefore it corresponds to the

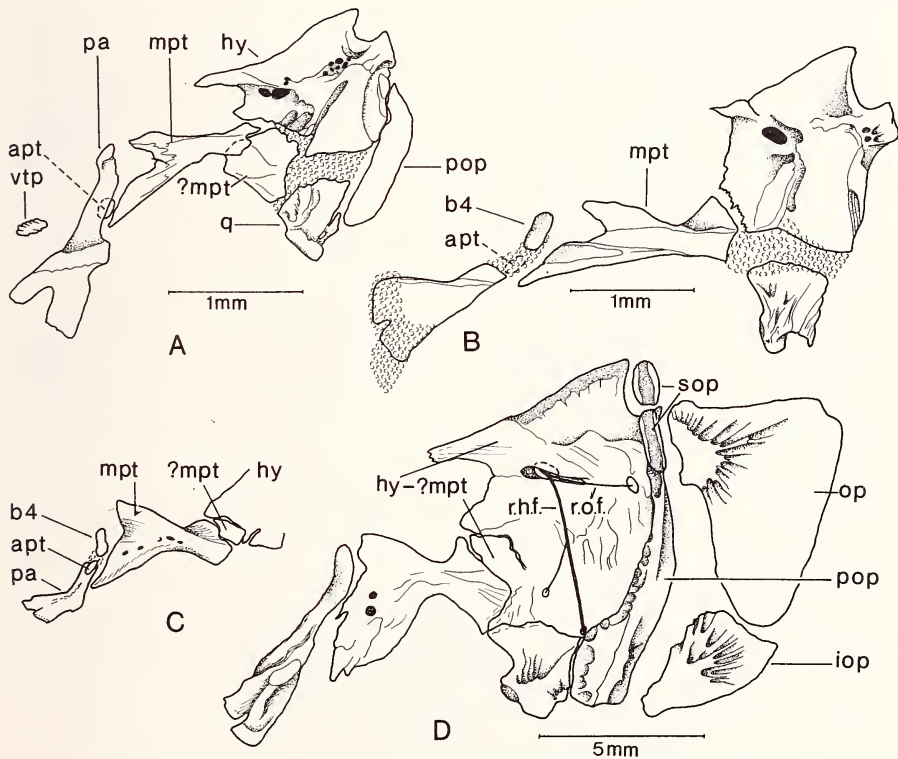


Fig. 25: *Diplomystes camposensis* n. sp. (PC 110276, 120276, 130276, KU 19257). — Suspensorium and opercular apparatus. — A: Lateral view, young specimen of about 28 mm standard length; B: Lateral view, young specimen of about 29 mm standard length; C: Medial view, large specimen; D: Lateral view, large specimen.

apt: additional pterygoid; b4: bone 4 of McMurrich; hy: hyomandibula; hy-?mpt: hyomandibula plus ?metapterygoid; iop: interopercle; mpt: metapterygoid; op: opercle; pa: palatine; pop: preopercle; q: quadrate; r.h.f.: ramus hyomandibular of facial nerve; r.o.f.: ramus interopercularis facialis; sop: suprapreopercles; vtp: vomerine tooth plate.

autopalatine. Palatine tooth plates are absent. When bone 4 (Fig. 25B, C) is present as a separate bone, it looks as a cup-like bone surrounding the posterior cartilage of the palatine.

In one specimen of about 29 mm standard length (Fig. 25A), a nearly square bone is present between the hyomandibula, metapterygoid and quadrate (on both sides of the specimen); it does not seem to result from fracture of one of the above mentioned bones. A partially separate piece of bone appears in the articular region between the hyomandibula and metapterygoid in some large specimens (Fig. 25D); at the moment, I name it as (?)metapterygoid, which is completely separated (Fig. 25A, C) in some young and adult specimens, whereas it is partially fused with the hyomandibula in others. The additional pterygoid (Fig. 25A—C) is absent in some specimens, on one or both sides of the head.

The lower jaw of adult specimens shows intraspecific variation in the size and shape of some bones. The dentary and angular do not overlap each other at their dorsal tips (Fig. 26C, D); in young specimens, a large coronoid cartilage (Fig. 26A, B, F) lies medially adjacent to the dorsal part of both bones; in larger specimens this cartilage is reduced in size; the coronoid cartilage is associated with the ligamentum primordiale extending mainly to the maxilla but also to the premaxilla. (For ligaments and tendons see description of *Diplomystes chilensis* in page 25, and Fig. 7A—D.) The dentary bears three or four rows of tall conic or incisiform teeth close to the symphysis; the bone does not form a ventroposterior flange close to the symphysis as in *D. nahuelbutaensis* n. sp.

In young specimens of about 28 or 29 mm in standard length, a broad Meckel's cartilage (Fig. 26A) is present posteriorly in the lower jaw; the large articular is already ossified; a small coronomeckelian bone (Fig. 26A) is partially hidden by the Meckel's cartilage. The articular prolongs below and posteriorly adjacent to the articular facet; another small elongate ossification (retroarticular) lies ventroposteriorly adjacent to the articular. In this stage of growth, the cartilage of the articular facet for the quadrate extends onto the articular (mainly), and also onto the retroarticular, and the angular.

Some noteworthy features of large specimens warrant discussion. The angular, articular and retroarticular may be identified because they retain incomplete joint lines in some parts of the posterior section of the lower jaw. A separate bone (?surangular) is present on the dorsomedial margin of the angulo-articular in SMF 7579. The exceptionally large articular develops strongly medially, and in some specimens this portion becomes partially or totally separated from the "main" articular (Fig. 26C). In one specimen, the angular plus retroarticular form laterally additional articular surface for the quadrate (Fig. 26E). (I have overtreated with NaOH [4 %] lower jaws of some of the largest specimens; I found that the articular has a heavily ossified region anteriorly; another large round ossification, as a bony ball, is placed in the posteromedial part.) The main component of the articular facet is the articular in the large specimens; the contribution of the angular is minor. The position of the posterior opening of the mandibular sensory canal is as in other diplomystids and the postarticular process is rudimentary (Fig. 26B, D)

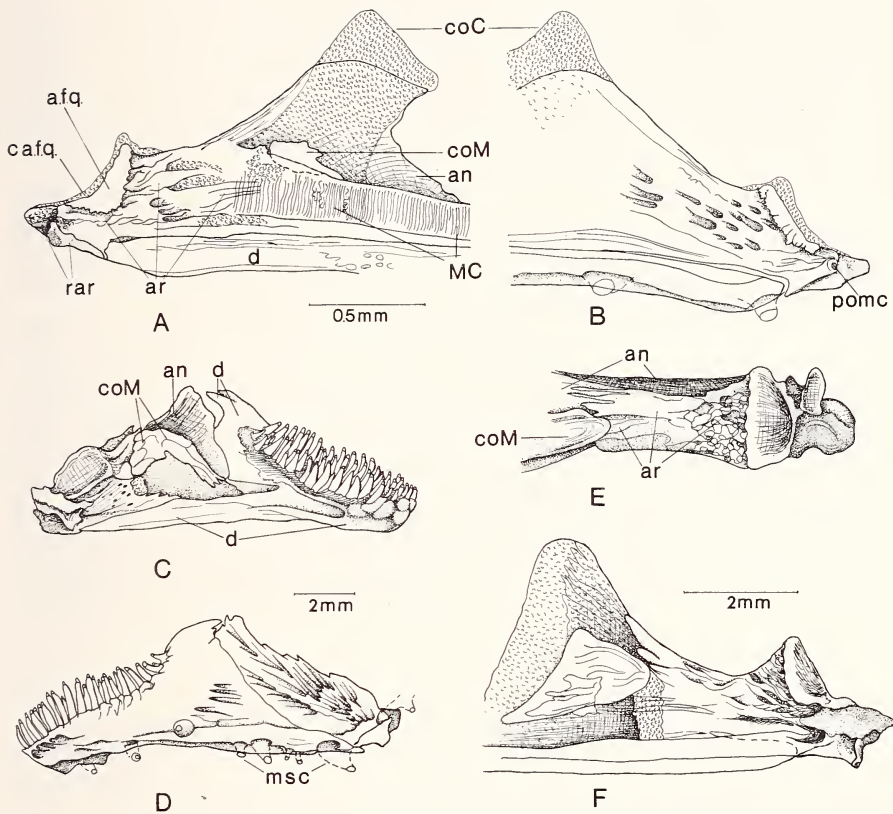


Fig. 26: *Diplomystes camposensis* n. sp. — Lower jaw. — A: Medial view, specimen of about 28 mm standard length; B: Lateral view, specimen of about 22 mm standard length; C—D: Medial and lateral views, sensory canal and pores of a large specimen; E—F: Dorsal and medial views of posterior part of the jaw.

a.f.q.: articular facet for quadrate; an: angular; ar: articular bone; ca.f.q.: cartilage covering the articular facet for quadrate; coC: coronoid cartilage; coM: coronomeckelian bone; d: dentary; MC: Meckel's cartilage; msc: mandibular sensory canal; pomc: posterior opening of mandibular sensory canal; rar: retroarticular.

The coronomeckelian bone (Fig. 26A, C, F) may vary in shape and size, being proportionally smaller in young specimens. For tendons and ligaments attached to the coronomeckelian bone see description of *Diplomystes chilensis* (page 26, Fig. 7A—D).

Hyomandibula, hyoid arch and opercular apparatus

There is a rudimentary or poorly developed levator arcus palatini crest, therefore the foramen (Fig. 25A, B, D) for the passage of the facial nerve is widely exposed in most

specimens. There are four foramina on the external surface of the hyomandibula; the facial nerve enters and leaves the bone through a common foramen (Fig. 25D); a second foramen for the ramus facialis opercularis is located posterior to the facial foramen; the hyomandibular branch of the facial nerve runs shortly on the lateral face of the hyomandibula, then bifurcates; one branch penetrates a small foramen close to the ventral part of the hyomandibula, whereas the other branch may penetrate the mandibularis foramen or just emerge in the posteroventral corner of the hyomandibula.

The interhyal is a small bone articulating weakly with the epihyal. The epihyal (Fig. 27A) is a nearly triangular hollow-like bone; anteriorly it contacts the ceratohyal through a weak articulation (Fig. 27C). The ninth and tenth branchiostegal rays are attached to the lower surface of the epihyal, and the eighth branchiostegal ray lies adjacent to the articulation of the ceratohyal-epihyal. The ceratohyal is an elongate thick bone; its dorsal margin is hollow-like and without a foramen. The first to seventh branchiostegal rays are suspended from the lower lateral surface of the ceratohyal. The latter produces anteriorly two articular facets for dorsal and ventral hypohyals. The dorsal and ventral hypohyals are nearly rectangular and of similar size. The dorsal hypohyals are joined medially and the ventral hypohyals are laterally displaced. Behind and below the median junction of the dorsal hypohyals and behind and below the ventral hypohyals is the urohyal. The urohyal has a characteristic shape and is perforated by

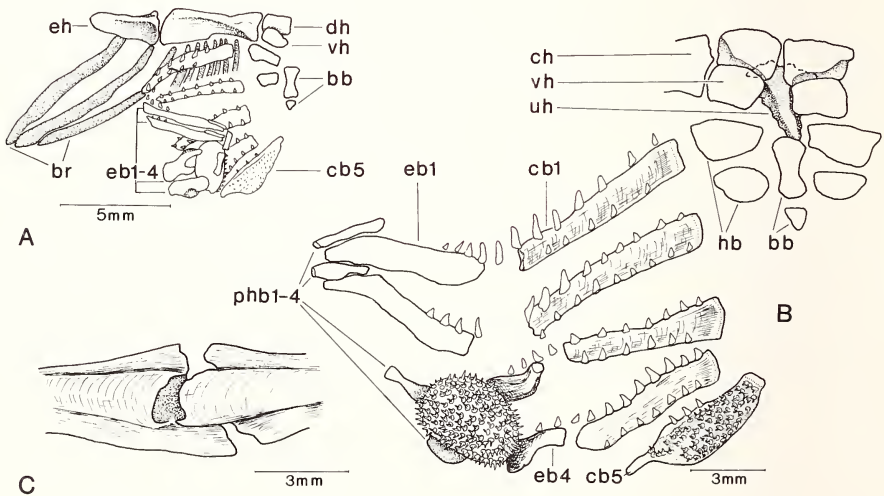


Fig. 27: *Diplomystes camposensis* n. sp. (PC 110276). — A: Hyoid arch and branchial apparatus, dorsal view; B: Inner view of branchial bones, hypohyals and urohyal; C: Articulation between ceratohyal and epihyal.

bb: basibranchials; br: branchiostegal rays; cb1–5: ceratobranchial 1–5; ch: ceratohyal; dh: dorsal hypohyal; eb1–4: epibranchial 1–4; eh: epihyal; hb: hypobranchial; phb1–4: pharyngobranchial 1–4; vh: ventral hypohyal; uh: urohyal.

a small oval foramen (Fig. 8C). The articular facets of the hypohyals, ceratohyals and epihyals are smooth, and the bones may be easily separated from each other.

The first to seventh branchiostegal rays are shorter and narrower than the eighth to tenth. The last three rays are slightly broader, but not greatly different in shape from the anterior branchiostegals.

Opercular series

The opercular bones differ slightly in shape from those of other diplomystids (compare Fig. 6B, 16 and 25D).

Branchial apparatus

The tooth plate of pharyngobranchial 4 has short conic teeth, whereas they are needle-like in *D. nahuelbutaensis* n. sp. Each epibranchial 1–4 bears a few gill rakers on the anterior margin; there is a small cartilaginous epibranchial 5. The bony part of the epibranchial is widely separated from the bony part of the ceratobranchial on each arch; one or two gill rakers lie over the cartilaginous articular region. The inner surface of ceratobranchial 5 is covered by conic teeth, whereas they are as needle-like in *D. nahuelbutaensis* n. sp. Both margins of ceratobranchials 1–4 bear gill rakers; ceratobranchial 5 bears one row of three gill rakers anteriorly.

Cephalic sensory canals

The cephalic sensory canals are similar to those described for *Diplomystes chilensis* and *D. nahuelbutaensis* n. sp. (compare Fig. 4A, 13 & 22A) with few exceptions. The mandibular canal (Fig. 26D) has five "main" tubules and pores and a few short additional tubules. Large pit organs were observed in a few specimens, in the same position as those of *Diplomystes chilensis* (see Fig. 4A).

Anterior vertebrae, Weberian apparatus and otoliths

The following description is based on a series of specimens of different sizes: The first five vertebrae are modified in comparison to the following abdominal vertebrae. Vertebrae 1 to 4 form the Weberian apparatus (Fig. 28A–C), and change slightly during ontogeny. The first two centra are longer in young than in adult specimens, and dorsally have an open space because they do not bear a neural arch and spine. In adults, centra 1–2 become shorter and the neural arch of vertebra 3 partially covers the dorsal part of centrum 2.

Centrum 1 (Fig. 28A) is a simple disc; it presents two dorsolateral depressions for the reception of the ventral sharp articular process of each scaphium. The intercalarium is placed dorsolaterally to centrum 2. Centra 2–4 (Fig. 28A) form a complex centrum. Centrum 2 has a ligamentous attachment to the os suspensorium (Fig. 28A, B). The parapophysis of the complex vertebra is a modification of the parapophysis of vertebra 4. The os suspensorium is placed ventrally to the parapophysis of the complex vertebra

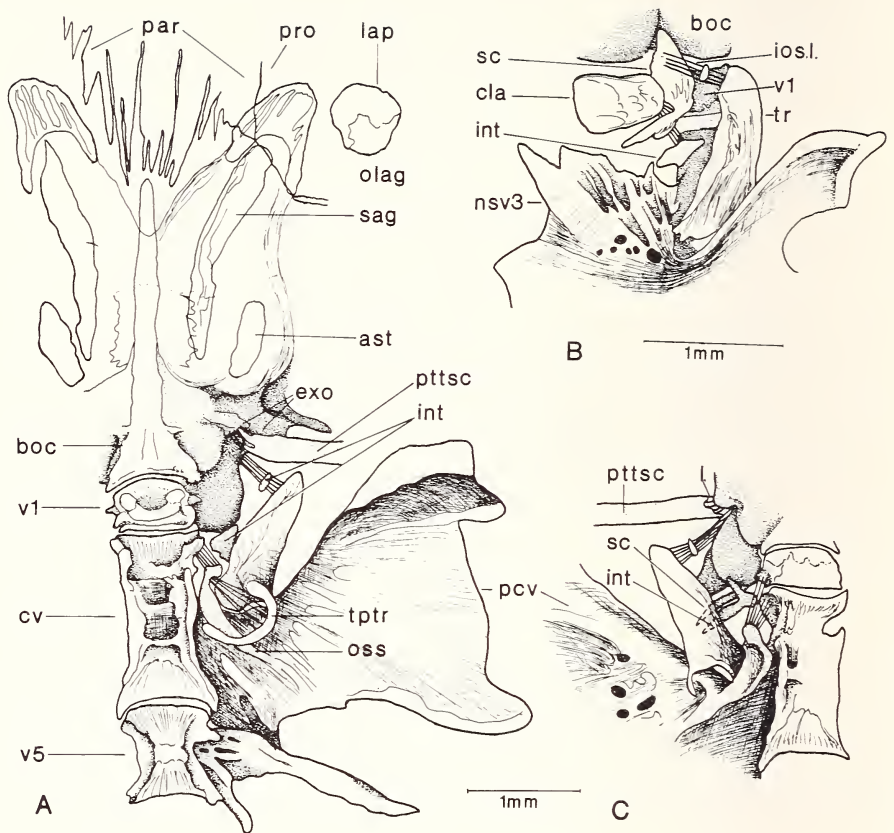


Fig. 28: *Diplomystes camposensis* n. sp. (PC 110276). — A: Posterior part of cranium, part of Weberian apparatus (left side), and first five vertebrae, ventral view; B: Dorsolateral view of part of Weberian apparatus (right side); C: Ventrolateral view of part of Weberian apparatus (right side) illustrating ligaments of the os suspensorium and shortening of the transformer process of the tripus.

ast: asteriscus; boc: basioccipital; cla: clastrum; cv: complex vertebra; exo: exoccipital; int: ascending process of intercalarium; ios.l.: interossicular ligament; lap: lapillus; nsv3: neural spine of vertebra 3; olag: ossified portion of lagena; oss: os suspensorium; par: parasphenoid; pcv: parapophysis of complex vertebra; pro: prootic; ptts: medial limb (or transcapular) of posttemporoprosupracleithrum; sag: sagitta; sc: scaphium; tr: tripus; tptr: transformer process of tripus; v1–5: vertebra 1–5.

and is fused with it by the dorsal end; the ventral end of the os suspensorium is directed to the lateral wall of the complex vertebra. A ligament (Fig. 28A) relates the os suspensorium to the transformer process of the tripus.

The tripus (Fig. 28A—C) is a complexly shaped bone. The crescentiform process of the dorsal crest of the tripus abuts a deep cavity in the anterolateral margin of the neural arch of centrum 3, and the parapophysis of the complex vertebrae; I have not seen a bony lamella attaching the tripus to the complex vertebra in young specimens. The tripus bears at least three ligaments. Its anterior end is connected with the scaphium through the interossicular ligament (ligaments 3 and 4 of Alexander 1962, 1964) which is intercepted by a small bone which appears in all specimens (part of the intercalarium) (Fig. 28B). (In one young specimen of about 29 mm in standard length, the intercalarium is complete, slender and of similar shape to that figured by Bridge & Haddon 1893: Pl. 11, Fig. 10.) Another ligament (Fig. 28A) connects the os suspensorium with the transformator process of the tripus (ligament 1 of Alexander); a third ligament extends from the dorsal crest of the tripus to the complex vertebra (ligament 2 of Alexander). The gasbladder is firmly attached to the ventrolateral region of the tripus.

The scaphium (Fig. 28B) is an L-shaped bone. Its anterior limb is broader than the dorsal limb and extends dorsal to centrum 1 and the posterior margin of the basioccipital; its concave surface faces anteromedially. The ascending limb projects back and upward. A small ligament extends between the scaphium and claustrum in young specimens; I have not seen it in larger specimens.

The claustrum (Fig. 28B) lies along the dorsal border of the scaphium and is roughly rectangular in shape.

All mentioned bones are well ossified from early ontogeny. The cartilage area and supraneural relationships are like those already described for *Diplomystes chilensis* (Fig. 9A—B); a supraneural 5 is found in front of the first dorsal pterygiophore (Fig. 29A).

The sinus impar (Fig. 28A) is elongate and narrow. It is weakly ossified in its anterior end, which extends forward beyond the bifurcation of the broad sinus endolymphaticus. The canalis communicans transversus connects with the anterior part of the lagenar region which forms an ossified shelf; the lagena is elongate and broad and the utricular region is comparatively smaller than the lagenar region. The two lagenar otoliths, sagitta and astericus, are greatly different in size. Of the three otoliths, the sagitta is the largest; it is especially long, lies close to the exoccipital shelf posteriorly and anteriorly lies against the ossified anterior shelf of the lagenar region. The lapillus is slightly larger than the asteriscus. The otoliths may be asymmetric in shape and size between sides of a specimen.

Especially noteworthy is the enlargement of the sinus impar prolonging forward beyond the anterior bifurcation of the sinus endolymphaticus; the cavum sinus imparis is a single small opening ventral to the foramen magnum; the sinus impar is separated from the spinal cord by a bony shelf formed by the exoccipitals.

