MORPHOLOGY OF THE LATERAL LINE SYSTEM AND OF THE SKIN OF DIPLOMYSTID AND CERTAIN PRIMITIVE LORICARIOID CATFISHES AND SYSTEMATIC AND ECOLOGICAL CONSIDERATIONS

by

GLORIA ARRATIA and LAURA HUAQUIN

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INTRODUCTION

Siluroids may have naked skin (e.g., Astroblepidae, Diplomystidae, Ictaluridae, Nematogenyidae, "Pimelodidae", Schilbeidae, Trichomycteridae) or armoured skin partially or mostly covered with bony plates (e.g., Doradidae, Callichthyidae, Loricariidae, Scoloplacidae) to which are attached denticles like placoid scales, with dentine and an outer layer formed by epidermal scales, apparently of enamel (Bhatti 1938, Whitear 1986, Sire 1993). The skin of catfishes without bony plates is generally smooth and with or without epidermal papillae; however, the skin of the flanks may become keratinized late in ontogeny in *Trichomycterus rivulatus* (Arratia 1987a). Keratinous skins are known in some siluroids, but apparently are not associated with breeding behavior (Wiley & Collette 1970, Mittal & Whitear 1979, Roberts 1982).

It has long been known that many fishes, especially catfishes, possess taste buds over the whole body surface (e.g., Herrick 1901, 1903a, Bardach & Atema 1971, Hara 1971). Literature on the histology of the skin is known from a few species such as *Ameiurus melas* (Herrick 1901), *Bagrus bayad*, *Clarias lacera, Chrysichthys auratus* (Hussaini & Lufty 1958), *Ictalurus nebulosus* (Bailey 1937), *I. punctatus* (Grizzle & Rogers 1979), *Rita rita* (Batti 1952, Singh & Kapoor 1967), *Silurus glanis* (Jakubowski 1987), and *Synodontis schall* (Lufty 1960). Literature on the ultrastructure and histochemistry of the skin is available for several genera of catfishes; *Bagarius* (Mittal & Whitear 1979), *Clarias* (Banerjee & Mittal 1975), *Corydoras* (Ovalle & Shinn 1977), *Heteropneustes* (Mittal et al. 1976, Agarwal et al. 1979), *Ictalurus* (Reutter 1978, Zuchelkowski et al. 1981, Yoakim & Grizzle 1982), several loricariids (e.g., *Ancistrus, Chaetostomus, Farlowella, Hypostomus, Loricaria*, and *Otocinclus*; Ono 1980), *Pimelodus* (Ferri 1982, 1983), *Plotosus* (Zaccone & Lo Cascio 1981), *Rita* (Mittal & Munshi 1969, 1970), and *Silurus* (Jakubowski 1987). Parts of the skin have been investigated by Scanning Electron Microscopy (SEM) in a few catfishes by Reutter (1978), Mittal & Whitear (1979), Ono (1980), Whitear (1986), and Arratia (1987a).

Even though the scaleless skin is a distinctive characteristic of catfishes (Regan 1911, Fink & Fink 1981), it has rarely been considered in either diagnoses or descriptions of catfishes. Exceptions are Arratia & Menu Marque (1981, 1984), Arratia (1983a, 1987a), Howes (1983), de Pinna (1988, 1992), and Schaefer et al. (1989). Armoured catfishes have received more attention, and the presence and number of plates and denticles have served to characterize certain taxa.

Of the thirty-four recognized Recent catfish families (Nelson 1994), the Diplomystidae is considered as the plesiomorphic sister group of all other families (Fig.1; Grande 1987, Mo 1991, Arratia 1992). A skin with large, simple or lobulated papillae embedded in a colloid-like substance is one of the diagnostic features of the family Diplomystidae (Arratia 1987a). The presence of white papillae on the lips and soft, grey elongate projections ("pelos" = hairs of Leybold) covering the entire body of fresh specimens was first mentioned by Leybold (1859) for *Arius carcharioides* (= *Diplomystes chilensis*). Considering the importance of the family for phylogenetic studies of siluroids, a detailed study of the neuromast lines and of the surface of the skin of *Diplomystes* is presented here. In addition, the neuromast lines and the skin of the loricarioid Nematogenyidae, a primitive family considered by some as the plesiomorphic sister group of the other loricarioids (Fig.1; Howes 1983, Schaefer 1987, Arratia 1990a, de Pinna 1992) is also investigated with light and SEM microscopy and it is compared with the skin of other loricarioids.

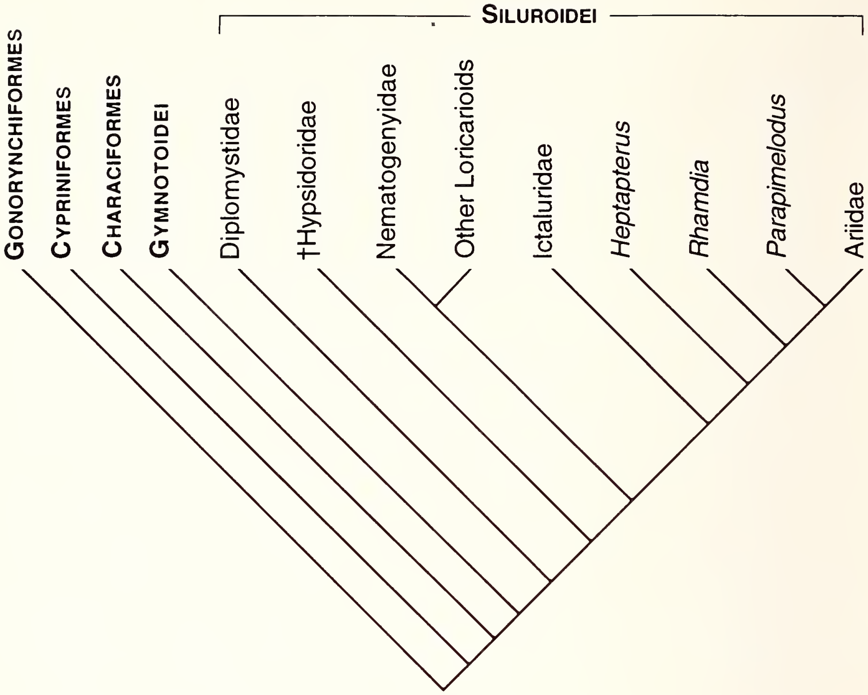

Fig.1: Scheme of an hypothesis of relationships of the catfishes studied and their phylogenetic position among ostariophysans (after Arratia 1992).
†: fossil group.

The goals of this research are: (1) Description of the lateralis system – mainly of the sensory canals associated with the skull roof – of certain catfishes such as *Diplomystes* spec., *Diplomystes* aff. *chilensis, D. camposensis, Nematogenys inermis, Trichomycterus areolatus, "Trichomycterus" mendozensis*, and *Hatcheria macraei* because the superficial neuromast lines commonly follow the path of the sensory canals. (2) Description of the superficial neuromasts, and pit lines in some catfishes. (3) Detailed description of the skin, mainly the epidermis, of *Diplomystes* spec., *Diplomystes* aff. *chilensis, D. camposensis, Nematogenys inermis, Trichomycterus areolatus, "Trichomycterus" mendozensis*, and *Hatcheria macraei* with comparative comments on other catfishes. (4) Interpretation of morphological characters and systematic and evolutionary significance of the variation observed. This point is strongly limited because the scarce information about most catfishes. (5) Comparison of the skin of benthic freshwater catfishes which have similar feeding diets, to test the hypothesis that the degree to which gustatory receptors are developed morphologically in different species is related to the environment, and in particular to the variety of food present in the latter (Meyer-Rochow 1981), and the existence of a correlation between the extent of development of the receptors and habits and/or ecology (Hoagland 1933, Moore et al. 1950, Lowenstein 1957, Branson & Moore 1962, Saglio 1992). The fourth point requires the description of the habitat and feeding of the species studied; such information is also presented. Therefore the description of the skin of each species is followed by an abbreviated description of its habitat preferences and diet.

Preparation of the samples for SEM of *Diplomystes* aff. *chilensis, Nematogenys inermis* and *Trichomycterus areolatus* were done by L. Huaquín, as well as most of the histological cross sections. Descriptions and interpretations are responsability of the senior author.

METHODS

The trajectory of the cephalic sensory canals and the presence of pores was checked in alcoholic specimens, dry skeletons, and cleared and stained specimens. Most of the specimens were cleared and double stained following Arratia & Schultze (1992); a few of them were prepared following Dingerkus & Uhler (1977).

Skins of siluroids of different sizes and of both sexes were examined by light microscopy (WILD M5 and M6 microscopes) to check for the presence of epidermal papillae, and superficial neuromasts on the body, fins, and also the palatal region and to check the pores of the lateralis system,

The barbels, upper lip, palatal region, dorsal region of the head between the eyes or between the nasal openings, body lateral line just posterior to the posttemporo-supracleithral region, pectoral, caudal, and adipose fins were prepared for observation with SEM. Parts of a few specimens were prepared for histological sections to check the SEM observations.

Specimens examined with SEM were anaesthetized with MS-222, killed by decapitation and fixed immediately after death. The specimens were not treated with mucolex. Fixation was in glutaraldehyde of various strengths (3–5 %), phosphate buffered to pH 7.4 and postfixation in osmium tetroxide. Dehydration was in graded acetone. The specimens were critical point dried (Anderson 1951) and sputter coated with gold (Polaron E 3000, E 5000) and examined in a Cambridge S4–10 or a Siemens Scanning Electron Microscope.

Specimens used for preparation of histological serial cross sections were fixed with alcoholic Bouin and stained with hematoxylin and eosin and three chromic of Mallory.

All illustrations were prepared by G. Arratia, the drawings were executed with the help of Wild FM5 and Olympus microscopes.

MATERIALS EXAMINED

Skins of catfish species prepared as serial cross sections and for SEM microscopy are listed below; part of the samples are kept at the Laboratorio of Biología, Facultad de Ciencias Forestales, Universidad de Chile, Santiago, and another part is kept by the senior author.

Ariidae

Galeichthys peru ianus Lütken: 175 mm standard length (SL) specimen from coastal region of Arica, northern Chile.

Diplomystidae

Diplomystes camposensis Arratia: Specimens of about 140–160 mm SL from San Pedro river in southern Chile.
Diplomystes aff. *chilensis* (Molina): Specimen of about 135 mm SL from the central part of Chile (Cachapoal river). The fishes are externally similar to *D. chilensis* but they differ in skin characters; other internal features have not been investigated due to the scarce number of specimens [2].
Diplomystes spec. (*sensu* Arratia 1987a): Specimens of 120–155 mm SL from the central part of Chile (Rapel and Maule basins).

Nematogenyidae

Nematogenys inermis (Guichenot): Specimens of 80–185 mm SL from central part of Chile (Cachapoal river).

"Pimelodidae"

Pimelodus spec.: Specimen of 180 mm SL from northern Argentina.

Trichomycteridae

Hatcheria macraei (Girard): Specimens of 145 mm SL from Coyaique, southern Chile; and specimens of 70–130 mm SL from western Argentinian Patagonia (Malargüe river, Mendoza).
Trichomycterus areolatus Valenciennes: Specimens of 60–125 mm SL from central part of Chile (Maipo basin).
"Trichomycterus" mendozensis Arratia, Chang, Menu Marque & Rojas: Specimens of 45–70 mm SL from Blanco river at Mendoza, Argentina.

The material listed below was used for comparative studies of the cephalic sensory canals, body lateral line, of epidermal papillae, superficial neuromast lines, and for preparation of serial cross sections.

Institutional abbreviations are as listed in Levinton et al. (1985) with the following exception: PC: private collection of G. Arratia. Species are listed alphabetically within each higher taxon. The abbreviations for cleared and stained material is "C & S"; for alcoholic specimens is "alc"; for examined specimens is "sp"; for dry skeleton is "dry skel."

Halecomorphi

Amia calva: KU 3883, 7 sp, C & S; KU 9051, 1sp, alc; KU 21290, 4sp, C & S; KU 21607, 1sp, C & S; and several dry skeletons. PC uncat., 4 sp, alc.

Elopomorpha

Elops affinis: SIO 69–187, 1sp, C & S; UCLA ST 0–29, 4 sp, C & S.
Elops hawaiensis: CAS-SU 35103, 1 dry skel.
Elops saurus: ANSP 147401, 2 sp, C & S; CAS(SU) 10847, 1 dry skel; CAS(SU) 45172, 1 sp, C & S; KU 3053, 3 sp, C & S; OS 5105, 2 sp, C & S; TCWC 0782–1, 3 sp, C & S; UMMZ 194313-S, 1 dry skel; UMMZ 194982-S, 1 dry skel. UNC 13093, 1 sp, alc.

Osteoglossomorpha

Hiodon alosoides: KU 16146. 6 sp. alc.; and numerous sp. alc.

Clupeomorpha

Chirocentrus dorab: KU 10518. 1 sp. alc.
Clupea harengus: PC 25986. 14 sp. C & S and 3 sp. alc.
Coilia nasus: KU uncat., 1 sp. C & S: PC 020989. 9 sp. C & S and 4 sp. alc.
Coilia ectenes: PC 170187. 3 sp. alc.
Denticeps clupeoides: MARC 73–32-P-4915–932. 3 sp. C & S: MRAC 76–32-P-4915–932. 1 sp. C & S: ZMUC 17169. 2 sp. C & S: NMC 63–0017. 1 sp. C & S; PC 515600. 3 sp. alc.
Dorosoma cepedianum: KU 16767. 3 sp. C & S: KU 21802. 36 sp. C & S and numerous sp. alc.
Engraulis encrasicholus: KU 19941. 8 sp. C & S.

Esocoidei

Esox americanus: KU 6041. 4 sp. C & S; KU 17864. 4 sp. C & S.
Esox lucius: KU 19092. dry skel.

Salmonidae

Onchorynchus mykiss: KU 12463. 13 sp. C & S: PC 080888. 15 sp. alc.
Prosopium williamsoni: PC 161046. 14 sp. C & S.
Thymallus thymallus: PC 161045. 2 sp. alc.. 40 sp. C & S.

Ostariophysi
Gonorynchiformes

Chanos chanos: CAS-SU 35075. 1 dry skel; CAS-SU 38340. 2 sp. C & S: FMNH 91775. 4 sp. alc; UMMZ 196864. 1 sp. C & S: PC uncat.. 1 sp. alc; PC uncat.. 1 sp.. alc; SIO 80–199. 7 sp. C & S.

Cypriniformes

Carassius aureatus: KU 14240. 1 sp. alc.
Cyprinus carpio: KU 3739. 1 sp. alc: KU 3790. 1sp. C & S: KU 15429. 1 sp. alc.
Dionda episcopa: KU 7427. 5 sp. C & S.
Notropis lutrensis: KU 12089. 2 sp. C & S; KU 15336. 1 sp. dry skel: KU 15793. 6 sp. C & S: KU 21377. dry skel; and numerous sp. alc.
Opsariichthys bidens: CAS-SU 32512. 2 sp. C & S; CAS-SU 68907. 2 sp. C & S: PC 22. 4 sp. C & S and 5 sp. alc.
Zacco platypus: KU 12320. 3 sp. alc: PC 21. 10 sp. C & S and 1 sp. alc.

Characiformes

Brycon argenteus: KU 10543. 2 sp. C & S; KU 10543. 3 sp. alc.
Cheirodon pisciculus: PC 130173. 10 sp. C & S; numerous sp. alc.
Gymnocharacinus bergi: KU 19199. 1 C & S: PC. uncat., 2 sp. alc.
Hoplias malabaricus: KU 13636. 3 sp. C & S: KU 13646. 2 sp. C & S and 3 sp. alc.
Xenocharax spilurus: CAS-SU 15639. 2 sp. C & S: CAS 115707. 1 sp. alc.

Siluroidei

Ariidae

Arius felis: KU 19590, 10 sp, C & S and 3 sp, alc.
Galeichthys peruvianus: ZMH 6667, 1 sp, alc.
Bagre marinus: KU 3053, 3 sp, C & S and 1 sp, alc; KU 21380, 1 dry cranium.

Astroblepidae

Astroblepus spec.: ANSP 138981, 14 sp, alc; KU 2010, 3 sp, C & S; numerous sp, alc.

Callichthyidae

Callichthys callichthys: KU 13721, 1 sp, alc; KU 13722, 3 sp, C & S.

Diplomystidae

Diplomystes camposensis: IZUA uncat., 5 sp, alc; KU 19209, 3sp, alc; KU 19210, 1 sp, C & S; PC 011086b, 3 sp, C & S; PC 220189, 17 sp, alc.
Diplomystes chilensis: CAS-SU 13706, 2 sp, alc; MCZ 8290, 2 sp, C & S.
Diplomystes nahuelbutaensis: CAS-SU 55423, 1 sp, alc, CAS-SU 55425, 1 sp, C & S; PC. 230186, 3 sp, C & S; IZUA uncat., 5 sp, alc.
Diplomystes spec.: KU 19255, 1 sp, alc; KU 19256, 1 sp, alc.
Olivaichthys viedmensis: FMNH 58004, 3 sp, C & S, and 5 sp, alc.

Ictaluridae

Ameiurus catus: KU 1741, 1 dry cranium; KU 8332, 2 sp, C & S; KU 10151, 3 sp, C & S; KU 10151, 10 sp, alc; numerous sp, alc.
Ameiurus melas: KU 1083, 1 sp, C & S; KU 14688, 3 sp, alc.; KU 15181, 2 sp, C & S; numerous sp, alc.
Ictalurus furcatus: KU 1747, 1 dry cranium; KU 5005, 2 sp, alc; KU 11343, 1 dry cranium.
Ictalurus punctatus: KU 4162, 32 sp, alc; KU 9657, 9 sp, C & S; an ontogenetic series.
Noturus exilis: KU 17229, 61 sp, C & S and 2 sp, alc; numerous sp, alc.
Pylodictis olivaris: KU 1746, 3sp, C & S; KU 2386, 1 sp, dry skel; numerous sp, alc.

Loricariidae

Plecostomus plecostomus: KU 13948, 2 sp, C & S.
Loricaria filamentosa: KU 13779, 2 sp, alc.
Loricaria uracantha: KU 17710, 2 sp, C & S.
Loricariichthys sp.: ANSP, 2 sp, C & S.

Nematogenyidae

Nematogenys inermis: KU 19238, 9 sp, alc; KU 19239, 6 sp, alc; PC 202, 10 sp, alc; PC 206, 3 sp, C & S; PC 214, 4 sp, alc; PC 010288, 1 sp, alc; PC 051188, 1 sp, alc; PC 30873, 6 sp, C & S.

"Pimelodidae"

Heptapterus mustelinus: KU 21235, 4 sp, C & S; PC 17583, 2 sp, C & S and 3 sp, alc.
Parapimelodus valenciennis: KU 21804, 10 sp, C & S; PC 010186, 5 sp, alc.

Pimelodus maculatus: PC 271282, 2 sp, C & S.
Pimelodus spec.: KU 21805, 2 sp, C & S; ZMH uncat., 1 sp, alc.
Rhamdia sapo: KU 21806, 3 sp, C & S; PC 100285, 3 sp, alc; PC 171887, 1 sp, alc.
Rhamdia wagneri: KU 20013, 3sp, C & S, and 3 sp, alc.

Trichomycteridae

Bullockia maldonadoi: KU 19371, 20 sp, C & S; PC 1374 1, sp, alc; PC 21986, 20 sp, C & S; numerous sp, alc.
Eremophilus mutisii: AMNH 56092, 1 sp, alc; CAS-SU 62920, 2 sp, C & S; PC uncat., 3 sp, alc.
Hatcheria macraei: KU 19202, 3 sp, alc; KU 19273, 2 sp, C & S; PC 126, 1sp, alc.
Malacoglanis gelatinosus: CAS(SU) 50755, 1 sp, C & S.
Ochmacanthus reinhardti: KU 13726, 1 sp, C & S; KU 131127, 1 sp, alc.
Sarcoglanis simplex: CAS(SU) 50189, 1 sp, alc.
Scleronema sp.: PC uncat., 2 sp, C & S, and 2 sp, alc.
Trichomycterus areolatus: KU 19308, 6 sp, C & S; KU 19423, 20 sp, C & s; KU 221081, 20 sp, C & S; PC 030882, 17 sp, alc; PC 070189, 9 sp, alc; PC 221185, 3 sp, alc.
Trichomycterus boylei : PC 230280–1, 14 sp, alc; PC 230280–2, 10 sp, alc.
Trichomycterus chiltoni: KU 19229, 9 sp, C & S and 15 sp, alc.
Trichomycterus metae: V-5852, 1 C & S and 1, sp, alc.
Trichomycterus nigricans: MNHN B.251, 1 sp, alc.
Trichomycterus rivulatus: CAS-SU 14851, 30 sp, alc; KU 19181, 3 sp, C & S; KU 19187, 25 sp, alc.
Trichomycterus roigi: PC 230281–1, 13 sp, C & S; numerous sp, alc.
"Trichomycterus" mendozensis: KU 19200, 30 sp, alc and 10 sp, C & S. This species will be removed from the genus *Trichomycterus* (Arratia, manuscript).
Tridentopsis pearsoni: CAS(SU) 56200, 2 sp, C & S; PC uncat., 2 sp, alc. and 2 C & S.
Vandellia cirrhosa: AMNH 20497, 1 sp, C & S; UMMZ 205178, 10 sp, C & S.

Gymnotoidei

Gymnotus carapo: KU uncat., 1sp, alc; KU 13793, 9 sp, C & S.
Gymnotus cylindricus: KU 1869, 2 sp, C & S.
Hypopomus brevirostris: KU 13800, 7 sp, C & S and 3 sp, alc.
Hypopygus lepturus: KU 20127, 1 sp, C & S.

TERMINOLOGY

The identification of the cephalic sensory canals follows Northcutt (1989). The identification of the cuticular layer follows Whitear (1970, 1986).

For comparative purposes the identification of taste buds (TBI, II, or III) according to their external morphology follows Reutter (1973, 1978) and Reutter et al. (1974) when possible; otherwise, the taste buds are identified as TBs. Taste buds that rise above the surface of the skin in high epidermal papillae, but are surrounded by deep furrows are identified as TBIs. Taste buds as volcano-like structure are identified as TBIIs. Taste buds that

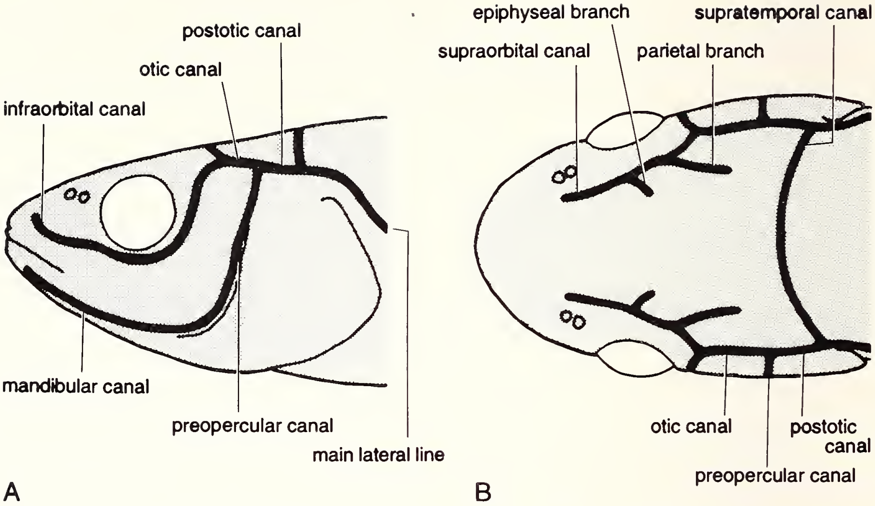

Fig.2: Diagrammatic representation of the cephalic sensory canal in advanced non-siluroid ostariophysans. A: Lateral view; B: Dorsal view.

do not arise above the surface of the skin are identified as TBIIIs. TB I is innervated mainly by cholinergic nerves, and TB II and TB III by aminergic and cholinergic nerves equally (Reutter 1973, Reutter et al. 1974). "Taste buds always are innervated by fibers derived from either the facial (VII), glossopharyngeal (IX), or vagal cranial nerves. This is true whether the taste buds are within the orobranchial cavity or spread across the animal's body surface, as in Ictaluridae and many Cyprinidae. The external taste buds are innervated by branches of the facial nerve; in many species (e.g., *Ictalurus*), a recurrent branch of the facial nerve exits from the skull caudally to innervate the taste buds on the flanks, fins, or tail." (Finger 1988: 349). The study of the innervation of taste buds in the diplomystids and loricarioids is outside the scope of the present paper.

Identification of pit-organs in catfishes follows Müllinger (1964) and Wachtel & Szamier (1969) for small pit-organs (= ampullary organs, electroreceptors), and Herrick (1903a), Flock (1971), and Coombs et al. (1988:565–567, fig.22.8) for large pit-organs or superficial neuromasts (mechanoreceptors). Superficial neuromasts as papillate neuromasts have been observed in the catfishes examined; they sit on a dermal stalk formed by the evagination of the basement membrane. The papillate pit-organ is elevated by a slight or pronounced evagination of the dermis, and it may sit in an intraepidermal pit (Coombs et al. 1988).

Identification of cell bearing protrusion follows Whitear & Mittal (1986) and of unculi and unculiferous plaques follows Roberts (1982).

The special terminology of Andean torrential rivers is briefly explained here. The Rhitron (Fig.2; Illies 1961, Ringuelet 1975, Campos 1984) is a section of a river characterized by high water speed, turbulence, and saturation of O_2, and low flow; the monthly average

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pore 1 of the otic canal; PA: parietal bone; po1: pore 1 of postotic canal; prec: preopercular canal; PT: pterotic; PTT: postemporal bone; s1–8: pores 1–8 of supraorbital canal; sobc: supraorbital canal; SOC: supraoccipital bone; SPH: sphenotic.

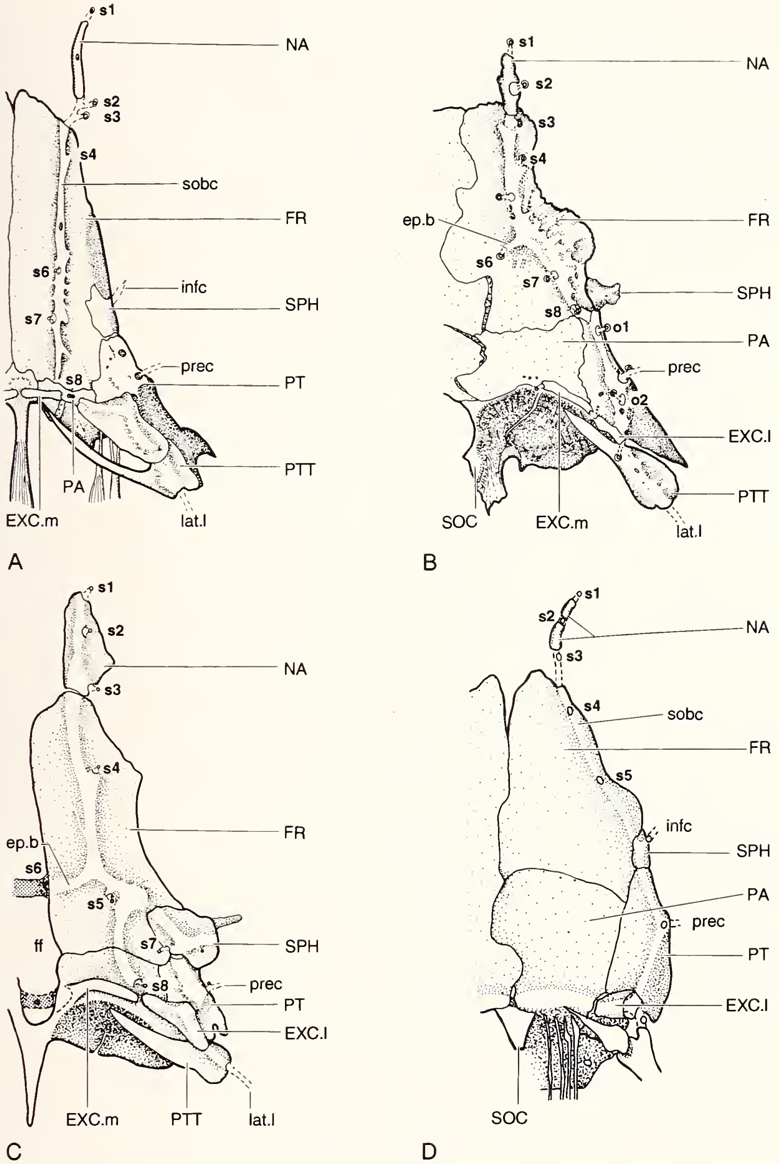

Fig.3: Trajectory of the sensory canals in the skull roof of certain primitive ostariophysans. A: gonorynchiform *Chanos chanos* Forsskål (CAS 38340); B: cypriniform *Opsariichthys bidens* Günther (CAS 15639); C: characiform *Xenocharax spilurus* Günther (CAS 32512); D: gymnotoid *Gymnotus cylindricus* (KU 18690). The supratemporal canal (not labeled) passes through the extrascapular bones.

ep.b: epiphyseal branch; EXC.l: lateral extrascapular bone; EXC.m: medial extrascapular bone; ff: frontal fontanel; FR: frontal bone; infc: infraorbital canal; lat.l: main lateral line; NA: nasal bone; o1:

water temperature is less than 20°C. The substratum is formed by fixed rocks, movable stones, gravel, and sand. The Rhitron is poor in plants and animals. Usually, a few small filamentous algae may survive fixed to the substratum. The Potamon is characterized by low water speed and turbulence. The turbidity is medium to high, with a deficit of O_2 and limited light. The monthly average water temperature is greater than 20°C. The substratum of the river is formed by mud, sand, or gravel.

The terms siluroids or Siluroidei are used herein for catfishes alone and the terms siluriforms and Siluriformes for catfishes and gymnotoids following the phylogenetic hypotheses of ostariophysan relationships by Fink & Fink (1981) and Arratia (1992).

LATERAL LINE SYSTEM

Primitively, the lateralis system of catfishes includes complete cephalic sensory system and a complete body lateral line. The cephalic sensory system (Figs.2A, B, 3A-D) in ostariophysans comprises the supratemporal, postotic or temporal, otic, supraorbital, infraorbital, preopercular, and mandibular canals. The cephalic sensory system in catfishes is formed by the same canals with the exception of the supratemporal which is missing (Figs.4B, 5B; e.g., Wright 1884, Collinge 1895, Pollard 1892, Lekander 1949, Chardon 1968, Taylor 1969, Lundberg 1982, Bailey & Stewart 1984, Skelton et al. 1984, Arratia 1987a). The generalized condition of the cephalic sensory canals in catfishes is as follows:

1) The otic canal runs in the extrascapular, pterotic, and sphenotic bones.
2) The supraorbital canal runs in the parieto-supraoccipital and in the frontal and nasal bones.
3) The infraorbital canal runs in the sphenotic, a series of infraorbital bones, and the antorbital bone [= infraorbital 1 or lacrimal according to some authors]. However, the bone identified here as the antorbital is the first to ossify among the circumorbital series in small diplomystids (Fig.6), nematogenyids, and ictalurids, as the antorbital does in other teleosts (see also Lekander 1949:66), and the dorsal branch or antorbital branch of the infraorbital canal is associated with the antorbital line or the caudal fork replacement of the infraorbital canal (see below).
4) In most catfishes the supraorbital, infraorbital, and otic canals unite with each other in the sphenotic. The union of the three canals is also observed in characiforms and gymnotoids (Fig.3C-D; Arratia and Gayet in press) but it was not observed in gonorynchiforms (e.g., *Chanos*) where the supraorbital canal extends posteriorly from the frontal to the parietal without reaching the sphenotic (Fig.3A) and in cypriniforms (Fig.3B; Lekander 1949: figs.20, 21, 24-27, 36).
5) The infraorbital canal exits from the sphenotic in most catfishes except ictalurids where it exits from the frontal (Lundberg 1982), commonly.
6) The preopercular canal exits from the pterotic bone.

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percle; p.potc: pore of postotic canal; PT: pterotic; pt.b: pterotic branch; p.sobc: pores of supraorbital canal; ro.l: rostral line (fork replacement of supraorbital canal); s1–8: pores 1–8 of supraorbital canal; sobc: supraorbital canal; SOC: parieto-supraoccipital bone; SPH: sphenotic; SPOP: suprapreopercle; stt.l: supratemporal accessory line.

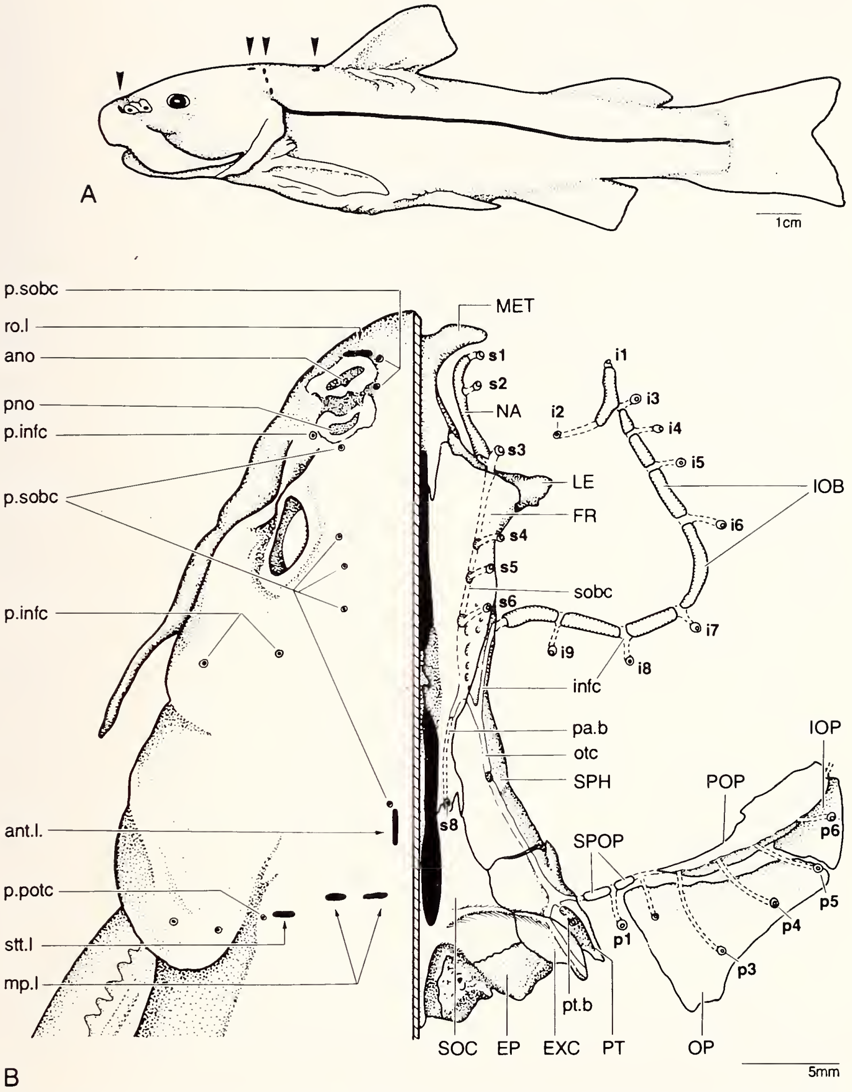

Fig.4: Cephalic sensory canals and superficial neuromast lines in *Diplomystes chilensis* (Molina). A: Superficial neuromast lines (indicated by arrowheads) and body lateral line enclosed by ossicles (thick black line); B: Distribution of superficial neuromasts and pores of the sensory canals (left) and their relationships to cranial, infraorbital, and opercular bones (right side).

anb.l: antorbital line; ano: anterior nasal opening; ant.l: anterior pit line; EP: epioccipital; EXC: extrascapular bone; FR: frontal bone; infc: infraorbital canal; i1–9: pores 1–9 of infraorbital canal; IOB: infraorbital bone; IOP: interopercle; LE: lateral ethmoid; MET: mesethmoid; mp.l: middle pit line; NA: nasal bone; OP: opercle; otc: otic canal; p1–6: pores 1–6 of preopercular canal; pa.b: parietal branch of supraorbital canal; p.infc: pores of infraorbital canal; pno: posterior nasal opening; POP: preo-

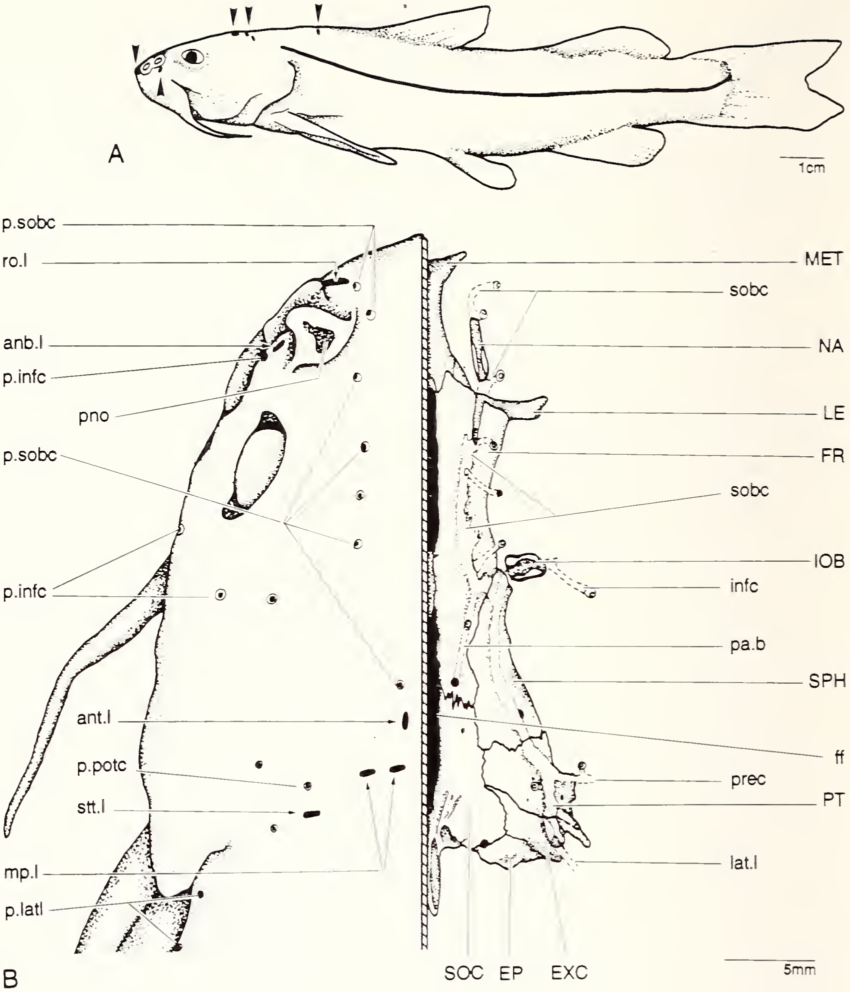

Fig.5: *Diplomystes camposensis* Arratia. A: Superficial neuromast lines (indicated by arrowheads) and main lateral line enclosed by ossibles (thick black line); B: Distribution of superficial neuromasts and pores of the sensory canals (left) and their relationships to cranial bones (right).
anb.l: antorbital line; ant.l: anterior pit line; EP: epioccipital; EXC: extrascapular bone; ff: frontal fontanel; FR: frontal bone; infc: infraorbital canal; IOB: infraorbital bone; lat.l: main lateral line; LE: lateral ethmoid; MET: mesethmoid; mp.l: middle pit line; NA: nasal bone; pa.b: parietal branch; p.infc: pores of infraorbital canal; p.latl: pores of main lateral line; pno: posterior nasal opening; p.sobc: pores of supraorbital canal; p.potc: pore of postotic canal; prec: preopercular canal; PT: pterotic; ro.l: rostral line (fork replacement of supraorbital canal); sobc: supraorbital canal; SOC: parieto-supraoccipital bone; SPH: sphenotic; stt.l: supratemporal accessory line.

In primitive teleosts the infraorbital canal bifurcates in the antorbital bone into the antorbital branch that extends dorsally and is associated with the caudal fork replacement of the infraorbital canal and an anterior branch which connects with the other side by the ethmoidal commissure. This is the condition observed in pholidophorids (Nybelin 1966) and in certain Recent teleosts (e.g., elopids; Nybelin 1967, Arratia 1987b, present paper). In ostariophysans the infraorbital canals do not connect by an ethmoidal commissure which is absent, the infraorbital canal is associated with a series of neuromasts belonging to the fork replacement line of the infraorbital canal.

The common condition in teleosts is the absence of an anterior union between supraorbital and infraorbital canals. However, the union of both canals is observed in some catfishes such as *Heptapterus mustelinus* where the antorbital branch of the infraorbital canal joins the second tubule of the supraorbital canal and only one pore is present at the confluence of both canals (Arratia 1987a: fig.39B). The confluence of both canals, without a pore, is found in *Heptapterus sympterygium* (Buckup 1988: fig.5). This condition in *Heptapterus* is interpreted herein as a derived character state. The union of both canals has also been described and illustrated in *Noturus exilis* by Taylor (1969: fig.1).

The supratemporal canal is unknown in catfishes, contrary to other ostariophysans where it passes through the extrascapular bones (compare Figs.3A-D and 4B, 5B, 7B). This absence is a synapomorphy of siluroids. Gayet (1988: figure on page 834) illustrated a series of pits placed transversally in the extrascapular bone running onto the supraoccipital which were identified in the figure as the supratemporal commissure. According to Gayet (1988: 834) the new fossil (†) genus *Andinichthys* and the new family †Andinichthyidae are characterized by the presence of a supratemporal commissure as a true canal running in the extrascapulae and extending as a groove onto the parieto-supraoccipital ("présence

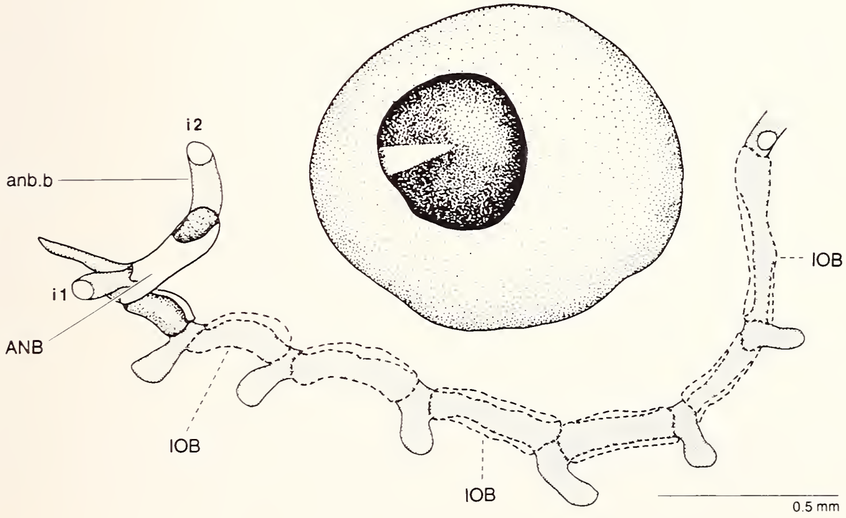

Fig.6: *Diplomystes camposensis* Arratia. Infraorbital canal (dotted) and its relationships to the antorbital bone (completely ossified) and infraorbital bones (which begin to ossify) in a young individual of 19 mm standard length. Note that pores 1 and 2 are open whereas all other tubules are still closed.
ANB: antorbital bone; anb.b: antorbital branch; IOB: infraorbital bones; i1–2: pores 1–2 of infraorbital canal.

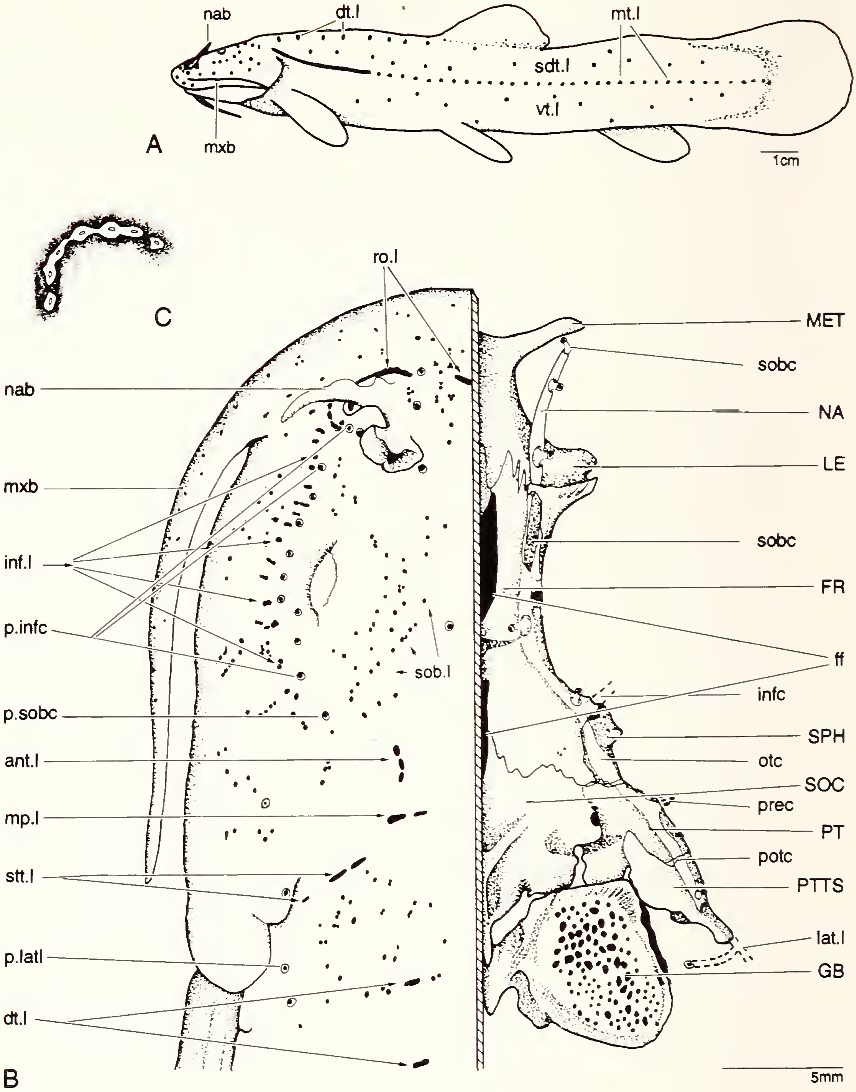

Fig.7: *Nematogenys inermis*(Guichenot). A: Superficial neuromast lines and body lateral line enclosed by ossicles (thick black line); B: Distribution of superficial pit lines, isolated superficial neuromasts, and pores of the cephalic sensory canal (left) and their relationship to cranial bones (right side); C: Enlargement of the rostral pit line.

ant.l: anterior pit line; dt.l: dorsal trunk line; ff: frontal fontanel; FR: frontal bone; GB: gas bladder capsule; infc: infraorbital canal; inf.l: infraorbital line; lat.l: main lateral line; LE: lateral ethmoid; MET: mesethmoid; mp.l: middle pit line; mt.l: middle trunk line; mxb: maxillary barbel; NA: nasal bone; nab: nasal barbel; otc: otic canal; p.infc: pores of infraorbital canal; p.latl: pores of lateral line; potc: postotic canal; prec: preopercular canal; p.sobc: pores of supraorbital canal; PT: pterotic; PTTS:

d'une commissure supratemporal existant, en tant que véritable canal, sur les extrascapulaires, et sous forme de gouttiére, sur le supraoccipital"). Gayet (1988:835) interpreted the presence of the "true" canal running medially in direction of its antimere as an argument to consider this canal-bearing bone a lateral extrascapula and the medial extrascapula, probably fused with the parieto-supraoccipital, as lost. Further study on the same material showed that a "true" supratemporal canal running in the extrascapular and parieto-supraoccipital is absent in the holotype of *Andinichthys*; but a rudimentary canal is present in one specimen (Arratia & Gayet in press: figs.2A, 3B).

There is variation in the organization of the lateralis system that may be formed by simple or ramified canals. Primitively, the cephalic sensory system in ostariophysans is formed by narrow, simple canals that give off short, narrow, and simple tubules that open to the skin surface by one pore per tubule. This is the generalized condition observed in a variety of catfishes such as diplomystids (Figs.4B, 5B; Arratia 1987a: figs.4A, 6B, 22A), nematogenyids (Fig.7B), other loricarioids (Figs.8C-F, 9A-F; Baskin 1970: figs.7, 14, 20; Arratia & Menu Marque 1984: figs.4A, 12A, B; Schaefer 1987: fig.4; see below), ictalurids (Wright 1884, Collinge 1895, Taylor 1969, Lundberg 1982, Arratia & Gayet in press), bagrids (Mo 1991), and †*Hypsidoris* and †*Astephus* from the Tertiary of North America (Arratia & Gayet in press). Advanced character states of the structure of the cephalic sensory system include:

1. The presence of broad and simple canals, observed in certain catfishes such as the "pimelodids" *Heptapterus* and *Rhamdia* (Fig.10A, B; Arratia & Gayet in press: fig.9A, B).
2. Canals that ramify during ontogeny, present in certain catfishes such as the "pimelodid" *Parapimelodus* (Arratia & Schultze 1990: fig.8B, Arratia and Gayet in press: fig.7B), and the ariid *Arius felis*, as shown by growth series of these species (Fig.10D). Ramified canals are also known from Plotosidae (Lekander 1949) and in Pimelodinae (Lundberg 1991). Probably, this condition was also present in the fossil catfishes †*Andinichthys*, †*Hoffstetterichthys*, and †*Incaichthys* from the Paleocene of Bolivia (Arratia & Gayet in press).

During the evolution of catfishes the lateralis system has undergone several changes that include (1) the loss of certain segments of the cephalic sensory system and of the body lateral line, and (2) appearance of some new sensory tubules.

Most catfishes, e.g., diplomystids, ictalurids, "pimelodids", ariids, and nematogenyids have a complete cephalic sensory system (Figs.4B, 5B, 7B, 8A, B), with the exception of the supratemporal canal which is absent. However, other catfishes such as certain loricarioids show a trend to loose some segments of the cephalic sensory system. For instance:

1) Supraorbital canal. The common pattern of the supraorbital canal is a continuous canal running in the frontal and nasal bones (Figs.4B, 5B, 7B, 8A, B) in Recent catfishes as well in most other primitive ostariophysans (Fig.3A-D). Among primitive loricarioids this condition is present in *Nematogenys* (Fig.8B), in the copionodontines *Copionodon* and *Glaphyropoma* (de Pinna 1992: fig.17), and in the trichomycterines *Hatcheria* (Fig.8F) and *Bullockia* (Fig.9A), whereas the canal is interrupted

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posttemporo-supracleithrun; ro.l: rostral line (fork replacement of supraorbital canal plus rostral fork replacement of infraorbital canal); sdt.l: subdorsal trunk line; sob.l: supraorbital accessory line; sobc: supraorbital canal; SOC: parieto-supraoccipital bone; SPH: sphenotic; stt.l: supratemporal accessory line; vt.l: ventral trunk line.

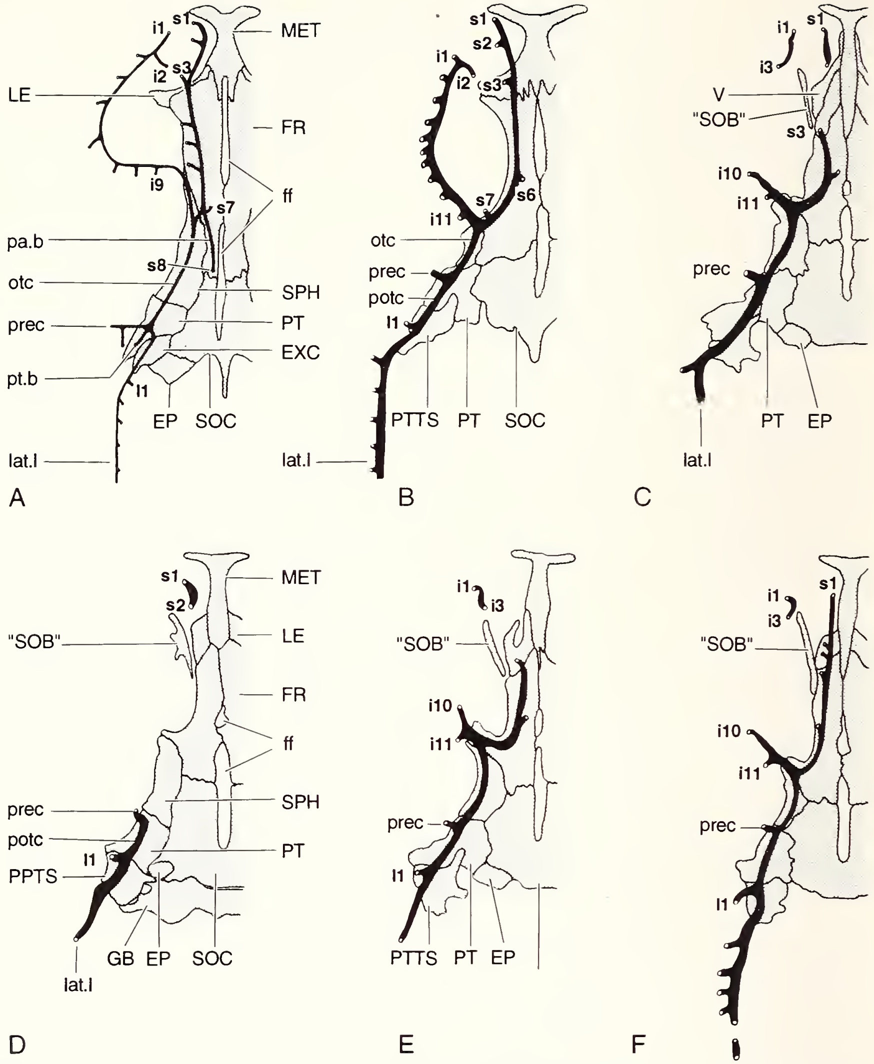

Fig.8: Diagrammatic dorsal aspect of the cranium of certain diplomystids and loricarioids illustrating the trajectory of the cephalic sensory canals (in black) and pores of the sensory canals. A: *Olivaichthys viedmensis* (Mac Donagh); B: *Nematogenys inermis* Guichenot; C: *Trichomycterus rivulatus* Valenciennes; D: *"Trichomycterus" mendozensis* Arratia et al.; E: *Eremophilus mutissi* Humboldt; F: *Hatcheria macraei* (Girard).

EP: epioccipital; EXC: extrascapular bone; ff: frontal fontanel; FR: frontal bone; GB: gas bladder capsule; i1–11: pores 1–11 of infraorbital canal; l1: pore 1 of main lateral line; lat.l: main lateral line and pores; LE: lateral ethmoid; MET: mesethmoid; otc: otic canal; pa.b: parietal branch; potc: postotic canal; prec: preopercular canal; PT: pterotic; pt.b: pterotic branch; PTTS: posttemporo-supracleithrum; s1–8: pores 1–8 of supraorbital canal; "SOB": tendon-bone supraorbital; SOC: parieto-supraoccipital bone; SPH: sphenotic; V: vomer.

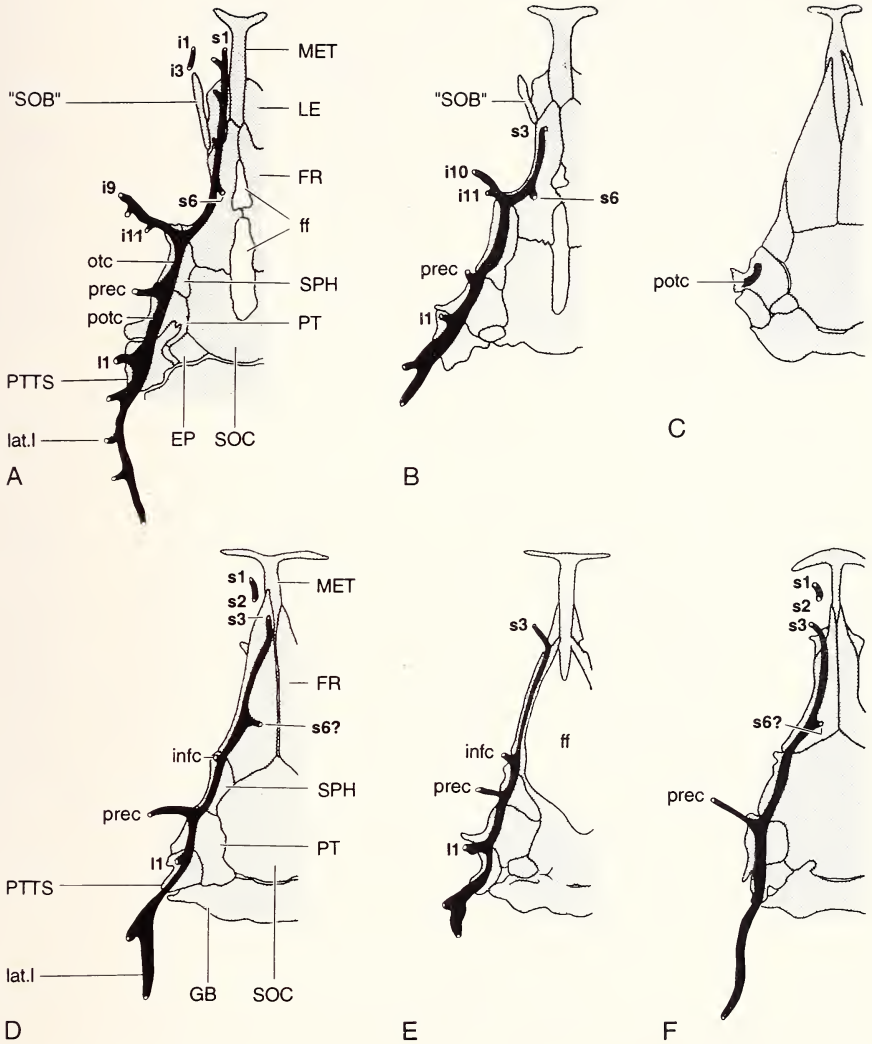

Fig.9: Diagrammatic dorsal aspect of the cranium of certain loricarioids illustrating the trajectory of the cephalic sensory canals (in black) and pores of the sensory canals. A: *Bullockia maldonadoi* (Eigenmann); B: *Scleronema* spec.; C: *Listrura nematopteryx* de Pinna (after de Pinna 1988); D: *Ochmacanthus rheinhardti* (Steindachner); E: *Tridentopsis pearsoni* (Myers); F: *Vandellia cirrhosa* Valenciennes.

EP: epioccipital; ff: frontal fontanel; FR: frontal bone; GB: gas bladder capsule; i1–11: pores 1–11 of infraorbital canal; infc: infraorbital canal; l1: pore 1 of main lateral line; lat.l: main lateral line and pores; LE: lateral ethmoid; MET: mesethmoid; otc: otic canal; potc: postotic canal; PT: pterotic; PTTS: posttemporo-supracleithrum; s1–6: pores 1–6 of supraorbital canal; "SOB": tendon-bone supraorbital; SOC: parieto-supraoccipital bone; SPH: sphenotic.