Vertebrae excluding the Weberian ossicles

On abdominal vertebrae four to eleven (at least) the neural spines (Fig. 29A) do not meet in the midline, and the supraneural 5 and pterygiophores extend ventrally between

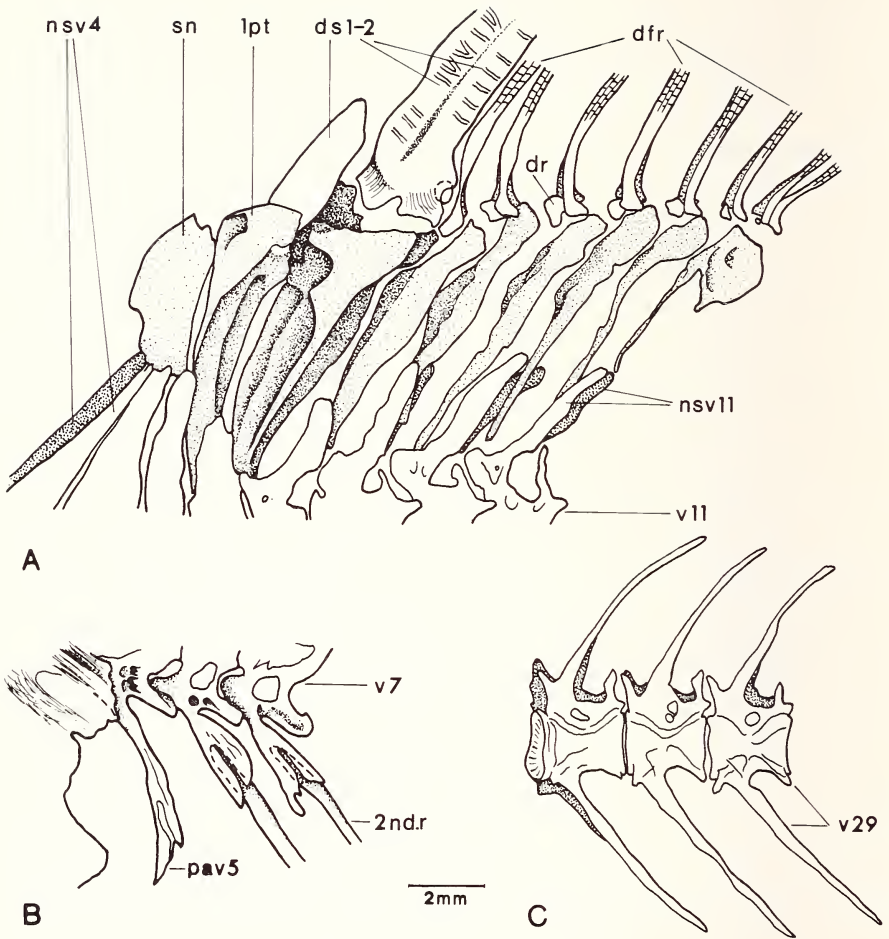


Fig. 29: *Diplomystes camposensis* n. sp. (PC 110276, 120276). — A: Supraneural 5, dorsal fin-rays, pterygiophores and neural spines, lateral view; B: Ventrolateral part of vertebrae 5 to 7 and ribs, lateral view; C: Vertebrae 27, 28 and 29, lateral view.

dfr: dorsal fin-rays; ds1-2: dorsal spines 1-2; dr: distal radial; nsv4-11: neural spine of vertebra 4-11; pav5: parapophysis of vertebra 5; sn: supraneural 5; v7,11,29: vertebra 7, 11, 29; lpt: first pterygiophore; 2nd.r: second rib.

the lateral elements. Neural spines of seventh to eleventh vertebrae are shorter than the following ones. The lateral faces of vertebrae six to nine may have large holes, and are curiously shaped, as noted by Chardon (1968). The neural spine sits on the anterior half of the neural arch and of the centrum.

The parapophysis of the fifth vertebra is elongate; a small rib lies below the distal tip of the parapophysis in small specimens; a separate pleural rib is not present in adult specimens; therefore, I assumed that the parapophysis of the fifth vertebra and the rib are fused. There are eleven pleural ribs attached to the parapophysis of vertebrae 6 to 16–18 (Fig. 29B).

Caudal vertebrae (Fig. 29C) bear elongate sharp neural and haemal spines, with the exception of the last vertebrae which have broader and flatter spines. The neural spine is a prolongation of the anterior half of the neural arch and it places on the anterior half of the centrum.

Pectoral girdle and fin

The pectoral girdle (Fig. 30A–C) does not differ significantly from that of other diplomystids (see page 30). Some additional information may be added based on young and adult specimens. The long ventromedial limb of the posttemporosupracleithrum or transcapular is weakly articulated with the exoccipital in young specimens; it is displaced ventroposteriorly reaching the lateral wall of the basioccipital in larger specimens. One short cartilaginous radial (sometimes ossified) and two long ossified proximal radials (Fig. 30A, D) occur in young and adult specimens. Cartilaginous proximal radial 2 fits into a cavity in the posterior part of the pectoral spine and the lateral halves

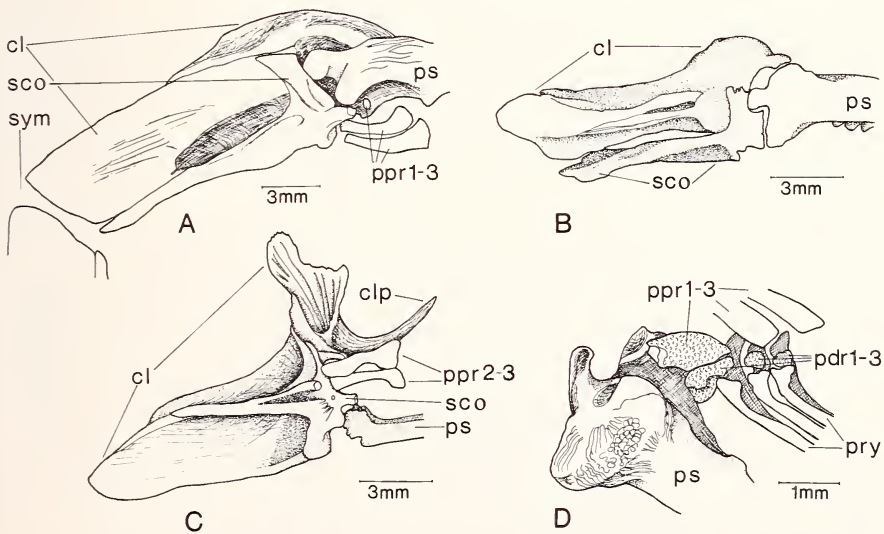


Fig. 30: *Diplomystes camposensis* n. sp. (PC 110276, 120276). — A: Pectoral girdle, spine and proximal radials, ventral view; B: Pectoral girdle, medial view; C: Posterior view of cleithrum and coracoid; D: Proximal and distal radials.

cl: cleithrum; clp: cleithral process; pdr1–3: pectoral distal radials 1–3; ppr1–3: pectoral proximal radials 1–3; pry: pectoral fin-rays; ps: pectoral spine; sco: scapulo-coracoid; sym: symphysis.

of the following soft-ray. Posteriorly, proximal radial 2 articulates with a slightly larger distal radial; there are two additional distal radials; all three distal radials remain cartilaginous (Fig. 30D) (some specimens do not have cartilaginous distal radials). They articulate with three soft rays.

The pectoral spine increases the number of serrae during growth (Fig. 18B, C), ten to twelve serrae are found in large specimens. The configuration of its posterior tip of the spine is different in shape from that of *Diplomystes nahuelbutaensis* n. sp. (compare Fig. 18A, C).

Pelvic girdle and fin

The pelvic girdle (Fig. 31A, B) frequently has three anterior elongate processes; in some specimens the two internal processes fuse, and this united process is then broader than the external one (Arratia et al. 1978: Fig. 16A). The pelvic girdle varies in shape in specimens of similar length; its median articular region is very elongate in some

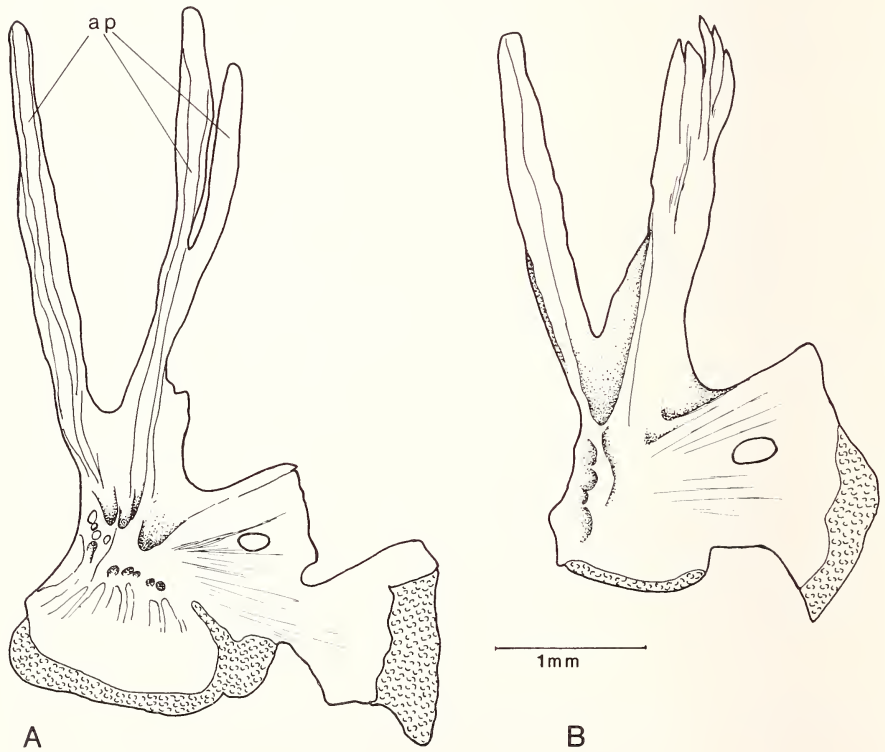


Fig. 31: *Diplomystes camposensis* n. sp. (PC 110276, 120276). — Pelvic girdle illustrating in-traspecific variation. — ap: anterior processes.

specimens, irregularly shaped in others. The posterior process is short or absent. No proximal or distal radials are present. There are six soft rays and one small bony splint; the distal region of the splint is segmented in one of the large specimens studied.

Dorsal fin

The dorsal fin (Fig. 29A) has two spines plus seven principal (branched and segmented) rays. The first spine of young and adult specimens is short and covered by skin, so commonly is inconspicuous. The second spine is long, strong, and formed by fusion of two modified lepidotrichia. Supporting the hypothesis of a fusion of two rays is the inner segmentation of the second spine, which shows two different sequences of segmentation belonging to two rays. The second dorsal spine, as the pectoral spine, has distally a plate formed by especially shaped segments; this portion permits its growth. Soft dorsal fin-rays are thin and small in comparison to the spine. All bear a distal radial. There are eight dorsal pterygiophores. The first two pterygiophores (Fig. 29A) are broad, strong, and extend deeply into the open space between the neural spines of vertebrae 6 to 8. The last pterygiophore is the smallest and its upper part is broad and slightly rounded. The supraneural 5 (Fig. 29A) lies anteriorly adjacent to the first pterygiophores; commonly it is nearly triangular in shape, but in some large specimens it is a rudimentary bone anteriorly adjacent to the first pterygiophore. The ventral tip of supraneural 5 is placed between the neural spines of vertebrae 4 and 5, and 6 in some specimens.

Anal fin

The anal fin has two simple rays plus eight to eleven principal rays (one specimen with four simple rays plus ten principal rays). The anal rays and their supports are similar to those of the dorsal rays. The first anal pterygiophore commonly is as long as the second one but shorter in a few large specimens. It is shorter in all juvenil specimens studied.

Caudal fin

The caudal fin is supported by the last seven vertebrae. The second ural centrum present in small specimens (absent in adults) is a rectangular bone posterodorsal to the compound centrum and dorsolaterally covered by a uroneural; it does not fuse with the base of hypural 3 or 4. Ural centrum 1 becomes atrophied through growth; as a consequence, the compound centrum (Fig. 32A) of adult specimens is formed mainly by the anterior half of preural centrum 1, and its posterior part produces a deep cavity in which articulate hypurals 3 and 4. The neural arch over the compound centrum is open dorsally; its halves are asymmetric and one of them, slightly elongate, supports the long epural. The epural is bifid in the lower part of all specimens examined.

The broad base of the parhypural is fused with the compound centrum. Hypural 2 bears a wide lateral wing close to the compound centrum; this wing produces a deep shelf of bone fitted closely against the elongate acute bases of hypurals 3 and 4. Hypurals 3 and 4 form also lateral wings close to the compound centrum; these wings are missing in hypurals 5 and 6.

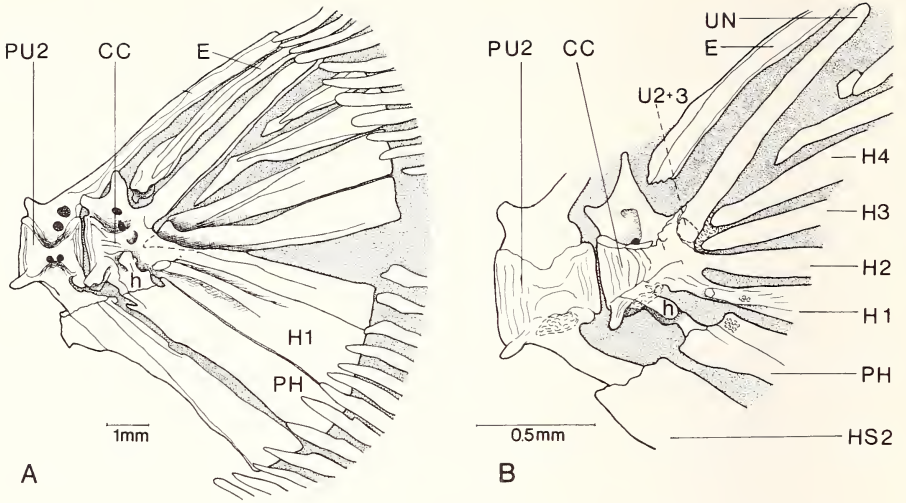


Fig. 32: Caudal skeleton, lateral view. — A: *Diplomystes camposensis* n. sp. (PC 110276); B: *Olivaichthys viedmensis* (specimen of about 30 mm standard length, from Chubut, Argentina). (AG, uncat.).

CC: compound centrum; E: epural; H1–4: hypural 1–4; h: hypurapophysis; HS2: haemal spine 2; PH: parhypural; PU2: preural centrum 2; sh: secondary hypurapophysis; U: second ural centrum; UN: uroneural.

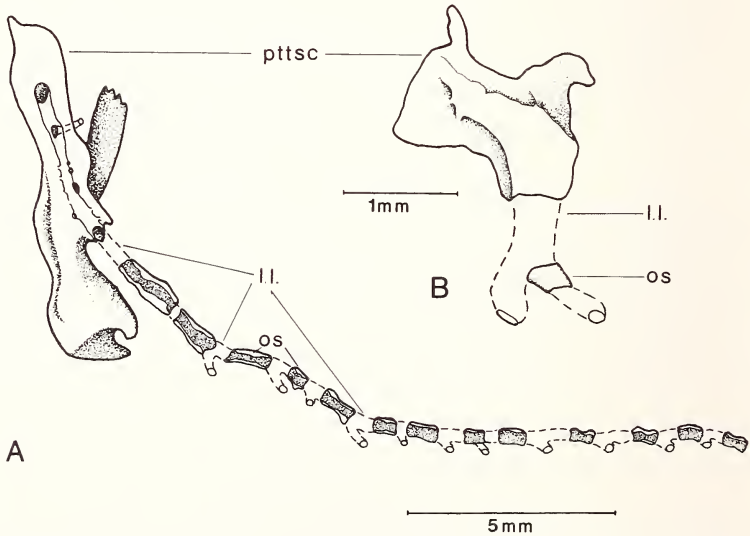


Fig. 33: Posttemporosupracleithrum and ossicles of lateral line. — A: *Diplomystes camposensis* n. sp. (PC 130276); B: *Trichomycterus roigi* (according to Arratia & Menu Marque 1984).

l.l.: lateral line canal; pttsc: posttemporosupracleithrum; os: ossicle.

There is a small sharp lateral hypurapophysis on the arch of the parhypural, it is present from early ontogeny. A secondary hypurapophysis is present on hypural 1; another thin lateral projection is developed on hypural 2.

There are 52—56 caudal rays. The upper lobe has two segmented unbranched rays (only one specimen with three) and the lower lobe has three segmented unbranched rays (two specimens with four). Most specimens have an equal number of rays in the upper and lower lobes (two specimens with one ray more in the upper lobe). The bases of the caudal rays are loosely attached to the hypurals, uroneural, and haemal and neural spines of the preural centra.

Lateral line

The lateral line, formed by ossicles (Fig. 33A), may be bifurcated distally in some specimens, a condition which I have not seen in other species of *Diplomystes*.

Diplomystes sp.

S y n o n y m s :

Diplomystes chilensis: Arratia, G. (1981 a): Bull. Mus. Nac. Hist. Natur., Chile, Pub. Ocas. 34: 44 (in part: Tinguiririca and Maule rivers). — (1982 a): Bol. Mus. Nac. Hist. Natur., Chile, 39: Fig. 7A, B (in part: specimen from Río Tinguiririca). — (1983 c): Studies on Neotropical Fauna & Env. 18 (4): 225, Tables 5, 6 (in part).

C o m m o n n a m e s : "tollo", "tollo de agua dulce".

S t u d i e d m a t e r i a l :

Diplomystes spec.: LBUCH 310883: 1 specimen; Río Copequén, Rancagua, Chile; coll. M. Arellano & F. Camilo; July 31, 1983. — PC 110275: 1 specimen (cl & st); Río Tinguiririca, Chile; coll. R. da Andrade & A. Chang; November 2, 1975. — KU 19256: 1 specimen; Río Tinguiririca, Chile; coll. L. Cid; February, 1976. — KU 19255: 1 specimen; Río Maule, Chile; coll. H. Diaz & A. Chang; December 2, 1974.

L o c a l i t i e s : Río Copequén, Río Tinguiririca, Río Maule; central Chile.

D e s c r i p t i o n : The specimens listed under this category are considered as *Diplomystes* undetermined until more material is available. The specimen from Río Copequén differs from all other diplomystids in that the whole skin has verrucose papillae, the skin of the dorsum and flank is greenish, with miniscule black spots, and the ventral region is whitish. The specimen from Río Maule (a juvenile) has the second dorsal spine longer than the first soft ray, unlike all other diplomystids. The specimens from Río Tinguiririca are similar to those of Río Maule, excepting the length of the second dorsal spine.

Genus *Olivaichthys* n. gen.

Synonyms:

Diplomystes: (?) Ringuélet, R. (1965): *Physis*, t. XXV. n. 69: 90. — (?) Ringuélet et al. (1967): *Los Peces Argentinos de Agua Dulce*, Buenos Aires: 263.

Geographical distribution: From Mendoza to southern Patagonia, Argentina. (Specimens from San Juan are not included here because I did not have the opportunity to examine them.)

Etymology: The prefix *Oliva* refers to Rubén Oliva and his wife, Beatriz Peñafort-Oliva, who have expended much effort, patience and money seeking for diplomystids in Argentina, with the Greek *ichthys* for fish.

Diagnosis: Sphenotic length less than 150 % of pterotic length. Short sphenotic lacking a long anterolateral process. Maxilla with two or more functional rows of teeth distally, many maxillary teeth in adult (23 or more) (*2). Elongate palatine bearing a tooth plate (usually asymmetric in shape and size) in adults (*1, *2). Five or six cartilaginous distal pectoral radials. One separate cartilaginous pelvic radial in early ontogeny. Pelvic girdle with three anterior processes in early ontogeny, frequently only two processes in adults. Skin smooth with short papillae on body, barbel, roof and floor of mouth. Buds as "rose" structure, forming a geometric figure, on skin at base of barbel (*2).

Type-species: *Olivaichthys viedmensis* (Mac Donagh, 1931)

The fishes that I assign to this new taxon, formerly called *Diplomystes viedmensis*, were thought by Ringuélet (1965, 1982) to comprise three subspecies or "geographic races" (his *D. viedmensis viedmensis*, *D. viedmensis cuyanus* and *D. viedmensis mesembrinus*) distinguishable by some body proportions (Table 4).

The diagnosis of the three subspecies is based on five specimens: *O. viedmensis viedmensis* (2), *O. viedmensis cuyanus* (2) and *O. viedmensis mesembrinus* (1). According to Ringuélet (1965, 1982), body proportions such as maximum depth of the head in head length, premaxillary and maxillary lengths in head length separate *viedmensis viedmensis* from *viedmensis cuyanus*. According to Ringuélet (1965) and later repeated by Ringuélet et al. (1967), *viedmensis viedmensis* is a "very characteristic catfish because the velvet-like skin, with very short papillae, short maxillary barbels, compressed at their bases, and lacks of mental barbel. The skin is soft." In contrast, *viedmensis cuyanus* has a more velvet-like and softer skin. This feature is difficult to evaluate because all diplomystids have a velvet-like skin. Ringuélet did not explain what some one should understand for "velvet-like" and "more velvet-like" skin, or "soft" and "softer" skin. According to Ringuélet (1982: 350) the maximum depth of head (55.4 % of standard length), length of premaxilla (19.3 % of head length), length of maxilla (16.9 % of head length), width of mouth (26 % of head width), depth of adipose fin

Table 4: Body proportions of subspecies of *Olivaichthys viedmensis* (according to Ringuélet 1982).

	<i>O. viedmensis viedmensis</i>		<i>O. viedmensis cuyanus</i>		<i>O. viedmensis mesembrinus</i>
	holotype	paratype	holotype	spec. San Juan	holotype
Predorsal length / standard length (%)	35.2	35.5	37.5	35.8	32.6
Preadipose fin length / standard length (%)	65.2	60.8	62.9	64.1	65.0
Head length / standard length (%)	24.5	23.7	28.5	25.3	22.5
Adipose base length / standard length (%)	27.5	25.6	25.8	23.3	20.6
Head depth / head length (%)	61.4	66.6	59.0	56.6	55.4
Adipose fin depth / adipose fin length (%)	13.3	17.5	22.1	18.2	28.9
Peduncle depth / standard length (%)	8.6	8.1	8.5	8.7	7.6
Maximum depth / standard length (%)	21.8	20.1	19.8	19.9	19.0
Head width / head length (%)	79.7	84.6	85.0	76.9	69.9
Mouth width / head length (%)	34.3	36.9	38.5	38.9	26.5
Interorbital width / head length (%)	35.3	36.0	34.2	40.7	33.7
Eye diameter / head length (%)	12.1	11.9	8.5	11.5	19.0

(28.9 % of adipose base length), are some of the body proportions (Table 4) of his new subspecies or "geographic race": *D. viedmensis mesembrinus*. If I consider that: a) the number of studied specimens is poor, b) the diplomystids, like other catfishes, are variable in body measurements, c) body proportions as premaxillary and maxillary lengths were not taken in cleared and stained specimens, thus the limits of the bones are not precisely determined, and d) most of body proportions overlap each others and also overlap those of the species of *Diplomystes* from Chile, then I conclude that there is no support at the moment to accept the three Argentinean "geographic races" of Ringuélet (1965, 1982).