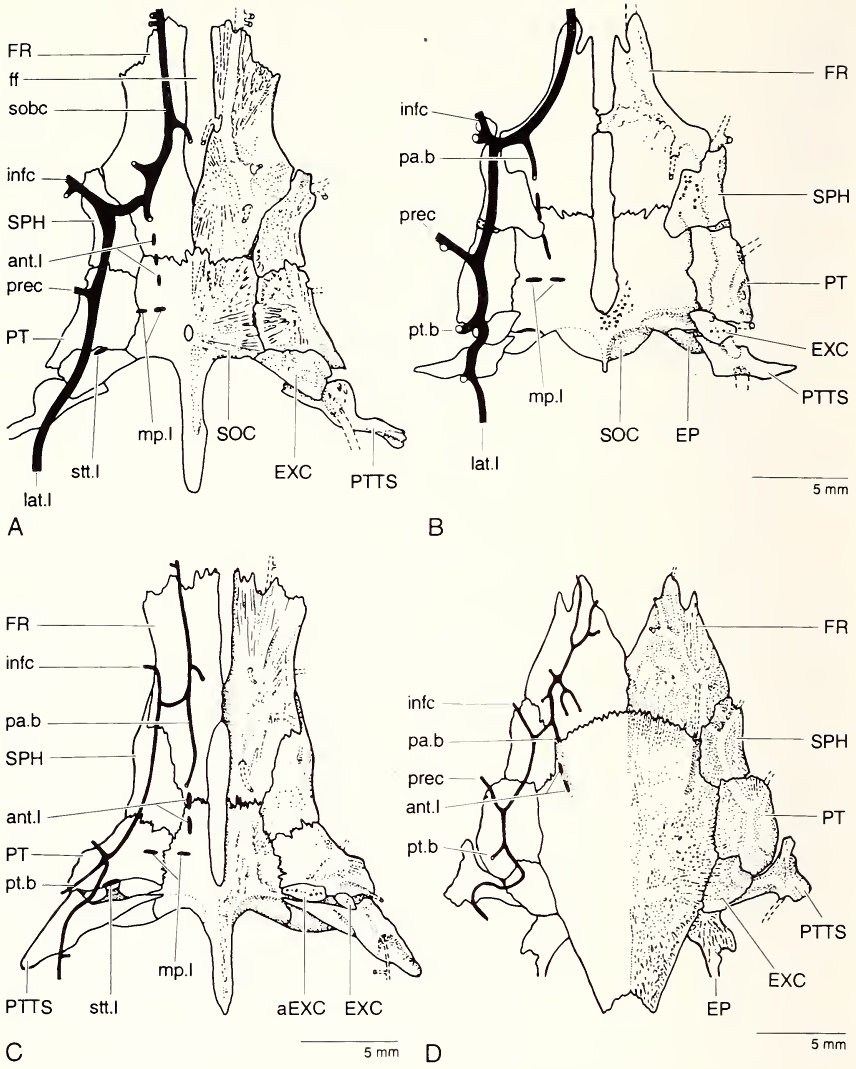

Fig.10: Posterior part of cranial roof and sensory canals. A: *Rhamdia sapo*; B: *Heptapterus mustelinus*; C: *Ameiurus catus*; D: *Arius felis*.
ant.l: anterior pit line; aEXC: additional extrascapular bone; EP: epioccipital; ep.b: epiphyseal branch; EXC: extrascapular bone; ff: frontal fontanel; FR: frontal bone; infc: infraorbital canal; lat.l: main lateral line; LE: lateral ethmoid; MET: mesethmoid; mp.l: middle pit line; NA: nasal bone; otc: otic canal; pa.b: parietal branch; potc: postotic canal; PT: pterotic; pt.b: pterotic branch; PTTS: posttemporo-supracleithrum; sobc: supraorbital canal; SOC: parieto-supraoccipital bone; SPH: sphenotic; stt.l: supratemporal accessory line.

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of infraorbital canal); sdt.l: subdorsal trunk line; smxb: submaxillary barbel; "SOB": tendon-bone supraorbital; SOC: parieto-supraoccipital bone; sobc: supraorbital canal; SPH: sphenotic; stt.l: supratemporal accessory line; V: vomer; vt.l: ventral trunk line.

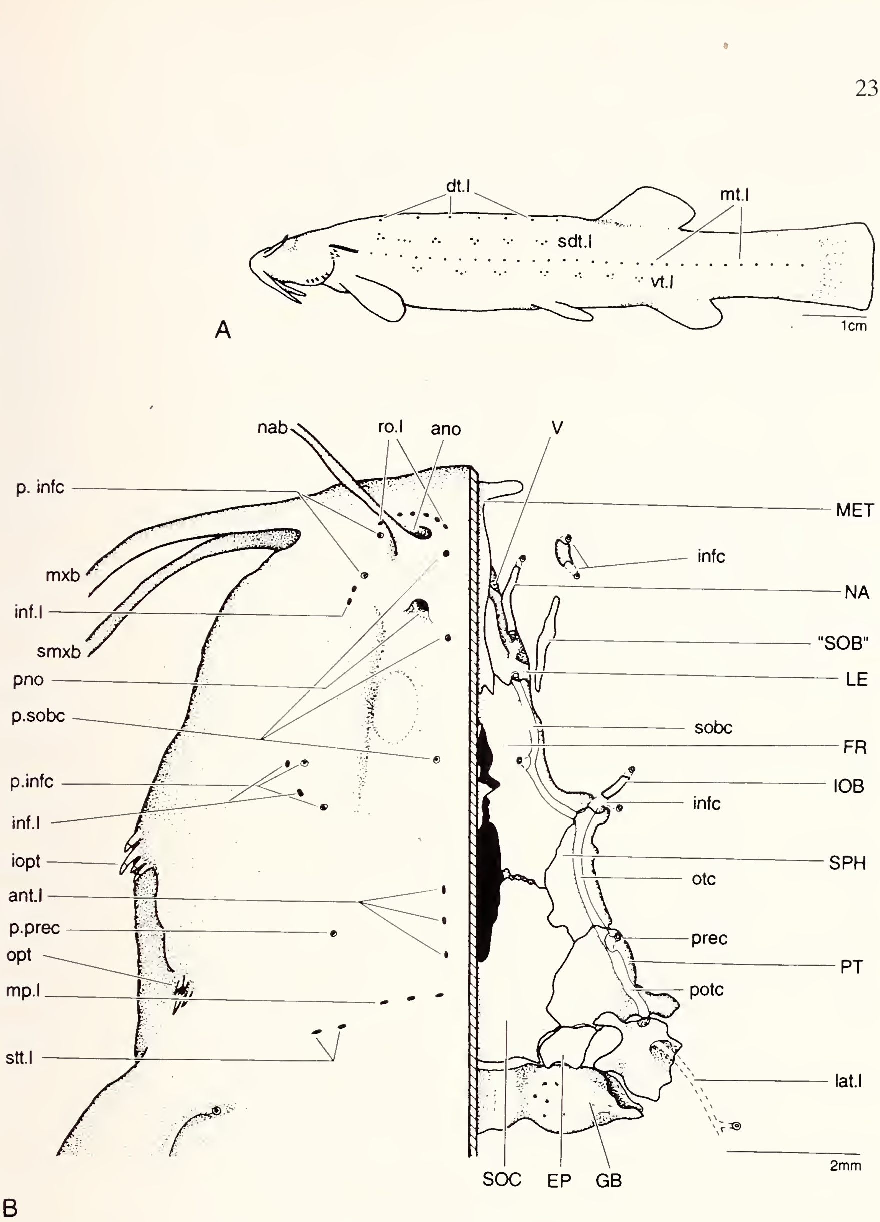

Fig.11: *Trichomycterus areolatus* Valenciennes. A: Superficial neuromast lines and main lateral line enclosed by ossicles (thick black line); B: Distribution of superficial pit lines, and pores of the cephalic sensory canal (left) and their relationship to cranial bones (right side).
ano: anterior nasal opening; ant.l: anterior pit line; dt.l: dorsal trunk line; EP: epioccipital; FR: frontal bone; infc: infraorbital canal; GB: gas bladder capsule; inf.l: infraorbital line; IOB: infraorbital bone; iopt: interopercular teeth; lat.l: lateral line; LE: lateral ethmoid; MET: mesethmoid; mp.l: middle pit line; mt.l: middle trunk line; mxb: maxillary barbel; NA: nasal bone; nab: nasal barbel; opt: opercular teeth; otc: otic canal; p.infc: pores of infraorbital canal; pno: posterior nasal opening; potc: postotic canal; p. prec: pore of preopercular canal; prec: preopercular canal; p.sobc: pores of supraorbital canal; PT: pterotic; ro.l: rostral line (fork replacement of supraorbital canal plus rostral fork replacement

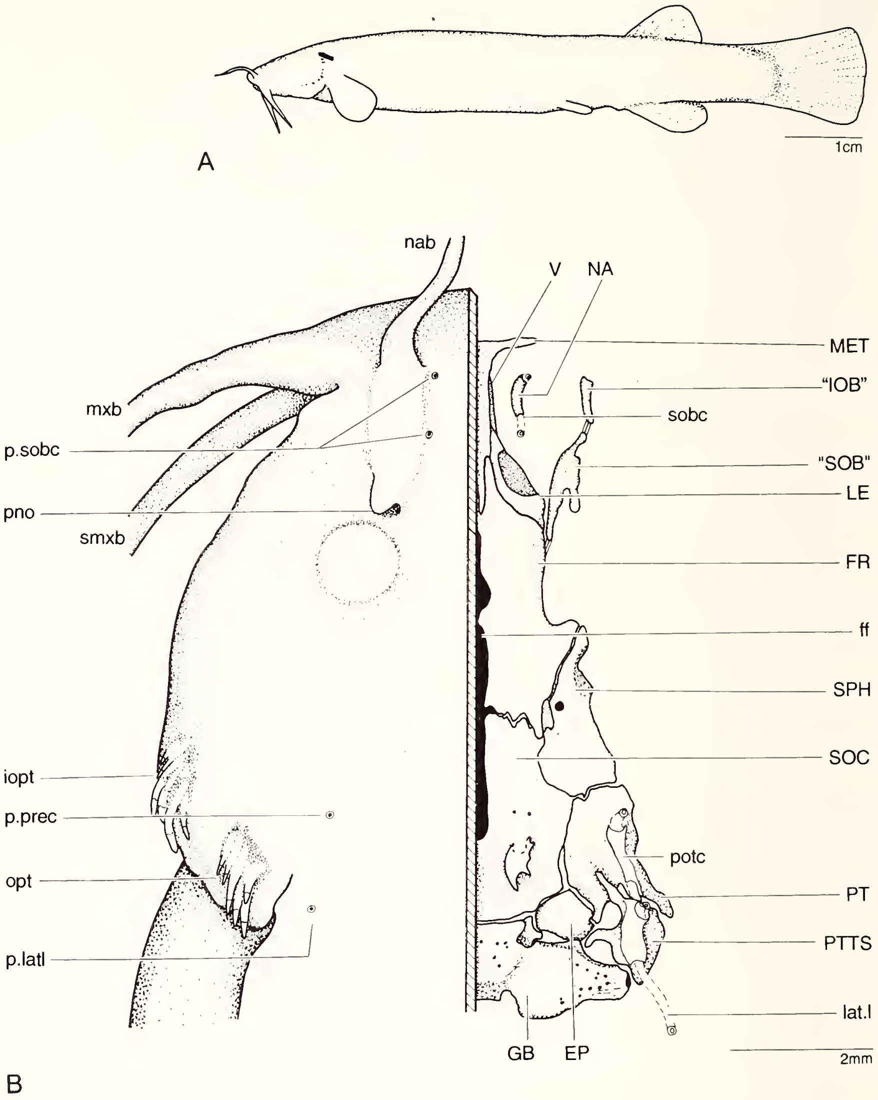

Fig.12: "*Trichomycterus*" *mendozensis* Arratia et al. A: Superficial neuromast lines and body lateral line enclosed by ossicles (thick black line); B: Distribution of pores of the cephalic sensory canal (left) and their relationship to cranial bones (right side).

EP: epioccipital; ff: frontal fontanel; FR: frontal bone; GB: gas bladder capsule; "IOB": tendon-bone infraorbital?; iopt: interopercular teeth; lat.l: lateral line; LE: lateral ethmoid; MET: mesethmoid; mxb: maxillary barbel; NA: nasal bone; nab: nasal barbel; opt: opercular teeth; p.latl: pores of lateral line; pno: posterior nasal opening; potc: postotic canal; p.prec: pores of preopercular canal; p.sobc: pores of supraorbital canal; PT: pterotic; PTTS: posttemporo-supracleithrum; smxb: submaxillary barbel; "SOB": tendon-bone supraorbital; sobc: supraorbital canal; SOC: parieto-supraoccipital bone; SPH: sphenotic; V: vomer.

between frontal and nasal bones in *Trichomycterus rivulatus* (Fig.8C), in most individuals of *T. areolatus* (Fig.11B), and in advanced trichomycterids such as *Ochmacanthus* (Fig.9D) and *Vandellia* (Fig.9F). Therefore, trichomycterines *sensu* Arratia (1990a) may have the supraorbital canal complete or interrupted; both conditions are found in species currently included in *Trichomycterus*.

Among trichomycterids the supraorbital canal shows further transformations. The anterior part of the canal is lost in *Eremophilus* (Fig.8E), *Scleronema* spec. (Fig.9B), and *Tridentopsis* (Fig.9E). The entire canal is lost in certain trichomycterids such as *Glanapteryx* (de Pinna 1989a: fig.5A), *Listrura* (Fig.9C; de Pinna 1988: fig.5A), and in "*Trichomycterus*" *mendozensis* (Fig.12B). This condition is also observed in most scoloplacids (Schaefer 1990), but it has evolved independently in certain trichomycterids and scoloplacids. The condition of the supraorbital canal in copionodontines and *Trichogenes* was not mentioned by de Pinna (1992), whose illustrations are not informative.

2) Epiphyseal branch of the supraorbital sensory canal. This is a medial branch of the supraorbital canal (Figs.2A, B, 3B, C) in front of, or close to the level of the epiphyseal bar. This branch is present in most ostariophysans and in most catfishes but it is absent in gymnotoids and diplomystids; however, a short branch in the position of the epiphyseal branch is found in certain specimens of *Olivaichthys* (Fig.8A) but not in *Diplomystes* (Figs.4B, 5B). Among loricarioids the condition varies. A short branch (Figs.7B, 8B) is present in *Nematogenys*, but a long branch reaching the interfrontal suture is present in certain loricarioids such as in the loricariid *Hypostomus* (Schaefer 1987: fig.4), in the scoloplacid *Scoloplax* (Schaefer 1990: fig.2A), in the trichomycterid sarcoglanidine *Malacoglanis* (Baskin 1970; herein) and in the trichomycterid stegophilinids *Pareiodon*, *Pseudostegophilus*, and *Apomatoceros* (Baskin 1970: figs.22, 24, 27). Although this is a homoplastic character among loricarioids, still it can be considered as an autapomorphy of *Malacoglanis* because the branch is absent in other sarcoglanidines (our interpretation of de Pinna's 1989a illustrations), and as a synapomorphy of the stegophilinids. The epiphyseal branch is missing in "*Trichomycterus*" *mendozensis* (Fig.9D), *Listrura* (Fig.9C), and *Tridentopsis* (Fig.9E; Baskin 1970).

3) Parietal branch of the supraorbital canal. A posteromedial branch of the supraorbital canal (Figs.2A, B, 3C, 4B, 5B) commonly runs from the frontal bone into (or above) the parietal bone in non-siluroid teleosts or parieto-supraoccipital in catfishes. The parietal branch is present in ostariophysans such as *Chanos* (Fig.3A), characiforms (Fig.3C), and most catfishes; the parietal branch is absent in primitive cypriniforms (Fig.3B) and gymnotoids (Fig.3D). Among catfishes the parietal branch may be long and reaching the parieto-supraoccipital bone (e.g., diplomystids, *Parapimelodus*, *Arius*), or short and not extending onto the parieto- supraoccipital bone (e.g., ictalurids, *Rhamdia*, and *Heptapterus*), or it may be absent. This branch is lost in *Nematogenys* (Figs.7B, 8B) and other loricarioids (Figs.8C-F, 9A-F; Baskin 1970, Arratia & Menu Marque 1981, 1984, Schaefer 1987, 1990, de Pinna 1988, 1989a, b); the absence of the parietal branch is considered herein a synapomorphy of loricarioids.

4) Infraorbital canal. This canal is complete (Figs.4B, 8A, B) in most catfishes and in other ostariophysans. It is complete in loricarioids such as *Nematogenys* (Fig.8B), copiodontines (de Pinna 1992: fig.17), *Trichogenes* (Britski & Ortega 1983), and *Hypostomus* (Schaefer 1987: fig.4), whereas it is reduced to its anterior and posterior segments in trichomycterines (Figs.8C, E, F, 9A). Further reductions include the loss of the anterior segment in *Scleronema* spec., *Ochmacanthus*, *Tridentopsis*, *Vandellia* (Fig.9D- F), and *Glanapteryx* (de Pinna 1989b: fig.5a), or the loss of the complete canal, e.g., "*Trichomycterus*" *mendozensis* and *Listrura* (Figs.8D, 9C; de Pinna 1988: fig.5A).

5) Antorbital branch of the infraorbital canal. The antorbital branch (Figs.2A, 4A) is the dorsal or posterodorsal tubule emerging from the main infraorbital canal in the antorbital bone in primitive fossil and Recent teleosts; an antorbital line or postnasal pit line is a dorsal continuation of the antorbital branch. In numerous modern teleosts the antorbital bone reduces or loses its sensory canal (Gosline 1961, Nybelin 1967; observation by G. Arratia), but still the antorbital line is present (e.g., *Coregonus*; Nybelin 1967). Therefore, "the position of the bone below the postnasal line strongly supports the opinion that it is an antorbital which has lost its sensory canal" (Nybelin 1967:244). In addition, numerous teleosts have a series of neuromasts that corresponds to the rostral fork replacement

line of the infraorbital canal that is mentioned in the literature by various names (Coombs et al. 1988:578, see below). The anteriormost bone of the infraorbital series in diplomystids and other catfishes have been commonly identified as infraorbital 1; however, the position of the bone, the presence of the antorbital branch (and of an antorbital line), the presence of the anterior branch of the infraorbital canal that is preceded by a series of neuromasts or the rostral fork replacement line in diplomystids (Fig.4B and below), and the early ossification of the bone during ontogeny support Arratia's (1987a) identification of this bone as the antorbital.

6) Preopercular canal. A complete preopercular canal (Fig.4B) is present in most catfishes and in other ostariophysans. The preopercular canal is present in *Nematogenys* and most loricarioids, except trichomycterids, some scoloplacids (Baskin 1970, Schaefer 1987, 1988, 1990), and some loricariids (e.g., *Otocinclus*; Schaefer 1991). An interrupted canal, restricted to a segment in the preopercle, is present in *Corydoras* (Schaefer 1988: fig.3a).

The loss of the preopercular canal is considered a synapomorphy of trichomycterids (Baskin 1970); however, the preopercular canal is very short and reduced to its upper portion and to one pore in the trichomycterids examined (Figs.8C, E, F, 9A, B); it is comparatively longer (but also bearing one pore) in advanced trichomycterids (Fig.9D, F); it is lost in other trichomycterids such as *Trichomycterus areolatus* (Fig.11B), "*Trichomycterus*" *mendozensis* (Figs.8D, 11B), and *Listrura* (Fig.9C). According to the available information it is more appropriate to consider the reduction (not the absence) of the preopercular canal to its upper section a synapomorphy of trichomycterids. The loss of the canal is interpreted herein as a derived character state found in certain trichomycterids.

7) Pterotic branch of the otic canal. Catfishes are characterized by the presence of the pterotic branch (Figs.4B, 5B, 8A), that is a lateroposterior branch of the postotic canal (or temporal canal) on the pterotic. Commonly, the pterotic branch opens through the skin (e.g., Diplomystidae), but it may continue into the posttemporo-supracleithrum joining the lateral line (e.g., *Parapimelodus*; Arratia & Gayet in press: fig.8B).

Although the presence of the pterotic branch is a synapomorphy of Siluroidei (Fink & Fink 1981, Arratia 1992, Arratia & Gayet in press), it is variably present in *Diplomystes* and *Rhamdia*, and is absent in loricarioids (Figs.7B, 8B-F, 9A-F, 11B, 12B). The absence of the pterotic branch is considered here a synapomorphy of loricarioids, and its pattern in *Parapimelodus* an autapomorphy of the genus.

8) Body lateral line. The main lateral line – enclosed by ossicles and numerous pores – extends along the flank to the base of the principal caudal rays in diplomystids (Figs.4A, 5A; Arratia 1987a) and in most other catfishes. About 55 to 60 short tubules each opening in a pore are found in *Diplomystes*. An unusual condition is found in the primitive trichomycterid copionodontines which have a complete lateral line devoid of ossicles according to de Pinna (1992); pores were not mentioned or illustrated for *Copionodon* and *Glaphyropoma* by de Pinna (1992). Many loricarioids have a reduced body lateral line. For instance:

a. The main lateral line ends anterior to the origin of the dorsal fin in *Nematogenys* (Fig.7A) and exits to the skin surface by about ten pores (Tab.1).
b. The main lateral line is reduced to its anteriormost part and exits to the skin surface by a few pores, e.g., in trichomycterids (Figs.8C-F, 9A, B, D-F, 11A, 12A; Tab.1).

A reduced body lateral line is considered here an apomorphic character state by comparison to the complete main lateral line found in diplomystids and in most other catfishes. The reduction of the main lateral line includes at least three character states, e.g., the moderately long main lateral line (with about ten pores); atrophied main lateral line (with one to three pores); and a divided and discontinuous line (this is an important character state for diagnosing species within *Otocinclus*; Schaefer, in litt.). A fourth state could be the complete absence of the main lateral line which was not observed in any of the examined loricarioids; however, this condition seems to be present in *Listrura nematopteryx* according to de Pinna's (1988: figs.2A, 5A) illustrations.

Table 1: Pores of the main lateral line, numbered from anterior to posterior (l1-ln), in diplomystids and certain loricarioids.
int: interrupted canal; ln: long lateral line reaching the base of the caudal fin, with more than 20 pores; * variable in both sides of the holotype specimen.

Taxa	Pores of the main lateral line													
	l1	l2	l3	l4	l5	l6	l7	l8	l9	l10	l11	l12	l13	ln
Diplomystes	l1	l2	l3	l4	l5	l6	l7	l8	l9	l10	l11	l12	l13	ln
Olivaichthys	l1	l2	l3	l4	l5	l6	l7	l8	l9	l10	l11	l12	l13	ln
Nematogenys	l1	l2	l3	l4	l5	l6	l7	l8	l9	l10	–	–	–	–
Bullockia	l1	l2	l3	l4	l5	–	–	–	–	–	–	–	–	–
Eremophilus	l1	l2	–	–	–	–	–	–	–	–	–	–	–	–
Hatcheria	l1	l2	l3	l4	l5	l6	int	l8?	l9?	–	–	–	–	–
Sarcoglanis	l1	l2	l3	–	–	–	–	–	–	–	–	–	–	–
Trichomycterus														
areolatus	l1	l2	l3	l4	–	–	–	–	–	–	–	–	–	–
boylei	l1	l2	l3*	l4*	–	–	–	–	–	–	–	–	–	–
duellmani	l1	l2	l3	l4	–	–	–	–	–	–	–	–	–	–
nigricans	l1	l2	l3	l4*	l5*	–	–	–	–	–	–	–	–	–
rivulatus	l1	l2	–	–	–	–	–	–	–	–	–	–	–	–
roigi	l1	l2	–	–	–	–	–	–	–	–	–	–	–	–
"*T.*" *mendozensis*	–	l2	–	–	–	–	–	–	–	–	–	–	–	–
Scleronema spec.	l1	l2	l3	–	–	–	–	–	–	–	–	–	–	–
Listrura	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ochmacanthus	l1	l2	–	–	–	–	–	–	–	–	–	–	–	–
Tridentopsis	l1	l2	–	–	–	–	–	–	–	–	–	–	–	–
Vandellia	–	–	l3?	–	–	–	–	–	–	–	–	–	–	–

A continuous main lateral line is the common condition in the catfishes examined, except by *Hatcheria* which may have an interrupted lateral line (Fig.8F).

The presence of ossicles (tube-like or half cylinder) enclosing the main lateral line is the generalized condition among siluroids. A lateral line devoid of ossicles seems to be unique to copionodontines.

Pores of the cephalic sensory canals

The canals of the lateralis system open to the skin surface by a series of pores; pores and the canals are connected by sensory tubules of variable length among the catfishes examined (also in *Noturus* and *Ictalurus* as described and illustrated by Taylor 1969: figs.1-2), however the sensory tubules are very short in other ostariophysans (Fig.3A-D). The cephalic sensory tubules are comparatively longer in diplomystids than in nematogenyids and trichomycterids (compare Figs.4B, 5B, 8A, and 8B-F, 9A-F, 11B, 12B). Each pore is commonly surrounded by a thickened border of connective tissue which may be paler than the surrounding skin. During growth, the border of the pore may become thicker and paler (e.g., *Nematogenys*), whereas they become difficult to observe in *Diplomystes*.

To facilitate comparisons, the pores opening in the skin are identified by numbers here. The number of pores in the skin and the number of openings in the bone do not always

Table 2: Pores of the supraorbital canal, numbered from anterior to posterior (s1-s8), in diplomystids and certain loricarioids.
?: unclear homology; *: only one pore at the conjuction of left and right sensory tubules 6.

Taxa	Pores of the supraorbital canal							
	s1	s2	s3	s4	s5	s6	s7	s8
Diplomystes	s1	s2	s3	s4	s5	s6	–	s8
Olivaichthys	s1	s2	s3	s4	s5	s6	s7	s8
Nematogenys	s1	s2	s3	–	–	s6	s7?	–
Bullockia	s1	s2	s3	s4	–	s6	–	–
Eremophilus	–	–	s3	–	–	s6	–	–
Hatcheria	s1	s2	s3	s4	–	s6	–	–
Malacoglanis	–	–	–	–	s5?	s6*	–	–
Sarcoglanis	–	–	–	–	s5?	s6*		
Trichomycterus								
areolatus	s1	s2	s3	–	–	s6	–	–
boylei	s1	s2	s3	–	–	s6	–	–
chiltoni	s1	s2	s3	–	–	s6	–	–
duellmani	s1	s2	s3	–	–	s6	–	–
nigricans	s1	s2	s3	–	–	s6*	–	–
rivulatus	s1	s2	s3	–	–	s6	–	–
roigi	s1	s2	s3	–	–	s6	–	–
"*Trichomycterus*"								
mendozensis	s1	s2	–	–	–	–	–	–
Scleronema spec.	–	–	s3	–	–	s6	–	–
Listrura	–	–	–	–	–	–	–	–
Ochmacanthus	s1	s2	s3	–	–	s6?	–	–
Tridentopsis	–	–	s3	–	–	–	–	–
Vandellia	s1	s2	s3	–	–	s6?	–	–

coincide; in addition, the number of pores varies during growth in some species, therefore young and large specimens were investigated to estimate the highest number present in each species. For instance, the number of pores [8] of the supraorbital canal present in young *Chanos chanos* (Fig.3A) decreases through growth, therefore pores 4, 5, and 6 are variably present. Despite the variation, the number of pores of the supraorbital canal is comparable between diplomystids and other primitive ostariophysans (Figs.3A, 4B, 5B, 8A). The variation of the number of pores of the otic, infraorbital, and preopercular canals makes comparison very difficult. In addition, there are more pores (e.g., infraorbital canal) in *Diplomystes* and other primitive catfishes than in the primitive members of the outgroups. Therefore, the numbering of the pores of the cephalic sensory canal in the siluroids examined is based on *Diplomystes* and then compared with other catfishes.

1) Pores of the supraorbital canal. The supraorbital canal exits to the skin through eight pores in primitive members of ostariophysan subgroups, and in the diplomystid *Olivaichthys* (Fig.8A; Tab.2) among catfishes; seven pores are commonly found in *Diplomystes* (Figs.4B, 5B). Pore 1 is at the anterior end of the supraorbital canal; it is the exit of the anteriormost, short nasal tubule. Pore 2 is close to the anterior end of the nasal bone, or to the anterior half of the nasal bone. Pore 3 is placed between the posterior end of the nasal bone and the anterior margin of the frontal. Pores 1 to 3 apparently are homologous among primitive ostariophysans (Figs.3A- D, 8A). Commonly,

there are four pores of the supraorbital canal associated with the frontal bone in *Diplomystes* (Figs.4B, 5B). Pores 4, 5, and 6 are the exit of short branches usually running lateral to the main canal; no epiphyseal branch is identifiable. However, another tubule and pore [7] is placed medial in *Olivaichthys viedmensis* (Fig.8A). *Diplomystes* misses one tubule and its pore [7] (Figs.4B, 5B). It is unclear whether tubule and pore 7 in *Olivaichthys* (Fig.8A) is homologous to the epiphyseal branch and pore [6] – which are interpreted here as the epiphyseal branch and pore by comparison with other ostariophysans (Fig.3B, C) and other catfishes with the complete series of pores (e.g., *Rhamdia*: Fig.10A) – in *Nematogenys* (Fig.7B, 8B) and some trichomycterids (Figs.9A, B, E, F). Pore 8 opens at the end of an elongate parietal branch that runs onto the posterior part of the frontal bone and anterior part of ́the parieto-supraoccipital bone (Figs.4B, 5B, 8A). Pores 6 and 8 are present in *Ictalurus* (Fig.10C), pores 6, 7, and 8 in *Rhamdia* (Fig.10A), pore 8 in *Heptapterus* (Fig.10B).

The number of pores of the supraorbital canal has strong variation among loricarioids. For instance, in *Nematogenys* the number of pores is reduced to five; pores 4, 5, and 8 are missing by comparison with *Diplomystes* (compare Figs.4B, 5B, and 7B).

The number of pores in trichomycterids is fewer compared with *Nematogenys*. There is a trend to lose pores 1 to 5, 7, and 8 (Figs.8C-E, 9B-F, 11B, 12B). The patterns of pores of the supraorbital canal seem to be diagnostic of certain trichomycterids. For instance, *Trichomycterus roigi, T. boylei, T. duellmani* (Arratia & Menu Marque 1984: figs.3A,

Table 3: Pores of the infraorbital canal, numbered from anterior to posterior (i1-i11), in diplomystids and certain loricarioids.

Taxa	Pores of the infraorbital canal										
	i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11
Diplomystes	i1	i2	i3	i4	i5	i6	i7	i8	i9	–	–
Olivaichthys	i1	i2	i3	i4	i5	i6	i7	i8	i9	–	–
Nematogenys	i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11
Glaphyripoma	–	i2	–	–	i5?	–	i7 ?	–	–	i10	–
Bullockia	i1	–	i3	–	–	i6	–	–	i9	i10	i11
Eremophilus	i1	–	i3	–	–	–	–	–	–	i10	i11
Hatcheria	i1	–	i3	–	–	–	–	–	–	i10	i11
Malacoglanis	–	–	–	–	–	–	–	–	–	–	i11
Sarcoglanis	–	–	–	–	–	–	–	–	–	–	i11
Trichomycterus											
areolatus	i1	–	i3	–	–	–	–	–	–	i10	i11
boylei	i1	–	i3	–	–	–	–	–	–	i10	i11
nigricans	i1	–	i3	–	–	–	–	–	–	i10	i11
rivulatus	i1	–	i3	–	–	–	–	–	–	i10	i11
roigi	i1	–	i3	–	–	–	–	–	–	i10	i11
"*Trichomycterus*"											
mendozensis	–	–	–	–	–	–	–	–	–	–	–
Scleronema spec.	–	–	–	–	–	–	–	–	–	i10	i11
Listrura	–	–	–	–	–	–	–	–	–	–	–
Ochmacanthus	–	–	–	–	–	–	–	–	–	–	i11
Tridentopsis	–	–	–	–	–	–	–	–	–	–	i11
Vandellia	–	–	–	–	–	–	–	–	–	–	–

13A, B). *T. rivulatus*, and *T. chiltoni* present pores 1, 2, 3, and 6, whereas "*Trichomycterus*" *mendozensis* has pores 1 and 2 only, a condition found also in *Listrura* (Tab.2). The loss of the parietal branch of the supraorbital canal and therefore of pore 8 seems to be a synapomorphy of loricarioids.

There is very little information in the siluroid literature about the cephalic sensory canals; some exceptions are Lekander 1949, Taylor 1969, Lundberg, 1975, 1982, Arratia 1987a, Schaefer 1988, and Arratia & Gayet in press. The present study shows that the presence of pores 4 to 8 of the supraorbital canal differs strongly among loricarioid catfishes.

2) Pores of the infraorbital canal. Commonly, the infraorbital canal gives off nine elongate branches in diplomystids (Figs.4B, 8A; Arratia 1987a: figs.4A, 22A). Each branch opens in a pore to the skin surface. The pores are identified here as pore 1 to 9, numbered from anterior to posterior. Pores 1 to 3 are associated with the antorbital bone, pore 2 is placed dorsally to the antorbital bone as the exit of the antorbital branch of the infraorbital canal.

Nematogenys commonly has eleven branches (Fig.8B), each opens in a pore; a high number of branches and pores is an autapomorphy of the family. In contrast, trichomycterids are characterized by reduction (or loss) of the infraorbital canal, which is represented by its anterior and posterior segments (Figs.8C-F, 9A-F, 11B; Tab.3). By comparison with *Nematogenys*, pores 1 and 3, and 10 and 11 are interpreted as commonly present in trichomycterines. This pattern of pores may be a synapomorphy of the subfamily Trichomycterinae. However, other members of the family lack pores 1 and 3 (e.g., *Scleronema* spec.) or possess only pore 11 (e.g., *Tridentopsis* and *Ochmacanthus*, which is considered a synapomorphy of tridentids); in addition, "*Trichomycterus*" *mendozensis, Listrura*, and *Vandellia* lack the infraorbital canal and therefore, the pores (Figs.8D, 9C, F). The copionodontines are unique among trichomycterids in having a complete infraorbital canal with a few pores. According to de Pinna (1992) *Glaphyropoma rodriguesi* has three pores in the infraorbital canal; however his fig.17 shows four pores (Tab.3). Since the same three pores were mentioned for *Copionodon* we are uncertain whether *Copionodon* has also four pores (as shown in fig.17) or only three. The homologization of the intermediate pores of the infraorbital canal in copionodontines is difficult because they could correspond to various pores in similar position in *Nematogenys*.

3) Pores of the otic canal. The otic canal does not give off any branch in the sphenotic bone, with the exception of *Trichomycterus roigi, T. boylei*, and *T. duellmani* (Arratia & Menu Marque 1984: figs.3A, 5A, B) where a short branch and its pore are present.

4) Pores of the postotic canal. The postotic or temporal canal gives off a short lateroposterior branch, the pterotic branch, with a pore in the pterotic in *Diplomystes* and most catfishes (Figs.4B, 5B, 8A). Branch and pore are absent in loricarioids (see above).

5) Pores of the preopercular canal. This canal gives off five or six elongate tubules, each ending in a pore, in *Diplomystes* (Fig.4B; Arratia 1987a: fig.6B), five in *Olivaichthys* (Schaefer 1988: fig.2a). In *Diplomystes* tubule 1 emerges between the suprapreopercles; tubule 2 between suprapreopercle and preopercle, it may be absent. Tubules 3–6 on preopercle. There are four elongate tubules in *Nematogenys* (Schaefer 1988: fig.2B; present paper); in contrast the canal is reduced to its upper section and opens through the skin by one pore in the trichomycterids examined (Figs.8C-F, 9A-F). The pore sits directly on the otic canal in some *Trichomycterus* with a very short tubule, whereas in other trichomycterids the pore is lateral to the pterotic (Fig.9D-F).

NEUROMAST LINES

Neuromast lines may consist of single neuromasts located at the bottom of shallow pits (pit lines), in grooves of the epidermis (groove lines), or enclosed in canals (canal lines) (Northcutt 1989:19). Superficial neuromasts are aligned in several lines on the dorsal and lateral part of the head in siluroids (Fig.13). For instance:

1) Fork replacement of supraorbital canal of Coombs et al. (1988); it has been termed rostral line or nasal line by various authors. – This line (Fig.13) is the continuation of the supraorbital canal anterior to the nasal bone, it lies medial to the fork replacement of the infraorbital canal. It is formed by a variable number of neuromasts placed anteromedial to the anterior nasal opening. It occurs in some catfishes (see below).

2) Rostral fork replacement of the infraorbital canal of Coombs et al. (1988); it is named rostral line, rostral commissure, or ethmoidal commissure by varios authors. – This line (Fig.13) is a continuation of the infraorbital sensory canal as already noted by Lekander (1949) for cypriniforms, Branson & Moore (1962) for centrarchids, Nybelin (1967) for coregonids, and Coombs et al. (1988) for different fishes. A rostral fork replacement of the infraorbital canal formed by a variable number of superficial

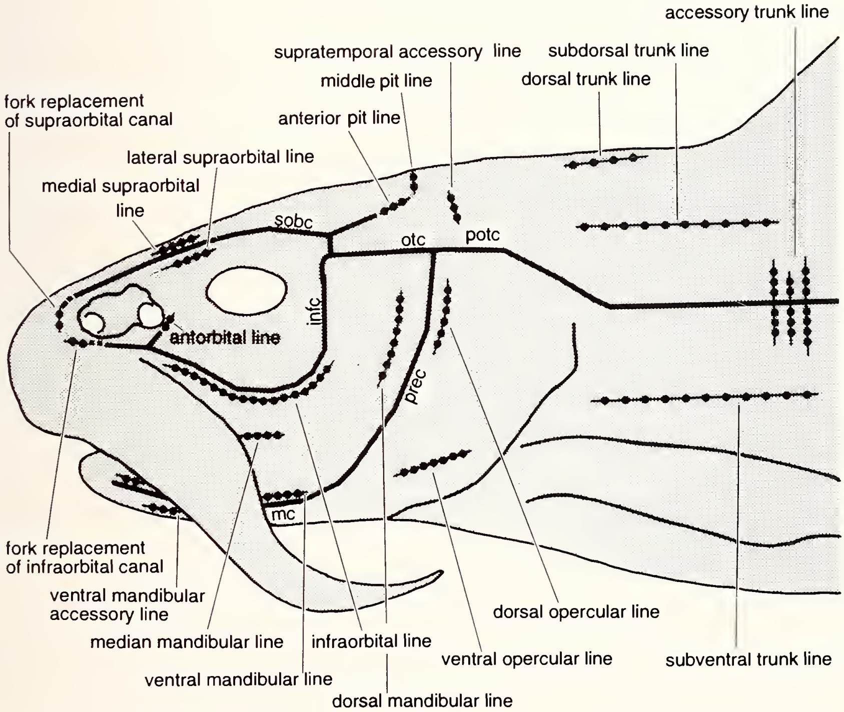

Fig.13: Diagrammatic representation of the lateral line canals and superficial neuromast lines in siluroids.
infc: infraorbital canal; lat.l: body lateral line; mc: mandibular canal; otc: otic canal; prec: preopercular canal; potc: postotic or temporal canal; sobc: supraorbital canal.

neuromasts is placed anterolateral to the anterior nasal opening in most catfishes examined.

3) Caudal fork replacement of the infraorbital canal of Coombs et al. (1988); it has been named antorbital line by various authors, and it is the name used herein. – The antorbital line (Fig.13) is a dorsal-caudal continuation of the antorbital branch of the infraorbital canal placed dorsal to the antorbital bone in teleosts. It occurs in some catfishes (see below).
4) Infraorbital line (name used herein), ventral accessory infraorbital line, or ventral infraorbital line. – A long line (Fig.13) formed by a series of superficial neuromasts lies ventral to the infraorbital sensory canal, forming the infraorbital line or a infraorbital field of neuromasts. It occurs in some catfishes (see below).
5) Supraorbital accessory line. – It is a line of superficial neuromasts placed lateral and/or medial to the supraorbital canal (Fig.13), above the frontal bone. A field of neuromasts is present in *Nematogenys*.
6) Anterior line, or anterior pit line (name used herein), or dorsal supraorbital line. – The anterior pit line (Fig.13) formed by a few large neuromasts is posterior to the parietal branch and pore 8 of the supraorbital sensory canal, on the skin above the posterior part of the frontal bone and/or the anterior portion of the large parieto-supraoccipital bone of some siluroids (see below).
7) Middle line, middle pit line (name used herein), or dorsal post-otic line. – It is a small line (Fig.13) formed by a few elongate neuromasts (two, three, or four) and is transversely placed on the parieto-supraoccipital bone, posterior to the anterior pit line in siluroids such as *Diplomystes chilensis*, *Nematogenys inermis*, *Heptapterus mustelinus*, and *Arius felix* (Figs.4B, 7B, 10B, D). The middle pit line is placed on the parieto-supraoccipital and pterotic bones in *Ictalurus* and *Rhamdia* (Fig.10A, C).
8) Supratemporal accessory line (name used herein), posterior line, or posterior pit line. – The supratemporal accessory line (Fig.13), commonly formed by one to three elongate superficial neuromasts, extends above the extrascapular and pterotic bones in a few catfishes such as *Diplomystes chilensis* and *Ictalurus* (Figs.4B, 10C); it extends on the extrascapular bone in *Rhamdia* (Fig.10A), and on the pterotic and post-temporo-supracleithrum in *Nematogenys* (Fig.7B).
9) Opercular lines. – Superficial neuromasts aligned in short lines or fields of superficial neuromasts are present on the opercular region in some siluroids (Fig.13) forming the dorsal and ventral opercular lines. They occur in some catfishes (see below).
10) Mandibular lines. – Superficial neuromasts aligned in short lines or field of superficial neuromasts are present on the hyomandibular region (dorsal mandibular line) and/or the mandibular region (median mandibular line, ventral mandibular line, ventral mandibular accessory line) (Fig.13).
11) Trunk lines of neuromasts (dorsal trunk or trunk accessories). – Superficial neuromasts may be aligned in different lines on the flank. A line dorsally placed on the flank, extending between the occiput and origin of dorsal fin is named the dorsal trunk line (Fig.13). The dorsal trunk line is innervated by a branch of the supratemporal dorsal accessory ramus (Northcutt 1985). In addition to this line, the superficial neuromasts may be aligned in a subdorsal trunk line placed between the dorsal trunk line and middle trunk line, and in a ventral trunk line placed below the middle trunk line. Trunk accessories are lines of neuromasts running in vertical lines on the flank.

Neuromast lines in *Diplomystes chilensis* and *D. camposensis*

Lines of superficial neuromasts are variable on left and right sides of body (Tab.4) in the same individual and among individuals of *Diplomystes camposensis* and *D. chilensis*. Neuromast lines are formed by one to three large, elongate neuromasts that are usually paler than the surrounding skin. A fork replacement line is placed in front of the anterior nasal opening (Figs.4B, 5B) in continuation of pore 1 of the supraorbital canal; because of individual variation it is uncertain whether the lateral portion of the line corresponds to the rostral fork replacement of the infraorbital canal or not. The antorbital line is occasionally present and formed by one or two elongate superficial neuromasts, placed dorsal to pore 2 of the infraorbital canal. The anterior pit line represented by one elongate neuromast placed posterior to pore 8 of the parietal branch of the supraorbital sensory canal, on the parieto-supraoccipital bone, may be found in *D. camposensis* and *D. chilensis*. The middle pit line is formed by two elongate neuromasts and is positioned above the parieto-supraoccipital bone, posterior to the anterior pit line. The supratemporal accessory line is represented by one elongate neuromast placed on the pterotic above the extrascapular bone or just in front of it. A supraorbital accessory line, a ventral infraorbital line, and opercular lines were not observed in any of the studied specimens of *Diplomystes*. One pair of superficial neuromasts of the dorsal trunk line is occasionally present on one side of the body in *D. camposensis* (Figs.4A, 5A). A true dorsal trunk line is not present in *Diplomystes*; sometimes one or a few elongate neuromasts may be irregularly present on the dorsal part of the trunk. Accessory trunk lines were not observed in *Diplomystes*, but a few unevenly distributed isolated superficial neuromasts were observed on the trunk.

Table 4: Intraspecific variation in absence (-) and presence (+) of superficial neuromast lines in 17 specimens of *Diplomystes camposensis* from one locality of San Pedro river, Valdivia, Chile. Left and right sides of body separated by slash.

Specimens	Neuromast lines						
	Rostral	Antorbital	Infraorbital	Anterior	Middle	Supra-temporal accessory	Dorsal trunk line
1	- / -	- / +	- / -	- / -	- / -	- / -	- / -
2	- / -	+ / -	- / -	+ / -	+ / -	- / +	- / +
3	+ / +	- / -	- / -	- / -	- / +	- / -	- / +
4	+ / -	- / -	- / -	- / -	- / -	- / -	+ / -
5	- / -	- / -	- / -	- / -	- / -	- / -	- / -
6	- / +	- / -	- / -	- / -	- / -	- / -	- / +
7	- / -	- / -	- / -	- / -	- / +	- / +	- / -
8	- / -	- / -	- / -	- / -	- / +	- / -	- / -
9	- / -	- / -	- / -	- / -	- / +	- / -	- / +
10	- / -	- / -	- / -	+ / -	- / +	- / +	- / -
11	- / -	- / -	- / -	- / -	- / -	- / -	- / -
12	- / -	- / -	- / -	- / -	- / -	- / -	- / -
13	- / -	- / -	- / -	- / -	- / -	- / -	- / +
14	- / -	- / -	- / -	+ / -	+ / -	- / -	- / +
15	- / -	- / -	- / -	- / -	- / -	- / -	- / -
16	- / -	- / -	- / -	- / +	+ / +	+ / +	+ / +
17	- / -	- / -	- / -	+ / +	- / -	- / -	- / -

In summary, a few specimens of *D. chilensis* and *D. camposensis* have superficial neuromast lines. The neuromast lines are highly variable bilaterally (Tab.4); such variation represents a trend toward loss of pit lines in these species.

Neuromast lines in *Diplomystes* spec. and *D.* aff. *chilensis*

Lines of superficial neuromasts are unknown from *Diplomystes* spec. and *D.* aff. *chilensis.*

Neuromast lines of *Nematogenys inermis*

The rostral line – commonly formed by seven to nine elongate, papillate, superficial neuromasts and an additional medial separate neuromast – lies on a pigment-free region of the skin in front of the anterior nasal opening (Fig.7B, C); each rostral line is separated from its antimere. The lateral portion of the rostral line is associated with the infraorbital canal and placed in front of pore 1, whereas its mesial portion is associated with the supraorbital canal just in front of pore 1 of this canal and corresponds to the rostral fork replacement of the supraorbital canal. Therefore, this line corresponds to both the rostral fork replacement of the infraorbital canal and the fork replacement line of the supraorbital canal.

A short antorbital line, usually consisting of two or three superficial neuromasts, is associated with pore 2 of the infraorbital canal, which is dorsally placed to the antorbital bone. An elongate infraorbital line composed by a variable number of rounded or ovoidal papillate superficial neuromasts lies ventral to the pores of the infraorbital canal. A field of numerous papillate superficial neuromasts (supraorbital accessory field) lies above and around the supraorbital canal (Fig.7B).

The anterior pit line is formed commonly by two or three elongate papillate superficial neuromasts, the middle pit line by two, and the supratemporal accessory line by one to three neuromasts (Fig.7B). The anterior pit line is placed at the suture between the frontal and parieto-supraoccipital bones. The supratemporal accessory line lies on the pterotic but its lateral superficial neuromast may lie on the suture between the pterotic and posttemporo-supracleithrum. Opercular lines were not clearly identified because the skin of the opercular region has numerous papillate superficial neuromasts irregularly placed as an opercular field. The position of these pit lines varies slightly among adults.

In addition to the superficial neuromast lines, groups of two, three, four or five superficial pit-organs are distributed as small fields on the head (Fig.7B). All superficial neuromasts are easily seen in large specimens, because they are papillate and commonly found in pigment-free spots of the skin (the last condition was described also in other fishes by Bennett 1971).

One or two trunk lines (identified here as dorsal and subdorsal trunk lines) of variable number of elongate superficial neuromasts are placed in the dorsal region of the body, between the occiput and the dorsal fin (Fig.7A). In addition, many isolated papillate superficial neuromasts are distributed on the flanks. They are not associated with the short body lateral line. A middle trunk line of superficial neuromasts extends from the end of the body lateral line to the base of the principal caudal rays; each neuromast is deeply sunk in a groove. Ventral to the body lateral line and middle trunk line is a ventral trunk line of papillate superficial neuromasts.

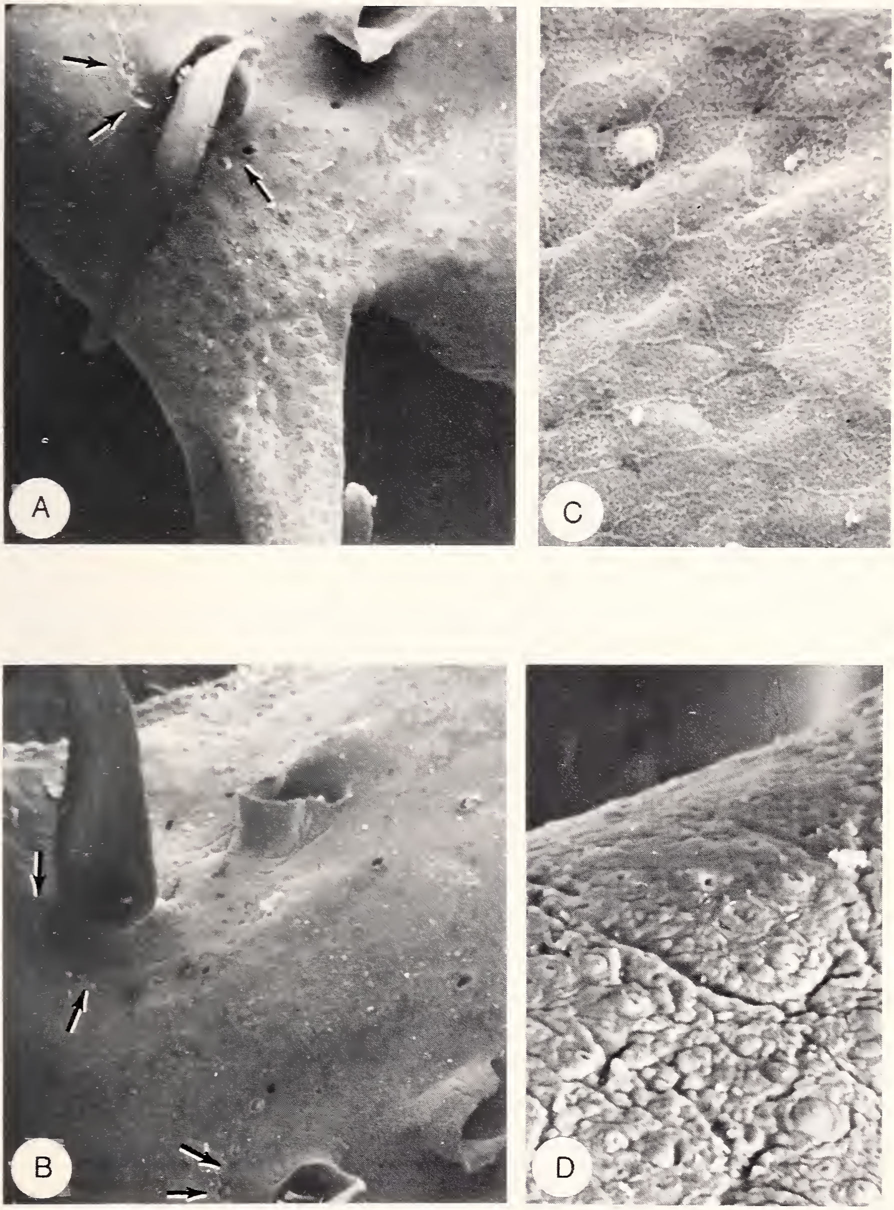

Fig.14: SEM of anterior part of the head in *Trichomycterus areolatus* Valenciennes. A: Dorsolateral view of head showing nasal openings and barbels. Rostral line and isolated superficial neuromasts are indicated by arrows (30x); B: Skin between nasal openings illustrating pores of the supraorbital canal and neuromasts forming the rostral lines (indicated by arrows) (30x); C: Skin lateral to posterior nasal opening showing a cell with domed protrusion (1,500x); D: Skin of the upper lip (260x).

Neuromast lines of *Trichomycterus areolatus*

Superficial neuromasts, isolated or as pit lines, were not observed in young *T. areolatus*, but they were observed in adults. They show strong variation between individuals. The rostral line (Figs.11B, 14A, B), formed by five to seven neuromasts, is placed anteriorly to the anterior nasal opening. This rostral line is associated laterally with the anterior portion of the infraorbital canal and therefore the lateral portion corresponds to the rostral fork replacement line; medially, it is associated with the supraorbital canal and corresponds to its fork replacement line; the limit between both cannot be decided from an external examination of the specimens. A short infraorbital line is placed posterior to the anterior portion of the infraorbital canal; another short infraorbital line may be placed in front of the posterior portion of the infraorbital canal; both are formed by a few neuromasts which are variably present from specimen to specimen.

The anterior pit line is formed by three elongate superficial neuromasts; it lies on the anterior part of the parieto-supraoccipital bone; the middle pit line which is positioned at the posterior part of the parieto-supraoccipital bone is formed by two or three neuromasts which are aligned with two or three neuromasts belonging to the supratemporal accessory line. This line lies on the posttemporo-supracleithrum, or pterotic and posttemporo-supracleithrum. A line of a few neuromasts is variably present on the skin covering the interopercle. Among the pit lines mentioned above, the rostral line (rostral fork replacement of the infraorbital canal plus fork replacement of the supraorbital canal) is the only one that is consistently present in adults.

The short main lateral line of the body is followed by a series of about 30 neuromasts forming the middle trunk line (Figs.11A, B, 15A). The neuromasts are placed between putative ampullary pits, forming a line that extends to the base of the principal caudal rays. The putative ampullary pit has an aperture of about 40 to 50 microns and the ampullary canal is short. The papillate superficial neuromasts of the middle trunk line are ovoid shaped, each is 80 to 90 microns long; they have an ovoidal surface bearing hair cells; this surface can bear single or multiple patches of hair cells.

Small fields of usually three to five ovoidal papillate superficial neuromasts are present on the body, similar to those of the middle trunk line. These ovoidal neuromasts are ordered in series. One series of neuromasts is just dorsal to the lateral line of the body and to the middle trunk line and it corresponds to the subdorsal trunk line. Another series extends from the posterior part of the head to the origin of the dorsal fin, forming a dorsal trunk line. Another series extends ventral to the lateral line of the body and to the middle trunk line; this series corresponds to a ventral trunk line that usually ends above the anal fin. In addition to these large ovoidal superficial neuromasts forming trunk lines, there are many papillate superficial neuromasts (Figs.15A, 16A, B) along the flanks; they are volcano-like structures and differ from the taste buds placed on the head (compare Figs.14A, B, 15A, C, 16A, B).

Neuromast lines of "*Trichomycterus*" *mendozensis*

The lateralis system is reduced to the postotic or temporal section of the cephalic sensory system and to the anteriormost portion of the lateral line of the body (Figs.8D, 12A, B) in "*Trichomycterus*" *mendozensis*. Most individuals do not have pit lines, independently of

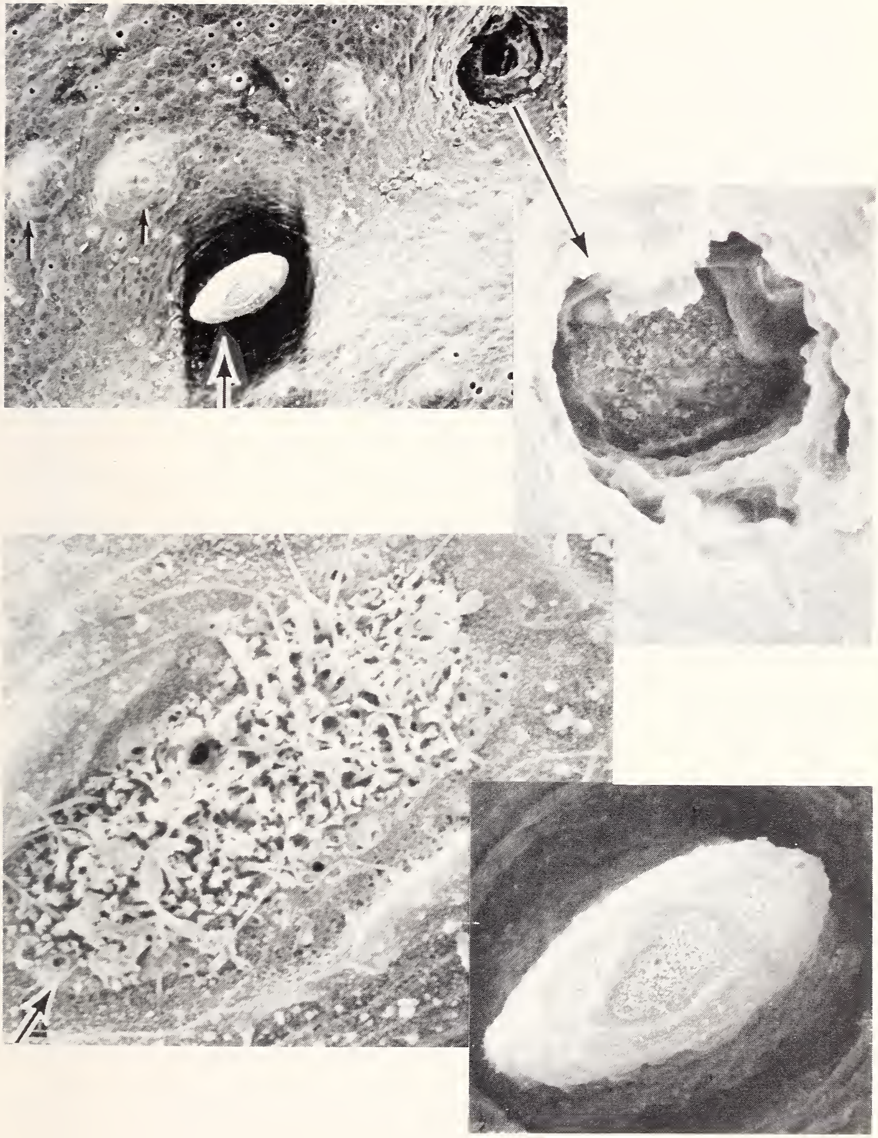

Fig.15: SEM of the skin of the middle region of the flank in *Trichomycterus areolatus* Valenciennes. A: Putative papillate pit (large arrow) and papillate superficial neuromasts (indicated by small arrows) of the middle trunk line (200x); B: Enlargement of the putative papillate pit (700x); C: Enlargement of a neuromast of the middle trunk line (700x); D: Enlargement (3,000x) of the patch of hair cells indicated by an arrow.

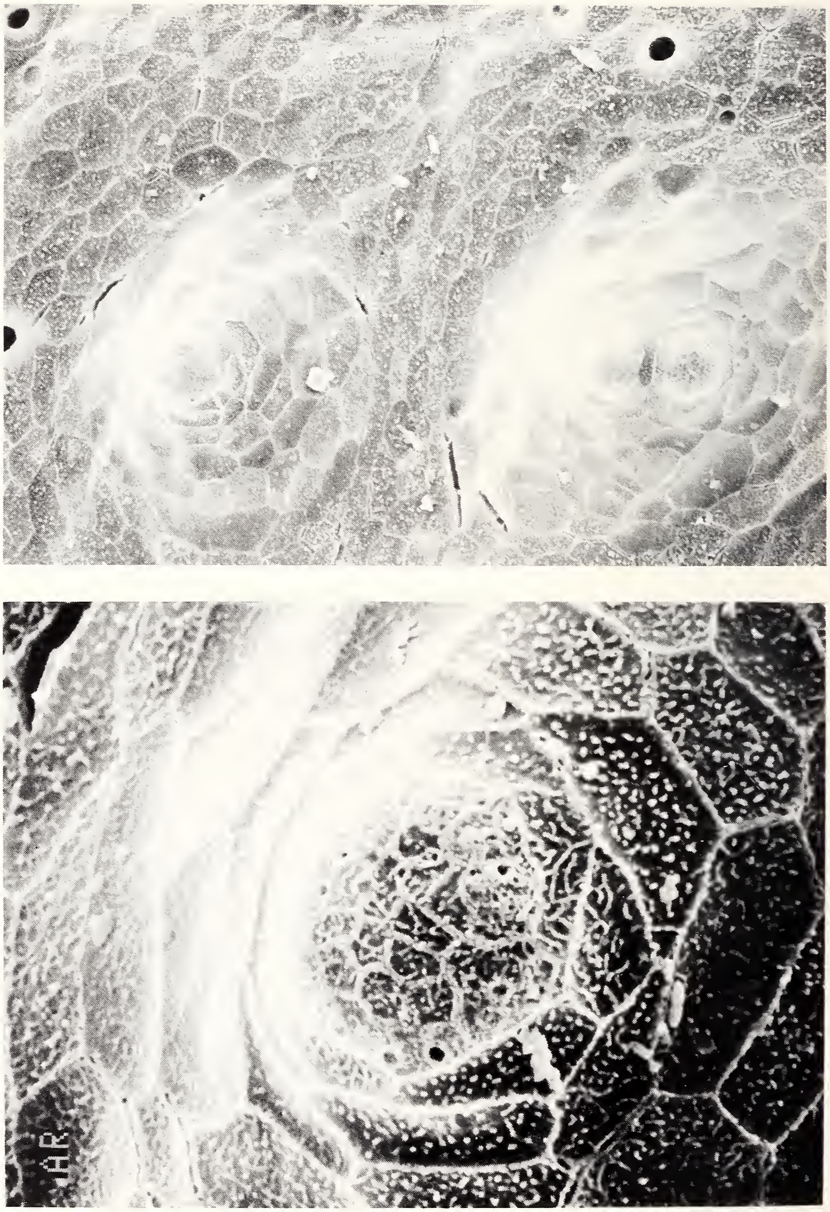

Fig.16: SEM of the skin of the middle region of the flank in *Trichomycterus areolatus* Valenciennes. A: Papillate superficial neuromasts and epithelial cells showing pores of goblet cells (700x); B: Enlargement of the cupula of one papillate superficial neuromast (3,000x).

size; the rostral line – similar to that of *Trichomycterus areolatus* (Fig.11B) – in front of the supraorbital canal is present in only one among 30 individuals examined. Only one fish among 30 individuals has middle pit lines and supratemporal accessory lines.