According to Ringuélet (1982), his "*D. viedmensis viedmensis*" is characterized because the tip of the dorsal fin-rays (when fin is folded) is distant from the origin of the adipose fin (this feature is also present in *Diplomystes camposensis* n. sp.), and that the distal tip of the pelvic fin is distant of the anal fin (this feature changes during growth, at least in the Chilean species of *Diplomystes*). Ringuélet (1982) considered his "*D. viedmensis mesembrinus*" from Río Senguier, in Chubut, as the "most modern

diplomystid" because of body proportions, whereas the evidence presented below, contradicts such statement.

I treat all these forms in the binomial, as *Olivaichthys viedmensis* (Mac Donagh), until more specimens (from different localities) become available for study.

Olivaichthys viedmensis (Mac Donagh, 1931)

(Figs. 32B; 34A–B; 35A–B; 36A–B; 37A–B; 38; Tables 3–4)

S y n o n y m s :

Diplomystes papillosus: Berg, C. (1901): Com. Mus. Nac. Buenos Aires, t.1 (9): 293. — Fisher, H. G. (1917): Ann. Carnegie Mus., XI (3–4): 405. — Lahille, F. (1922): Mrio. Agric. Nac., Lab. Zool.: 13.

Diplomystes viedmensis: Mac Donagh, E. (1931): Not. Prelim. Mus. La Plata (1): 65–66. — (1938): Rev. Mus. La Plata, 1, Zool. (5): 137–142. — Pozzi, A. (1945): Gaea VII (2): 259. — Ringuélet, R. A., & R. A. Aramburu (1957): Mrio. Asuntos Agrarios, Buenos Aires, publ. 119: 5. — (1961): Agro, año III (7): 41. — Ringuélet, R. (1965): Physis XXV (69): 90–92. — (1980): Neotrópica: 246. — (1982): Limnobiós 22, fasc. 5: 349–351. — Ringuélet et al. (1967): Los Peces Argentinos de Agua Dulce, Buenos Aires: 263–265. — Cei et al. (1978): Pub. Ocas. Inst. Biol. Animal, Univ. Nac. Cuyo, ser. cient. 2: 33, map 29. — Arratia, G., & S. Menu Marque (1981): Zool. Anz. 207 (1/2): 108. — Arratia, G. (1982 a): Bol. Mus. Nac. Hist. Nat. Chile, 39: 55, cuadros 1–2. — Arratia et al. (1985): Deserta 7: 58, 60, 63, 64, 67, 69, 70, 72. — Peñafort, M. B. (1981): Bol. Mus. Cienc. Natur. & Antrop. "Juan Cornelio Moyano" (2): 35, 48, 54, 57.

C o m m o n n a m e : "otuno", "bagre aterciopelado", "gatuno", "atún".

S t u d i e d m a t e r i a l :

Paratype: CIMLP 19-III-31-1 and 19-III-31-2: 2 specimens; Río Negro, Viedma, Argentina. (Data were provided by Dr. A. Miquelarena).

A d d i t i o n a l m a t e r i a l :

CIMLP 18-12-81-1: 1 specimen; desembocadura Río Senguer, Lago Musters, Chubut. CIMLP 13-V-32-3: 1 specimen; Río Yaucha, Vilucó, Mendoza. — Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (IADIZA) (uncat.): 2 specimens (1 cl & st); Río Mendoza, Uspallata and Río Salado; coll. R. Oliva & B. Peñafort-Oliva; 1980. — Private collection Dr. A. Gosztonyi, Puerto Madryn, Chubut, Argentina: 1 specimen (cl & st); Río Chubut. — BMNH 1983-12-3-4: 2 specimens; Río Quillén, Viedma; coll. O. Caranza; February and September, 1983.

T y p e - l o c a l i t y : Río Negro in Viedma, Argentina.

D i a g n o s i s : Same as the genus, page 66.

D e s c r i p t i o n : Elongate diplomystids which reach about 280 mm total length (278.5 mm maximum length known, Ringuélet 1982).

Mac Donagh (1931: 138) stated that the main difference between the Chilean and Argentinean diplomystids (though he recognized that he did not have the possibility to study Chilean diplomystids) is the skin, without papillae in *Olivaichthys viedmensis* but with a fine "grain aspect". My studies reveal that the skin of the body and fins of the Argentinean diplomystids has few papillae in young. In adults, few, short, somewhat rounded or conic papillae are all over the body; the region close to the mouth and the maxillary barbel has smaller rounded papillae than those of *Diplomystes camposensis* n. sp. (Fig. 21A—B); the skin of the dorsoposterior region of the barbel has small conic papillae (Fig. 34A); each papilla has usually a central taste bud which is surrounded by five or six taste buds producing a very regular figure (Fig. 34B); the papillae of the roof of the mouth are similar to those of *Diplomystes chilensis* (see Fig. 2C).

The ground color is pale purple with abundant black spots on dorsum and flanks (fresh material; according to Mac Donagh 1931: 66). With many black spots on a purple-greyish ground (Mac Donagh 1938: 138). Violet-greyish or purple, with black spots (Ringuélet et al. 1967: 265). Pale brownish on dorsum and flanks, and whitish ventrally,

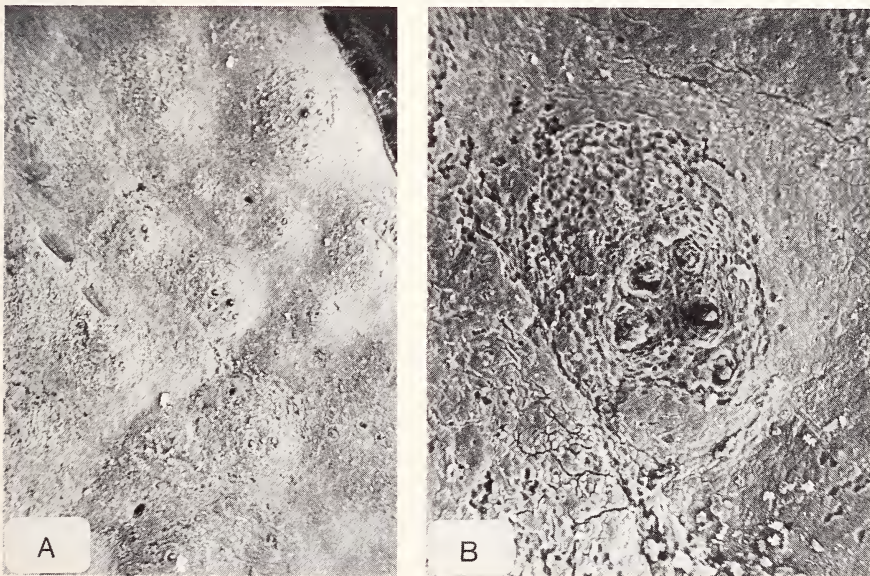


Fig. 34: *Olivaichthys viedmensis* (BMNH 1983-12-3-4). — Skin of the dorsoposterior region of the maxillary barbel. — A: Distribution of papillae and buds (SEM 38x); B: Enlargement of papillae and buds illustrated on A (SEM 176x).

in one juvenile specimen from Mendoza river. The coloration varies from one locality to the other, and in the same locality (see Table 3 for comparison of coloration of species of Diplomystidae).

The maxillary barbel has a central rod as in the other diplomystids. It is interesting to remark that this rod is partially ossified and the barbel slightly rigid in the largest specimen of Mendoza.

The lateral line, enclosed by ossicles, extends slightly posteriorly to the base of the principal caudal fin-rays in the young specimen from Chubut; in adult specimens it ends close to the base of the principal caudal rays.

A shorter sphenotic and larger pterotic (Fig. 35A), which is the condition usually seen in teleosts. The young specimen from Chubut has a short, broad sphenotic, about 70 %

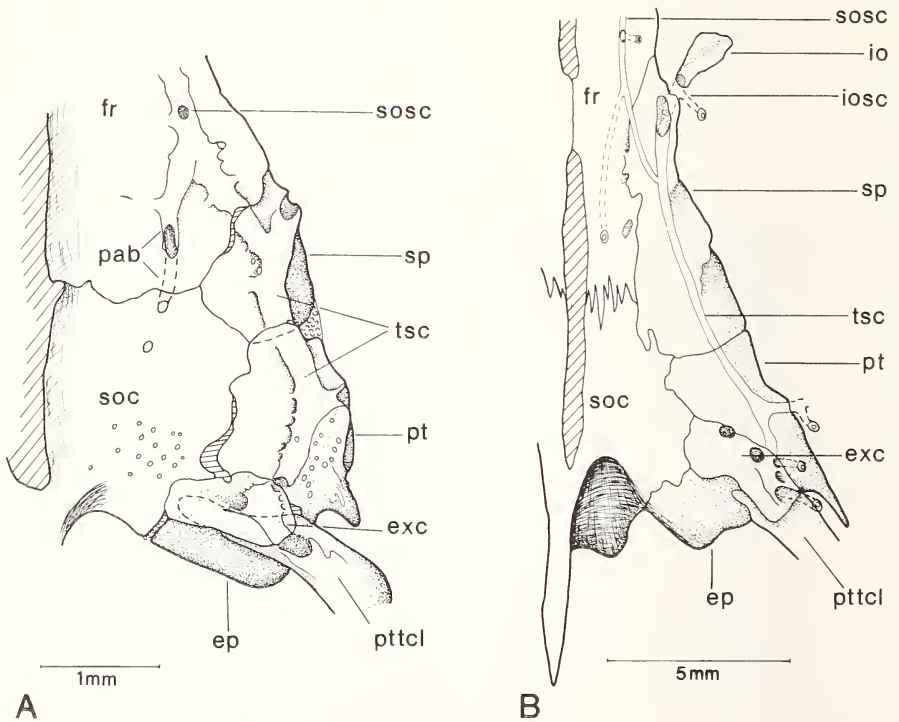


Fig. 35: Part of cranium in dorsal view. — A: *Olivaichthys viedmensis* (AG, uncat.); B: *Olivaichthys viedmensis* (IADIZA, uncat.).

ep: epioccipital; exc: exoccipital; fr: frontal; io: last infraorbital bone; iosc: infraorbital sensory canal; pab: parietal branch of the supraorbital sensory canal; pt: pterotic; pttcl: posttemporosupraclathrum; soc: supraoccipital; sosc: supraorbital sensory canal; sp: sphenotic; tsc: temporal sensory canal.

as long as the pterotic, lacks the long anterolateral projection bearing the infraorbital sensory canal and also lacks a sphenotic spine. In adult specimens, the sphenotic is a little longer than the pterotic (Fig. 35B), about 130 % of the pterotic length; the bone has not developed the long anterolateral projection present in *Diplomystes*.

The frontal (Fig. 35A) is broader posteriorly in the little specimen from Chubut as in young *D. camposensis* n. sp. (a condition found in most teleosts). This pattern is not found in any of the adult Chilean and Argentinean diplomystids.

The extrascapular (Fig. 35A—B) is similar in its position and relationships to this bone in the Chilean diplomystids. The young diplomystid from Chubut shows an opening and a groove in the position of the supratemporal commissure.

In the young specimen from Chubut, the cephalic sensory canal runs in a broad bony tube (Fig. 35A), while in young specimens of *Diplomystes camposensis* n. sp. it runs partially in a groove and during growth becomes completely enclosed by bone.

The infraorbital sensory canal is enclosed by infraorbitals as bony tubes, like those in *Diplomystes chilensis* and *D. nahuelbutaensis* n. sp., whereas they are half-cylinder or tube-like bones in *D. camposensis* n. sp. (Table 3); the preopercular sensory canal is partially enclosed by two or three suprapreopercular tube-bones; the preopercular sensory canal gives off four or five tubules and pores, as in the other diplomystids mentioned above.

The premaxilla and maxilla of the adult specimens (Fig. 36A) have shorter and slender teeth than the Chilean *Diplomystes chilensis* and *D. camposensis* n. sp. The teeth are shorter than those of *D. nahuelbutaensis* n. sp. which bears needle-like teeth. The innermost rows of premaxillary teeth are especially short and slender in comparison to the species of *Diplomystes*.

The maxilla has three or more rows of teeth anteriorly and two or more rows posteriorly (Fig. 36A), 23—35 teeth may be found in each maxilla of large *Olivaichthys viedmensis*; the number of maxillary teeth of the Argentinean diplomystids is significantly higher than that of the Chilean *Diplomystes* (with 8—18 teeth). *Diplomystes* bears one row less along the maxilla.

The palatine (Fig. 36A) is elongate as in most specimens of *Diplomystes camposensis* n. sp. (Fig. 24B), therefore longer than in *Diplomystes chilensis* (Fig. 6A) and *D. nahuelbutaensis* n. sp.

The palatine bears a tooth plate in adult specimens (with the exception of CIMLP 19-III-31-1, a large specimen of 227 mm standard length, observation by Dr. A. Miquelarena); frequently one patch is larger than the opposite (Fig. 36A); the teeth are slightly spatulate and elongate, like the mandibular teeth. This feature separates *Olivaichthys* n. gen. from *Diplomystes*.

Two autogenous vomerine plates (Fig. 36A), separated in the midline, bear short, broad, conic teeth which are shorter than those of the species of *Diplomystes*.

The dentary lacks a developed ventroposterior flange, as do *Diplomystes chilensis* and

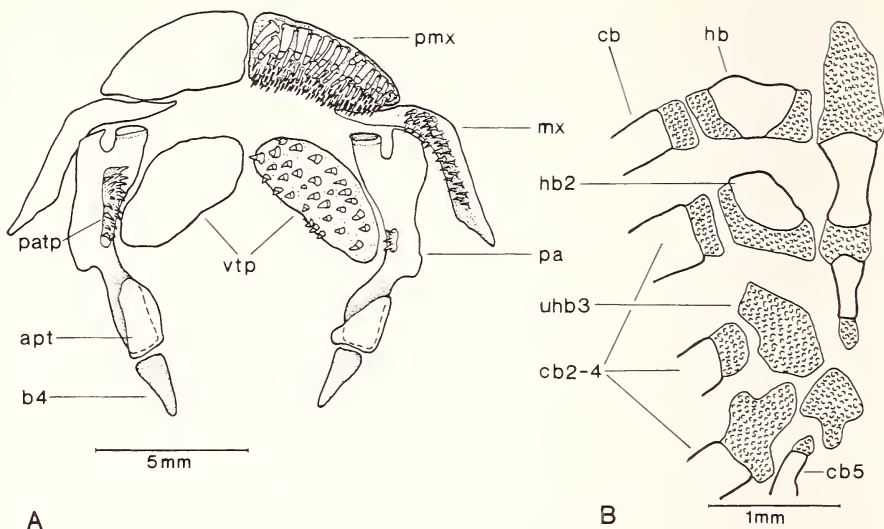


Fig. 36: *Olivaichthys viedmensis*. — A: Premaxilla, maxilla, palatine, vomerine tooth plate, and additional pterygoid, ventral view; B: Cartilage areas in branchial apparatus of a young specimen of about 30 mm standard length. (AG, uncat.).

apt: additional pterygoid; b4: bone 4 of McMurrich; cb1–5: ceratobranchial 1–5; hb1–3: hypobranchial 1–3; mx: maxilla; pa: palatine; patp: palatine tooth plate; pmx: premaxilla; u: unossified; vtp: vomerine tooth plate.

D. camposensis n. sp. (it is present in *Diplomystes nahuelbutaensis* n. sp.). The mandibular canal gives off four or five tubules and pores.

The branchiostegal ray count is low (8–9) as in *Diplomystes chilensis* (see Table 2).

The branchial skeleton (Fig. 36B) in the young specimen from Chubut has a cartilage plate (unossified hypobranchial 3) with a shape similar to hypobranchial 2. A separate median cartilage plate, basibranchial 4, placed posteriorly to basibranchial 3. These cartilage plates, present in early ontogeny, do not ossify in any adult specimen of Argentinean and Chilean diplomystids. The urohyal presents many small lateral projections in the young specimen from Chubut but it is T-shaped in the large specimens, whereas the shape is different in species of *Diplomystes* (Fig. 8A–C).

40–43 vertebrae are present; the count does not differ from that of the Chilean *Diplomystes* (see Table 2).

The posttemporosupracleithrum of the adult specimens has nothing remarkable, but the Chubut specimen has a long dorsal limb (Fig. 35A) (shorter in the young Chilean diplomystids) which extends medially below the extrascapular, therefore I assume that a shortening of the dorsal limb of the posttemporal characterizes the adult diplomystids.

The pectoral girdle of adult diplomystids bears two or three ossified proximal radials.

The Chubut specimen has a second row of five cartilaginous distal radials (Fig. 37A), whereas six cartilaginous distal radials are present in adults. Only three distal radials are present in young specimens of *Diplomystes camposensis* n. sp., three or none are present in adults; no distal radials have been observed in *D. chilensis*. The adult cleared and stained specimens have 13–14 serrae in the pectoral spine, whereas 16–17 serrae were determined by Ringuelet et al. (1967). I have not found such high count in any of the largest specimens of the species of *Diplomystes* (*D. chilensis* with 12 serrae, *D. nahuelbutaensis* n. sp. with 8–9 serrae, and *D. camposensis* n. sp. with 9–12 serrae).

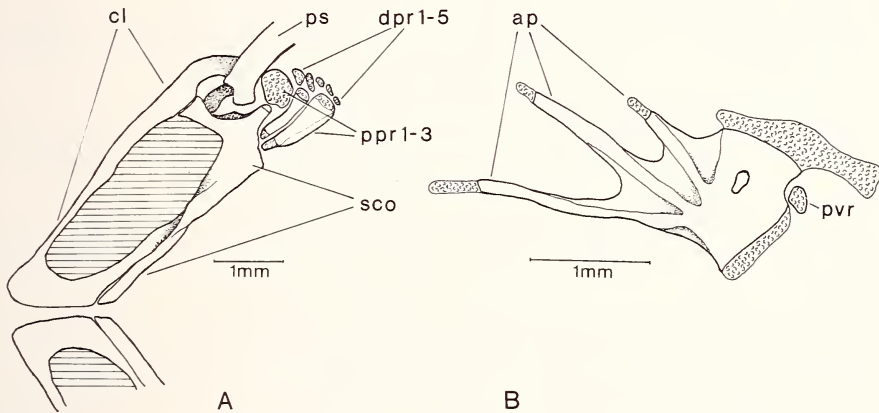


Fig. 37: *Olivaichthys viedmensis* (AG, uncat.). — A: Pectoral girdle and spine, ventral view; B: Pelvic girdle.

ap: anterior pelvic processes; cl: cleithrum; dpr1–5: distal pectoral radials 1–5; ppr1–3: proximal pectoral radials 1–3; ps: pectoral spine; pvr: pelvic radial; sco: scapulo-coracoid.

The pelvic girdle and fin of adult Argentinean diplomystids is similar to that of *Diplomystes chilensis*, whereas the young specimen of Chubut has three anterior elongate processes (Fig. 37B), a condition more like that of *Diplomystes nahuelbutaensis* n. sp. and *D. camposensis* n. sp. This specimen also shows a free unossified pelvic radial (Fig. 37B) not present in young specimens of *Diplomystes camposensis* n. sp. I have not seen a free unossified or ossified pelvic radial in any adult diplomystid, thus I assume that it is lost or fused to the pelvic girdle during growth. The pelvic splint of the largest studied specimens is segmented distally as in one large specimen of *D. camposensis* n. sp.

The caudal skeleton of adult Argentinean diplomystids is more similar to that of *Diplomystes camposensis* n. sp. in the broadening of the base of the parhypural. The little specimen of Chubut differs from young specimens of *D. camposensis* n. sp. in the presence of a cartilaginous area (Fig. 32B) between the base of hypurals 3 and 4 and the rudimentary second ural centrum. The base of hypural 6 fuses to an incomplete ural centrum.

ANALYSIS OF DIAGNOSTIC FEATURES OF GENERA AND SPECIES OF DIPLOMYSTIDAE

The following features are unique derived characters of Diplomystidae within the Siluroidei and within ostariophysans:

- 1) Skin of the whole body covered with large simple or lobulated papillae and buds embedded in a colloid-like substance.
- 2) Sagitta, the largest otolith.
- 3) Pterosphenoid lacking a suture with the parasphenoid.
- 4) Large, broad rhomboidal vomer (not T- or arrow-shaped).
- 5) Dorsal margin of hyomandibula extending onto pterosphenoid, sphenotic, prootic and pterotic.
- 6) "Lap" joint between hyomandibula and metapterygoid.
- 7) Large coronomeckelian bone in adults.
- 8) Palatine with two articular facets anteriorly articulating with two facets of the maxilla.
- 9) Separate second ural centrum present in young, lost in adult.
- 10) Maxilla with more than one row of functional teeth along most of its ventral margin.

Even though primitive features are not considered in a cladistic analysis, I list here the primitive features unique to the family Diplomystidae within all recent Siluroidei.

- 11) Dentate maxilla, also present in some characiforms.
- 12) Long maxilla (longer than premaxilla), broad posteriorly, and with long medial process as in primitive teleosts.
- 13) Four ossified pharyngobranchials of similar length as in other ostariophysans where the pharyngobranchial 4 is often cartilaginous.
- 14) Ossified supraneurals 3–4 present as in some ostariophysans.
- 15) 9/9 principal caudal rays, primitive within Siluroidei only but advanced over other ostariophysans.

All these characters (1–15) are discussed in chapter VII "Features of diplomystids and comparison with other siluroids". The numbers are used in the cladogram illustrating the relationship of diplomystids (Fig. 38).

Diagnostic features of genera

16) Palatine tooth plate: A patch of teeth (Fig. 36A) associated with the autopalatine was found only in adult specimens of *Olivaichthys* n. gen., and on one side of one specimen of *Diplomystes chilensis*, within siluroids. Teleosts such as *Elops* (Taverne 1974; pers. obs.), *Denticeps* (Greenwood 1968) and *Percilia* and *Percichthys* (Arratia 1982 b) have teeth on the dermal portion of the palatine; ontogenic fusion of the autopalatine and dermopalatine is described for *Salmo* (de Beer 1937) and for *Esox* (Jollie 1975). This information about palatine teeth in some diplomystids differs from Fink & Fink's (1981) conclusion that a dermopalatine is absent in ostariophysans.

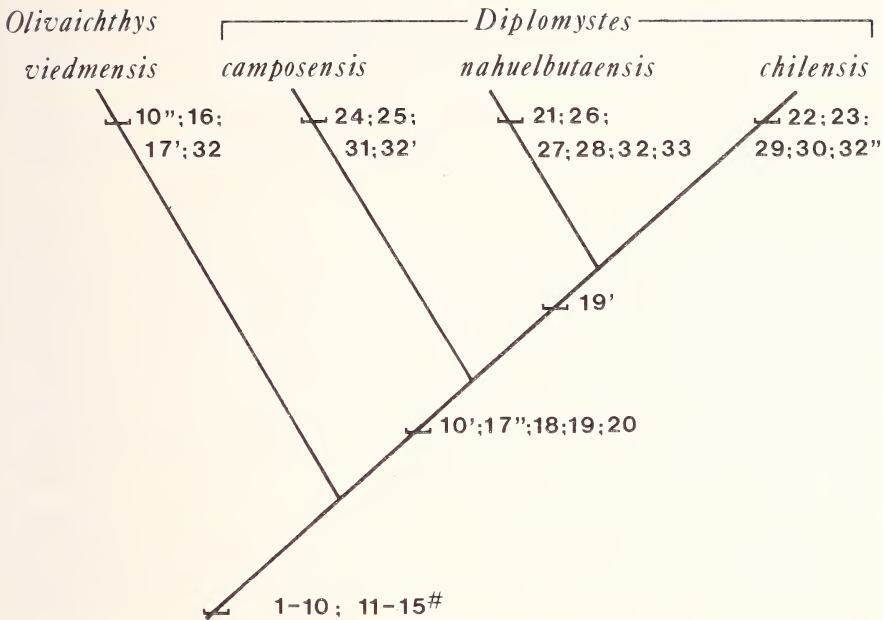


Fig. 38: Interrelationships of diplomystids. (primitive features apparently unique to diplomystids). (For explanation see page 74 to 89).

Characters: 1: Skin of the whole body covered with large simple or lobulated papillae and buds embedded in a colloid-like substance; 2: Sagitta, the largest otolith; 3: Pterosphenoid lacking a suture with the parasphenoid; 4: Large, broad rhomboidal vomer; 5: Dorsal margin of hyomandibula extending well onto the pterosphenoid; 6: "Lap" joint between hyomandibula and metapterygoid; 7: Large coronomeckelian bone in adults; 8: Palatine with two articular facets anteriorly articulating with two facets of maxilla; 9: Separate second ural centrum present in young, lost in adult; 10: Maxilla with more than one functional row of teeth along most of its ventral margin; 10': Two functional rows of maxillary teeth anteriorly, one posteriorly; few teeth; 10'': Three or more rows of maxillary teeth; many teeth; 11: Dentate maxilla; 12: Long maxilla, broad distally, and with long medial process; 13: Four ossified pharyngobranchials of similar length; 14: Ossified supraneurals 3-4 present; 15: 9/9 principal caudal fin-rays; 16: Palatine tooth plate present; 17: Sphenotic longer than pterotic; 17': Sphenotic less than 130 % of pterotic length; 17'': Sphenotic over 150 % of pterotic length; 18: Long anterolateral process of sphenotic; 19: Three pectoral distal radials present; 19': Absence of pectoral distal radials; 20: Absence of pelvic radial; 21: Smallest relation preorbital length/standard length; 22: Origin of pelvic fin anterior to the half of standard length; 23: Fused anterior processes of palatine; 24: Articular facets for a cartilage joining with mesethmoid, vomer, lateral ethmoid and orbitosphenoid and lateral ethmoid at about the first third of palatine; 25: Small levator arcus palatini crest; foramen for facial nerve exposed in the lateral face of hyomandibula; 26: One vomerine tooth plate present; 27: Bony flange present in the ventroanterior part of dentary; 28: Needle-like mandibular and branchial teeth; 29: Few procurrent caudal fin-rays; 30: Two segmented unbranched rays in both dorsal and ventral lobes of caudal fin; 31: Few or none pectoral axillary glands; 32: Buds producing a "rose-shaped" structure on skin of dorsoposterior region on barbel; 32': Buds distributed along an axis in large rounded epidermal papillae on skin of dorsoposterior region of barbel; 32'': Eight to ten buds supported by a long basal papilla on skin of dorsoposterior region of barbel; 33: Posterior nostril widely exposed.

Teeth on the palate region are often associated with the vomer or some pterygoid bones in catfishes (Regan 1911, Tilak 1961, Jayaman 1966). Premaxillary teeth sit on a posterolateral bony process which covers the anterior part of the palatine in the pimelodid *Heptapterus*. Only in *Olivaichthys* n. gen. the patch of teeth is on the palatine itself. The toothed palatine of this diplomystid is considered here as an advanced feature within siluroids; the presence of a palatine tooth plate separates *Olivaichthys* n. gen. from *Diplomystes*.

17–18) Length of the sphenotic (17), and anterolateral process of sphenotic (18): The sphenotic is a bone moderately large but shorter than the pterotic in primitive and most extant teleosts. The sphenotic may be longer than the pterotic in catfishes such as ictalurids (McMurrich 1884 a, Lundberg 1982). A shorter sphenotic and longer pterotic, or both bones of similar length, occur in several catfishes such as Nematogenyidae, Trichomycteridae, Loricariidae, Pimelodidae. The sphenotic (Fig. 4A; 13; 22A; 35B) is longer than the pterotic in all diplomystids (17). The sphenotic is less than 130 % (17') of the pterotic length in *Olivaichthys* n. gen. while it is over 170 % (17'') in *Diplomystes*.

The sphenotic (Fig. 35A) lacks a long anterolateral process in young diplomystids (representative of the primitive condition). A rudimentary or short process (Fig. 35B) is present in *Olivaichthys* n. gen. while a long anterolateral process (advanced condition, 18) is present in adult *Diplomystes* (Fig. 4A; 13; 22A).

19) Pectoral distal radials: Distal radials or secondary pterygials are reported for several catfishes (Tilak 1963: Table 1). The maximum number of distal radials found by Tilak is five (= four, because he counts the first proximal radial as a distal one; see his figures 1–23). I find the primitive number of five or six distal radials in young (Fig. 36A) and adult *Olivaichthys viedmensis*, and in young specimens of *Callichthys callichthys* (KU 13722), while only three (19) in *Diplomystes camposensis* n. sp., and none (19') in *Diplomystes chilensis* and *Diplomystes nahuelbutaensis* n. sp. No distal radials are found in *Clarias* and *Heteropneustes* (Tilak 1963: Table 1). Neither cartilaginous or ossified distal radials are found in any stage of development of trichomycterids and nematogenyids. There is a trend to lose distal radials in siluroids. I interpret the high number (five or six) as primitive within siluroids which is also found in some characiforms (Weitzman 1962; a higher number is found in the characid *Gymnocharacinus*, Miquelarena & Aramburu 1983). *Olivaichthys* n. gen. represents the primitive condition within the diplomystids; fewer (19) or absence of distal radials (19') is the derived condition (*Diplomystes*).

20) No pelvic radials: The cartilaginous pelvic radial (Fig. 37B) present in the young specimen of *Olivaichthys viedmensis* is not found in any other diplomystid or in any siluroid. Nevertheless I cite here its presence in adult *Noturus exilis* (a small round cartilaginous radial; KU 17229). There may be forwarded two hypotheses for the loss of the pelvic radial of diplomystids, (a) fusion to the girdle or (b) loss during growth. Based on the shape of the posterior margin of the girdle in adult diplomystids, I prefer the second hypothesis. The presence of a pelvic radial in early ontogeny of *Olivaichthys viedmensis* is interpreted here as primitive within Diplomystidae, and siluroids; ossified

radials are found in characids. This feature separates young *Olivaichthys* n. gen. from young *Diplomystes* (without cartilaginous or ossified pelvic radial in every growth stage).

Diagnostic features of species of *Diplomystes*

21–22) Body proportions: Since *Diplomystes chilensis* was supposed to be the only diplomystid, little information is known on body proportions (Eigenmann & Eigenmann 1890, Eigenmann 1927), and in number of dorsal and anal rays. Body proportions are known mainly from the Argentinean *Olivaichthys viedmensis* (Ringuelet 1965, 1982, Ringuelet et al. 1967) (Table 4). Most body proportions of diplomystids are variable (see Table 1, based on many specimens), a situation already established for other catfishes by Arratia et al. (1978), and Arratia & Menu Marque (1981, 1984). Only few ratios of diplomystids may be used as diagnostic features (in combination with other) of species:

21) Preorbital length/standard length: The relation preorbital length to standard length of *Diplomystes nahuelbutaensis* n. sp. is the smallest within the species of *Diplomystes* (see Table 1); this ratio is considered as a derived feature because a long preorbital length is the early ontogenetic condition of diplomystids.

22) Prepelvic length/standard length: The origin of the pelvic fin lies anterior to the half of the standard length in *Diplomystes chilensis*; it is about half the length or posterior in *D. nahuelbutaensis* n. sp. and posterior in *D. camposensis* n. sp. (see Table 1) and *Olivaichthys* n. gen. The origin of the pelvic fin closer to the snout than to the base of the caudal fin is interpreted as the advanced condition within diplomystids.

23) Anterior process of palatine: Two (separate) anterior processes of the palatine (Fig. 14B; 24B; 25A–D; 36A) in diplomystids is a unique condition within siluroids (feature 8) (see chapter VI, page 86). *Olivaichthys viedmensis*, *Diplomystes nahuelbutaensis* n. sp. and *D. camposensis* n. sp. share the presence of two separate processes (feature 8) but they are fused (23) (Fig. 6A) in *Diplomystes chilensis*.

24) The articular facets for the cartilage joining with mesethmoid, vomer (mainly), lateral ethmoid and orbitosphenoid are placed at about the midlength of the palatine in *D. chilensis* (Fig. 6A), in *D. nahuelbutaensis* n. sp. and in *Olivaichthys viedmensis*, whereas they are at about the first third of the palatine in *D. camposensis* n. sp. (Fig. 24B; 25A, D). The condition present in the latter is interpreted here as advanced within diplomystids.

25) Levator arcus palatini crest: Young diplomystids have a rudimentary levator arcus palatini crest on the lateral surface of the hyomandibula. Adult specimens of *Olivaichthys viedmensis*, *Diplomystes chilensis* and *D. nahuelbutaensis* n. sp. have a well developed levator arcus palatini crest (Fig. 6B–C, 16), whereas the crest (Fig. 25A, B, D) is rudimentary in *D. camposensis* n. sp.

As result of the development of the levator arcus palatini crest, the foramen for the facial in the hyomandibula is hidden by the crest in large *Olivaichthys* and some large *Diplomystes* (Fig. 6B, C), while large *Diplomystes camposensis* n. sp. have the foramen for the facial (Fig. 25A, B, D) widely exposed on the hyomandibula. Rudimentary levator arcus palatini crest, and the foramen for the facial nerve exposed (in the hyomandibula) in *Diplomystes camposensis* n. sp. is interpreted as a neotenic feature; the development of the crest in the primitive *Olivaichthys* is interpreted as secondarily acquired.

26) Vomerine tooth plate: Eigenmann (1927: 37) stated for diplomystids "vomer with two patches of teeth in the young which coalesce into a subcircular, much larger patch in the adult". That statement is not completely correct because in *Diplomystes camposensis* n. sp. the plates remain broadly separated in most specimens, regardless of age. In *Diplomystes nahuelbutaensis* n. sp., there is a trend for the tooth plates to fuse during early ontogeny; thus already juvenile specimens have partially or totally fused plates. The presence of one vomerine tooth plate in *D. nahuelbutaensis* n. sp. is interpreted here as advanced within Diplomystidae. Separate vomerine tooth plates are found in *Olivaichthys* n. gen. and in several catfish groups, but they are lost in some advanced catfishes such as loricariids.

Larger (conic) teeth on the vomer than on the jaws (Fig. 14B; 35A) is a condition present in Diplomystidae, and a few other catfishes such as the bagrid *Rita* and Plotosidae; the presence of large vomerine teeth is presumably associated with feeding specialization according to Gosline (1975: 12).

27) Dentary: A bony flange is present in the ventroanterior part of the dentary, close to the symphysis in *D. nahuelbutaensis* n. sp., whereas it is absent in all other diplomystids.

28) Mandibular and branchial teeth: The mandibular teeth and the teeth of the tooth plate of the pharyngobranchial 4, and of the ceratobranchial 5 are tall and conic, needle-like in *D. nahuelbutaensis* n. sp.; in contrast, small conic, spatulate or incisiform teeth are found in all other diplomystids.

29) Number of procurrent caudal fin-rays: The number of dorsal and ventral procurrent caudal fin-rays is high in diplomystids (see Table 2) as in some trichomycterid siluroids. Few dorsal (14–18) and ventral (14–17) procurrent rays are present in *D. chilensis*, compared to other diplomystids. The low number of dorsal and ventral procurrent rays of *D. chilensis* is interpreted as the advanced condition within diplomystids.

30) Number of segmented, unbranched caudal fin-rays: Diplomystids usually have three or four segmented, unbranched rays in both dorsal and ventral lobes of the caudal fin. *D. chilensis* is an exception having only two segmented, unbranched rays in each lobe.

31) Pectoral axillary gland: Pectoral axillary glands are known in several catfishes (Kner 1855, Sorensen 1884, Pawlowsky 1914, Reed 1924); they have not been described

for other teleosts. None to three glands may be found in diplomystids; the gland appears in early ontogeny, and in both sexes. In *Diplomystes camposensis* n. sp., there is an evident trend to lose this structure (the most common pattern in this species is one on one side of the body / none on the opposite side). I interpret the presence of this gland as advanced for siluroidei. Within diplomystids, *Diplomystes chilensis* has 2/2, *Diplomystes nahuelbutaensis* n. sp. 3/3, and *Olivaichthys viedmensis* 1/3 glands; while the decreasing of the number of glands in *Diplomystes camposensis* n. sp. (0/1) may be interpreted as a secondary reduction.

32) Skin: The comparison of similar areas of the skin of diplomystids (the dorso-posterior region of the maxillary barbel taken as example) reveals that the structure (Fig. 12A, B; 34A, B) of the buds has evolved in parallel. Buds producing a "rose-shaped" structure are present in *Olivaichthys* n. gen. and *Diplomystes nahuelbutaensis* n. sp. (32), buds distributed along an axis in large rounded epidermal papillae (Fig. 21A, B) are found in *Diplomystes camposensis* n. sp. (32'), whereas groups of eight to ten buds are supported by a long basal papilla (Fig. 2A, B) in *Diplomystes chilensis* (32"). Because it is not possible to postulate a sequence of change at present, each feature is taken as unique for each species.

33) Nostrils: Anterior and posterior nostrils are surrounded by a small skin fold in *Diplomystes nahuelbutaensis* n. sp., the posterior nostril is widely exposed. In contrast, *Olivaichthys viedmensis*, *Diplomystes chilensis* and *D. camposensis* n. sp. have large skin folds around both nostrils, the longest in *D. camposensis* (the posterior nostril completely covered by the skin fold). I interpret the rudimentary skin fold of *D. nahuelbutaensis* n. sp. as the advanced condition within Diplomystidae.

Phylogenetic relationships of diplomystids (Fig. 38)

The family Diplomystidae is characterized by ten autapomorphies (1 to 10). There are several other advanced features shared with other catfishes which are discussed in chapter VI. Other five features, primitively unique to Diplomystidae (11 to 15) within the Siluroidei also characterize the family.

The Argentinean diplomystid *Olivaichthys* n. gen. is characterized by one autapomorphy (16) which is unique within Diplomystidae and also within ostariophysans, and other three autapomorphies (10", 17', 32). Several primitive features are unique to *Olivaichthys* n. gen. within the Diplomystidae as: a) a sphenotic longer than the pterotic but less than 130 %, b) lack of the long anterolateral process of the sphenotic, c) five or six cartilaginous pectoral distal radials, and d) a separate cartilaginous pelvic radial in young stage.

The genus *Diplomystes* is separated by five derived characters (10', 17", 18, 19, 20) from *Olivaichthys* n. gen.. *Diplomystes chilensis* is characterized by five (22, 23, 29, 30, 32") advanced features, *D. nahuelbutaensis* n. sp. by six advanced features (21, 26, 27, 28,

32, 33), and *D. camposensis* n. sp. by four advanced features (24, 25, 31, 32'). Within the species of *Diplomystes*, *D. camposensis* n. sp. is the most primitive species in having a) the most posteriorly placed pelvic fin, b) the largest adipose fin, c) the highest number of dorsal and ventral procurrent caudal rays, d) a joint between the parasphenoid and the pterosphenoid in some specimens (see chapter VI), e) three pectoral distal radials in some specimens, and f) three separate anterior processes in the pelvic girdle in most specimens.

Diplomystes nahuelbutaensis n. sp. and *D. chilensis* can only be united on one advanced character (19'), even though each of the two species has only few of the primitive characters which occur together in *D. camposensis* n. sp. In the pelvic girdle, adult *D. nahuelbutaensis* n. sp. and *D. chilensis* possess only two separate anterior processes like *Olivaichthys* n. gen., while the three processes of the juvenile are not reduced during ontogeny in most specimens of *D. camposensis*. The reduction of the three processes could be interpreted as advanced feature of *D. nahuelbutaensis* n. sp. and *D. chilensis*, occurring in parallel in *Olivaichthys*.

V. NOTES ON ECOLOGY AND DISTRIBUTION

The members of the family Diplomystidae are strict freshwater fishes of the southern part of the Austral Subregion of South America (terminology by Ringuelet 1975, Arratia et al. 1985) and not only from central Chile and central Argentina as stated by Darlington (1957) and illustrated by Berra (1981: 69). Although former references cite *Diplomystes chilensis* from the Aconcagua basin southward throughout Chile, this species was commonly found in the Aconcagua and Maipo basins only. It is apparently now extinct in both basins. Members of the genus *Diplomystes* are confined to central and southern Chile; *D. chilensis* and *D. nahuelbutaensis* n. sp. are taxa of the Chilean biogeographic province; *Diplomystes camposensis* n. sp. is a characteristic taxon of the Valdivian region, in the Chilean side of the Patagonian province, whereas *Olivaichthys* n. gen. with its single species *viadmensis* occupies the Argentinean territory from (?) San Juan to southern Patagonia (Sub-andino Cuyana and Patagonian provinces, according to Arratia et al. 1985).

Information about habits and habitats of diplomystids is scarce and based only on *Diplomystes camposensis* n. sp. (in Arratia 1983 a); information about reproductive periods, sites of breeding, feeding, and so on, is entirely lacking. According to my observations in the field, there is no especial difference in the habitat preference within the species of *Diplomystes*. Young specimens prefer the benthic part of the Rhitron of montane rivers while adults prefer the benthic part of the Potamon (terminology by Illies 1969); *Diplomystes* is found in fast rivers or in fast sections of sluggish rivers, in opposition to *Nematogenys*, which prefers quiet or slow-running water. Most but not all specimens were collected in sections of rivers lacking plants. *Diplomystes camposensis* n. sp. is also found in lakes of the south of Chile.

Diplomystid species occupy regions from a few meters to about 2000 m above sea level (Arratia et al. 1985: Fig. 15, 16). The Chilean diplomystids have been collected in lower regions than the Argentinean ones (*D. chilensis*, from few meters above sea level to about 650 m; *D. nahuelbutaensis* n. sp., from few meters above sea level to about 214 m; and *D. camposensis* n. sp., from few meters above sea level to about 120 m). The Argentinean *Olivaichthys viadmensis* occurs over a wide range of altitudes (from few meters above sea level to about 1900 m).

The diet of adult diplomystids seems to be exclusively carnivorous; complete crustaceans of the genus *Aegla*, larvae and adult insects, and annelids are commonly found in their stomachs (only one large prey item or several smaller ones); I have not found specimens with empty stomachs.

VI. FEATURES OF DIPLOMYSTIDAE AND COMPARISON WITH OTHER SILUROIDS

The only recent attempt to classify the families of siluroids into higher categories is that by Chardon (1968). He recognized thirty families grouped into seven suborders within the order Siluriformes. This classification leaves many problems; some of the suborders seem to be unnatural assemblages, as Chardon acknowledged, and Roberts attested (1973). Several diagnostic characters of the families of Siluroidei (suborder of Fink & Fink 1981) overlap each other (see for instance Regan 1911, Ringuélet et al. 1967); this unsatisfactory situation is repeated in subfamilies and genera.

Greenwood et al. (1966) pointed to some difficulties which arise with phylogenetic analysis of siluroid families. Since then, our knowledge of the suborder Siluroidei has not improved so much that a cladogram could be produced which includes most of the families.

The Diplomystidae has been traditionally recognized as the most primitive family of the suborder Siluroidei. According to Chardon (1968: 33), *Diplomystes camposensis* n. sp. (his *D. papillosus*) presents a series of primitive features approaching cypriniforms which other siluroids have lost, two advanced features compared with other siluroids (loss of the articular and ascending process of the intercalarium, large parapophysis of the 4th vertebra covering the anterior camara of the gasbladder), and some unique features. The unique characters were not listed. Roberts (1973: 391) maintained that *Diplomystes* is more primitive than any other catfish, citing their lack of unique specializations. However, Roberts noted that *Diplomystes* does have apparently unique specializations involving the articulation of the hyomandibula (extending onto the pterosphenoid) and the pattern of jaw muscle invasion of the skull roof. Recently, Lauder & Liem (1983: 141) remarked that "the most primitive family of catfishes, the relict Diplomystidae of South America, are the only catfish to retain a toothed maxillary bone. With the exception of this family, the phylogenetic position of the other catfish families is uncertain and further work is badly needed on the interrelationships of catfishes".

In the following, I will discuss characters of Diplomystidae which I consider important for systematics and for evaluating the relationships within Siluroidei.

S k i n : The name papilla (round or conic epidermal outgrowth of the skin of many siluroids) should not be used as synonym of bud or taste bud (or end-bud of Wright 1884, or terminal bud of Herrick 1901) because some catfishes present simple or complex papillae lacking the so-called taste buds (skin of the trunk in diplomystids) (Fig. 2D & 21D), other catfishes present the skin strongly verrucose or papillose but only a few small taste buds are found (skin of dorsal region of the trunk in the trichomycterid *Hatcheria*), and other catfishes have a smooth skin lacking the conic or round structure defined as epidermal papilla but they present taste buds (skin of dorsal region of the trunk in *Galeichthys*). SEM of siluroid taste buds skin have been published by Reutter & Breipohl (1975), Ovalle & Shinn (1977), Reutter (1978), Ono (1980) and Lane &

Whitear (1982). In all studied siluroids the papilla bearing a taste bud is smaller than in diplomystids. I have not seen solitary sensory cells in the skin of diplomystids. (A paper on the skin of several siluroids will be published elsewhere).