The short lateral line of the body (Fig.12A) has one (occasionally two) pores; it is followed by a middle trunk line formed of minuscule neuromasts deeply sunk in short vertical skin grooves. Commonly this series of neuromasts ends in front of the anal fin. A dorsal trunk line composed of five minuscule neuromasts, also positioned in vertical grooves, extends from the occiput to the dorsal fin in a few specimens. Neuromasts were not observed in the ventral part of the flank.

SKIN

The description of the skin of certain catfishes is preceded by a general characterization of the skin, particularly of the epidermis.

The skin of the catfishes studied is composed of the epidermis, the underlying dermis, and the hypodermis or subcutaneous layer that lies beneath the dermis of which it is a continuation. The dermis is composed of dense connective tissue and the hypodermis by loose connective tissue and adipose tissue. Melanophores are located in the epidermis, dermis, and hypodermis, and also in the central rod of the barbels. Melanophores may be distributed all over the body, including the skin covering the eye as in *Nematogenys inermis*.

A large, ovoidal or rounded eye is present in *Diplomystes*. The eye is comparatively larger in *Diplomystes* than in *Nematogenys* and most trichomycterids, which have a small eye. Among the members of the subfamily Trichomycterinae, *Bullockia* has the largest eye. In certain catfishes the skin is interrupted around the eye, so that the eye lies in direct contact with the water (e.g., *Diplomystes, Ictalurus, Rhamdia*), or the eye is covered by the skin (e.g., *Nematogenys*, trichomycterines, *Noturus, Heptapterus*). In the latter condition, the skin presents different patterns of pigmentation. The skin is pigmented and therefore the fish may be blind or partially blind (e.g., *Nematogenys*); or the skin covering the eye is unpigmented (e.g., *Bullockia*), or has a few melanophores (e.g., *Trichomycterus areolatus*).

Epidermis

The general description of the epidermis is based on *Diplomystes*. The epidermis (Fig.17A, B) is a stratified squamous epithelium with a basal layer of columnar cells which produce additional cells. The epidermis presents goblet or mucous cells, club or alarm substance cells, solitary cells, unicellular unculi, taste buds, and pit-organs. The quantity and distribution of these elements and the richness of the epidermis vary along the skin of one individual in different regions of the body and among individuals of different species (see below).

The squamous epithelium with the basal layer is well developed in the epidermis of the barbels, lips, and everywhere where epidermal papillae are present. The squamous epithelium is thin, almost absent in certain parts of the skin of the body (e.g., in grooves of the skin behind the head).

The squamous epithelium of the epidermis of the barbels (Figs.17A, 18A, B) is composed of about ten to fifty cell rows which change in shape and orientation from the surface to the basal part of the epithelium. Those just below the cuticle commonly are flat cells placed parallel to the dermis. The basal layer is usually composed of one or two layers of co-

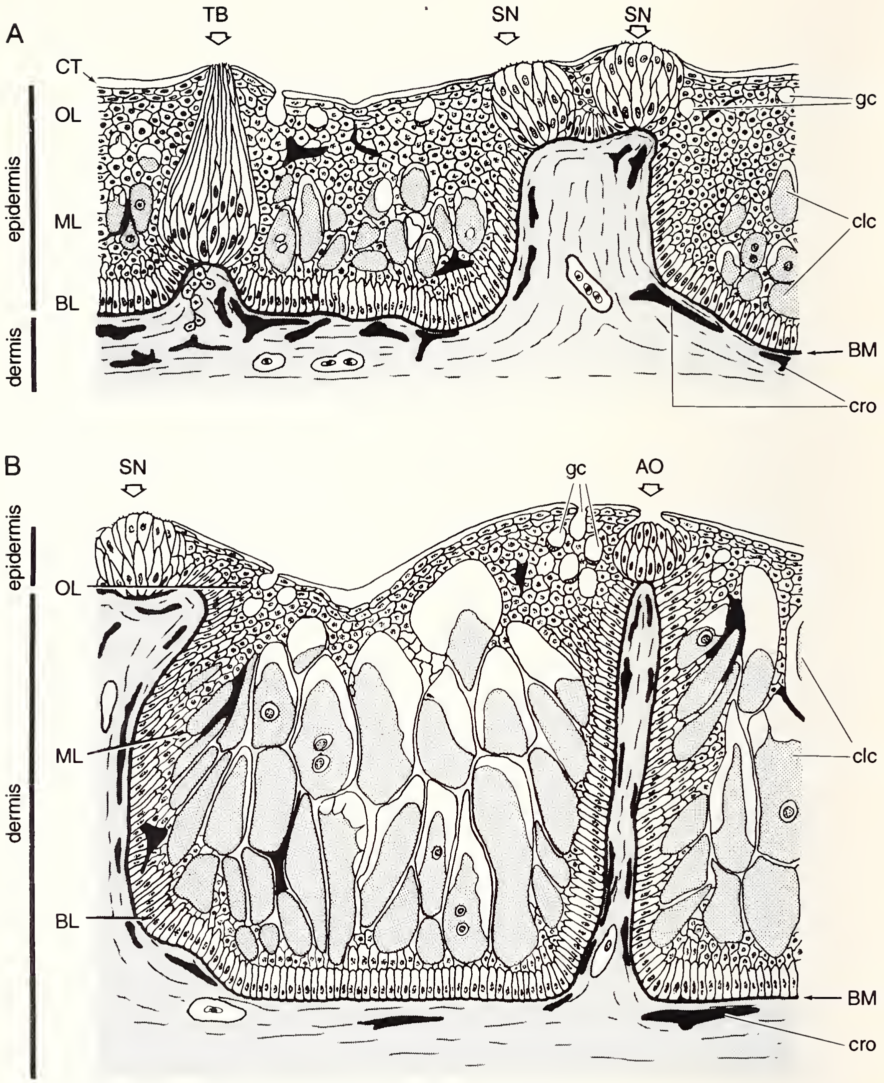

Fig.17: Diagrammatic cross section of the skin based on histological sections of *Diplomystes*. A: Skin of maxillary barbel; B: Skin of dorsal part of body, behind head.
AO: ampullary organ; BL: basal epithelial cell layer; BM: basal membrane; clc: club cell; cro: chromatophores; CT: cuticle; gc: goblet cell; ML: middle epithelial cell layers; OL: outer epithelial cell layers; SN: superficial neuromast (papillate pit of Coombs et al. 1988); TB: taste bud.

lumnar cells, with ovoidal or round nuclei, lying just above the dermis. The epithelial cells, of the middle layer, placed between the superficial and basal cells, are usually polyhedrical, and the epithelium looks glomerular-like. Goblet cells placed between the squamous

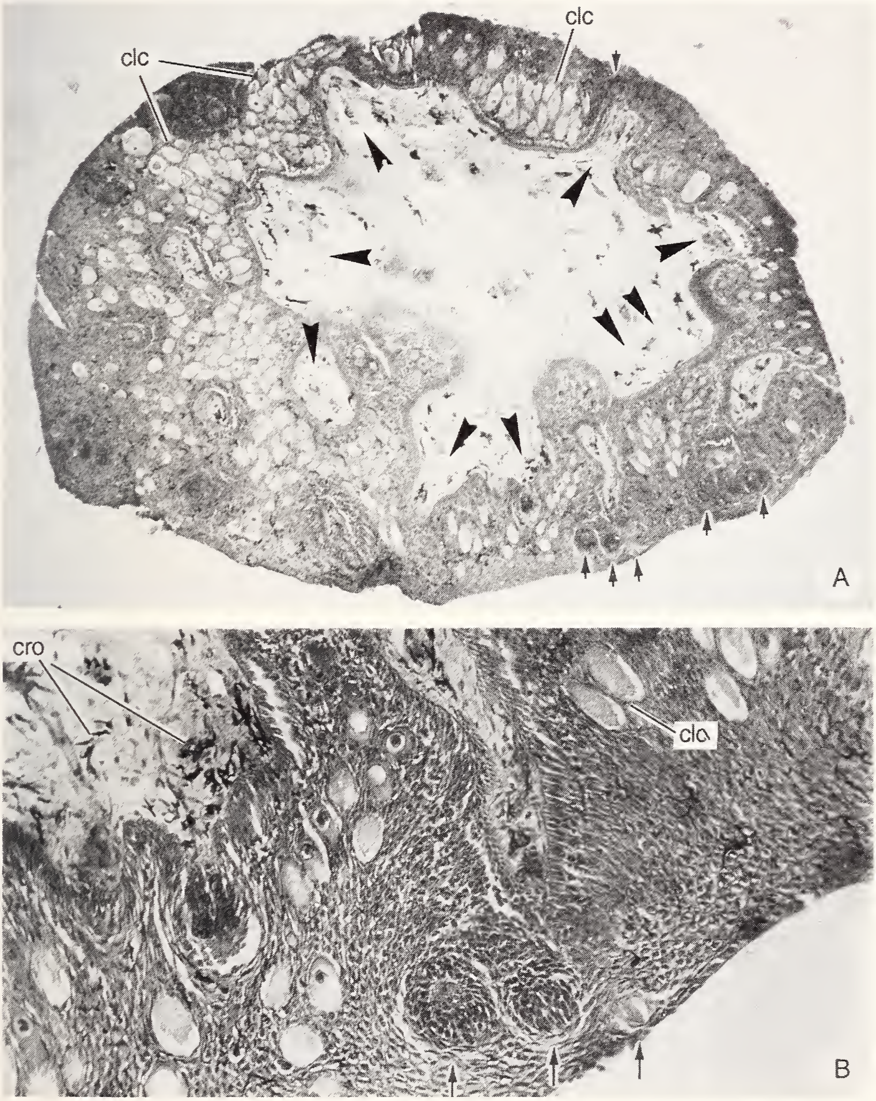

Fig.18: Cross section of the maxillary barbel and skin of *Diplomystes*. A: Arrowheads point to dermal papillae and small arrows to taste buds; B: Enlargement out of A illustrating the structure of the epidermis; arrows point to taste buds.
clc: club cell; cro: chromatophores.

cells are near the superficial epithelium; the diameter of their external aperture ranges between 5 to 10 microns. Club cells are above the basal layer, occupying most of the middle layer of the epidermis. The quantity of club cells varies strongly among species. They are large, round or ovoidal unicellular glands, with one or two large nuclei. Similar structures are present in the epidermis of the lips. However, the epidermis of the body varies considerably.

The squamous epithelium of the epidermis of the body (Figs.17B, 19A, D) is composed of a few cell rows that are concentrated at the surface, and rows of elongate cells separating the club cells and reaching the columnar cells of the basal layer. The goblet cells and taste buds are in lesser quantity than in the epidermis of the barbels and lips. The ampullary organs and the superficial neuromasts are irregularly present along the body skin. The main element of the epidermis of the body are the elongate, large mononucleated or binucleated club cells organized in two or more rows. The club cells may be expanded close to the skin surface.

Taste buds are irregularly distributed on the skin of barbels, head, and body; they are aligned in rows on lips and mouth. They may be placed on epidermal papillae or not. Groups of cells forming a taste bud extend from a dermal papilla to the surface of the epidermis. Taste buds have a characteristic flask shape (Fig.17A). Three cell types are present: receptor cells in the center of the organ, supporting cells located peripherally between the receptor cells and the surrounding epithelial cells, and basal cells at the base of the taste buds. The receptor cells have big, elongate, basal nuclei and long sensory processes which form the apical portion of the taste bud.

Commonly, the ampullary organs are irregularly placed in the skin of the head and body, but they are present in greater number on the lips, pectoral rays, and adipose fin when present. The ampullary organs are located at the bottom of depressions of the epidermis; they are formed by sensory cells bearing microvillae that project into the lumen of the ampulla and supporting cells with basally located nuclei. The apical surfaces of the receptor cells do not bear cilia. In regions of thick epidermis a long tube opening in a pore leads to the surface (see skin of *Trichomycterus areolatus*). Putative ampullary organs with pores of different sizes have been identified in the catfishes examined: Unusually large pores ranging from 100 to 500 microns, pores of 0.2 to 2 microns, and minuscule pores of 0.2 to 0.6 microns; the lumen of the minuscule ampullary organ is observed at about 5,000 (x) magnification. We do not know whether the ampullary organs of different sizes present in diplomystids have the same function or not; because of their similar structure we identify them as ampullary organs.

Superficial neuromasts sitting on dermal papillae (Fig.17A) are variably present in the catfishes studied. Each organ (papillate neuromast) lies on an evagination of the dermis and reaches the surface of the skin; its apical portion is generally wider than that of an ampullary organ (see below). It is composed of sensory and supporting cells.

The papillate superficial neuromasts forming a pit line are large structures, 1–3 mm long, in the diplomystids studied. Similar large structures are unevenly distributed on the entire body in *Nematogenys*; small putative papillate superficial neuromasts, unevenly distributed on the entire body, are found in *Diplomystes*. These small putative neuromasts are observed at high magnification (see below). The large papillate superficial neuromasts may be elongate (e.g., in *Diplomystes, Ameiurus, Ictalurus, Heptapterus*), round or ovoidal (e.g., *Nematogenys* and *Trichomycterus*).

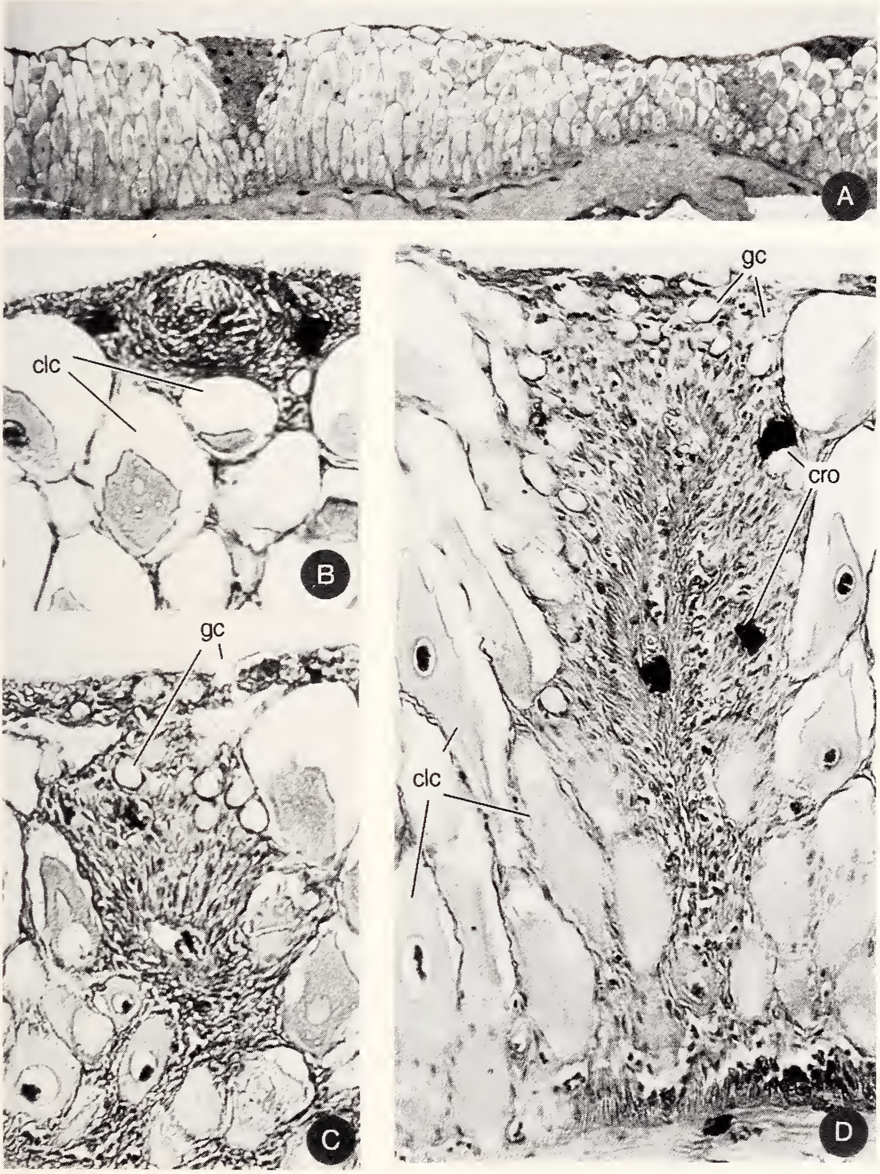

Fig.19: Cross sections of the skin of dorsal part of body, behind the head, in *Diplomystes*. A: Section of the epidermis and underlying dermis (cuticle removed); B: Small putative superficial neuromast and club cells; C: Squamous epithelium, goblet cells, and club cells; D: Enlargement of one cellular "pillar" placed between the club cells.
clc: club cell; cro: chromatophores; gc: goblet cell.

Skin of *Diplomystes* spec.

The surface of the skin is soft, covered by a thick cuticle or colloid-like substance. The colloid-like substance is greyish and transparent enough to reveal subsurface chromatophores that are present in the epidermis, dermis, and hypodermis according to cross sections.

The epidermis is greatly developed in comparison with the dermis. Because of the thickness of the epidermis, dermal papillae can invade the epidermis deeply, so that basal layer and receptors are closer to the external surface. The invasion of the dermis into the epidermis of the barbel produces numerous evaginations that more or less radiate from the axis of the barbel which is slightly displaced anterodorsally in diplomystids (Figs.17A, 18A). The epidermal epithelium of the barbel is thicker at the posterior and inner regions where the major concentration of club cells is found (Fig.18A). The epithelium is comparatively thinner anterodorsally. Taste buds are abundant anterodorsally and anteroventrally. About ten rows of cells are found in the thinnest part of the epidermis, whereas more than fifty rows of cells are present in the thickest epidermal areas. Usually more than two taste buds are associated with one dermal papilla.

Ovoidal-shaped club cells are abundant in the barbel. Most club cells are closer to the basal layer than to the external surface of the epithelium. In the barbel, the ovoidal or rounded club cells are placed between compartments formed by the evaginations of the dermis (Fig.17A).

The epidermal basal layer is commonly formed by one row of columnar cells with ovoidal or round nucleus placed in the lower half of the cell. Occasionally, more than one row of columnar cells are present on the dermal evaginations.

Numerous melanophores of irregular shape are found in the epidermis, dermis, and hypodermis of the barbel (Figs.17A, 18A, B), and also in the central rod of the barbel.

The whole base of the maxillary barbel, the gular region, and part of the branchiostegal region are covered by numerous, large, ovoidal or rounded epidermal papillae, separated from each other by deep furrows (Fig.20A). The papillae are formed by proliferation of the epidermis. The cuticle is usually thinner at the top of the papillae being thicker at the grooves between them. The epidermal papillae of the barbel bear small pit-organs and numerous TBIIs (Fig.20D), whereas the papillae of the gular and branchiostegal regions bear numerous taste buds (Fig.20E, F). The cell surfaces are completely covered by short, irregularly shaped microridges (Fig.20B).

The number of epidermal papillae and taste buds decreases distally along the maxillary barbel. Epidermal papillae bearing taste buds occur mainly at the anterior margin of the barbel. Numerous taste buds, slightly sunk between the epithelial cells, are partially surrounded by a deep furrow; they are found in epidermal papillae. Many sensory cell terminals of different sizes are on each taste bud. As shown by SEM microscopy, the external surface of the epithelial cells is often polyhedrical in shape and the surface is completely covered with irregular microridges (Fig.20B, D). The middle part of the barbel has TBIIs (Fig.20D). The anteroventral part of the dorsal lip bears TBIIs; the sensory cell terminals are of only one type.

Large epidermal papillae (Fig.20E) of different sizes, usually ovoidal-shaped and separated from each other by deep furrows, are found in the gular region. The number of TBIs and TBIIs ranges from 5 to 18 per papilla (Fig.20E, F).

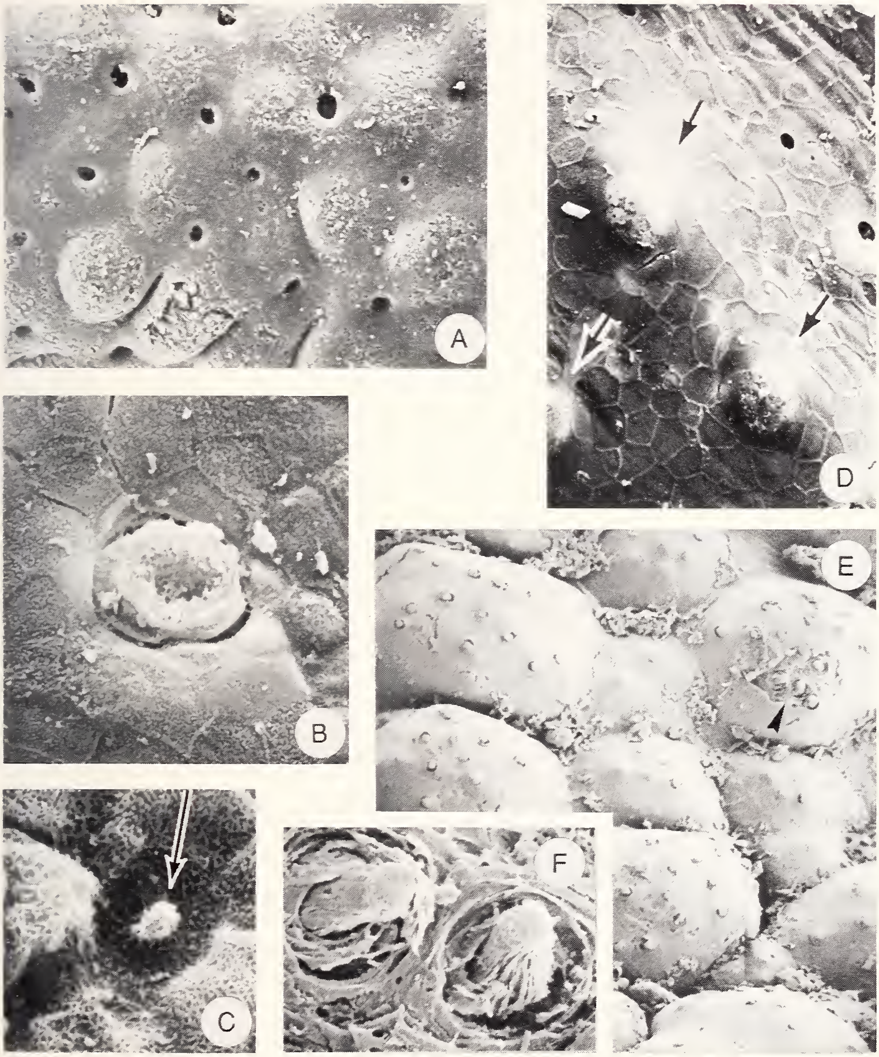

Fig.20: SEM of the skin of *Diplomystes* spec. at the base of maxillary barbel. A: Pores of goblet cells and epidermal papillae (40x); B: Enlargement (1,250x) of a putative pit-organ and epithelial cells; C: Cell bearing protrusion, indicated by an arrow (2,500x); D: Taste buds (indicated by arrows) and pores of goblet cells of the middle part of the maxillary barbel (640x); E: Epidermal papillae bearing taste buds in the gular region (76x); arrowhead points to the taste buds that are enlarged in F; F: Apical region of taste buds (640x).

The thickness of the epidermis of the body is more than the double of that of the dermis. The main component of the epidermis are the club cells (Fig.19A, D) which occupy the space between the basal layer and the superficial epithelial cells. There are four to six rows of ovoidal club cells of variable size that are interrupted by "pillar" of squamous epithelium, basal layer, and dermal papillae along the body. The "pillars" extend from just above the dermis to the cuticle, giving to the epidermis the aspect of being divided into compartments (Figs.17B, 19A, D). Many goblet cells and putative small superficial neuromasts are found on the "pillars". The small superficial buds are composed of a few sensory and basal cells. The small buds resemble taste buds in shape because the sensory cells possess elongate sensory terminals and basal nuclei, but the small buds have no supporting cells; it is uncertain whether the small buds have receptor cells bearing cilia on their apical surfaces.

Few, small epidermal papillae which are usually whitish and completely embedded in the colloid-like substance are observed on the pectoral and dorsal fins; a few ampullary organs occur on the pectoral fins. A few small epidermal papillae and two or three rows of large ampullary organs whose apertures range between 100 and 500 microns are observed on the adipose fin (Fig.21A); these round pores are so large that they are seen at low magnification (20x) with a stereoscope. Higher magnification reveals the ampullary lumen inside the short canal of the ampullary organ (Fig.21B). Only one very small TBIII was observed at high magnification (2,500x) on the adipose fin.

The skin surrounding the main lateral line has numerous ampullary organs with pores ranging from 0.2 to 1 micron of diameter. Taste buds were not observed close to the lateral line.

The surface of the entire body presents pores of variable diameter (50 to 100 microns) belonging to goblet cells; they are observed at low magnification (Figs.20A, D, 21B). Goblet cells are especially abundant on the lips, barbels, and oral cavity. The goblet cells are ovoidal or round-shaped and the elongate nuclei have a basal position.

A few cells bearing a domed protrusion (Fig.20C) are found in the dorsal part of the head; they look exactly like those described and figured by Whitear & Mittal (1986: pl.IV, fig.d) in the scorpaeniform teleost *Agonus cataphractus*. The domed protrusions are small structures whose diameter is about one or two microns; they are irregularly placed on the skin of the head.

Unicellular unculi, multicellular horny tubercles, and superficial neuromast lines were not observed on the skin of head and body.

Skin of *Diplomystes* aff. *chilensis*

The surface of the skin is so markedly papillose, that the skin appears as verrucose to the naked eye. It is covered by a thin colloid-like substance on the head and trunk. The lips, the base of maxillary barbel, and the gular and branchiostegal regions are completely covered by large, ovoidal or round epidermal papillae. The skin on the base of the barbel and adjacent area has, in addition, numerous elongate epidermal papillae separated by deep grooves (Fig.22A). Epidermal papillae are found on the skin of pectoral and dorsal spines and fin-rays, and at the base of the adipose fin (Fig.21C, D). A few ampullary organs are found on the pectoral rays. Many small, elongate or round pores of 1 to 1.6 microns diame-

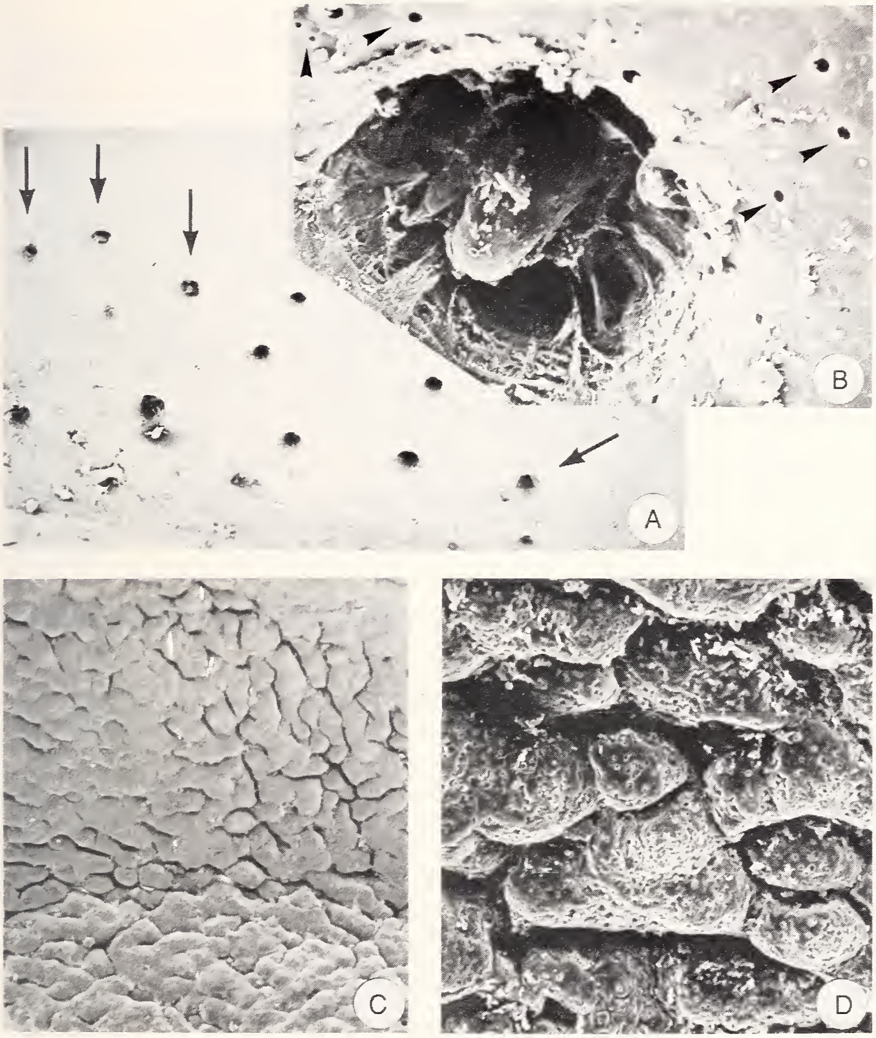

Fig.21: SEM of the skin of adipose fin. A: *Diplomystes* spec.: skin of the lateral side of the fin, close to its base; the presence of ampullary organs is indicated by arrows (26x); B: *Diplomystes* spec.: enlargement (416x) of an ampullary organ illustrating the ampullary lumen, and pores of goblet cells indicated by arrowheads; C: *Diplomystes* aff. *chilensis*: skin of the lateral side of the fin, close to its base (240x); D: *Diplomystes* aff. *chilensis*: enlargement (104x) of some papillae illustrated in C; note the presence of many pores.

ter belonging to ampullary organs (Fig.21D) are located on each epidermal papilla of the adipose fin. Pores of goblet cells were not observed on the barbels.

Papillate superficial neuromasts, probably at different activity stages because of their aspect, and taste buds are present along the barbel from the base to the distal tip (Figs.22A-

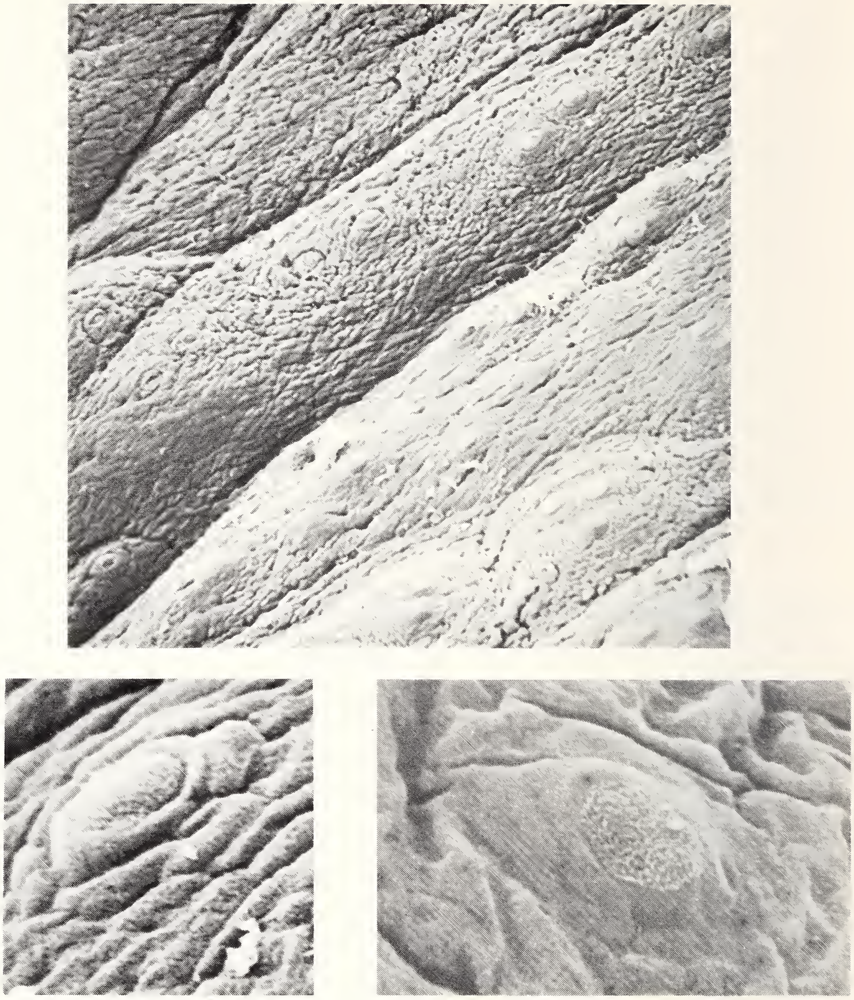

Fig.22: SEM of the skin of the base of the maxillary barbel in *Diplomystes* aff. *chilensis*. A: Distribution of papillate superficial neuromasts and taste buds (130x); B: A papillate superficial neuromast in active stage (1,300x); C: A taste bud (1,300x).

C, 23A-E). The large epidermal papillae bear large taste buds (Fig.23A), which do not rise above the surface of the skin and may be surrounded by deep furrows. The large epidermal papillae are situated between elongate epidermal projections which are separated from each other by deep grooves. Taste buds rising just above the surface of the skin (Fig.23B) were observed together with slit-like structures (Fig.23A-C). These structures are interpreted as papillate superficial neuromasts whose cupulae are sunken in this particular individual at the time when it was prepared. These sunken neuromasts are presumed to be able to rise to the surface at some later time. This assumption is supported by *Nema-*

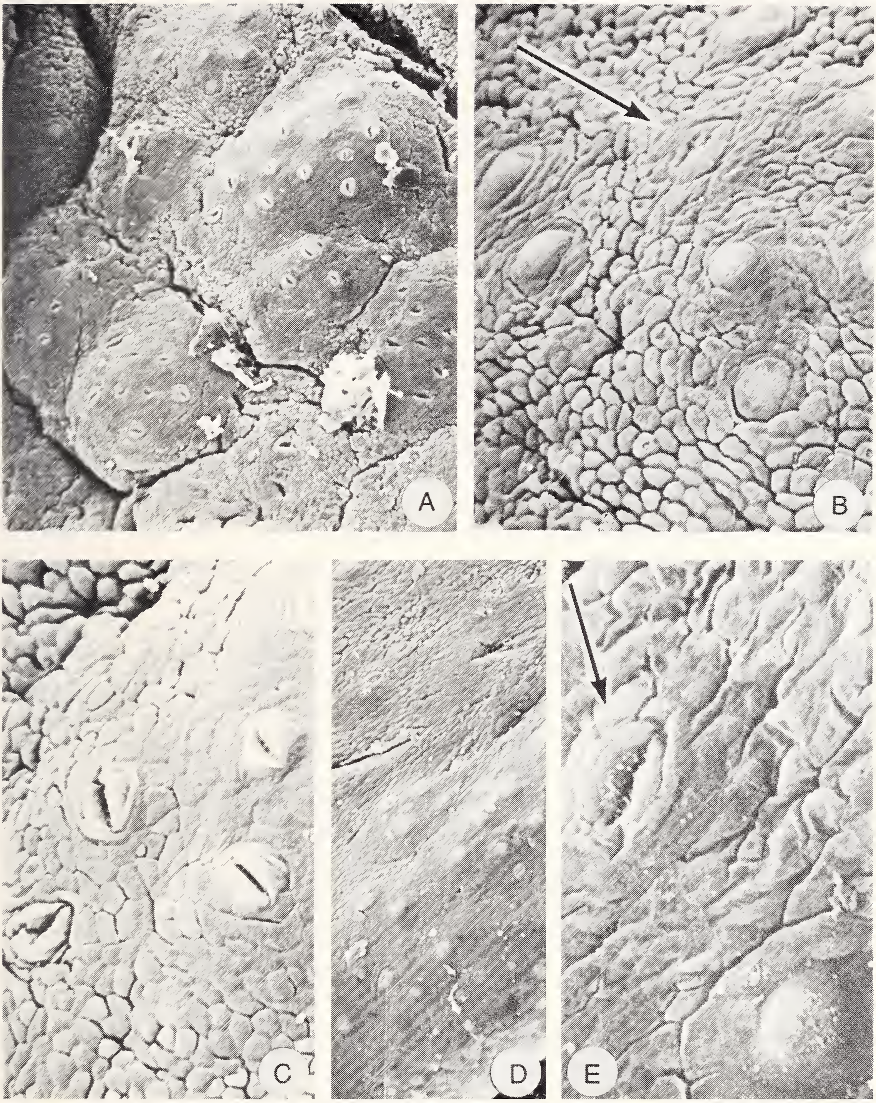

Fig.23: SEM of the skin of the maxillary barbel in *Diplomystes* aff. *chilensis*. A: Taste buds, slit-like structures or papillate superficial neuromasts, and epidermal papillae at the base of the maxillary barbel (130x); B: Enlargement (520x) of taste buds at the base of the barbel, a papillate neuromast (indicated by an arrow), and micropapillae forming the epidermal papillae; C: Enlargement of slit-like structures at the base of the barbel; D: Taste buds and papillate neuromasts in the middle region of the maxillary barbel (130x); E: Enlargement (1,040x) of a taste bud and a slit-like structure (indicated by an arrow).

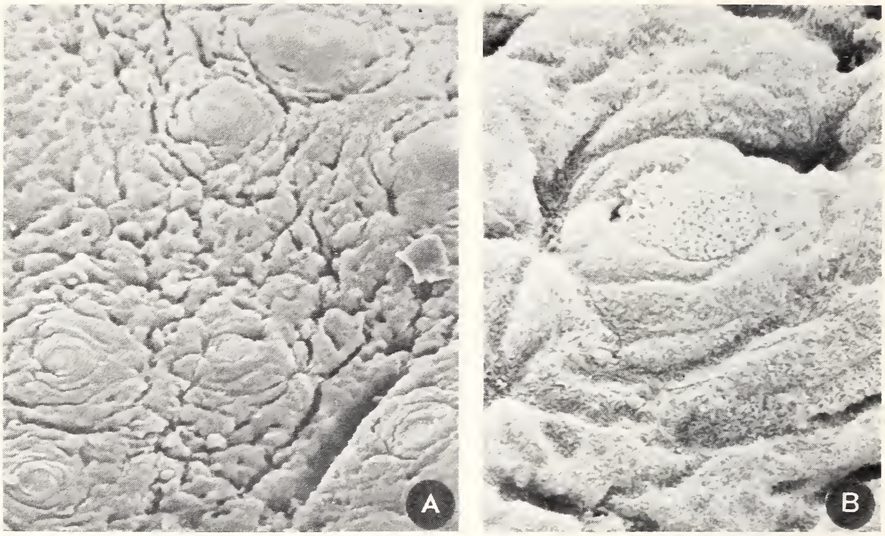

Fig.24: SEM of the skin of *Diplomystes* aff. *chilensis*. A: Epidermal papillae and taste buds (300x) in the skin between the vomerine tooth patchs; B: Enlargement (1,500x) of a taste bud.

togenys. The apical portion of the papillate superficial neuromasts and of the taste buds in *Nematogenys* show different degrees of exposure between neuromasts and taste buds (see below, p. 59, Fig.30B-D). A similar condition of the taste buds was described and illustrated by Jakubowski (1983: fig. 1D, E) in the bottom dweller *Cobitis taenia* and was interpreted as morphological protection of the sensory terminals against damage when the fish swiftly digs itself into the sand.

The middle region (Fig.23D) of the barbel has numerous small epidermal papillae bearing taste buds and superficial neuromasts. The distal end of the barbel is covered by irregularly shaped epidermal papillae; a few large taste buds (Fig.23E) and slit-like structures or papillate superficial neuromasts were observed.

Different types of taste buds are found in the mouth. For instance, many volcano-like TBIIs are found in the skin of the mouth between the premaxillary and vomerine teeth. The skin between the vomerine tooth patches (Fig.24A) is covered with many small epidermal papillae, separated by deep furrows. Rose-like taste buds (Fig.24B), with the sensory terminal area at the horizon of the skin, and a few large volcano-like TBIIs are also found in this area. The whole surface of the epidermal cells is covered by microridges.

Unicellular unculi, multicellular horny tubercles, large superficial neuromasts, and neuromast lines were not observed on the skin of the specimens examined.

Skin of *Diplomystes camposensis*

The skin of *D. camposensis* commonly presents numerous short, blunt papillae (Fig.25A) that are covered by the colloid-like substance. Young specimens have smoother surface than that of adults.

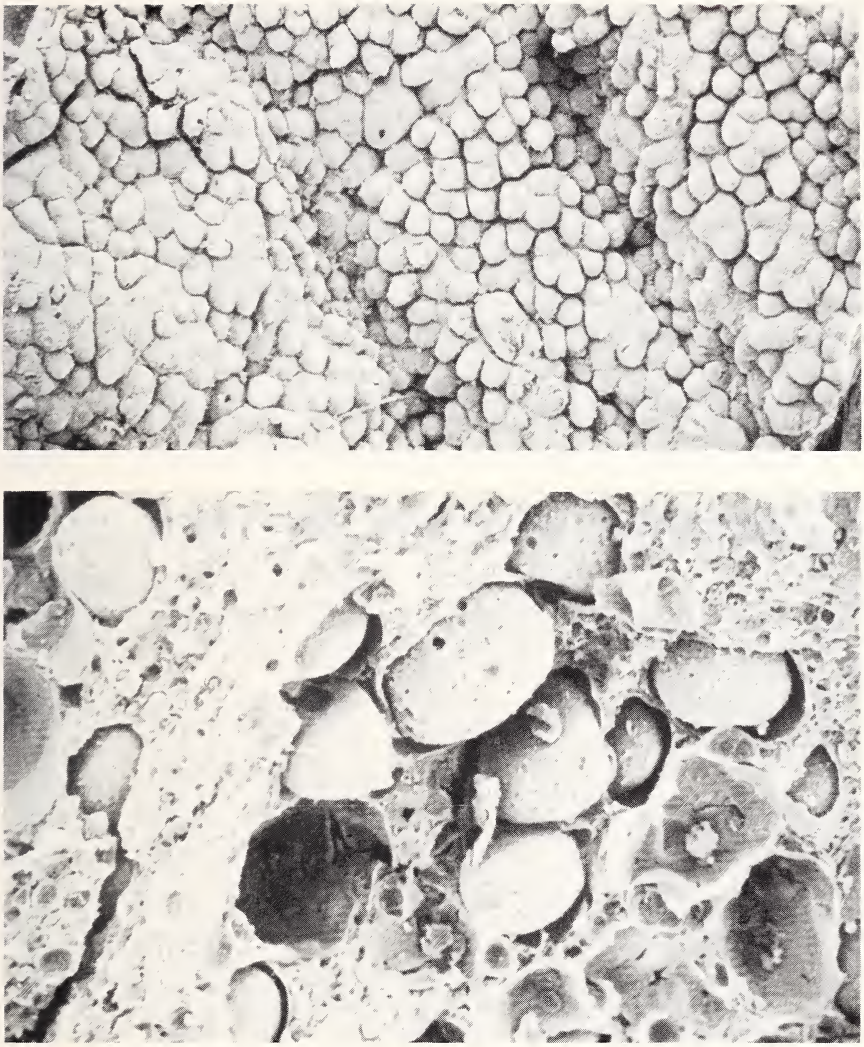

Fig.25: SEM of the skin of *Diplomystes* aff. *chilensis*. A: External view of the skin of the middle region of the flank (20x); B: Cuticle and superficial epidermis removed to illustrate the club cells (320x).

The micromorphology of the skin of *D. camposensis* is similar to that described above for *Diplomystes* spec., except for the following features: The whole surface of the epithelial cells of the flanks is covered by a dense reticulum of microridges and by a pronounced ridge on one side of each cell (Fig.26A, B). These microridges cover the epithelial surface of the entire body. Microridges are less dense in the palatal region (Fig.27A) than on the flanks. This kind of ornamentation is unique to *D. camposensis* among species of *Diplomystes*.

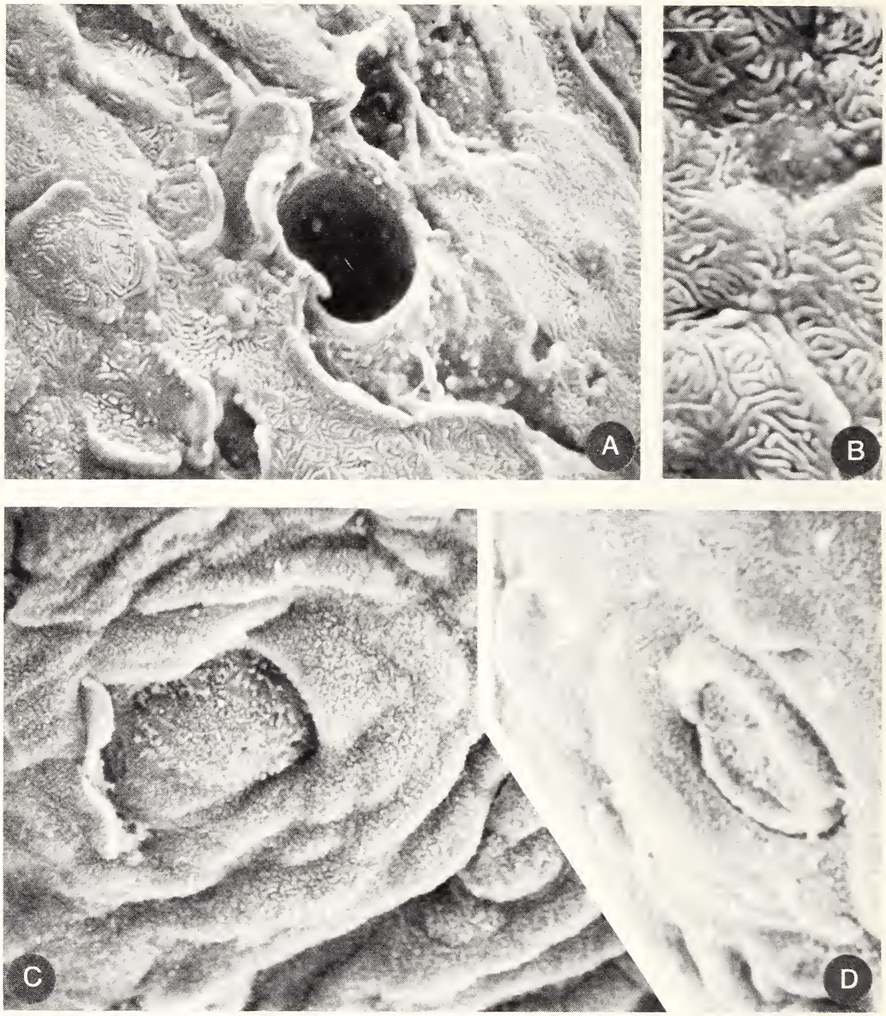

Fig.26: SEM of the skin of *Diplomystes camposensis* Arratia. A: Pore of the lateral line and skin surface posterior to pectoral girdle (2,500x); B: Enlargement of the epidermal surface (5,000x); C: Rose-like taste bud of upper lip (2,500x); D: Small rose-like putative superficial neuromast from dorsal lip (2,500x).

Slit-like structures that correspond to papillate superficial neuromasts (according to cross sections) are observed in the upper lip of *D. camposensis*. Numerous rose-like taste buds are positioned on the maxillary barbels, lips, and in the palatal region (Fig.26C); they are small structures which can be observed at high magnification (about 2,000x). The skin of the flanks presents numerous pores of about 30 microns in diameter; inside the pore is a

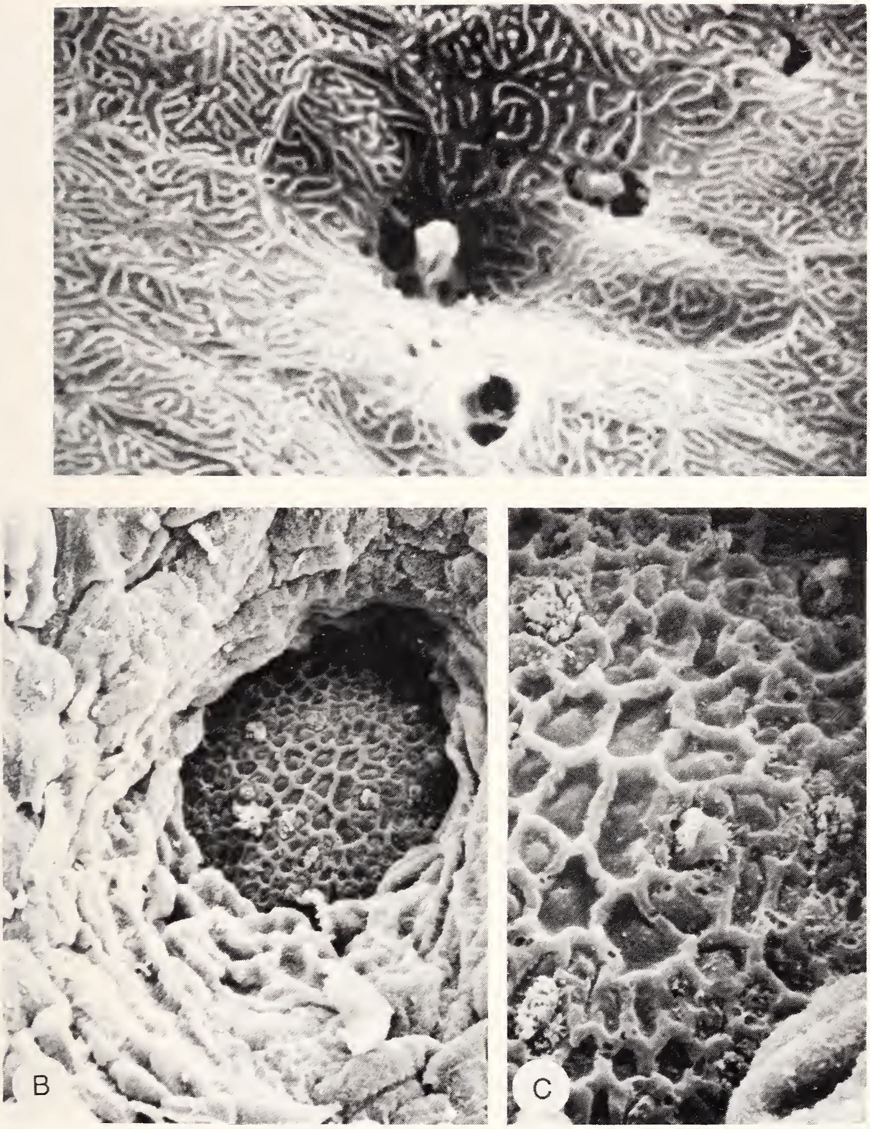

Fig.27: SEM of the skin of *Diplomystes camposensis* Arratia. A: Skin of the palatal region in between the vomerine tooth plates. Note that the microridges are not so dense as on the skin covering the trunk; B, C: Skin of the dorsal part of the flank showing an unidentified pore and structure at 1,000x and 3,000x, respectively.

structure whose surface is covered by thick ridges forming a regular pattern (Fig.27B, C). These unidentified structures were observed with SEM microscopy only.

Remarks

Numerous taste buds are concentrated on maxillary barbels, lips, branchiostegal membranes, and oral cavity in diplomystids. Rose-like taste buds are found in *D. camposensis* (Fig.26C), whereas they are volcano-like TBIIs or barely arising over the surface of the skin (TBs) in *Diplomystes* spec. and *Diplomystes* aff. *chilensis* (Figs.20D, 22C, 23E). Taste buds of the palatal region lie between large furrows and are placed on elongate epidermal papillae in *D. chilensis* (Arratia 1987a: fig.2C), unlike in other diplomystids where furrows and papillae are comparatively shorter and unevenly distributed.

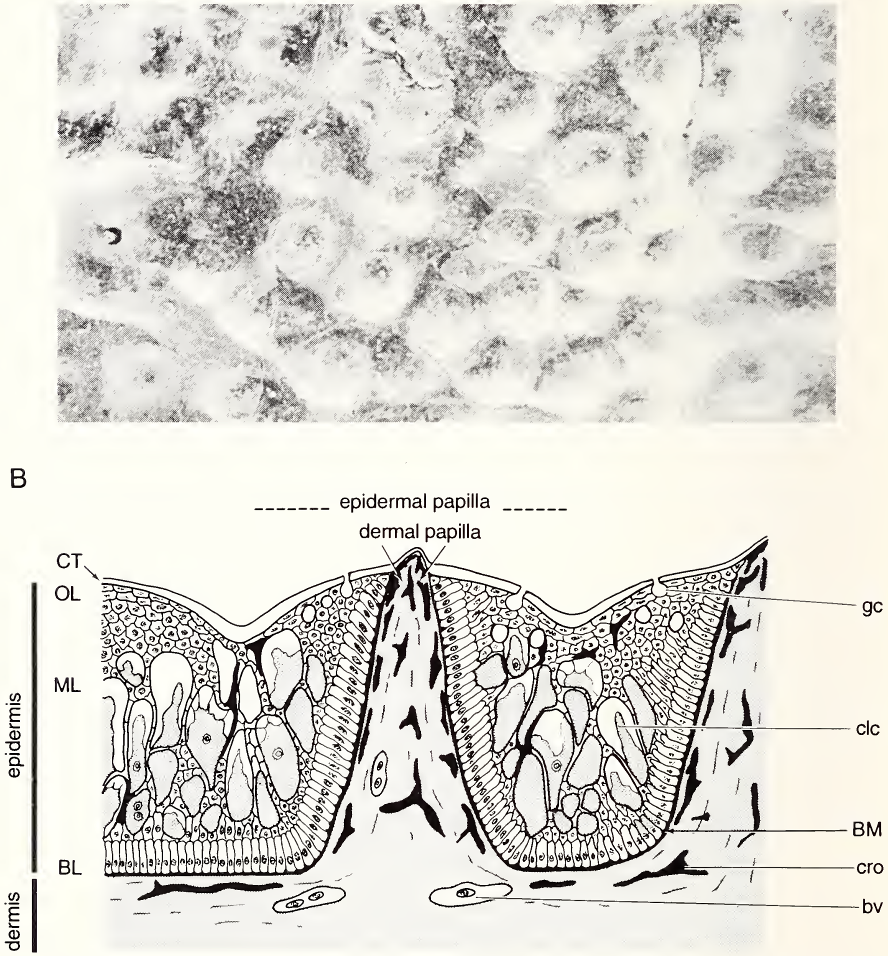

Fig.28: Skin of an adult *Nematogenys inermis* (Guichenot) of 27 cm standard length. A: SEM of the skin of the dorsal part of the flank posterior to the pectoral girdle (30x); B: Diagrammatic representation of a cross section of this region to show the growing of the dermal papillae.
BL: basal layer; BM: basal membrane; bv: blood vessel; clc: club cell; cro: chromatophores; CT: cuticle; gc: goblet cell; ML: middle epithelial cell layers; OL: outer epithelial cell layers.

Numerous putative ampullary organs (Fig.21A-D) with large pores (100 to 500 microns of diameter) are present on head and body of *Diplomystes* spec., but small ampullary organs (pores of 0.2 to 2 microns of diameter) are found in *D.* aff. *chilensis.*

Numerous isolated papillate superficial neuromasts are unevenly distributed on the head of *Diplomystes* and also in the mouth. The superficial neuromasts are particularly abundant in the entire maxillary barbel in *Diplomystes* aff. *chilensis*, whereas they are especially abundant at the base of the maxillary barbel and lips in *D. camposensis.*

Skin of *Nematogenys inermis*

The external aspect of the skin of *Nematogenys inermis* varies with age, being soft on the body and with epidermal papillae on the lips, base of barbels, and branchiostegal region in young individuals. Large specimens have numerous large, round, whitish papillae on the whole body with the exception of the distal tip of the barbels (few or none), and distal parts of the dorsal, anal, and caudal fins. Numerous epidermal papillae are distributed in rows on the skin of pectoral and pelvic rays, and also on the first dorsal ray. Adult individuals over 250 mm standard length show in each large epidermal papillae a conical, blackish structure which can emerge above the epidermal surface (Fig.28A, B). Each of these structures is the result of extended growth of a dermal papilla whose surface is covered with melanophores. These papillae are found on the dorsal part of the head and body, being more numerous just behind the head; taste buds and pit-organs were not observed on these papillae. In large individuals, the skin surrounding the pores of the lateral line is whitish and becomes keratinized.

The skin is composed of epidermis, dermis, and hypodermis with different thickness along the body. The cuticle, colloid-like (Fig.29B-E), is thicker along the head and body, being particularly thick on furrows of the skin and thinner on the barbels. The epidermis has goblet cells, club cells, taste buds, and pit-organs like in *Diplomystes*, but there are important differences to be noticed.

Nematogenys inermis has a pair of nasal pseudobarbels (sensu Arratia 1987a) posterior to the anterior nasal opening, a long pair of maxillary, and a short pair of mental barbels. Epidermal papillae of different sizes are present on the dorsoposterior part of the base of the maxillary barbel, and also on the anterior part close to the base of the barbel. The surface of the maxillary barbel is irregular, with grooves and elongate projections.

The epidermis (Fig.29A) is thicker at the anterior part of the maxillary barbel than at its posterior part. In general it is comparatively thicker than the dermis; on the maxillary barbel, the dermis does not produce evaginations extending into the epidermis like those in diplomystids. The squamous epithelium (Fig.29B, C) of the maxillary barbel is well developed, with ten to twenty rows of epithelial cells and with many round or ovoidal goblet cells. There are goblet cells on the entire skin and also in the oral cavity; however, their number varies along the body being more abundant in the epidermis of the maxillary barbels, lips, and mouth; the whole dorsal surface of the head has many goblet cells.

Commonly, there is one layer of few ovoidal or round club cells (Fig.29A, C) lying above the basal membrane in the epidermis of the maxillary barbel and separated from each other by a thick basal layer composed of three or four rows of columnar cells. They are

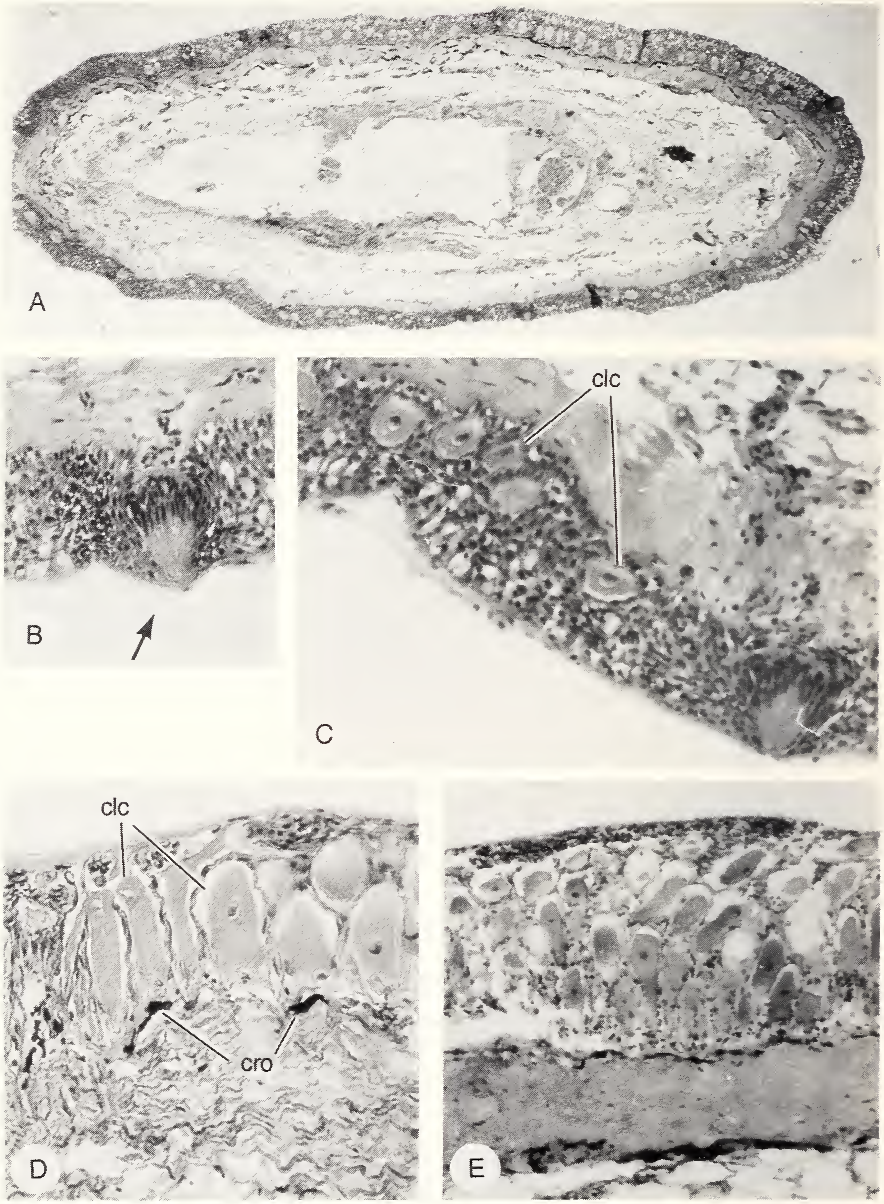

Fig.29: Maxillary barbel and skin of *Nematogenys inermis*. (Guichenot). A: Cross section of the maxillary barbel. Note the thickness of the epidermis with respect to that of dermis; B: Section of the skin of the maxillary barbel illustrating a taste bud indicated by an arrow; C: Section of the skin of the maxillary barbel illustrating the squamous epithelium, taste bud, and club cells; D, E: Section of the skin of the body just posterior to head illustrating differences in the epidermis.
clc: club cell; cro: chromatophores.

comparatively fewer than in diplomystids (compare Figs.18A, 29A) and most of them present only one nucleus. Large taste buds (Fig.29B, C) and superficial neuromasts, as deep as the thickness of the epidermis are found in the maxillary barbel.