The enormous development of the papillae of diplomystids is one of their most relevant features already noted first by former workers (e. g. Leybold 1859). The papillae of *Diplomystes chilensis* are so long in some specimens that they reach one or two millimeters, thus it is possible to distinguish them easily. The papillae of the skin of *Diplomystes camposensis* n. sp. are broader, rounded, with an irregular surface and not so long as those of *D. chilensis* (compare Figs. 2A—D & 21A—D) but also relevant; the differences in the skin of the two genera of diplomystids can be observed with a stereo microscope; I used SEM as a way to get more information. It could be questioned that the specimens were fixed in alcohol; all diplomystids studied with SEM here have been in alcohol for several years, thus the information is comparable.

A soft papillate ("hairy") or verrucose skin whose papillae are embedded in a coloid-like substance is characteristic of Diplomystidae. Length and shape of the papillae vary from species to species, being extremely long and either simply or lobulated (Fig. 2A—D) in *Diplomystes chilensis*, short, conic and mainly simple (Fig. 34A, B) in *Oliveichthys* n. gen., and short, round and either simple or lobulated (Fig. 21A, B) in *Diplomystes camposensis* n. sp. The distribution of the papillae seems to follow an "order" in *D. chilensis*. Their position and direction is symmetric in both sides of body. The papillate roof of the mouth has the papillae (bearing taste buds) distributed in rows and also placed on elongate folds which are ordered in rows in all diplomystids. I have no explanation for the distribution of the papillae neither on the skin nor on the roof and floor of the mouth.

A papillate roof of the mouth and papillate branchiostegal membranes are one feature in common to Diplomystidae and Nematogenyidae (Howes 1983 a). This feature is also found in pimelodids (e. g. *Heptapterus*) and some trichomycterids (Arratia & Menu Marque 1984: 506).

A papillate skin is common for many catfishes; there are interspecific and intergeneric differences in the shape and distribution of the epidermal papillae in those species sharing this character (Arratia 1983: 72, 76; Arratia & Menu Marque 1981: 506, 514, 515).

Wiley & Collette (1970) described nuptial tubercles in ostariophysans, noting that they have a well developed keratinous cap. Keratinous tubercles are known in some siluroids but do not appear to be associated with breeding behavior. Large keratinized tubercles are found in some uncommonly large females and males of *Trichomycterus* from the Bolivian Altiplano; the keratinized tubercles are present on the flanks, just posterior to the pectoral girdle; I have not seen similar structures in other trichomycterids. Diplomystids do not have keratinous tubercles. The papillae seem to be not associated with breeding behavior since they are present in specimens of different sizes, different sexes, and permanently, although the skin of young specimens is smoother and with fewer papillae than that of adults. The diplomystid type of "hairy" skin with elongate papillae all over the body is uncommon within siluroids and within teleosts; the papillae

show different shape, length and complex structure along the body. I believe these complex structures on the skin of the body have some sensory function, but they differ from the typical taste buds described for other teleosts (see for instance Reutter et al. 1974, Ovalle & Shinn 1977).

I n n e r e a r a n d o t o l i t h: According to Fink & Fink (1981: 343) in otophysans there is a posteromedial extension of the perilymph system, the sinus impar, which communicates to the ear vibrations transmitted from the gasbladder by modified skeletal structures of the anterior vertebrae; the sinus impar is separated from the spinal cord by a shelf of bone formed by the exoccipitals. Those are the conditions found in some siluroids such as diplomystids and *Nematogenys* (Arratia & Menu Marque 1984). In Astroblepidae, Loricariidae and Callichthyidae the sinus impar is so short that it is not distinct of the sinus endolymphaticus and the exoccipitals do not produce a shelf of bone, a condition also found in *Trichomycterus* (Chardon 1968, Arratia & Menu Marque 1984). This probably results from secondary reduction of the structures as the Weberian apparatus became more compact in those fishes.

According to Chardon (1968), the lagena is larger than the utricular region and the asteriscus is the largest otolith in diplomystids; Chardon considered this feature as primitive and similar to the cyprinid condition.

Table 5: Largest region of the auditory organ and largest otolith within some siluroids.

	Auditory region	Otolith
<i>Ageneiosus</i>	utriculus	lapillus
<i>Aspredo</i>	utriculus/lagena	asteriscus
<i>Astroblepus</i>	utriculus	lapillus
<i>Bagarius</i>	utriculus	lapillus
<i>Bagre</i>	utriculus	lapillus
<i>Callichthys</i>	utriculus	lapillus
<i>Chaca</i>	utriculus	lapillus
<i>Chrysichthys</i>	utriculus	lapillus
<i>Diplomystes</i>	lagena	sagitta
<i>Doras</i>	utriculus	lapillus
<i>Galeichthys</i>	utriculus	lapillus
<i>Helogenes</i>	utriculus	lapillus
<i>Heteropneustes</i>	utriculus	lapillus
<i>Ictalurus</i>	utriculus	lapillus
<i>Malapterurus</i>	utriculus	lapillus
<i>Nematogenys</i>	utriculus	lapillus
<i>Plotosus</i>	utriculus	lapillus
<i>Rhamdia</i>	utriculus	lapillus
<i>Schilbe</i>	utriculus	lapillus
<i>Selenaspis</i>	utriculus	lapillus
<i>Trichomycterus</i>	utriculus	lapillus
<i>Wallago</i>	utriculus	lapillus

Fink & Fink (1981) maintained that the lagenar otolith is equal in size to or larger than the utricular otolith. In *Diplomystes chilensis* and *Diplomystes camposensis* n. sp., the lagena is larger than the utricular region (Table 5), a primitive condition apparently unique within siluroids (lagenar and utricular regions of about similar size in *Aspredo*, Table 5).

According to Frost (1925), the asteriscus is the largest otolith of *Diplomystes papillosus* (read *D. chilensis*) a statement repeated by later authors; curiously, the sagitta figured by Frost (Pl. 22, Fig. 3) is widest anteriorly, unlike that in any diplomystid checked by me. However, a sagitta with such shape is found in the other large Chilean catfish, *Nematogenys*; unfortunately Frost did not present catalogue numbers of the specimens he studied. At least in *Diplomystes* the sagitta is the largest otolith, but we must be aware that these elements commonly vary in size and shape. In most catfishes (Table 5), the largest otolith is the lapillus; the sagitta as the largest otolith is interpreted here as a unique condition in diplomystids.

P t e r o s p h e n o i d — p a r a s p h e n o i d: The pterospheoid joins the parasphenoid in most catfishes but not in Diplomystidae (representative of the advanced condition). The presence of a large foramen for facial, trigeminal and optic nerves in Diplomystidae does not permit the joint of both bones. A few specimens of *Diplomystes camposensis* n. sp. have the large foramen divided into two foramina by a narrow prolongation of the pterospheoid joining the parasphenoid, therefore some specimens of *D. camposensis* still keep the primitive condition.

V o m e r: This bone has a characteristic T- or arrow-shape in most catfishes. An elongate teardrop vomer is found in *Trogloglanis*, "a condition uniquely derived among ictalurids" (Lundberg 1982: 40). A needle-like vomer is found in *Hipophthalmus* (Howes 1983 b); the bone is variable in size in catfishes. The vomer of diplomystids (Fig. 5A; 23A) is somewhat rhomboidal and greatly broader and larger than that of other siluroids, a feature also noted by Alexander (1965); this seems to be a condition uniquely derived in Diplomystidae within siluroids.

H y o m a n d i b u l a r a r t i c u l a t i o n w i t h t h e c r a n i u m: One of the important variables of the hyomandibula is the location of its articulation with the cranium. Chardon (1968) uses this feature to identify some families of siluroids: a) hyomandibula articulating with sphenotic and pterotic (Diplomystidae, Siluridae, Bagridae, Pimelodidae and *Malapterurus*); b) hyomandibula articulating only with sphenotic (*Helogenes*, Amplycipitidae); c) hyomandibula articulating with pterotic, sphenotic and alisphenoid (Plotosidae).

It is necessary to distinguish between the articular area of the hyomandibula and its "contact" area. A long articular area (Fig. 5B; 23B) for the hyomandibula on the pterotic, the sphenotic-prototic joint, and the pterospheoid is present in diplomystids. In other catfishes I examined, the hyomandibula articulates with the pterotic, sphenotic and anteriorly "contact" the pterospheoid (e. g. *Ictalurus*, *Nematogenys*), or is not

prolonged anteriorly (Trichomycteridae, Loricariidae, Callichthyidae). The joint between the hyomandibula and cranium is located mainly along the sphenotic-prootic joint in the Diplomystidae; the contribution of the pterotic is minor. In other catfishes (e. g. Trichomycteridae) with a large pterotic, the articular area comprises the sphenotic-prootic joint and pterotic. This last feature is commonly found in siluroids, and I interpret the condition of Diplomystidae as a derived one, apparently unique.

"Lap" joint between hyomandibula and metapterygoid: A suture (usually a sutura dentata or serrata) is commonly joining the hyomandibula and the so-called metapterygoid in siluroids, whereas a synchondral joint is present in some catfishes. An overlap of both bones producing a "lap" joint has been observed only in diplomystids within siluroids.

Coronomeckelian bone: The coronomeckelian bone, comparatively small in young diplomystids, becomes larger in larger specimens, which is unusual in siluroids and in teleosts (some siluroids have a small coronomeckelian bone as adults, e. g.: *Nematogenys*, or it lacks, e. g. *Trichomycterus*). The enormous development of the coronomeckelian bone is interpreted here as an advanced condition apparently unique for diplomystids.

Palatine - maxilla: Different relations between the maxilla, palatine and antorbital can be found within catfishes:

a. Maxilla with two articular facets (Fig. 14B; 23A; 24B) articulating directly with two facets of the palatine (only in Diplomystidae).

b. Maxilla with two small rounded facets, one articulating with the anterior facet of a rod-like palatine, the other connected through a cartilage with antorbital (Fig. 39A, B) (e. g.: *Nematogenys*, *Ictalurus*, *Heptapterus*).

Similar relationships are found in Trichomycteridae, with the following differences: the palatine is broader anteriorly and dorsally contacts the (?)cartilaginous plate supporting the nasal barbel (Fig. 39C), and it has a small articular facet for the premaxilla (at least in *Bullockia* and *Hatcheria*).

c. Maxilla bearing one facet articulating with one facet of the palatine, and lacking contact with orbital bones (Fig. 40A) (e. g.: *Plecostomus*, *Callichthys*).

According to my present knowledge, the condition "a" is found only in Diplomystidae within siluroids. A double-headed palatine is also found in cyprinids (Gosline 1975), but its articulation differs from that of diplomystids.

Second ural centrum: A separate second ural centrum is present in early ontogeny of diplomystids (Arratia 1982 a, present paper), but the centrum is lost in adults (Gosline 1961, Lundberg & Baskin 1969, Arratia 1982 a, present paper). In contrast, in the majority of catfishes a reduced second ural centrum fuses with the base of one or more hypurals, or it fuses with the compound centrum (Lundberg & Baskin

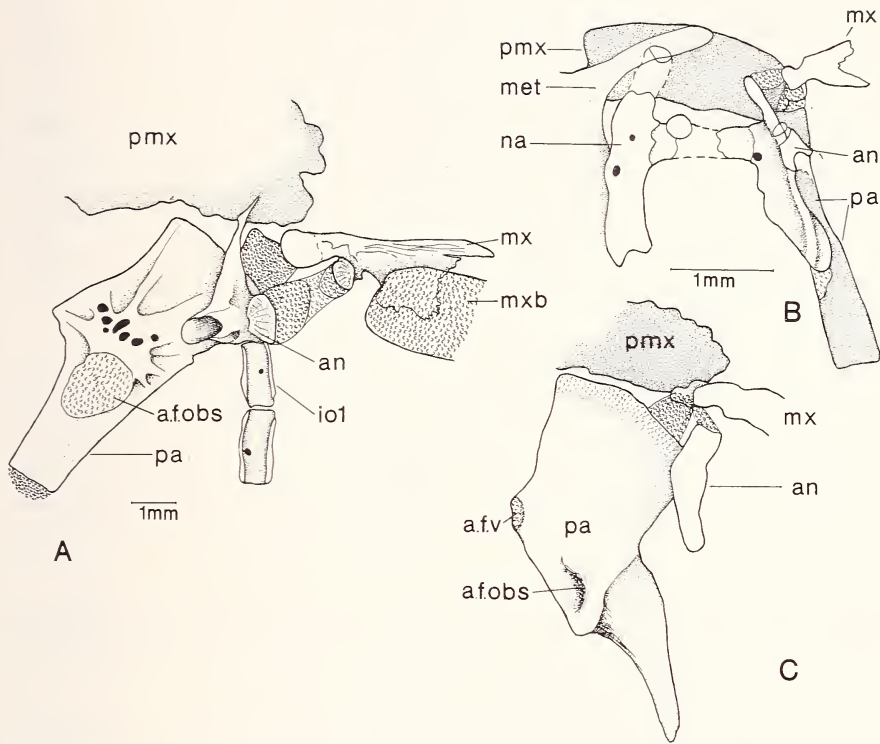


Fig. 39: Relationships among palatine, maxilla and antorbital. — A: *Nematogenys inermis* (LBUCH 30873); B: *Heptapterus mustelinus* (KU 21135); C: *Trichomycterus oroyae* (NMNH 16786).

a.f.obs: articular facet for lateral ethmoid-orbitosphenoid complex; a.f.v: articular facet for vomer; an: antorbital; iol: first infraorbital; met: mesethmoid; mx: maxillary; mxb: maxilla barbel and its support; na: nasal; pa: palatine; pmx: premaxilla.

1969, Arratia 1982 a, 1983 c). "A separate, well developed ural centrum occurs in some members of four specialized and unrelated families. This is interpreted as independent redevelopment of a presumably primitive pre-ostariophysan condition" (Lundberg & Baskin 1969: 46). Recently, Patterson (1984) described a separate second ural centrum in the fossil otophysan *Chanoides*.

I interpret the presence of a separate second ural centrum in young and its loss in adult diplomystids as an advanced condition apparently unique to Diplomystidae.

Rows of maxillary teeth: The presence of a dentate maxilla is primitive within Siluroidei, one functional row of maxillary teeth can be found in characid ostariophysans. Maxillary teeth are apparently present in the Eocene siluroid

Hypsidoris farsonensis; the teeth occupy less than a third of the ventral margin of the maxilla, but the maxilla is reduced in size (Lundberg 1975 b, Lundberg & Case 1970) in comparison to diplomystids. Within recent Siluroidei only the Diplomystidae have a functional dentigerous maxilla, but the quantity of teeth and the number of functional tooth rows vary within diplomystid genera. More than one row of functional maxillary teeth is considered here advanced within diplomystids. There are three or more rows of functional teeth (10'', Fig. 38) with 23 or more teeth in adults along the ventral margin of the maxilla in large *Olivaichthys* n. gen., whereas fewer tooth rows (10') (two rows anteriorly, one posteriorly) and fewer teeth (8–19 teeth in adults; Table 2) are found in larger *Diplomystes*; therefore, *Diplomystes* is more primitive within diplomystids than *Olivaichthys* in having less maxillary teeth.

Dentate maxilla: A dentate maxilla is only present in Diplomystidae within recent Siluroidei. The presence of maxillary teeth is interpreted here as primitive because this condition is shared with some characiforms ("teeth are absent from some families and reduced in others", Greenwood et al. 1966: 383). Maxillary teeth have not been reported for gonorynchiforms and cypriniforms (see for instance: Ramaswami 1955 a, b, Monod 1963, Roberts 1973, Taverne 1981, Sawada 1982, Patterson 1984, Gayet 1986).

Size and shape of maxilla: A maxilla (a) not reduced in size, (b) being narrow anteriorly, broad posteriorly and (c) bearing a large medial process has been considered primitive for Diplomystidae (Fink & Fink 1981).

(a) The maxilla (Fig. 14B; 23A; 24B; 36A) of diplomystids is longer than the premaxilla; it is not reduced in size as in all recent catfishes with the exception of *Trichomycterus boylei* (Arratia & Menu Marque 1984: Fig. 12A). Fink & Fink (1981) considered the maxilla (not reduced in size) of diplomystids as primitive because it is also present in primitive teleosts (the primitive teleosts used for comparison are not mentioned). A small maxilla is widely distributed in gonorynchiforms, cypriniforms and siluroids, whereas a large maxilla is found in some cypriniforms (Roberts & Kottelat 1984) and in characiforms (see for instance Weitzman 1962, Roberts 1969). The presence of an elongate maxilla in characiforms and in diplomystids may be interpreted as a reappearance of the condition present in primitive fossil teleosts such as pholidophorids and leptolepids (Nybelin 1966, 1974).

(b) The maxilla of diplomystids is narrow anteriorly and broad posteriorly as in other ostariophysans such as gonorynchiforms, cypriniforms and characiforms; the distal part of the maxilla is comparatively broader than in other ostariophysans, being the posterior margin truncate in diplomystids (see Figs. 14A, 24A). Commonly, the posterior part of the maxilla is slightly rounded in other ostariophysans (see for instance: Roberts 1969: Fig. 3, Weitzman & Kanazawa 1976: Fig. 5, 11, Weitzman & Géry 1980: Fig. 5, Patterson 1984: Fig. 6, Gayet 1986: Fig. 12).

(c) A long medial process of the maxilla is found only in diplomystids within the Siluroidei, a condition present in other ostariophysans.

Pharyngobranchials: The branchial apparatus (Fig. 17A, B; 27A, B) of Diplomystidae has four separate ossified pharyngobranchials of similar length, which is primitive and unique within siluroids; in other siluroids with four pharyngobranchials usually the first (or second one) is very small, or unossified; only pharyngobranchial 4 has a tooth plate. Within siluroids there is a trend to lose one (Tilak 1961) or two (Nawar 1954, Arratia & Menu Marque 1984) pharyngobranchials. Only epibranchial 3 bears an uncinat process in diplomystids; epibranchials 1–3 bear an uncinat process in trichomycterids (Arratia & Menu Marque 1984), as they do in primitive teleosts (Rosen 1973). Thus, an uncinat process confined to the third epibranchial is interpreted here as a derived condition for siluroids.

Supraneurals: Fink & Fink (1981) identified absence of the supraneural above the second neural spine as an otophysan synapomorphy; "Since *Chanooides* has this bone, and since the two enlarged supraneurals of cypriniforms are apparently homologous with those in *Chanooides*, this is wrong" (Patterson 1984: 445). "Absence of the second supraneural is a characiphysan character", according to Patterson (1984: 445); this conclusion is wrong because *Diplomystes chilensis* has a second cartilaginous supraneural (Fig. 9A). A large third supraneural fused with the fourth supraneural which is separate as a small bone (Fig. 9B) is present in some specimens of *D. chilensis*. Two separate supraneurals are present above centra 3–4 in the characid *Gymnocharacinus bergi* (Miquelarena & Aramburu 1983: Fig. 10; a large supraneural 3 and a small 4), therefore, characiphysans do not have only one supraneural as stated by Fink & Fink (1981). A fifth supraneural is present in few catfishes such as diplomystids (figured also by Alexander 1965). The fifth supraneural (Fig. 29A) of diplomystids is placed among the neural spines of vertebrae 4 to 6.

The number of supraneurals (Fig. 9A–B; 29A) of diplomystids (a probable second unossified supraneural, a compound supraneural 3+4, or separate supraneurals 3 and 4, and a fifth small supraneural which appears to be fused with the first pterygiophore in some specimens) is considered here as a primitive condition within ostariophysans.

Principal caudal fin-rays: The most primitive caudal ray count (9/9) occurs only in Diplomystidae within the Siluroidei. The count 9/9 is nearer than 10/9 count of other ostariophysans and primitive teleosts than the 8/9 or less of other siluroids (Lundberg & Baskin 1969, Arratia et al. 1978, Arratia 1982 a, 1983 c).

Commonly, only the numbers of procurrent and principal caudal rays are mentioned. I suggest to determine also the number of segmented unbranched rays of each lobe in young and adult specimens of siluroids. During growth, the dorsal and ventral procurrent rays become progressively segmented in *Nematogenys* (Arratia 1982 a, 1983 c), an unusual condition within teleosts and not described for other siluroid. The count of segmented unbranched rays may be helpful separating species, or in phylogenetic interpretations, therefore, this is a feature which should be more investigated in siluroids.

Barbel: The presence of only one pair of barbels has been interpreted (Eigenmann 1927, Roberts 1973, etc.) as primitive within siluroids but not unique to

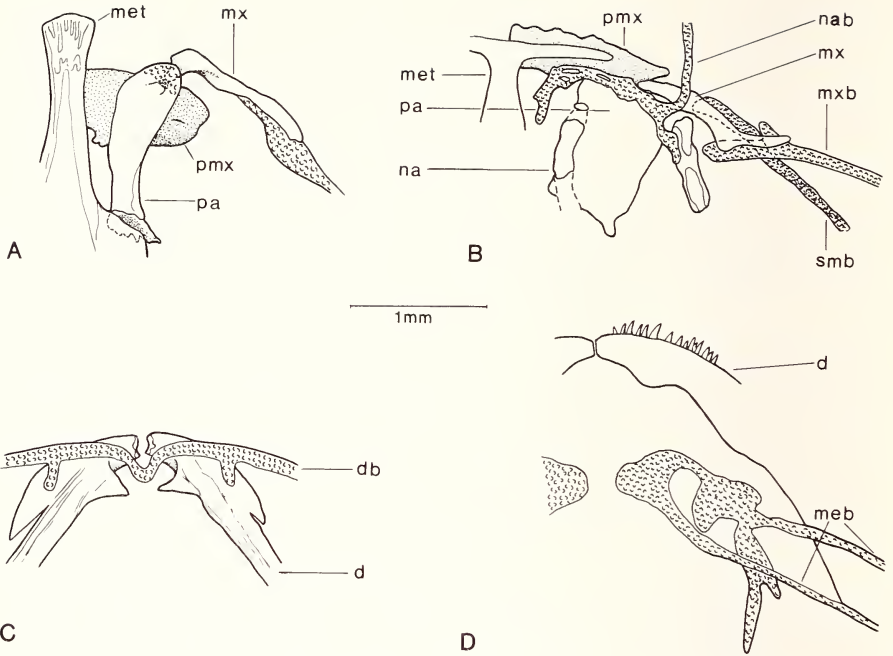


Fig. 40: Cartilaginous support of barbels and associated bones. — A: *Plecostomus* sp. (KU 21135); B: *Trichomycterus roigi* (according to Arratia & Menu Marque 1984); C: *Callichthys callichthys* (KU 13722); D: *Cetopsorhamdia* sp. (ANSP 13890).

d: dentary; db: dental barbel and its (?)cartilaginous support; meb: mental barbel and its (?)cartilaginous support; met: mesethmoid; mx: maxilla; mxb: maxillary barbel and its (?)cartilaginous support; na: nasal; nab: nasal barbel and its (?)cartilaginous support; pa: palatine; pmx: premaxilla; smb: submaxillary barbel and its (?)cartilaginous support.