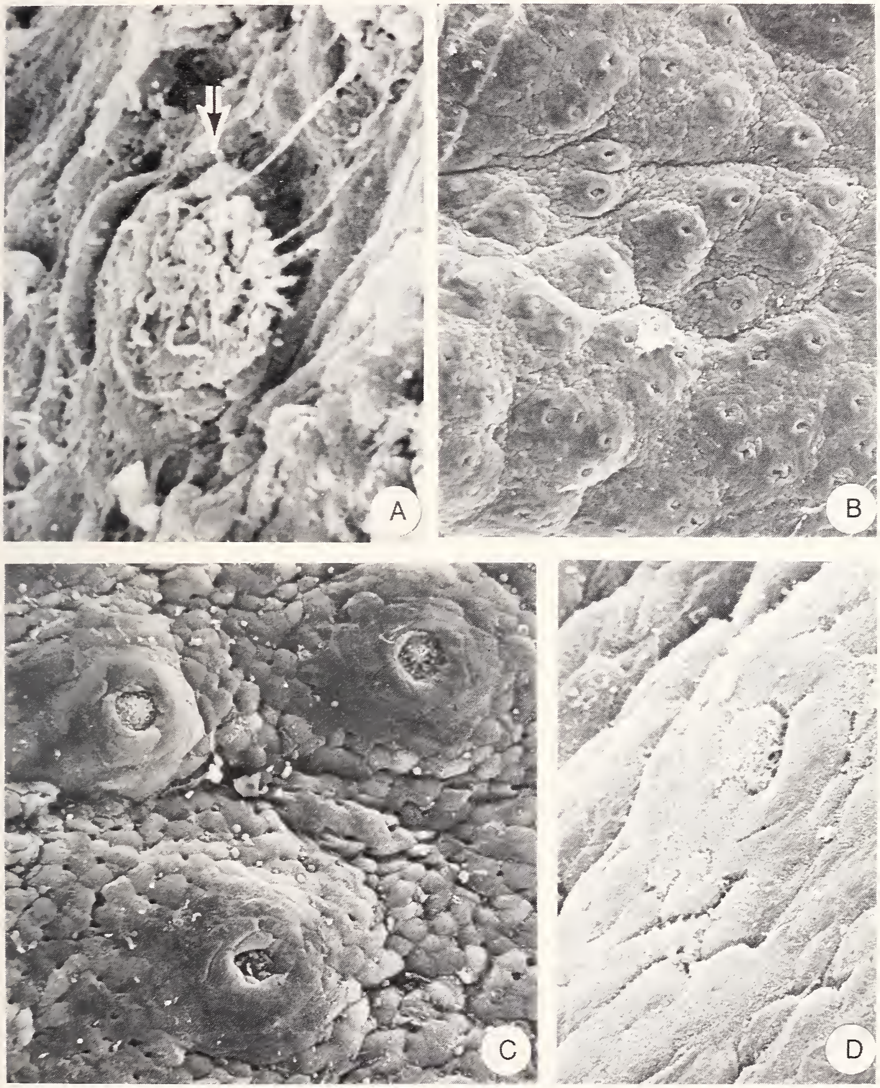

Fig.30: SEM of the skin of *Nematogenys inermis* (Guichenot). A: A putative mechanoreceptor and projections (indicated by arrows) from the anterodorsal region of the maxillary barbel (1,500x); B: Epidermal papillae and taste buds at the base of the maxillary barbel (170x); C: Enlargement (640x) of a section of B; note the pores and small droplets of goblet cells; D: Superficial neuromast of the middle region of the maxillary barbel (1,800x).

No melanophores are present in the epidermis of the barbels in *Nematogenys*; all melanophores are concentrated in the dermis and subjacent layers. A similar condition is also observed in the epidermis of the body, where most melanophores are concentrated in the dermis.

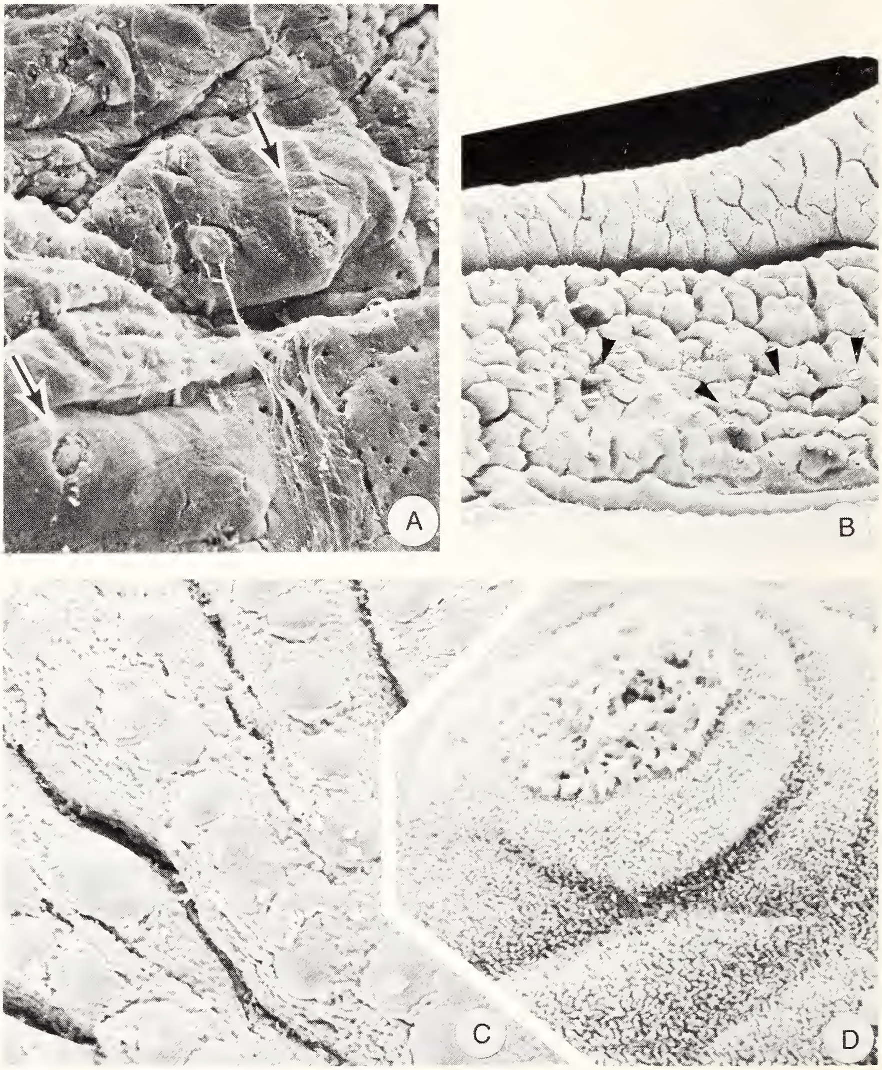

Fig.31: SEM of the skin of *Nematogenys inermis* (Guichenot). A: Anterior part of upper lip (640x). Superficial neuromasts are indicated by arrows; B: Ventral part of the upper lip and skin between premaxillary teeth indicated by short arrows; note the distribution of the epidermal papillae (34x); C: Position of taste buds in the skin of the palatal region (340x); D: Enlargement of a taste bud of the palatal region (3,600x).

The epidermis is of similar thickness or is thinner than the dermis in the skin of the head and body. The superficial epidermis on the body just posterior to the head is formed by a thin epithelium that presents a curious characteristic that has not been observed in the other catfishes examined: The presence of one or two rows of elongate club cells that can be placed horizontal to the epidermal surface, just below the cuticle. Club cells in horizontal position are irregularly placed along the body.

Two or more layers of elongate club cells (Fig.29D, E), not so large as those in *Diplomystes*, form most of the epidermis of the body. The club cells separate from each other by the squamous epithelium composed usually by a few layers of cells and for the basal layer. A well-defined middle layer of cells is not observed in the epidermis of *Nematogenys*. The club cells are placed in compartments limited by cellular "pillars" as those described and figured for diplomystids (Figs.17B, 19A, D).

Taste buds are irregularly distributed on the skin of barbels, head, and body, but they are aligned in rows in the skin of the mouth. They can be placed on epidermal papillae or not. The demarcation between the epidermal papilla bearing taste buds and the surrounding epithelium is sharp, formed by a deep furrow. Many volcano-like TBIIs, with their sensory terminals usually sunk in the pore of the bud (Fig.30B, C) are found in the maxillary barbel; in some of them, the sensory cell terminals are not seen at all because they are sunken deeply into the crater of the volcano-like TBIIs. A few taste buds barely protrude above the surface of the skin in the middle and distal regions of the maxillary barbel. Isolated papillate superficial neuromasts (Fig.30A) are unevenly distributed at the base of the maxillary barbel.

The number of taste buds decreases in the middle part of the maxillary barbel. Superficial neuromasts that barely extend above the surface of the skin (Fig.30D) are found in this region. The epidermal papillae at the middle of the barbel are irregular in shape but extremely large and elongate, in comparison to those found at the base of the maxillary barbel.

The skin of the anterior part of the upper lip (Fig.31A) has an irregular surface due to large epidermal papillae and deep furrows. Here the scarce taste buds, many pores of deeply sunk ampullary organs, isolated papillate superficial neuromasts, and pores of goblet cells are present. On the ventral side of the upper lip and on the skin between the premaxillary teeth, elongate epidermal papillae (on the lip) or irregular small papillae (between the teeth) appear which are separated by deep grooves (Fig.31B). The epidermal papillae have numerous pores of goblet cells and a variable number of TBIIs which are distributed in rows (Fig.31C) on the lips. A similar arrangement of taste buds is observed in the palatal region; the sensory cell terminals of the taste buds may be slightly sunk, or on the top of the buds (Fig.31D).

Many conical epidermal papillae of different sizes, each bearing a TBI, are found on the dorsal and lateral parts of the head (Figs.31A, 32A, B). The whole skin in this region has numerous pores of goblet cells (Fig.32C).

The skin posterior to the cleithrum, in the middle of the flank, has epidermal papillae of different sizes and shapes lacking taste buds (Fig.33A-C). Dorsal to this area, there is a narrow region composed of many long, simple or lobulated microprojections or unicellular unculi (Fig.33D) that look similar to the unicellular unculi figured by Roberts (1982: fig.19G-I) for the sisorid *Pseudecheneis sulcatus*.

Numerous papillate superficial neuromasts, isolated or in groups, or lines, are found on the head (Figs.30A, D, 32D) and body. They are more evident in large individuals than in the young. They are numerous on the upper lip, the base of maxillary barbel, around the eye, cheek, and opercular region. Commonly, they have a round or ovoidal area of hair cell epithelium protruding from the mantle cells which surround it completely (Fig.32D).

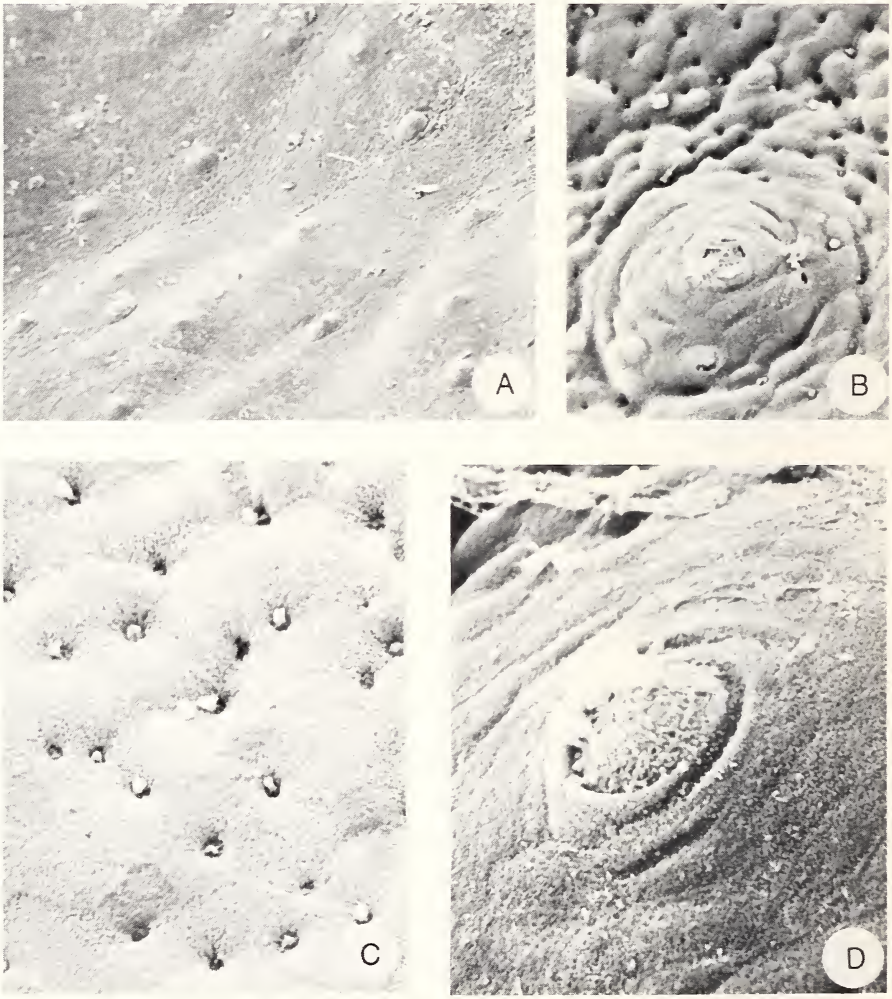

Fig.32: SEM of the skin of the dorsal part of the head, between the eyes, in *Nematogenys inermis* (Guichenot). A: Skin between the eyes showing taste buds (30x); B: Taste bud, pores and droplets of goblet cells (600x); C: Epithelial cells and droplets of goblet cells (1,600x); D: Papillate superficial neuromast (1,500x).

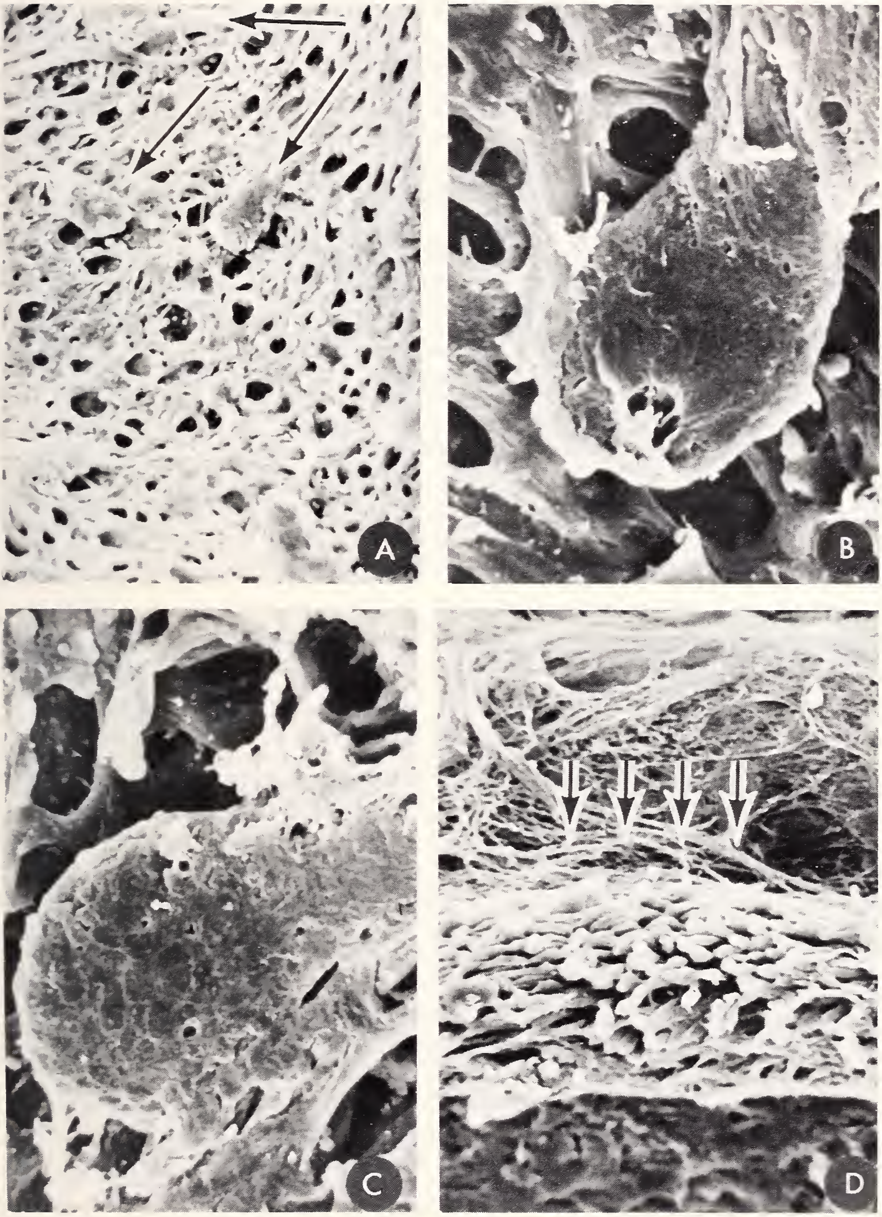

Fig.33: SEM of the skin dorsal to the main lateral line region behind pectoral girdle in *Nematogenys inermis* (Guichenot). A: 300x; arrows indicate epidermal papillae; B, C: Enlargement (600x) of epidermal papillae; D: Unicellular unculi indicated by arrows (300x).

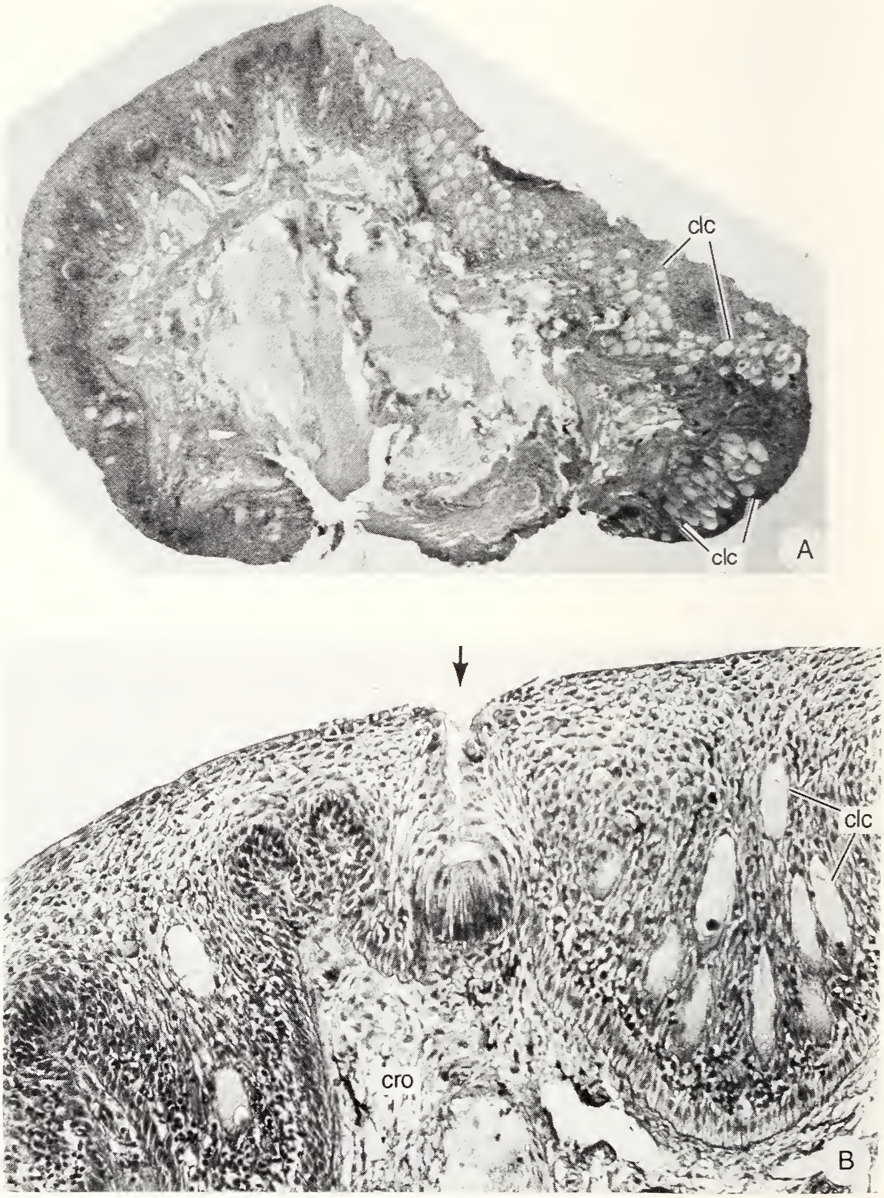

Fig.34: Maxillary barbel and skin of *Trichomycterus areolatus* Valenciennes. A: Cross section of the maxillary barbel; B: Enlargement of a section of the skin of the maxillary barbel illustrating the structure of the epidermis; a deeply sunk ampullary organ is indicated by an arrow.
clc: club cell; cro: chromatophores.

Skin of *Trichomycterus areolatus*

The skin of young specimens appears smooth under low magnification. Adult specimens have large, round, translucent epidermal papillae on the whole surface of maxillary and submaxillary barbels, lips, and branchiostegal region. Few, small, slightly conical epider-

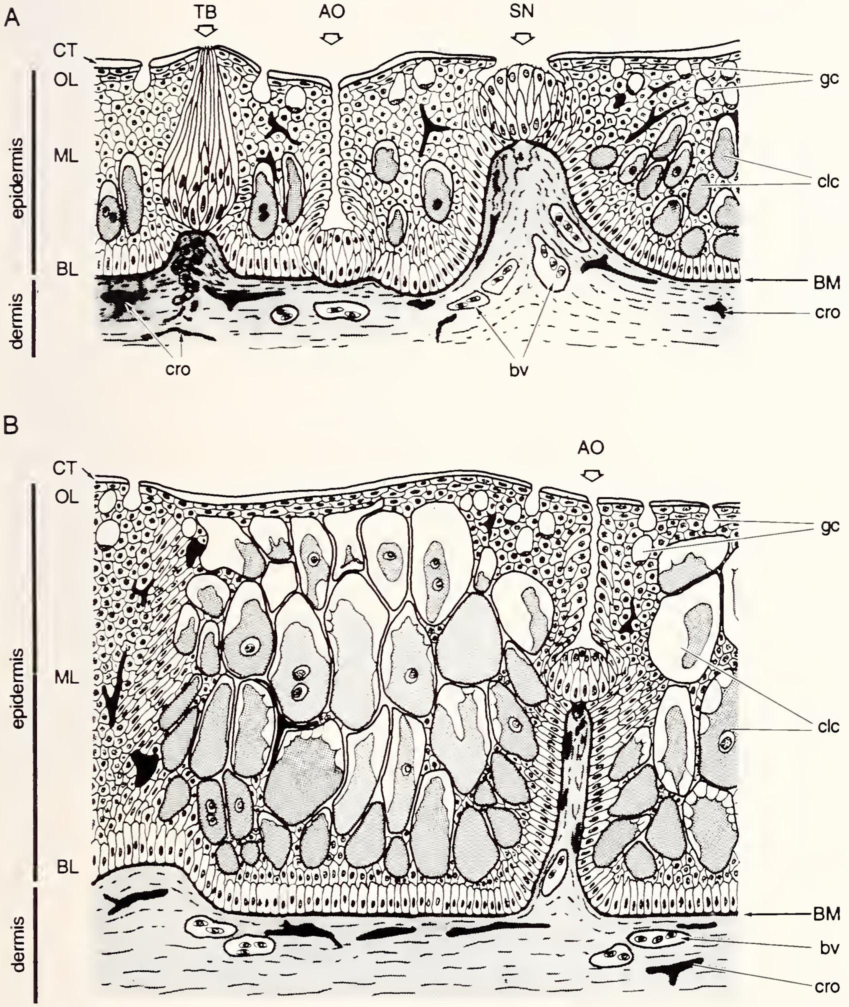

Fig.35: Diagrammatic cross section of the skin of *Trichomycterus areolatus* Valenciennes, based on histological sections. A: Skin of the maxillary barbel; B: Skin of dorsal part of body behind head.
AO: ampullary organ; BL: basal layer; BM: basal membrane; bv: blood vessel; clc: club cell; cro: chromatophore; CT: cuticle; gc: goblet cell; ML: middle epithelial cell layers; OL: outer epithelial cell layers; SN: superficial neuromast (papillate pit of Coombs et al. 1988); TB: taste bud.

mal papillae are distributed all over the body including the first pectoral ray, first principal dorsal and anal rays, and base of the principal caudal rays. Differences in quantity and distribution of epidermal papillae in males and females were not observed. Large individuals (not even the largest known, a 125 mm specimen) do not present the development of conical dermal evaginations on the surface of the skin as described above for *Nematogenys* (Fig.28A, B).

The thickness of the epidermis varies along the body as in the other catfishes examined. The epidermis (Fig.34A, B) of the maxillary barbel is thicker than the dermis. The squamous epithelium is formed by many rows of cells and it has different thickness because of the deep evaginations of the dermis into the epidermis (Figs.34A, B, 35A). The epidermis of *T. areolatus* resembles that of *Diplomystes* in the presence of numerous irregularly distributed club cells (compare Figs.17A, 18A, 34A, B, 35A). There are numerous taste buds, commonly two or more associated with a dermal evagination, and a variable number of ampullary organs deeply sunk in the epidermis (Figs.34B, 35A). The epidermis is thicker at the posterior half of the maxillary barbel than in the anterior half. The posterior half bears numerous club cells, whereas the anterior half bears numerous taste buds and a few ampullary organs which are deeply sunk into the epidermis.

The skin of the body is similar to that above described for *Diplomystes* being the club cells the most numerous elements of the epidermis (Fig.35B).

Trichomycterus areolatus has three pairs of barbels, e.g., nasal, maxillary, and submaxillary. The first one (Fig.14A, B) is a projection of the membrane posteriorly surrounding the anterior nasal opening. The complete skin of the nasal barbel appears reticulate under examination with SEM; gustatory receptors were not observed. The skin of the maxillary and submaxillary barbels is markedly papillate (Figs.14A, B, 36A, 37A), with epidermal papillae of different sizes which are separated by deep grooves; each epidermal papilla bears a variable number of taste buds and epidermal micropapillae. The quantity of epidermal papillae, epidermal micropapillae, and taste buds varies along the barbel; they are numerous on the proximal region (Fig.37A), dorsoanterior surface, and distal tip of the barbel (Fig.36A).

Examination of each epidermal papilla with SEM microscopy reveals the presence of numerous TBIs and a few TBIIs on each at the base of the maxillary and submaxillary barbels and on lips. Each taste bud is placed in a round protuberance arising from the surface of the epidermal papilla. Each taste bud (Figs.36A-D, 37A, B) has numerous sensory cell terminals. Many irregularly shaped epidermal micropapillae lie between the apical portions of the taste buds; numerous, small, round or conic evaginations of the epidermis that look paler than the sourrounding structures, are found along the whole surface of the barbels; these evaginations were not observed in cross sections.

The upper lip (Fig.14D) has a verrucose surface with deep grooves and numerous taste buds and isolated papillate superficial neuromasts.

The skin of the dorsal part of the head around and between the nasal barbels is highly papillose and with few TBIs; higher magnification (1,500x) reveals a few cells bearing domed protrusion (Fig.14C). The microridges of the epithelial cells on the skin of the head are evident at about 1,500x whereas they are not seen at such magnification in the skin of the barbels. The epithelial cells are of irregular shape and size. The skin (Fig.37C, D) of the dorsoposterior part of the head and anterior part of the trunk just posterior to the short main lateral line is smooth and with a few or without epidermal papillae and taste buds.