Diplomystidae. The supporting system of the maxillary barbel in diplomystids (contra Ghiot & Bouchez 1980) and other catfishes is a small plate placed ventroposteriorly to the maxilla (Fig. 40A, B). Siluroids with three or four pairs of barbels have a large plate supporting the barbel (Fig. 40B–D) (Howes 1983 b, Arratia & Menu Marque 1984). The central rod of the barbel has been assigned as cartilage at least for some catfishes (e. g. Pollard 1895, Baecker 1926, Nagar & Mathur 1959, Reutter 1978), as "infantile fibrous cartilage" changing into precartilage in *Silurus glanis* (Hoffmann 1923), as chondroid supporting tissue (with hyaline cells = cartilage-like tissue) for *Silurus glanis* (Schaffer 1930) and as a elastin net surrounded by longitudinal fibers of collagen in *Pimelodus clarias* (Ghiot & Bouchez 1980). Information about many families is missing and the actual information is variable as Pollard (1895: 416) noted: "In Siluroids much more complicated differentiations have arisen. The tentacles are not of similar histological nature in different families".

The study of the plates supporting the barbels clarifies statements of former authors. For example: 1) *Nematogenys* is said to have three pairs of barbels. My studies of ontogenetic series of the rudimentary nasal barbel of this fish show that the barbel is a projection of the skin around the nostrils, and it lacks a cartilaginous support. Thus, this fish lacks a "true" nasal barbel, and has only two pairs of barbels. 2) The support of the so-called mental barbel may be related to the dentary (Fig. 40C) or not (Fig. 40D). I propose to establish the relationships of the plates supporting the barbels of different catfishes because it could be a helpful taxonomical feature.

Differences in position and relationships of the maxillary barbel of siluroids and cypriniforms were cited by Fink & Fink (1981), who conclude that barbels of siluroids and cypriniforms appear to have evolved independently. I could add that histological studies of the maxillary barbel (e. g. Pollard 1895, Schaffer 1930, Sato 1973 a, b, Sato & Kapoor 1957, Nagar & Mathur 1959, Reutter 1978, Ghio & Bouchez 1980) show differences between barbels of both groups, but there are also histological differences between species within each group so that it is difficult to evaluate this feature.

N a s a l c a p s u l e : Alexander (1965) noted that the nasal cavities are bounded medially by the mesethmoid and posteriorly by the lateral ethmoid in most siluroids. The surrounding bones of the nasal capsule within siluroids seem to be more varied than recognized by Alexander (1965) and Howes (1983 a). The nasal capsule is surrounded by the mesethmoid, lateral ethmoid and laterally by the palatine in *Nematogenys* (Howes 1983 a); I have to add that the antorbital also borders the capsule. The nasal capsule is mainly surrounded by the broad palatine in Astroblepidae and according to Howes (1983 a) in *Trichomycterus rivulatus*, uniquely within Trichomycteridae. Based on my observations, the broad palatine occurs in most *Trichomycterus* species, and also the antorbital is bounded by the nasal capsule laterally.

The nasal capsule is placed in a cavity of the lateral ethmoid in loricariids; these catfishes have two patterns (Howes 1983 a). The nasal capsules of Diplomystidae are large and have many sensory folds; each capsule sits in a cavity bounded by the mesethmoid, lateral ethmoid, a cartilaginous area related to vomer, palatine, maxilla and the antorbital. On the basis of our present knowledge of siluroids, it seems to me that the combination of bones framing the nasal capsule in diplomystids is a derived feature within siluroids.

M e s e t h m o i d - l a t e r a l e t h m o i d - v o m e r : The space at the juncture of these three bones, mainly mesethmoid and lateral ethmoid, is filled with cartilage in adult specimens of *Diplomystes* (Fig. 5B). This fontanelle is absent or very small in larger specimens of *Diplomystes camposensis* n. sp. (Fig. 23B). The largest known cartilaginous areas are found in the ictalurid *Trogloglanis* (Lundberg 1982: Fig. 7). A large cartilaginous area is found in other ostariophysans (de la Hoz & Chardon 1975: Fig. 2, 3, 4, 7; Fink & Fink 1981: Fig. 2A, C, E). Unfortunately this is a feature difficult to evaluate because information on adult specimens of many families is missing, and the available information may be referred to young or to adult specimens (the

lengths are not mentioned, and/or the scales are missing on the figures, e. g. in de la Hoz & Chardon 1975, Fink & Fink 1981).

Mesethmoid: According to Fink & Fink (1981), "in most siluroids the mesethmoid is flatter and broader dorsally than in *Diplomystes*; this feature appears to be associated with a general broadening of the head and it is hypothesized to be secondary". According to my studies, many siluroids have the mesethmoid dorsally as slender as diplomystids, or even more (e. g. *Plecostomus*, *Trichomycterus*, *Astroblepus*). I hesitate to relate the dorsal broadening of the mesethmoid with that of the head, since fishes with greatly different snout widths (*Diplomystes*, *Oliveichthys* n. gen., and *Trichomycterus*) may have either a compressed or a slender mesethmoid. On the other hand, fishes with similarly broad snouts (*Trichomycterus* and *Nematogenys*) show different widths of the mesethmoid.

The elongate T-shaped mesethmoid, often with a median anterior notch and producing two elongate lateral horns, is considered (Fink & Fink 1981) to be a primitive condition, not unique in Diplomystidae (also in catfishes such as Nematogenyidae, Trichomycteridae, Ictaluridae, Pimelodidae).

Frontal: The posterior part of the frontal is broad in young diplomystids (Fig. 35A) and narrower in adults (Fig. 4A; 13; 22A; 35B). The early ontogenetic condition is interpreted here as primitive, while the posterior narrowing of the frontal in adults is a derived feature. Some other catfishes with a narrow frontal posteriorly are *Ictalurus* and *Eutropiichthys*.

A broader frontal posteriorly is a condition found in young and adult specimens of catfishes such as Nematogenyidae, Trichomycteridae, Pimelodidae, Plecostominae.

Sphenotic spine: Primitive teleosts bear a sphenotic spine (Nybelin 1966, 1974, Patterson & Rosen 1977, Arratia 1981 b, Arratia & Schultze 1985). It is found in many extant teleosts, including some siluroids such as trichomycterids (Arratia et al. 1978, Arratia & Menu Marque 1981, 1984), *Callichthys*, *Heptapterus* (pers. obser.) and some ictalurids (Lundberg 1982: Figs. 11, 12, 15, 17, 18). Diplomystids lack the sphenotic spine (Alexander 1965, present paper), a derived feature (not unique for diplomystids) within siluroids.

Parietal: The presence or absence of a parietal in siluroids is not clear cut. It appears to be present but fused to the supraoccipital during ontogeny in *Galeichthys* (Bamford 1948), in one young specimen of *Diplomystes camposensis* n. sp. and in some juvenile and adult specimens of trichomycterids (Arratia et al. 1978, Arratia & Menu Marque 1984). Chardon (1968: Fig. 15) figured a separate parietal in *Diplomyste papillosus* (read *Diplomystes camposensis* n. sp.); contrary to Chardon, I have not found a separate parietal in SMF 7579, the specimen studied by Chardon. According to Hoedemann (1960), separate ossification of the parietal does not occur in ontogeny of *Callichthys* and *Hoplosternum*. It seems possible that the parietal fuses with the

supraoccipital in early ontogeny of some siluroids, but is lost in others. The parietal branch of the supraorbital sensory canal runs enclosed by bony tube on the frontal (not running on the supraoccipital), nevertheless the parietal branch extends posteriorly as a tubule ending in a pore. In young *Oliveichthys* n. gen. (Fig. 35A), the tubule extends onto the supraoccipital; in young *Diplomystes camposensis* n. sp., it extends onto the parietal. The study of the parietal branch throughout ontogeny may be helpful in the identification of a parietal or a parietosupraoccipital in different catfishes.

Extrascapular: Different names have been used for bones of the upper part of the pectoral girdle and extrascapular in the literature. I follow here the nomenclature of Fink & Fink (1981), however, I was not able to see two separate ossifications in the posttemporosupracleithrum in young diplomystids.

The extrascapular is present in all diplomystids. It is closely bound to the pterotic, supraoccipital and epioccipital in large specimens. Laterally, the extrascapular (Fig. 4B; 13; 22A, B; 35A, B) carries the main lateral sensory canal enclosed in a bony tube in all studied diplomystids. I have not seen a "normal" supratemporal commissure although usually one short tube, one or more openings in the bone, and a groove are present. I hypothesize that the supratemporal commissure (probably rudimentary in youngest specimens) is lost in diplomystids; that seems to be a general condition for siluroids.

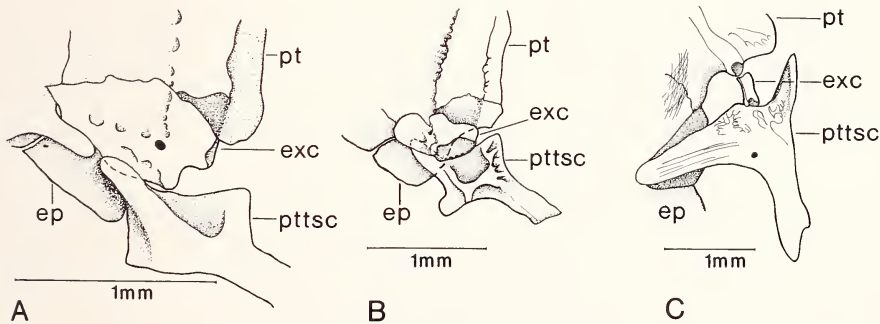


Fig. 41: Extrascapular and surrounding bones. — A: *Heptapterus mustelinus* (KU 21135); B: *Cetopsorhandia* sp. (KU 16395); C: *Bunocephalus coragooides* (ANSP 139313).

ep: epioccipital; exc: extrascapular; pt: pterotic; ptsc: posttemporosupracleithrum.

Within siluroids there is a trend to lose the extrascapular. A "well-developed" plate-like bone is found in all diplomystids (the largest bone is in *Oliveichthys* n. gen. (Fig. 35A, B). The bone is reduced in size in pimelodids (Fig. 41A, B). It is represented only by the tube enclosing the main lateral canal in ictalurids (posttemporal bone of Greenwood et al. 1966, Lundberg 1982) and *Bunocephalus* (Fig. 41C). Loss of the bone occurs in other catfishes such as nematogenyids and trichomycterids.

Foramen for facial, trigeminal and optic nerves: The optic nerve may share a common foramen with the trigemino-facialis nerve (*Diplomystes chilensis*, *D. nahuelbutaensis* n. sp., some *Diplomystes camposensis* n. sp., Nematogenyidae, Trichomycteridae, Siluridae, Bagridae in part, Clariidae, Callichthyidae), or these nerves may emerge separately through two foramina. The latter condition is usually found in siluroids (Howes 1983 b).

Table 6: Bones surrounding the trigemino-facialis foramen in some siluroids. — (according to present paper, and figures by Jayaman 1966 (2), Lundberg 1982 (3), Howes 1983 b (4), and Howes in *litteris* (5); + = presence).

	ptero- sphenoid	orbito- sphenoid	supra- sphenoid	para- sphenoid	prootic	sphenotic
<i>Auchenipterus</i> (4)			+	+	+	
<i>Chrysichthys</i> (2)	?+			+	+	+
<i>Diplomystes</i> (most species)	+	+		+	+	
<i>Diplomystes</i> <i>camposensis</i> (part)	+			+	+	
<i>Hatcheria</i>	+				+	+
<i>Hoplosternum</i> (4)	+				+	
<i>Hypophthalmus</i> (4)	+		+		+	+
<i>Ictalurus</i> (3)	+	+	?+	+	+	
<i>Nematogenys</i>	+				+	+
<i>Noturus</i> (3)	+		?+	+	+	
<i>Trichomycterus</i>	+				+	+
<i>Trogglanis</i> (3)	+		?+	+	+	
<i>Pterodoras</i> (5)	+			+		+

The trigemino-facialis foramen or the common foramen for the trigemino-facialis and optic nerves are situated very differently among siluroids (Table 6). The foramen is usually surrounded by four bones; of those the only common elements in most of the siluroids in Table 6 are the pterosphenoid and prootic. The combination of parasphenoid, pterosphenoid, orbitosphenoid and prootic is presented only in *Diplomystes*. Some members of *Diplomystes camposensis* n. sp. have only three bones (Table 6) which is also unique. Howes (1983 b) figures mistakenly the trigemino-facialis foramen limited by pterosphenoid, orbitosphenoid and frontal in *Pterodoras*; the trigemino-facialis foramen in *Pterodoras* is limited by pterosphenoid and sphenotic (Howes in litt.). The suprasphenoid of Howes (1983 b) is present in some catfishes but not in Diplomystidae, Nematogenyidae and Trichomycteridae, not in *Clarias* and *Heteropneustes* (Srinivasachar 1958).

Different patterns of the bones surrounding the optic foramen (Table 7) are also found in siluroids. No single bone consistently borders the foramen. The pterosphenoid usually is present, but it does not border the foramen in *Auchenipterus*. From two to four

Table 7: Bones surrounding the optical foramen in some siluroids (according to present paper, Lundberg 1982 (2) and Howes 1983b (3); + = presence).

	para-sphenoid	supra-sphenoid	orbito-sphenoid	ptero-sphenoid	prootic
<i>Auchenipterus</i> (3)	+	+			
<i>Diplomystes camposensis</i> (part)	+		+	+	
<i>Hoplosternum</i> (3)			+	+	+
<i>Hypophthalmus</i> (3)		+		+	
<i>Ictalurus</i> (2)		?+	+	+	
<i>Noturus</i> (2)		?+	+	+	
<i>Pterodoras</i> (3)	+	+	+	+	
<i>Trogloglanis</i> (2)	+	?+	+	+	

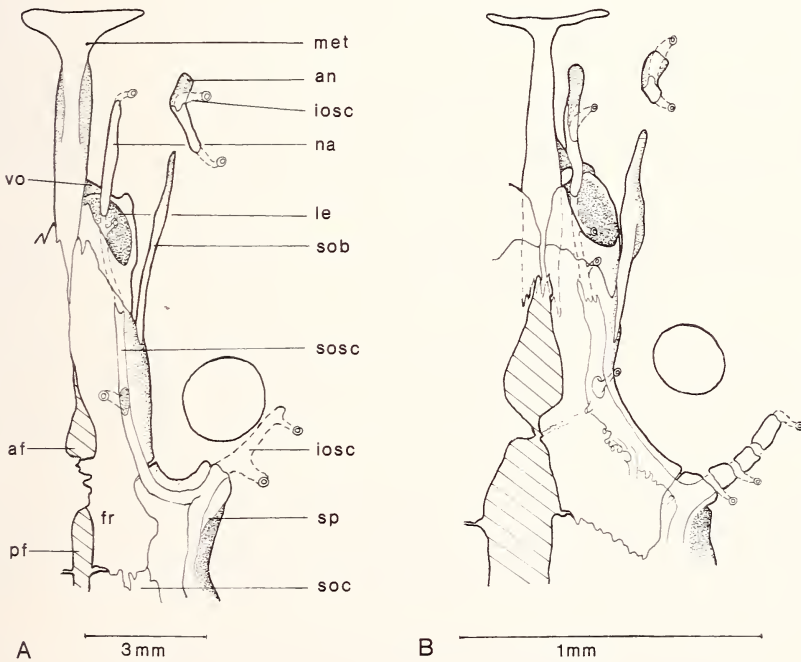


Fig. 42: Dorsal view of cranium illustrating the relationships of the supraorbital bone. — A: *Hatcheria macraei* (PC 126, KU 19204); B: *Bullockia maldonadoi* PC 1374, KU 19224).
 af: anterior frontal fontanelle; an: antorbital; fr: frontal; io: last infraorbital bone; iosc: infraorbital sensory canal; le: lateral ethmoid-orbitosphenoid complex; met: mesethmoid; na: nasal; pf: posterior frontal fontanelle; sob: supraorbital bone; soc: supraoccipital; sosc: supraorbital sensory canal; sp: sphenotic; vo: vomer.

bones can surround the foramen. Howes (1983 b) recognized the optic foramen bounded by the suprasphenoid (at least) as synapomorphic for Auchenipteridae and Doradidae (see Table 7). I suggest a comprehensive review of this feature in siluroids before judging its phylogenetical importance.

Circumorbital bones and eye: According to Roberts (1973) and Fink & Fink (1981), the supraorbital bone is absent in siluriforms. Such statement is correct for some catfishes such as diplomystids, ictalurids, nematogenyids. A supraorbital bone is present in trichomycterids (Arratia et al. 1978, Arratia & Menu Marque 1981, 1984, Arratia 1983 b, present paper), in *Heteropneustes* (Kapoor 1960), and probably in loricarioids (Howes 1983 a), as in primitive teleosts. Thus diplomystids present a derived condition, not unique within siluroids.

The supraorbital bone (Fig. 42A, B) may be a long needle-like bone in the trichomycterids *Hatcheria* and *Bullockia*, or a short bone in *Trichomycterus*. The supraorbital is placed alongside the frontal and lateral ethmoid in *Hatcheria* and *Bullockia* (Fig. 42A, B). In *Trichomycterus*, the supraorbital is mainly placed alongside the lateral ethmoid (Arratia et al. 1978, Arratia & Menu Marque 1984: Fig. 3A, 12A, B).

The bone placed anteriorly to the first infraorbital in diplomystids and nematogenyids is considered here as the antorbital (Figs. 4A; 13; 22A; 39A) because of (a) its shape (slightly comma-shaped), (b) the anterior ending of the infraorbital sensory canal and (c) its relationships. The antorbital bone presents different shapes in siluroids (e. g.: Fig. 39A—C; 42A, B; Arratia & Menu Marque 1984: Figs. 3A, 12A, B).

The infraorbital series of siluroids consists mainly of tubes or half-cylinders bearing the infraorbital canal (Fink & Fink 1981). That description is right for several catfishes but not for all. A complete series of bones (6—9) bearing the sensory canal is found in some catfishes such as diplomystids (Fig. 4A; 13; 22A), ictalurids, nematogenyids. The usual number is seven to nine in *Diplomystes* and *Oliveichthys* n. gen. Such high number of infraorbital bones is not found in any other teleost, fossil or recent. I interpret the high number of infraorbital bones in diplomystids as the result of fragmentation of some of them and as an advanced condition shared with nematogenyids (with seven to nine bones). In siluroids as in other teleosts, there is a trend to reduce or lose infraorbital bones; the loricariids (Howes 1983 a), callichthyids, and pimelodids (pers. obs.) are examples. The strongest loss of bones is found in trichomycterids which keep only the last infraorbitals (Fig. 42A, B) (Arratia et al. 1978, Arratia & Menu Marque 1984).

The infraorbital bones lack bony plates in most siluroids. Small bony plates are found in the last infraorbital of *Diplomystes nahuelbutaensis* n. sp. (Fig. 13), in the last three infraorbital bones of *Diplomystes camposensis* n. sp., and in some advanced siluroids such as loricariids and callichthyids (Fink & Fink 1981).

Sclerotic bones are supposed to be absent in siluriforms; nevertheless, a shelf of bone supporting the eye-ball is found in young specimens of *Callichthys* (KU 13722). This bony shelf is not connected with the infraorbital sensory canal, and it appears as in in-

dependent ossification in early ontogeny of the fishes examined here. It is unclear whether this feature corresponds to a sclerotic bone, or if it is neomorphic.

The eye of siluroids may be covered by the skin or not. A naked eye is found in catfishes such as Diplomystidae, Pimelodidae in part (e. g. *Parapimelodus*, *Pimelodus*), in Loricariidae (e. g. *Loricaria*, *Plecostomus*, *Xenocara*), and in Ictaluridae in part (e. g. *Ictalurus*). The eye is covered by the skin in other groups, such as Ageneiosidae, Auchenipteridae, Ictaluridae in part (e. g. *Noturus*), Pimelodidae in part (e. g. *Hep-tapterus*, *Iheringichthys*, *Microglanis*, *Myoglanis*), Cetopsidae and Trichomycteridae. A covered or naked eye can be present in different genera within one family. Habits and habitat of the fish do not explain the difference between fishes of similar habits and habitat may have either condition.

Palatine's articulations: In diplomystids the palatine bears dorsally two articular facets placed at about the midpoint of the bone, or in its first third (Fig. 6A; 24B); the medial one articulates with a cartilage joining mesethmoid, vomer (mainly in adults), lateral ethmoid and the orbitosphenoid, and the lateral one with the lateral ethmoid. Actually, this condition is difficult to evaluate since there are different patterns in siluroids; for instance:

- a. The palatine bears dorsoposteriorly one large facet articulating with both the lateral ethmoid (a small area) and the orbitosphenoid (*Plecostomus*).
- b. The palatine bears dorsally one facet in the posterior half of the bone, articulating with the lateral ethmoid (Lundberg 1982; per. obs.) (*Ictalurus*).
- c. The palatine bears dorsally one facet (placed just behind the midpoint of the bone) articulating with the lateral ethmoid-orbitosphenoid complex (Fig. 39A) (*Nemato-genys*).
- d. The palatine bears dorsally two facets. The dorsolateral one, at about the midpoint of the bone, articulates with the lateral ethmoid-orbitosphenoid complex; the inner one, placed on the medial margin of the bone, articulates with the vomer (Fig. 39C) (*Trichomycterus*).

Pterygoid bones: Different names have been used for the pterygoid bones in catfishes (see Gosline 1975). The presence of metapterygoid, ectopterygoid and mesopterygoid in *Diplomystes* has been stated by Alexander (1965) and Fink & Fink (1981). Alexander points out that the ectopterygoid is small or absent in *Diplomystes*. Gosline (1975) could not find a mesopterygoid in the specimen examined by him. According to my studies, two pterygoid bones are present in diplomystids: the metapterygoid and an additional pterygoid; the additional pterygoid is occasionally present.

The bone traditionally named as metapterygoid in diplomystids is united by a "lap" joint with the hyomandibula and by a small synchondral joint with the quadrate. A small sutural region is present between the hyomandibula and quadrate in large diplomystids. The "lap" joint between hyomandibula and metapterygoid seems to be

unique to diplomystids. At the moment, I have no interpretation for the small bone, ?metapterygoid, present in young *Diplomystes camposensis* n. sp. This feature should be checked when more young specimens are available. The small additional pterygoid found in some specimens of diplomystids (and sometimes on only one side of the fish) may be the "ectopterygoid" of other authors; it seems to me that the position of this bone (below the palatine) in diplomystids is not homologous with that of the ectopterygoid in other teleosts. This small pterygoid appears as an additional element of the series and it could represent a neomorphic feature; it does not seem to be a fracture of the mesopterygoid (Fig. 25A, C). A similar bone was described for some other siluroids by Howes (1983 a).

The bone 4 of McMurrich (1884 a) has been considered as a mesopterygoid by other authors. This bone is connected to the palatine in diplomystids (see above); it partially encloses the posterior cartilage of the palatine, it appears irregularly in some young (Fig. 25B) and adult (6B; 25C; 36A) specimens, on both or only one side of the body, and it cannot be interpreted as belonging to the pterygoid series. I interpret it as a neomorphic feature.

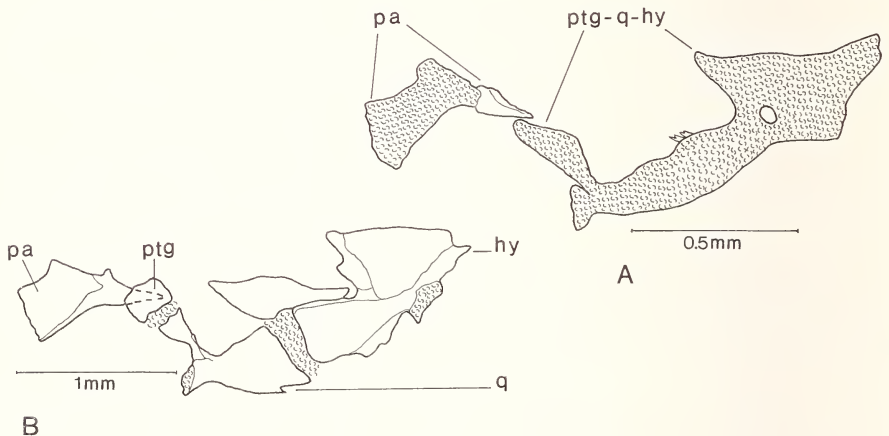


Fig. 43: Palatopterygoquadrate arch and palatine in *Trichomycterus areolatus* (PC 1218 & 11282). — A: Specimen of 11 mm standard length; B: specimens of 15–22 mm standard length. hy: hyomandibula; pa: palatine; ptg: pterygoid; ptg-q-hy: pterygoid-quadrate-hyomandibular plate.

The interpretation of the pterygoid bones within different catfishes is complicate. It should be accompanied by studies of ontogenetic series of different groups, and may even then be confusing. For example, there is a plate of undifferentiated cartilage (pterygoid, quadrate, hyomandibula) in small trichomycterids of about 11 mm in standard length; the palatine (formed by cartilage anteriorly, while it is already ossified

distally) is clearly separated from this plate. From this stage of cartilage well differentiated bones appear abruptly (Fig. 43A—B), without a gradual succession of changes. A separate pterygoid and the quadrate are easily identified in fishes of about 15 mm in standard length; the quadrate presents an anterior projection which during growth acquires a dorsal flange; the latter grows anteroventrally reaching the free pterygoid. What pterygoid is the latter? I have named it as an endopterygoid in former papers about trichomycterids; a bone in a similar position (in *Malapterurus*) has been named as endopterygoid by Howes (1985: Fig. 13). According to the ontogenetical development in *Trichomycterus areolatus*, this bone could be interpreted as a) the metapterygoid, or b) the mesopterygoid (= endopterygoid); the second hypothesis encloses the assumption of an early fusion between metapterygoid and quadrate, or between metapterygoid and hyomandibula.

A bone in a similar position as the so-called metapterygoid of diplomystids is found in young *Parapimelodus valenciennesi* (ZMH 6669). The "metapterygoid" of *Parapimelodus* bears teeth on its anterior part unlike in any other siluroid. Is this bone only the metapterygoid or is this bone the result of an early fusion between the metapterygoid and the ecto- or mesopterygoid? The young specimens studied here give no information about a fusion between pterygoid bones. To complicate the subject, a thin long J-shaped bone lies below the palatine, its distal curved part lies against the lateral ethmoid. The bone has not the shape and not the relationships of the ectopterygoid, not of the mesopterygoid. (A similar bone in *Pimelodus* was identified as the mesopterygoid by Gosline 1975.) What bone is it? I have no answer at the moment, but these examples are presented to illustrate the need of careful studies on the hyomandibula and pterygoid bones of catfishes.

Lower jaw: The lower jaw of diplomystids shows intraspecific variation in the shape and the development of some structures through growth. The cartilage of the articular facet for the quadrate extends extensively posteriorly, over the retroarticular (Fig. 26A—B) in young *Diplomystes camposensis* n. sp. The dentary may produce lateral expansions close to its dorsal tip, to accommodate more rows of teeth in larger specimens of *D. camposensis* n. sp.

I am uncertain about the relationships in the posterior part of the lower jaw; for instance, is the large "articular" really only an articular or the articular plus part of the retroarticular? The posteromedial development of the articular (Fig. 15C; 26A, C, E) in diplomystids could be functionally related to the work of the jaw, but that hypothesis fails in that *Nematogenys*, which has a similar diet, lacks such medial development of the articular. Curiously, *Nematogenys* does not show the ossification identified here as the retroarticular; the posterior end of the jaw is a thin bone and not heavily ossified. Young specimens of *Nematogenys* show that Meckel's cartilage extends just below the articular facet for the quadrate, but a posteroventral ossification (retroarticular) is missing; the strong ligament connecting with the interopercle is fixed to the angular. The present understanding of the lower jaw of diplomystids and other catfishes is quite unsatisfactory, and I present the problem without solution.

In teleosts with a separate retroarticular, a ligament extends between its posterior part and the interopercle. In siluroids the ligament extends from the retroarticular-articular to the interopercle in diplomystids (Fig. 7A—C). A second ligament is found on the posterior surface of the angular and retroarticular; it is connected with epihyal and interhyal (Fig. 7A—C). The condition of these ligaments of diplomystids are as those found in other teleosts (Lauder 1982).

A ligament extending from the maxilla to the dorsal tip of the anguloarticular at the coronoid process of the lower jaw is synapomorphic for siluroids and gymnotoids (Fink & Fink 1981); Howes (1983 a) has given contrary evidence for other siluroids, not including diplomystids. In the latter, the ligamentum primordiale (Fig. 7A—D) extends from a coronoid cartilage placed medially in the lower jaw (and not in the osseous coronoid process of the jaw) to the maxilla and premaxilla (and to the palatine in one specimen). The attachment of the ligamentum primordiale to the premaxilla and the palatine has not been described for other siluroids and it is apparently unique to diplomystids. The lower external part of the adductor mandibulae attaches muscoulously on the medial part of the dorsoposterior part of the lower jaw (angulo-articular). Most of the muscle inserts on the medial coronoid cartilage dorsal to the coronomeckelian bone through several strong tendons; this insertion on the coronoid cartilage and on the enormous coronomeckelian bone is apparently unique within siluroids. (Other insertions have been mentioned for some other siluroids, not diplomystids e. g. McMurrich 1884 b, Takahasi 1925, Nawar 1955, Howes 1983 a, b).

According to our present knowledge, the relationships of the ligamentum primordiale and the extensive insertion of the adductor mandibulae on the coronomeckelian bone are apparently unique for diplomystids. Nevertheless, more research on other siluroids is needed to make some conclusion.

H y o i d a r c h : The hyoid arch of different fishes was reviewed by McAllister (1968), who gave brief information of siluriforms. According to my studies, there are some aspects of interest:

a) Ontogenetic changes: The hyoid arch is developed from a continuous cartilaginous bar in most siluriforms; this bar differentiates into one or two hypohyals, a ceratohyal, epihyal and interhyal. The branchiostegal rays articulate with the ceratohyal and epihyal. This pattern is present in small diplomystids and other catfishes, nevertheless I find some exceptions (*Loricarichthys* and *Callichthys*).

In early ontogeny of *Loricarichthys*, a cartilaginous elongate plate extends ventroanterior to the articular area between the ceratohyal and epihyal; this elongate plate lies adjacent to the bases of the first three branchiostegals (Fig. 44A). A broad cartilaginous area joins the ceratohyal and epihyal in *Callichthys* (Fig. 44B); this area extends ventroanteriorly. Three separate cartilage bars connect the branchiostegals with the cartilage between the ceratohyal and epihyal. The first and longer bar bears two slender branchiostegals, the second bar articulates with the broadest, last branchiostegal. This ontogenetic character apparently differentiates *Loricarichthys* and *Callichthys* from other siluroids, but information is missing from many siluroids.

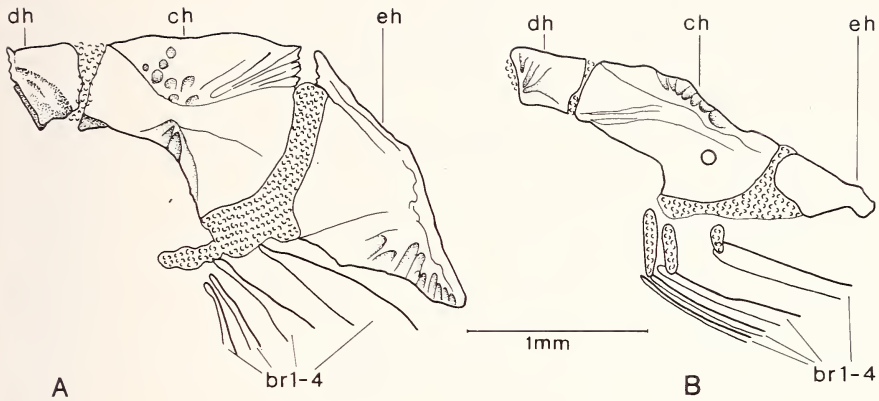


Fig. 44: Branchiostegal rays and relationships with ceratohyal and epihyal in young specimens. — A: *Loricarichthys* sp. (ANSP 131612); B: *Callichthys callichthys* (KU 13722). br1-4: branchiostegal rays 1-4; ch: ceratohyal; dh: dorsal hypohyal; eh: epihyal.

b) Hypohyals: Dorsal and ventral hypohyals (Fig. 27A—B) have similar size and shape in diplomystids. They differ slightly in ictalurids, and the ventral hypohyal is rudimentary in *Nematogenys*, *Heptapterus*, and also in *Eutropiichthys* (Tilak 1961). No ventral hypohyal exists in trichomycterids. I interpret the condition of Diplomystidae as primitive, and hypothesize a trend toward loss of the ventral hypohyal in siluroids.

c) The articular facets between the ceratohyal and epihyal are smooth and weakly joined in Diplomystidae (Fig. 27C) and Trichomycteridae. The articulation between those bones is produced by a dentated suture in *Ictalurus* and *Nematogenys*; in the latter, both interdigitating surfaces become partially fused in the largest specimens. I interpret the last condition as derived within siluroids.

O percular series: Diplomystids lack a subopercle, as do most catfishes. The presence of one to three suprapreopercles in diplomystids is shared with other siluroids such as ictalurids, nematogenyids, pimelodids, other ostariophysans, and some primitive teleosts (Nybelin 1974). The preopercle of diplomystids lacks a ventral limb, as in other siluroids. Fink & Fink (1981) state that the interopercle is shortened considerably on an antero-posterior axis, so the interopercle is a short triangular bone in siluroids. A short slightly triangular bone is present in several siluroids, including diplomystids, ictalurids (Lundberg 1982), hypophthalmids (Howes 1983 b), and *Nematogenys* (Arratia et al. 1978). A large elongate bone is present in trichomycterids (Arratia et al. 1978, Arratia & Menu Marque 1984); thus, this feature cannot be considered as an apomorphy for siluroids.

Fink & Fink (1981) stated that the triangular shape of the opercle is synapomorphic for the siluroids and gymnotoids. Howes (1983 a: 34) disagrees with this conclusion;

diplostyid species show differences in the shape of the opercle (compare Figs. 6B, 16 & 25D), and trichomycterid species show a highly modified opercle which is not triangular at all (Arratia 1983: Fig. 5, Arratia & Menu Marqué 1984: Fig. 9).

Weberian apparatus: There are important differences in the Weberian apparatus of siluroids, such as the position and number of the Weberian ossicles.

In diplostyids as in several siluroids, the Weberian ossicles are placed posterior to the cranium and externally to the anterior centra, and the gasbladder is not enclosed in lateral expansions of the complex vertebra. One modification is presented in *Nematogenys* (Fig. 45A): the Weberian ossicles are enclosed into modified vertebrae and into the posterior part of the braincase, and there are camarae of the gasbladder enclosed in osseous lateral expansions from the complex vertebra. The complex vertebra is formed by three modified vertebrae (3–5). Another modification of the Weberian ossicles is represented in *Trichomycterus*: the Weberian ossicles are located mainly within the braincase (Fig. 45B); the complex vertebra is formed by two modified

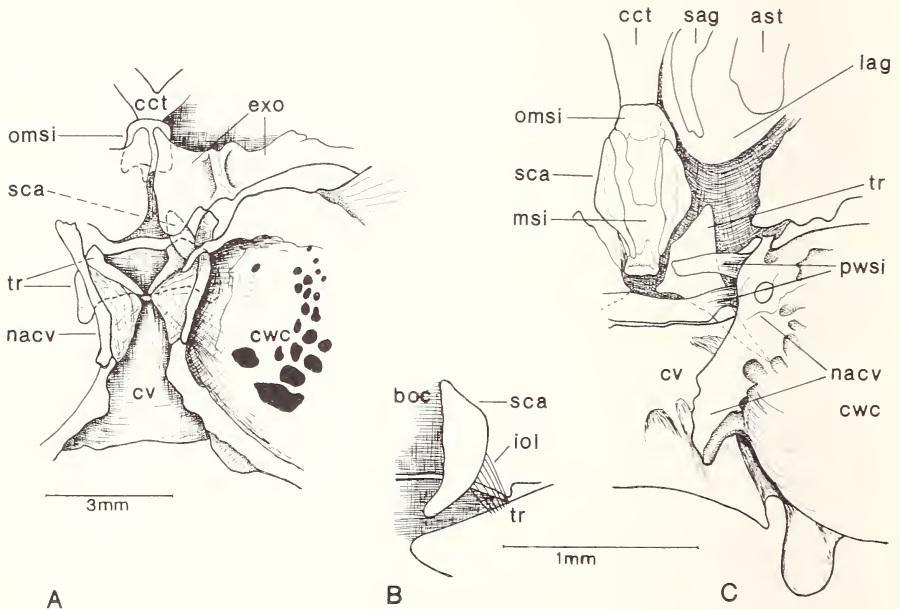


Fig. 45: Weberian apparatus and related bones, dorsal view; roof of the cranium and neural arch of complex vertebra removed. — A: *Nematogenys inermis* (LBUCH 30873); B: Interossicular ligament between scaphium and tripus in *N. inermis*; C: *Trichomycterus areolatus* (KU 19416). ast: asteriscus; boc: basioccipital; cct: canalis comunicans transversus; exo: exoccipital; cv: complex vertebra; iol: interossicular ligament; lag: lagena; msi: membrane of sinus impar; nacv: broken neural arch of complex vertebra; omsi: ossification of the membrane of sinus impar; pws: posterior wall of sinus impar; sag: sagitta; sca: scaphium; swc: gasbladder capsule; tr: tripus.

vertebrae (4–5; not 3 and 4 as is in Arratia & Menu Marque 1984, and occasionally by vertebrae 3, 4 and 5); the complex vertebra becomes fused to the basioccipital in largest specimens of some species of trichomycterids; thus, this feature changes throughout growth, and besides, it varies intraspecifically in *Trichomycterus*.

The position of the Weberian apparatus and the number of ossicles (4) of diplomystids and silurids for example, are similar to those of characiforms and cypriniforms. In siluroids there is a trend to lose some Weberian ossicles. For instance, the Trichomycteridae have only two ossicles (scaphium and tripus).

In otophysans, the first neural arch is modified to form the scaphium and claustrum (Rosen & Greenwood 1970). The claustrum is secondarily absent in gymnotoids (Fink & Fink 1981), and also absent in several siluroids such as trichomycterids, nematogenyids (Fig. 45A–B), loricariids and others (see Chardon 1968). According to Fink & Fink (1981), the scaphium has a characteristic rounded outline anteriorly and a small process which articulates with the first centrum. That is not the condition for all otophysans since in trichomycterids, nematogenyids, loricariids and others the scaphium lacks the small articular process (Fig. 45A–B); after its incorporation into the braincase, the scaphium lacks a connection with the first centrum in the fishes mentioned above. Fink & Fink (1981) maintain that in characiphysans, the scaphium extends well anteriorly to the border of centrum 1, but in some siluroids (at least trichomycterids, nematogenyids, and loricariids), the scaphium is situated even anteriorly and centrum 1 is lost altogether.

Former authors have stated that the tripus represents the rib or/and the parapophysis of the third centrum (see Karandikar & Masarekar 1954: 20). Watson (1939) suggested a more complex origin (basiventral plus rib of vertebra 3 plus ossification of the interossicular ligament, mass of mesenchyme and ossification in the wall of the gasbladder). Matveiev (1929) (for cyprinids) and Hoedemann (1960 a) (for a siluroid) have suggested other origin for the tripus. The assumption of a tripus derived from the rib and/or parapophysis of the third centrum is difficult to accept for catfishes with this bone mainly enclosed in the braincase, supposedly lacking the transformator process (see Chranilov 1929, Chardon 1968), and the third vertebra placed posterior to the basioccipital region, contributing to the formation of the complex vertebra. Unfortunately, the smallest specimens (12 mm in total length) which I checked have the tripus already ossified; therefore, assumptions about the origin of the tripus in siluroids should be reviewed developmentally in species having different patterns of the Weberian apparatus.

The tripus attached to the complex vertebra by a thin dorsal bony lamella has been interpreted as a synapomorphy of characiphysans; in cypriniforms, *Chanos*, and other primitive teleosts it is autogenous (Fink & Fink 1981). This statement is not completely correct because young and adult specimens and some other primitive siluroids (e. g. *Ictalurus melas*) present this crescentiform process or "bony" lamella closely articulated or abutted on a deep cavity into the lateral wall of the third centrum of the complex vertebra; but an important number of siluroids, including loricariids and callichthyids

(considered as advanced siluroids) have the tripus mainly enclosed in the braincase cavity and the tripus may be attached to the complex vertebra or not; the character is intraspecifically variable in some trichomycterids, and the so-called "bony" lamella — when it is present — is formed by mineralized dense connective tissue. Each tripus is united to its partner by the "bony" lamella which is attached to the complex vertebra in *Nematogenys*.

The intercalarium is part of the Weberian apparatus and unique to otophysans (Fink & Fink 1981). In siluroids, the articular process of the intercalarium is lost; in some catfishes the intercalarium consists only of a nodule of bone (see Chardon 1968, Howes 1983 b). In diplomystids, the ascending process is separate from the nodule, with the exception of one young specimen of *Diplomystes camposensis* n. sp., bearing the ascending and horizontal processes as described for *Macrones* (= *Mystus*, according to Fink & Fink 1981) by Bridge & Haddon (1893: 83). According to Fink & Fink (1981: 329), "*Diplomystes* appears unique (and not representative of the condition primitive for siluroids) in that the ascending process is separate from the nodule in the interossicular ligament". At least one young diplomystid studied here (*Diplomystes camposensis* n. sp.), keeps the primitive condition presented by *Mystus*. The intercalarium is lost in some other catfishes such as loricariids (Chardon 1968), trichomycterids and nematogenyids.

Centra 2–4 are fused into a complex vertebra in siluroids (one of the characters of Fink & Fink 1981); such fusion occurs in several groups such as diplomystids and ictalurids; the centra 5–6 are included in the complex vertebra in some catfishes such as Loricariidae, Astroblepidae and Ageneiosidae (Chardon 1968, Howes 1983 b); only centra 4–5 (occasionally the centrum 3 also) are incorporated into the fusion in trichomycterids of the genus *Trichomycterus*; in largest specimens, the complex centrum fuses to the basioccipital. A separate first vertebral centrum is present in diplomystids and it is hypothesized here as primitive; this free centrum is not present in adult specimens of *Trichomycterus* and *Nematogenys* and apparently is lost or possibly fused to the basioccipital in some trichomycterids.

An elongate anterior horizontal process of the os suspensorium has been stated as a synapomorphy of siluroids and gymnotoids by Fink & Fink (1981); at least trichomycterids, nematogenyids and other catfishes (Chardon 1968) with Weberian ossicles enclosed in the braincase lack the os suspensorium.

L i g a m e n t s o f t h e W e b e r i a n a p p a r a t u s : The ligaments of the Weberian apparatus have been numbered differently (see for instance Alexander 1962, 1964, Rosen & Greenwood 1870). To avoid confusion with one or the other nomenclature I name them here according to the names of the bones which are joined by the ligament. The study of the ligaments in diplomystids is easier in young than in large specimens because bones become closer during growth. Alexander (1964) distinguished three ligaments between the tripus and other bones in Siluri (which are also found in cypriniforms): ligaments 3 and 4 joining the tripus with the intercalarium, ligament 2 joining the tripus with the complex centrum and ligament 1 joining the

tripus with os suspensorium. These three ligaments exist in diplomystids; besides these three ligaments, additional ligaments are present in diplomystids. (For example, a short ligament between the scaphium and claustrum probably is a modification of the oblique interneural ligament 1 of Rosen & Greenwood 1970; another short ligament extends between the ascending process of the intercalarium and the scaphium and probably corresponds to a section of the oblique interneural ligament 2. A ligament extends between the os suspensorium and the transformator process of the tripus, but the os suspensorium also connects by thin ligaments to centra 1 and 2; probably all these ligaments are derivatives of the intercostal ligaments.)

In siluroids with an encapsulated gasbladder there is a reduction of Weberian ossicles coupled with loss of the transformator process of the tripus and os suspensorium and their ligaments. The simplicity in number of structures and the partial incorporation of the tripus in the braincase cavity, together with the action of these ligaments, probably permits faster transmission of vibrations or other distortion of the wall of the gasbladder. I interpret the condition of the ligaments of diplomystids (more similar to that of cypriniforms) as primitive.

Aorta and posterior cardinal veins: The middle position of the aorta and the lateral position of the cardinal veins in the ventral part of the complex vertebra of diplomystids is similar to that figured by Alexander (1964: Fig. 2d) for a primitive siluroid, with the following differences: the os suspensorium extends down to the ventral surface of the complex centrum and the cardinal veins are slightly ventrally placed to that position figured by Alexander. No additional ossifications protect or enclose these blood vessels.

Anterior abdominal vertebrae excluding the first four: Separation of the fifth vertebra from the complex vertebra is one of the features used by Regan (1911) in his diagnosis of Diplomystidae and later by Chardon (1968) for his *Diplomystoidei* new suborder. The unfused fifth vertebra is not unique to diplomystids, it is also present in troglodytic ictalurids (Lundberg 1982). There is no posterior extension of lamellar bone over the ventral surface of the fifth centrum in diplomystids; this feature is present also in troglodytic ictalurids (Lundberg 1982). Therefore, these two characters, interpreted as primitively unique to Diplomystidae by former authors, are not unique to diplomystids within the Siluroidei.

The 4th to 16–17th abdominal vertebrae of diplomystids are characterized by having the neural spines separate medially, as in *Elops* (Taverne 1974; per. obs.) and in some recent clupeids (Arratia & Schultze 1985). The curious lateral aspect of these vertebrae (Fig. 29B) in *Diplomystes camposensis* n. sp., was already noted and commented upon by Chardon (1968). No other catfish seems to have similar anterior vertebrae, but information to that effect is incomplete.

Baudelot's ligament: The posttemporosupracleithrum produces an ossified medial limb or transcapular which contacts the basioccipital in adult catfishes

such as diplomystids, ictalurids, and bagrids; this limb was interpreted as a transcapular by Kindred (1919) and as the ossified Baudelot's ligament by Fink & Fink (1981). If this is the ossified Baudelot's ligament, its ossification must occur very early, because it is completely ossified from early ontogeny in the diplomystids and ictalurids I studied. I could detect no discontinuity between the posttemporosupracleithrum and this medial limb or transcapular. I doubt the homology of this structure with Baudelot's ligament and name it as the medial limb of the posttemporosupracleithrum or transscapular. A short ligament is present between the medial limb or transcapular and the basioccipital in adult diplomystids examined here and it may represent a rudimentary Baudelot's ligament. The medial limb or transcapular is firmly sutured with the cranium in some catfishes as *Pimelodus*, *Synodontis*, Ariidae and Doradidae (Alexander 1965). The medial limb or transcapular is very short in catfishes such as trichomycterids; I have not seen a ligament relating the medial limb or transcapular and the basioccipital in trichomycterids; I hypothesize that Baudelot's ligament is rudimentary in some catfishes and it is lost in those with an enclosed gasbladder fused or partially fused to the cranium.

Pectoral proximal radials: "Always two primary pterygials" (= proximal radials) are found in siluroids (Tilak 1963: 147). I have found three proximal radials in diplomystids (Fig. 30A, B, D; 37A), commonly one cartilaginous and two ossified radials (the first one ossified but extremely small in some specimens); three elongate ossified radials in nematogenyids; and only one large ossified radial in trichomycterids (Arratia et al. 1978). A second radial remains cartilaginous in most trichomycterids with the exception of some large specimens of *Trichomycterus roigi*, where it is ossified (Arratia & Menu Marque 1984). I do not know of any catfish with four proximal radials, the number commonly found in teleosts. Diplomystids and nematogenyids with three proximal radials represent the primitive condition in siluroids.

Pectoral spine: Most catfishes bear pectoral and dorsal spines; pelvic and dorsal spines are also found in other teleosts. A strong pectoral spine seems to be a specialization of catfishes, but it is absent in some siluroids such as trichomycterids. The pectoral spine may have a smooth anterior and posterior surface (trichomycterids), or bear teeth (plecostomids, nematogenyids).

The pectoral spine of some siluroids has been accurately studied in its main ossified region; siluroids often lose the distal end of the spine during preparation, thus the literature about this region is scarce. I call attention to the distal part of the pectoral spine because it may be a diagnostic feature of some catfish groups (Fig. 18A—C; 46A—C). The end of the spine is preformed in characteristically shaped membrane plates in diplomystids (Fig. 18A—C); or it may be preformed by small plates, each one finely branched distally (*Ictalurus*, Fig. 46A); it may be formed by the segments of a modified ray finely branched laterally (*Noturus*, Fig. 46B); it may be formed by squared plates, separated from each other (*Nematogenys*, Fig. 46C). The spine of *Nematogenys*

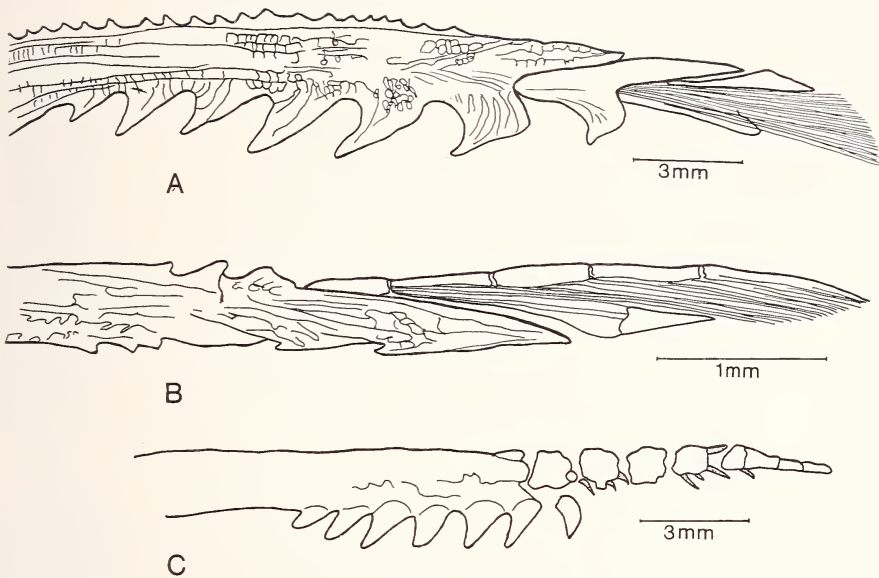


Fig. 46: Pectoral spine (distal tip). — A: *Ictalurus punctatus* (KU 9657); B: *Noturus flavus* (KU 2539); C: *Nematogenys inermis* (LBUCH 30873).

superficially appears toothless, but microscopic examination of the ventral view of the spine of the largest specimens reveals many small teeth which may not emerge from the skin.

Pelvic girdle and splint: The pelvic girdle (Fig. 31; 37B) of young specimens of *Olivaichthys viedmensis* and most specimens of young and adult *Diplomystes camposensis* n. sp. have three anterior processes; two of them fuse or partially fuse in larger *Olivaichthys* n. gen., and *Diplomystes chilensis* and *D. nahuelbutaensis*. Three anterior processes in the pelvic girdle is a feature found in Siluridae (Shelden 1937, Tilak 1967); most catfishes have two anterior processes in the pelvic girdle, and callichthyids seem to have a single process anteriorly (Hoedeman 1960 b: Fig. 13b—c). The early ontogenetic stage with three anterior separate processes is interpreted here as primitive.

Diplomystids have a small pelvic splint which is also found in other catfishes (see for instance Shelden 1937, Arratia et al. 1978, Howes 1983 a). According to Howes (1983 a: 336), "a pelvic splint is recorded only in the Trichomycteridae, Astroblepidae, Loricariidae and Diplomystidae". This statement is not completely correct because a pelvic splint is also present in Callichthyidae and Schilbeidae. The pelvic splint was considered as a "rudimentary spine" by Howes (1983: 337), in contrast, the pelvic splint

is segmented in the largest diplomystids studied and it has the structure of a rudimentary half-ray.

Cephalic sensory canals and lateral line: The supraorbital canal of diplomystids usually gives off one or more tubules (and pores) more than that of other catfishes (Herrick 1901, Allis 1904, Lekander 1949, Kapoor 1960, 1961, Lundberg 1975, 1982, Arratia & Menu Marque 1984), as does the infraorbital canal. *Nematogenys* is exceptional in having even more infraorbital tubules and pores (10 or 11). The supraorbital canal gives off a parietal branch in diplomystids (Fig. 4A; 13; 22A) (primitive condition); such a branch is lost in *Trichomycterus* (Arratia & Menu Marque 1984: Fig. 3A; 12A, B), in *Hatcheria* (Fig. 42A) and in *Bullockia* (Fig. 42B). The supraorbital canal does not give off a tubule on the sphenotic in diplomystids (Fig. 4A; 13; 22A; 35A, B), like most other catfishes (Kapoor 1960, 1961, Lundberg 1975), except that sphenotic tubule and pore are found in some *Trichomycterus* species of the Altiplano (Arratia & Menu Marque 1984: Fig. 3A; 12A, B). The supratemporal commissure apparently is lacking in siluroids (see above), as noted by Lekander (1949).

The supra-, infraorbital and temporal canals join the sphenotic in siluroids; the juncture of the three canals occurs on the first third of the sphenotic in diplomystids (Fig. 4A; 13; 22A; 35A, B) and ictalurids, and about in the middle or in the posterior part of the bone in many other catfishes. The point of branching of the parietal branch in the frontal in diplomystids and some other siluroids (such as ictalurids, *Brachiglanis* and some *Liocassis* [Lundberg 1982: 36]) is associated with jaw muscle invasion of the skull roof. Lundberg (1982) interprets this feature as a derived condition within siluroids "but one which has evolved in parallel a few times".

The infraorbital sensory canal is complete in many catfishes, as in most recent teleosts; it is reduced to its end (Fig. 42A—B) in trichomycterids (advanced condition, apparently unique within siluroids). The infraorbital canal ramifies into two branches. The antorbital branch (Fig. 4A; 13; 22A) prolongs over the dorsal margin of antorbital in diplomystids, while the lower branch is very short. The infraorbital canal ending in the antorbital is a condition found in pholidophorids and other fossil teleosts, and also in some recent primitive teleosts as in *Elops* (Taverne 1974), and in the clupeid *Sardinops*. I interpret the end of the infraorbital sensory canal in diplomystids as a shared primitive teleostean feature.

The infra- and supraorbital sensory canals do not join in their anterior ends in most catfishes. An anterior juncture is found in the pimelodids *Heptapterus* (Fig. 39B) and *Pimelodella* (KU 21225); a neomorphic feature?

The preopercular sensory canal gives off four tubules which extend over the opercle and interopercle (Fig. 6B) in diplomystids. These tubules do not branch as they do in some other catfishes; an especially ramified preopercular sensory canal is found in *Hypophthalmus* (Howes 1983: Fig. 2).

Large pit organs organized as a rostral, an anterior and a middle pit-line have been described for a few catfishes (Herrick 1899, Allis 1904, Lekander 1949). Lekander (1949:

60) also noted "some organs around anterior nasal opening". All these pit-line organs or pore-tube commissure were clearly evident in the specimens MNHN 92082 (*Diplomystes chilensis*), and SMF 7579 and KU 66045 (*Diplomystes camposensis* n. sp.). This feature was difficult to confirm in other specimens because the pit organs are easily confused with the elongate papillae, and in some specimens seem minute or absent (under the magnification and resolution I used). I have not seen these structures in the trichomycterids *Hatcheria* and *Trichomycterus*. More information on the distribution of this feature in siluroids is needed.

The lateral line runs along the flank, to or beyond the base of the principal caudal fin-rays in diplomystids and other catfishes such as *Ictalurus* and *Heptapterus*. At the opposite extreme a very short canal represented by one or two ossicles and two or three pores occurs in some trichomycterids (compare Figs. 33A, 33B). The length of the lateral line, number of ossicles and pores is a helpful taxonomical feature separating some siluroid groups.

Absent structures: Siluroids are characterized by the loss of several bones (Greenwood et al. 1966). The following structures are absent in diplomystids: intercalar, basiptyergoid process, suprasphenoid, supraorbital, sclerotic bones, supramaxilla, ectopterygoid, mesopterygoid, symplectic, subopercle, epineurals, epipleurals, trigemino-facialis chamber, posterior myodome and supratemporal commissure. The reduction in number of the bones is also accompanied by fusion of some of them: (?)parietal — supraoccipital, and posttemporal — supracleithrum.

Additional bones: Diplomystids (and other siluroids) have some additional bones which are not commonly found in other recent teleosts, for example: bone 4 of McMurrich (Fig. 6B; 25A—C), an additional small pterygoid (Fig. 6B; 25A—C) 7—9 infraorbital bones (Fig. 4A; 13; 22A), 2—3 suprapreopercles (Fig. 16; 25D) and 1 or 2 intermandibular—preopercular ossicles (Fig. 16).

VII. FINAL CONCLUSION

The analysis of features of Diplomystidae and other siluroids shows that the members of Siluroidei are highly variable. The statement "generalized catfish pattern" should be avoided. The information presented above reveals that some anatomical characters vary strongly from group to group, and lack of information in several groups makes comparison difficult. Detailed ontogenetic studies of different structures in different groups are needed as base for a future phylogenetic interpretation of the relationships of the families of Siluroidei.

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IX. ABSTRACT

Traditionally, the Diplomystidae have been recognized as the most primitive within the about thirty-two families of Siluroidei. Most knowledge of the group is based on few specimens of *Diplomystes*. Following detailed studies of many specimens of Diplomystidae, I propose one new genus and two new species. *Diplomystes* is restricted to central and south of Chile, and contains four species (*D. chilensis* [Molina], apparently now extinct, *D. nahuelbutaensis* n. sp., *D. camposensis* n. sp. and *Diplomystes* spec.). *Oliveichthys* n. gen. with the species *viadmensis* is distributed in Argentina (Subandino Cuyana and Patagonian provinces).

Ten unique derived features characterize the Diplomystidae: the skin of the whole body covered with large simple or lobulated papillae and buds embedded in a colloid-like substance; sagitta the largest otolith; pterosphenoid lacking a suture with the parasphenoid; large, broad rhomboidal vomer; dorsal margin of hyomandibula extending well onto the pterosphenoid; "lap" joint between hyomandibula and metapterygoid; large coronomeckelian bone in adults; palatine with two articular facets anteriorly articulating with two facets of the maxilla; separate second ural centrum in young, lost in adult; maxilla with more than one functional row of teeth along most of its ventral margin. Several advanced features of diplomystids are shared with other siluroids, as for instance: nasal capsule bounded by mesethmoid, lateral ethmoid, cartilage of vomer, palatine, maxilla, and antorbital; presence of pectoral (1) and dorsal (2) spines; invasion of the adductor mandibulae on frontal, pterotic, sphenotic, extrascapular and supraoccipital; sphenotic longer than pterotic; sphenotic spine absent; six to nine infraorbital bones present, etc. Five primitive features are apparently unique to diplomystids within recent siluroids: presence of a dentate maxilla; long maxilla, broad posteriorly and with a long medial process; presence of four ossified pharyngobranchials of similar length; presence of ossified supraneurals 3—4; 9/9 principal caudal rays. In addition, many primitive features are shared with other siluroids (e. g. one pair of maxillary barbels; moderately large extrascapular bone; dorsal and ventral hypohyals present; complex vertebra not fused with fifth vertebra and lacking lateral lamellae bone; six hypurals).

A comparative analysis of features of the Diplomystidae and other catfishes is presented. Siluroids are characterized by high morphological diversification (e. g.: in the structure of the skin, of the barbels, of the pterygoid bones, of the supraneurals when they are present, of the auditory region; in the structure and relationships of bones forming the circumorbital series, bones framing the nasal capsule, of the bones framing the optical and trigeminofacial foramina, of the bones of upper and lower jaws, of the bones forming the suspensorium), and knowledge of most families is not adequate for complete phylogenetic resolution.

X. ZUSAMMENFASSUNG

Gewöhnlich werden die Diplomystidae als primitivste der ungefähr 32 Familien der Siluroidei angesehen. Unser Wissen der Familie ist auf wenigen Exemplaren einer einzigen Art begründet. Nach eingehendem Studium vieler Exemplare der Diplomystidae stelle ich eine neue Gattung und zwei neue Arten auf. *Diplomystes* tritt nur im zentralen und südlichen Chile auf und umfaßt vier Arten (*D. chilensis* [Molina], vermutlich bereits ausgestorben, und *D. nahuelbutaensis* n. sp., *Diplomystes camposensis* n. sp. und *Diplomystes* spec.). *Olivaichthys* n. gen. mit der Art *viadmensis* ist in Argentinien (subandine cuyanaische und patagonische Provinzen) verbreitet.

Zehn einzigartige abgeleitete Merkmale charakterisieren die Diplomystidae: Haut des gesamten Körpers bedeckt mit großen einfachen oder kleinlappigen Papillen und Tuberkeln, eingebettet in eine kolloid-ähnliche Substanz; Pterosphenoide ohne Naht mit dem Parasphenoide; großes und breites rhomboidales Vomer; dorsale Artikulation des Hyomandibulare reicht weit auf das Pterosphenoide; überlappende Verbindung zwischen Hyomandibulare und Metapterygoide; großer coronomeckelischer Knochen in adulten Exemplaren; Palatinum mit zwei Gelenkflächen, die mit zwei Gelenkflächen des Maxillare artikulieren; gesondertes zweites urales Zentrum in Jugendformen, das in adulten Formen verlorengelassen; am ventralen Rand des Maxillare mehr als eine Reihe in Funktion stehender Zähne. Mehrere abgeleitete Merkmale sind den Diplomystidae und anderen Siluroidei gemeinsam, wie zum Beispiel: Nasenkapsel gebildet vom Mesethmoid, lateralem Ethmoid, Knorpel des Vomer, Palatinum, Maxillare und Antorbitale; ein Brustflossenstachel und zwei Rückenflossenstachel vorhanden; der adductor mandibulae reicht bis zum Frontale, Pteroticum, Sphenoticum, Extrascapulare und Supraoccipitale; Sphenoticum länger als Pteroticum; kein stachelförmiger Fortsatz am Sphenoticum; sechs bis acht Infraorbitale. Fünf primitive Merkmale sind augenscheinlich innerhalb der Siluroidei auf die Diplomystidae beschränkt: bezahntes Maxillare; langes Maxillare mit langem medialem Fortsatz und am Hinterende breit; vier verknöcherte Pharyngobranchialia ungefähr gleicher Länge; Supraneuralia 3–4 verknöchert; und 9/9 Hauptstrahlen in der Schwanzflosse. Viele primitive Merkmale haben die Diplomystidae zusätzlich mit anderen Siluroidei gemeinsam (z. B.: ein Paar maxillarer Barteln; verhältnismäßig großes Extrascapulare; dorsale und ventrale Hypohyalia vorhanden; komplexer Wirbel des Weberschen Apparates nicht verschmolzen mit dem fünften Wirbel und ohne lateralen lamellaren Knochen; sechs Hypuralia).

Eine vergleichende Analyse der Merkmale der Diplomystidae und anderer Weise schließt die Arbeit ab. Die Siluroiden sind durch sehr große morphologische Mannigfaltigkeit (z. B.: der Struktur der Haut; der Barteln; der Pterygoide, der Supraneuralia, sofern vorhanden; der Gehörregion; der Struktur und Beziehung der Knochen der zirkumorbitalen Serie; der Knochen, die die Nasenkapsel umgeben; der Knochen, die die Foramina des Opticus und des Trigemino-facialis umgeben; der Knochen des Ober- und Unterkiefers; der Knochen des Suspensoriums) ausgezeichnet; unsere Kenntnis der meisten Familien ist nicht ausreichend für eine vollständige phylogenetische Analyse.

XI. RESUMEN

Tradicionalmente se ha reconocido a Diplomystidae como la más primitiva entre las aproximadamente treinta y dos familias del suborden Siluroidei. El conocimiento del grupo se basa fundamentalmente sobre unos pocos especímenes de *Diplomystes*. El estudio de numerosos ejemplares de Diplomystidae me permite proponer un nuevo género y dos nuevas especies. *Diplomystes* está restringido a las regiones central y sur de Chile y contiene cuatro especies (*D. chilensis*, aparentemente extinto actualmente, *Diplomystes nahuelbutaensis* n. sp., *D. camposensis* n. sp. y *Diplomystes* spec.). *Oli-vaichthys* n. gen. con su especie *viadmensis* se distribuye en Argentina (provincias biogeográficas Sub-andino Cuyana y Patagónica).

Diez caracteres avanzados y únicos caracterizan a la familia Diplomystidae: la piel del cuerpo cubierta con papilas largas, simples o lobuladas y "buds" que están embebidas en una substancia de aspecto coloidal; sagitta el otolito más grande; pteroesfenoides carece de sutura con el paraesfenoides; vomer grande y romboidal; articulación dorsal del hiomandibular extendiéndose extensivamente sobre el pteroesfenoides; articulación "sobrepuesta" entre hiomandibular y metapterigoides; hueso coronomeckeliano grande en adultos; palatino con dos carillas articulares articulando con dos carillas del maxilar; segundo centro ural independiente en jóvenes, ausente en adultos y maxila con más de una hilera de dientes funcionales a lo largo de su borde ventral. Varios caracteres avanzados de diplomystidos son compartidos con otros siluroídeos, como por ejemplo: cápsula nasal limitada por mesetmoides, etmoides lateral, cartilago del vomer, palatino, maxila y antorbital; presencia de espinas pectoral (1) y dorsal (2); invasión del adductor mandibulae sobre frontal, pteriótico, esfenótico, extraescapular y supraoccipital, esfenótico más largo que pteriótico; espina esfenótica ausente; seis a ocho huesos infraorbitales presentes. Cinco caracteres son aparentemente únicos de Diplomystidae dentro de los Siluroidei actuales; ellos son: presencia de maxilar dentado; maxila larga, ancha posteriormente y con un largo proceso medial; presencia de cuatro faringobranquiales osificados y de similar longitud; presencia de supraneurales 3 y 4 osificados y 9/9 rayos principales caudales. Varios caracteres primitivos son compartidos con otros siluroídeos (ej.: un par de barbillas maxilares, hueso extraescapular moderadamente grande, hipohiales dorsal y ventral presentes, vértebra compleja no fusionada a la quinta vértebra y careciendo de hueso laminar lateral, seis hipurales).

Se presenta un análisis comparativo de caracteres de Diplomystidae y otros siluroídeos. Siluroidei está caracterizado por un alto grado de diversificación morfológica (ej.: en la estructura de la piel, de las barbillas, de los huesos pterigoídeos, de los supraneurales cuando están presente, de la región auditiva; en la estructura y relaciones de los huesos que forman la serie orbital, de los huesos que rodean la cápsula nasal, de los huesos limitantes de los forámenes de los nervios óptico y trigeminofacial, de los huesos de las mandíbulas, de los huesos que constituyen el suspensorio) y el conocimiento actual sobre la mayoría de las familias no es adecuado o suficiente para presentar alguna interpretación filogenética.

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