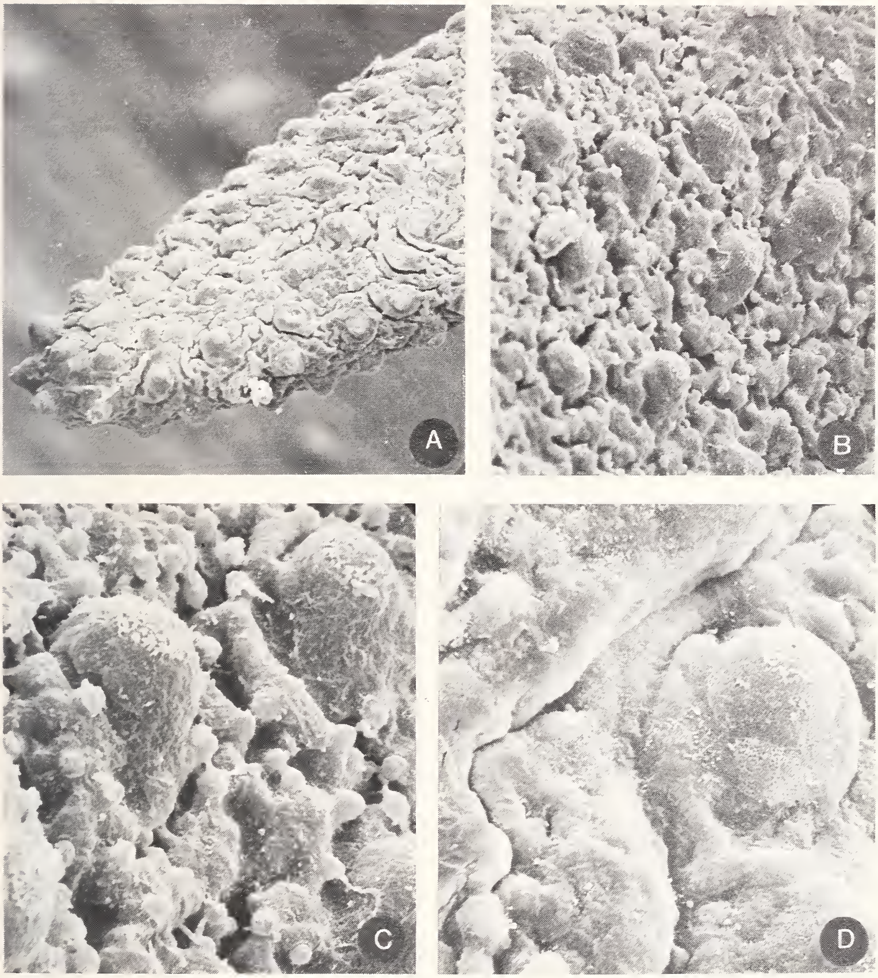

Fig.36: SEM of the skin of the distal part of maxillary barbel (A- C) and of the submaxillary barbel (D) in *Trichomycterus areolatus* Valenciennes. A: Distal part of maxillary barbel (340x); B: Enlargement (1,500x) of taste buds and epidermal papillae; C: Enlargement of part of A (1,500x); D: Taste bud and epidermal papillae at the base of the submaxillary barbel (1,500x).

However, higher magnification (over 5,000x) shows many microscopical papillae covering the cellular surface.

Trichomycterus areolatus has a short main lateral line on the body (Fig.10A) like in other species of *Trichomycterus* (Arratia & Menu Marque 1984). The main lateral line of the body opens to the skin surface by small, round pores; the lateral line ends just posterior to the posttemporo-supracleithrum. The skin surrounding the last pore is irregularly papillate; taste buds were not found in this region. The surface of the body epidermal papillae is covered by round microprojections or micropapillae and a net of irregularly distributed

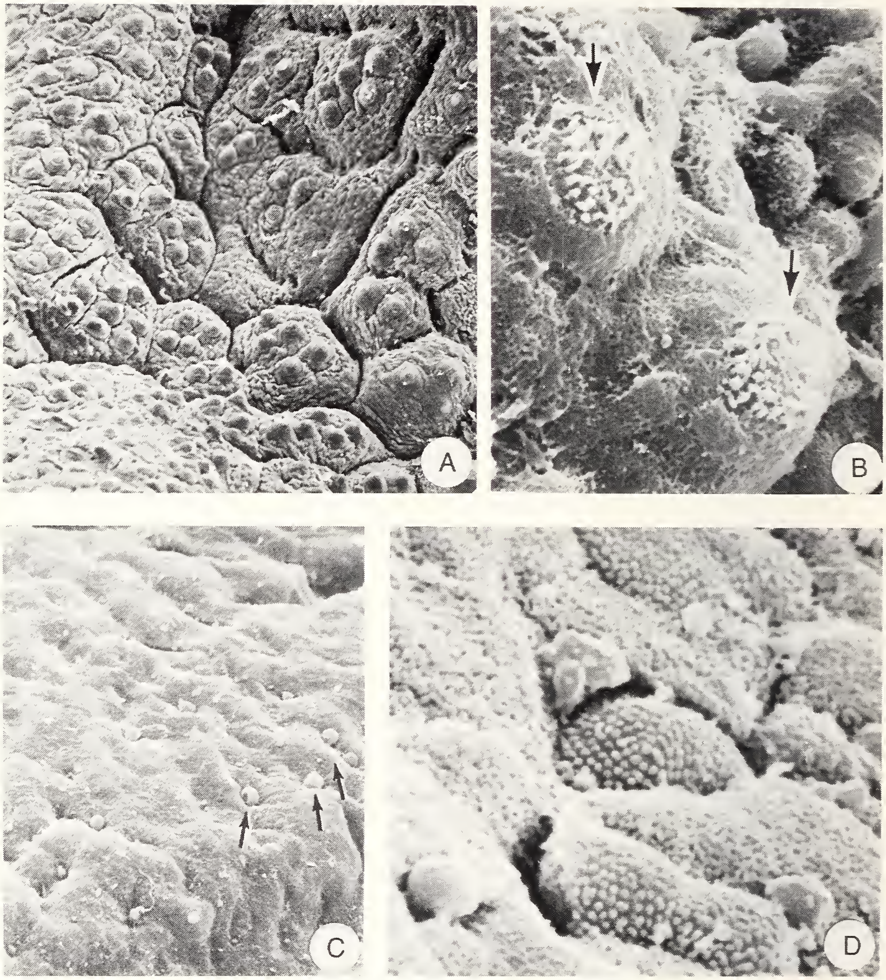

Fig.37: SEM of the skin of *Trichomycterus areolatus* Valenciennes. A: Distribution of taste buds on epidermal papillae (300x) at the base of the maxillary barbel; B: Enlargement (1,500x) of a taste bud; note gustatory terminal processes indicated by arrows; C: Skin posterior to the pectoral girdle in *Trichomycterus areolatus*; a few droplets of goblet cells are indicate by arrows (1,500x); D: Enlargement (5,600x) of a section of the skin posterior to the pectoral girdle.

microridges; droplets of different sizes of goblet cells are observed at high magnification (Fig.37C).

The skin of adult individuals shows numerous pores along the flanks; the pores belong to putative ampullary pits (40 to 50 microns), to goblet cells, and some of the smallest to ampullary organs which are deeply sunk in the epidermis.

Fig.38: SEM of the skin of "*Trichomycterus*" *mendozensis* Arratia et al. A: Skin of the middle region of the flank, posterior to pectoral girdle, illustrating the presence of pores of ampullary organs and papillate superficial neuromasts (320x); B: Enlargement of a neuromast and of a cell bearing protrusion (indicated by an arrow) (2,500x).

Skin of "*Trichomycterus*" *mendozensis*

The skin of young individuals is soft, without epidermal papillae, but the papillae appear during growth. Among adults, males have more epidermal papillae than females, so that the whole surface of males is papillose and covered with numerous, large pores of ampullary organs (Fig.38A). Volcano-like taste buds are present mainly on the barbels and lips. They are similar to those described above for *Trichomycterus areolatus*.

The most remarkable feature of the skin of "*T.*" *mendozensis* is the large quantity of pores of ampullary organs (diameter ranges between 1.7 and 4.5 microns) which appear all over the skin surface (similar to the condition described in *Silurus glanis* by Jakubowski 1987) and the presence of translucent, conical epidermal papillae bearing papillate superficial neuromasts (Fig.38A, B). The papillae bearing neuromasts are unevenly distributed on the entire surface of the body. A few cells bearing protrusion of about 5 microns in diameter are irregularly present in the skin of the dorsal part of head and body. The surface of the epithelial cells is covered by a net of microridges that are observed at high magnification (Fig.38B). "*Trichomycterus*" *mendozensis* does not have micropapillae on the epidermal papillae in contrast to *Trichomycterus areolatus* (Figs.36B, C, 37D) and *Hatcheria*.

Skin of *Hatcheria macraei*

The skin of *Hatcheria macraei* resembles that of *Trichomycterus areolatus* in having numerous taste buds, epidermal papillae, and micropapillae of different sizes on the barbels (see above). The skin of the body just posterior to the cleithrum is similar to that of *Nematogenys* (Fig.33D); an elongate mass of microprojections is found in the skin in the middle

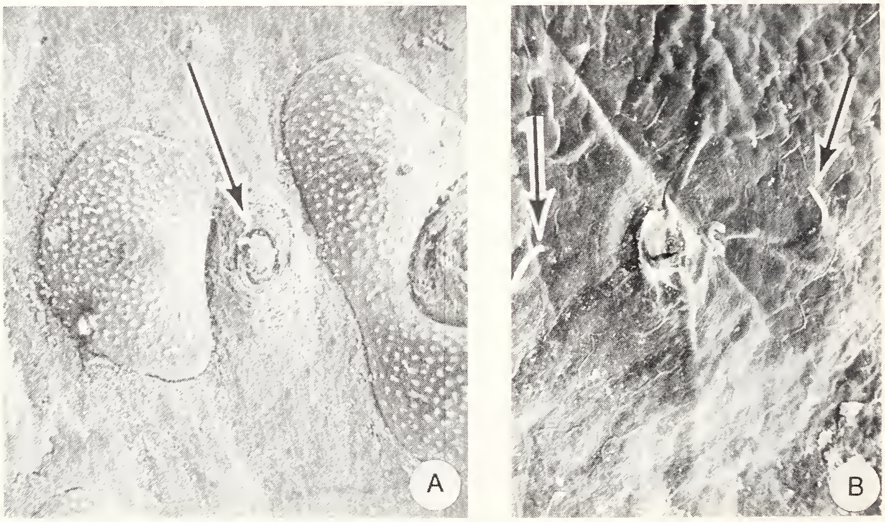

Fig.39: A: SEM of the skin of the dorsal region of the head in *Pimelodus* spec. (220x); arrow indicates an unculiferous plaque; B: Skin of the dorsal region of head of *Galeichthys peru ianus* Lütken. Solitary cells indicated by arrows.

region of the flank just posterior to the cleithrum and they are interpreted here as unicellular unculi.

Despite the overall similarities, *Hatcheria* has fewer papillate superficial neuromasts than *Nematogenys*, and apparently, the rostral line (rostral fork replacement of the infraorbital canal plus fork replacement of the supraorbital canal) is the only pit line consistently present in *Hatcheria*.

Skin of *Pimelodus* spec.

Though the skin of large *Pimelodus* spec. appears smooth under low magnification, high magnification reveals hill-like unculiferous plaques (Fig.39A) that become keratinized during growth and are irregularly distributed in the dorsolateral region of the head. Each plaque does not have taste buds but many conical arrow-like microprojections or unculi. Between the plaques, a few volcano-like TBIIs are present.

Unculi have been described from *Pimelodus maculatus* by Ferri (1982, his horny-like cells). The unculiferous cell is filled by filaments embedded in an amorphous matrix (Ferri 1982: fig.15).

Skin of *Galeichthys peruvianus*

Among the species examined, *Galeichthys peruvianus* is the only marine representative. The skin of *Galeichthys peruvianus* is smooth, lacking large epidermal papillae or tubercles. The skin on the dorsal region of the head has a few taste buds, which are just at the surface of the skin. The gustatory surface of each taste bud bears two kinds of simple sensory cell terminals, one thicker than the other. Isolated papillate superficial neuromasts have an elongate strip of hair cell epithelium flanked by mantle cells on both sides. Solitary cells (Fig.39B) are observed on the dorsolateral region of the head; each solitary cell has a simple apical process; the apical process is slightly broader than the base and has tubular structures. Solitary cells were not observed in the other species studied.

HABITATS

Habitat of *Diplomystes* spec.

Two young specimens from this species were collected in the "dead zone" (below the stones, where the water speed is zero according to the definition by Dussart 1966:2254) of the Rhitron (Fig.40A, B), whereas the larger specimens (n=4) were collected in the Potamon of Andean torrential rivers (Rapel and Maule basins). The six specimens are the only known representatives of this undescribed catfish.

Diplomystes spec. has been collected together with another siluroid, *Trichomycterus areolatus* (many individuals), the percichthyids *Percichthys trucha* and *P. melanops* (few individuals), many individuals of the decapod crustacean *Aegla laevis*, and a few specimens of a few species of trichopterids, ephemeropterids, plecopterids, chironomids, and other insects.

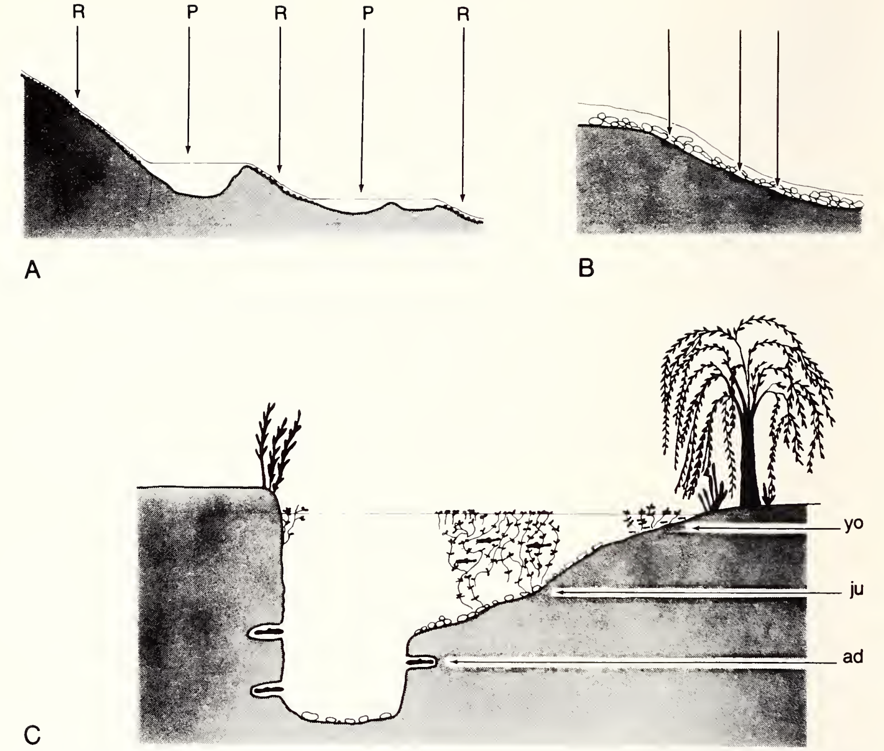

Fig.40: Diagrammatic sections of an Andean torrential river. A: Altitudinal section illustrating the Rhitron (R) and Potamon (P); B: Section of the Rhitron illustrating the "dead zone" (indicated by arrows) among the stones where the adult trichomycterids live; C: Section of the Potamon illustrating habitat preferences of *Nematogenys inermis* of different ages (after Arratia 1983b).
ad: adult; ju, juvenile; yo: young individuals.

Food items are known from two specimens: pieces of one individual of *Aegla laevis* per fish, partially digested.

Habitat of *Diplomystes* aff. *chilensis*

The only two known specimens, recently collected, were found in Potamonal sections of streams of Cachapoal river. One specimen was collected at about 80 cm depth in a stony stream surrounded by trees; other fishes inhabiting the stream were the catfishes *Nematogenys inermis, Trichomycterus areolatus*, the atherinid *Basilichthys australis*, the perciform *Percichthys trucha*, and the characid *Cheirodon pisciculus*. The second specimen of *Diplomystes* was collected in a section of a stream with muddy bottom and abundant vegetation (e.g., *Myriophyllum* and *Azola*). The crustacean *Aegla laevis*, plus larvae and adult insects of the family Hydrophyllidae spp., are especially abundant.

Food items are known from one specimen: pieces of one specimen of *Aegla laevis*.

Habitat of *Diplomystes camposensis*

The habitat of *D. camposensis* was described by Arratia (1983b) and later confirmed (Arratia 1987a, present paper) by more specimens collected in the region of Valdivia, Chile. Young specimens prefer the benthic section of the Rhitron of montane rivers while adults prefer the benthic section of the Potamon of rivers and lakes placed from a few meters above sea level to about 650 m. Specimens over 130 mm total length prefer to live below 60 cm depth, where the superficial water speed ranges between 0.5–1.6 m/sec, and the temperature of the surface water ranges between 14° to 18°C in summer (no other data available; Arratia 1983b: Tab.4).

Young specimens have been collected together with adult individuals of *Trichomycterus areolatus*. Adult specimens have been collected together with *Percichthys trucha* and different species of salmonids which are exotic fauna introduced in southern Chile.

The diet seems to be exclusively carnivorous; intact *Aegla laevis*, larvae and adult insects, and annelids are found in their stomachs (fifteen stomachs were examined).

Habitat of *Nematogenys inermis*

Nematogenys inermis is a typical habitant of the Potamonal section of Andean torrential rivers, mainly of 'spring waters' in central Chile. They live in Potamonal sections of the rivers that are about sea level or a few meters above. The habitat preferences (Fig.40C) of *N. inermis* change throughout life (Arratia 1983b:220–223). Young specimens (below 50 mm total length) prefer shallow (1–20 cm), flowing (0.10–0.26 m/sec) clear water. Juvenile specimens, sexually immature (60–180 mm total length) prefer deeper water (40–70 cm) with vegetation (e.g., *Myriophyllum brasiliense* and *Elodea chilensis*), and with surface speed of the water ranging between 0.10 and 0.70 m/sec. Large specimens, sexually mature (about 190–300 mm total length; contra de Pinna 1992:215 who interpreted 220 mm specimens as senescent individuals) prefer deep regions (below 70 cm); they live in caves on the walls of the rivers, at grooves in the bottom, and/or between the roots of *Salix chilensis* when those grow into the water.

Juveniles of *N. inermis* have been collected together with few specimens of the perciliid *Percilia gillissi*, the percichthyid *Percichthys trucha*, many larval and adult individuals of *Aegla laevis*, trichopterids, ephemenopterids, plecopterids, and chironomids. Larval and adult insects are abundant within the aquatic vegetation and on the water surface. Large individuals were mainly or only collected with *Aegla laevis*.

Adults of *N. inermis* are carnivorous; commonly one or a few intact prey organisms are found in the stomachs (twenty individuals were examined). The food items of *N. inermis* from central Chile were mainly *Aegla laevis*; they also eat adult and larval aquatic insects.

Habitat of *Trichomycterus areolatus*

Trichomycterus areolatus is a typical inhabitant of Andean torrential rivers in Chile; it lives at altitudes ranging from sea level to about 2,400 m (Arratia et al. 1985: fig.16).

Habitat preferences of *T. areolatus* change throughout growth (Arratia 1983b:223–225; Manríquez et al. 1988:91). Specimens of 7.6–24 mm total length prefer quiet waters (0 to

0.5 m/sec) close to the shore (0.5 to 10 mm depth), with a muddy and/or sandy bottom and small stones. Specimens of 25–60 mm total length prefer waters close to the shore and with vegetation; they move between the "dead zone" of the Rhitron and vegetation close to the shore. Adult specimens (70–120 mm total length) prefer the "dead zone" of the Rhitron with stony substratum where the speed of surface water varies between 0.10 and 2 m/sec from season to season (Arratia 1976, 1983b). The minimum length of mature *T. areolatus* is 56.7 mm for males and 51.1 mm for females which correspond to about the half of the maximum length which the species reach (Manríquez et al. 1988).

Young individuals of *T. areolatus* usually coexist in the "dead zone" with the crustacean *Aegla laevis*. Juvenile individuals, and breeding males and females, are found between plants living together with a variety of fish species such as *Cheirodon* spp., *Basilichthys chilensis, Percilia* spp., and *Percichthys* spp. Juvenile individuals, like the adults, do not school, although numerous individuals may live together in the same sector of a river.

Adult individuals of *T. areolatus* are carnivorous with no preference for one specific item (Duarte et al. 1971); the diet (thirty specimens examined) mainly comprises of complete *Aegla laevis*, and/or aquatic insects and insect larvae, gastropods, and oligochaetes.

Habitat of "*Trichomycterus*" *mendozensis*

"*Trichomycterus*" *mendozensis* is a typical inhabitant of the "dead" zone of the Rhitron of small rivers (Blanco river and El Salto and Las Mulas streams) that drain in Mendoza river, at about 1,500 to 1,700 m above sea level (Arratia et al. 1978, Arratia et al. 1985). "*T.*" *mendozensis* concentrates in some sectors of the rivers. The water speed ranges between 1.8 and 2.5 m/sec. The average annual water temperature is 8°C to 13°C (Peñafort 1981:48). This species is the only fish species living in these streams; it is endemic to these streams. The rest of the fauna comprises abundant *Aegla* crustaceans and many larvae of Plecoptera. Its diet is similar to that of *Trichomycterus areolatus* described above.

Habitat of *Hatcheria macraei*

Habitat preferences of *Hatcheria macraei* are similar to those of *T. areolatus* with some differences in the quality of the river bottoms, and water speed (Arratia 1976, Arratia & Menu Marque 1981: Tab.6; Peñafort 1981). The habitat preferences of *H. macraei* changes through growth (Arratia & Menu Marque 1981:107–107). Specimens of 10–20 mm total length prefer quiet water (0 to 0.5 m/sec) close to the shore (1–50 cm depth), with a sandy bottom and small stones. Specimens over 70 mm total length prefer the "dead zone" of the Rhitron with stony and sandy substratum, where the speed of the surface water varies between 0.10 and 3.20 m/sec. The depth of the water is less than 50 cm. The largest specimens were found in the presence of *Aegla* spp., but not together with other fish species. Juvenile *Hatcheria* were collected with the characid *Cheirodon* spec., the cyprinodontiform *Jenynsia linneata*, the catfish *Olivaichthys viedmensis*, the perciform *Percichthys* spec., and salmonids which have been introduced in Patagonia.

Juvenile and adult individuals of *H. macraei* do not school (Arratia & Menu Marque 1981).

Adult *H. macraei* is carnivorous. It feeds mainly on the crustacean *Aegla* and aquatic insects.

COMPARISON AND DISCUSSION

Superficial neuromasts

Neuromasts occur superficially in pits in the epidermis, in grooves, or in sensory canals. Superficial neuromasts are different from those enclosed in canals; they differ in size, structure, development, and possibly innervation (Satô 1956, Jakubowski 1965, 1966, Hama 1978, Münz 1979, Münz & Claas 1983, Coombs et al. 1988, Webb 1989a, b, Northcutt 1989). There is significant variation in the structure of superficial neuromasts and in the terminology used to describe them. Recently, Coombs et al. (1988) proposed a classification of neuromasts based on the relationships between neuromasts, dermal and epidermal layers, and basal epidermal layer. Among neuromasts, Coombs et al. (1988) distinguished:

1) The epidermal pit-organs which sit in pits formed by a gap in the epidermis and that are morphologically similar to the large pit-organs in ictalurid catfishes as described by Herrick (1901) and in catfishes and other ostariophysans by Satô (1955).
2) The ampullary pit-organs which are superficially similar to the ampullary electroreceptive organs present in siluroids (Herrick 1901, 1903a, Müllinger 1964) and non-siluroid teleosts (Jakubowski 1966, Roper 1981).
3) The superficial papillate neuromasts which are known from different teleosts, including the catfishes examined here.

Superficial neuromasts are often grossly apparent, e.g., *Diplomystes chilensis* (Fig.4B; Arratia 1987a), *Diplomystes camposensis* (Fig.5B), *Ictalurus punctatus* (Grizzle & Rogers 1979), *Nematogenys inermis* (Fig.7B), *Trichomycterus areolatus* (Fig.11B), *Rhamdia sapo* (Fig.10A), and *Pimelodus* spec. They are often surrounded by a small unpigmented area. Superficial neuromasts were not found in *Diplomystes* spec. and *D.* aff. *chilensis*; they are totally lacking in *Plotosus anguillaris* (Lekander 1949).

The presence of superficial neuromasts is intraspecifically variable (Tab.4; Grizzle & Rogers 1979, Arratia 1987a, Coombs et al. 1988); commonly, they are less numerous in young than in adults (e.g., in *Nematogenys*). They also vary between specimens of similar length; for instance, they are irregularly present in specimens of *Diplomystes camposensis* from the same locality (Tab.4).

In general, the superficial neuromast lines are poorly known in ostariophysans. There is information from a few cypriniforms (with the best known pit lines), characiforms, and siluroids. The skin of gymnotoids has received more attention, but superficial neuromast lines have not been described in that group.

Superficial neuromasts may occur as isolated elements, neuromast fields, or distinct rows or pit lines which follow the path of the lateralis system in catfishes such as *Silurus* (Allis 1904), *Ictalurus punctatus* (Herrick 1901, Grizzle & Rogers 1979), *Parasilurus* (Atoda 1936, Satô 1949a, 1955), *Plotosus* (Lekander 1949), *Diplomystes chilensis* (Fig.4B; Arratia 1987a), *D. camposensis* (Fig.5B), *Nematogenys inermis* (Fig.7B), and *Trichomycterus areolatus* (Fig.11B). Superficial neuromasts may be aligned in several pit lines on the dorsolateral part of the head in siluroids. For instance:

1) Rostral fork replacement of the supraorbital canal. – Rostral lines in front the anterior nasal openings may be present in ostariophysans. The limits between left and right lines can hardly be decided in certain fishes by studying the

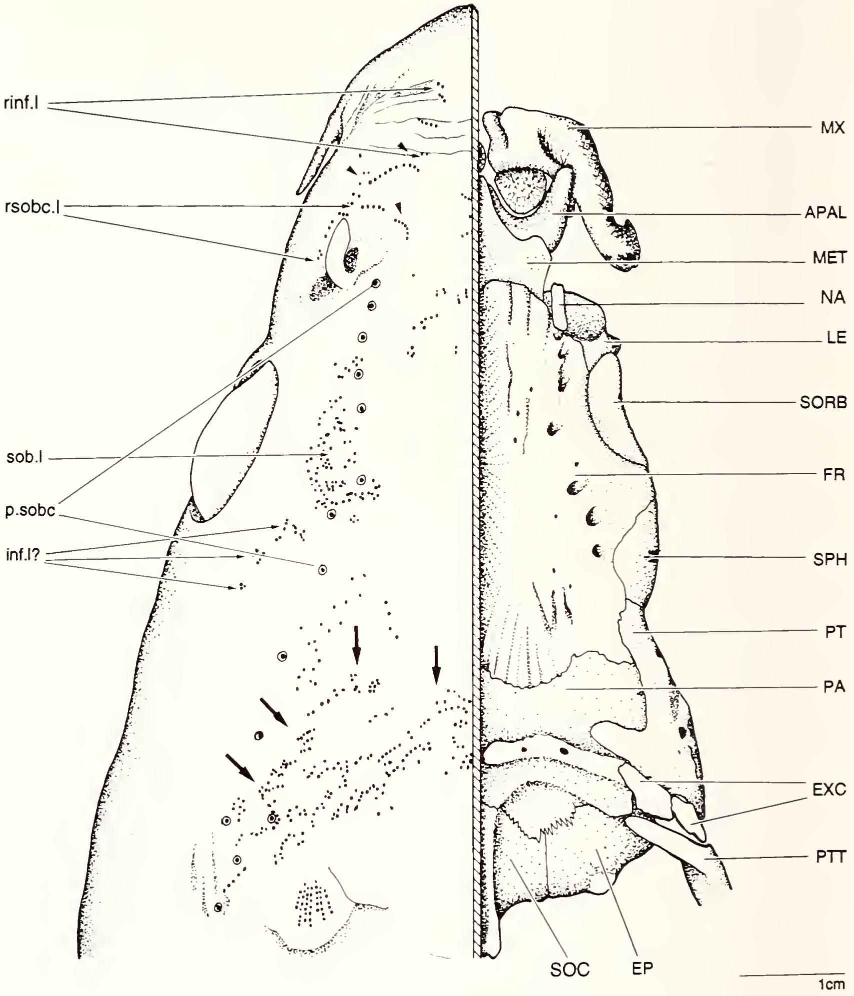

Fig.41: Distribution of lines of superficial neuromasts as field of neuromasts (left) in *Cyprinus carpio* Linnaeus and their relationship to cranial bones (right side). Note that there is no clear distinction between the anterior, middle, and posterior pit lines (indicated by large arrows). The rostral and nasal lines, in front of the anterior nasal opening are represented by several rows of superficial neuromasts (indicated by arrowheads); there is no clear separation between both pit lines.
APAL: autopalatine; EP: epioccipital; EXC: extrascapular bones; FR: frontal bone; if.l?: infraorbital line?; LE: lateral ethmoid; MET: mesethmoid; MX: maxilla; NA: nasal bone; PA: parietal; p.sobc: pores of supraorbital canal; PT: pterotic; PTT: posttemporal; rinf.l: rostral replacement of infraorbital canal; rsobc.l: fork replacement of supraorbital canal; sob.l: supraorbital accessory line: SOC: supraoccipital; SORB: supraorbital bone; SPH: sphenotic.

skin surface; in addition, as already noted above, it is difficult to establish the limit between the rostral fork replacement of the infraorbital canal and the fork replacement of the supraorbital canal.

A fork replacement line of the supraorbital canal was observed in *Diplomystes chilensis* and *D. camposensis*, and in most other catfishes examined. This line has been observed in cyprinids by Lekander (1949, his nasal line: figs.11, 15, 20, 24, 26, 28) and Satô (1949b: fig.1; 1955: figs.5a, b, 6a, b, 7a, b). *Cyprinus carpio* has several rows of superficial neuromasts medial and in front of the anterior nasal opening (Fig.41); they are identified here as the rostral fork replacement line of the supraorbital canal, in front of which there is another series of neuromasts which corresponds to the rostral fork replacement of the infraorbital canal (= rostral commissure of Satô 1955: fig.5A). This line is also present in characiforms; for instance, in *Hoplias* it is formed by fields of neuromasts (Fig.42) placed medial and in front of the anterior nasal opening. This line has been observed here also in *Chanos chanos*, cypriniforms, characiforms, and in primitive catfishes.

2) Rostral fork replacement of the infraorbital canal. – This line which is commonly identified as the rostral commissure was described first for siluroids by Allis (1904) in *Silurus*, and later by Lekander (1949) and Satô (1955). Arratia (1987a) described large neuromasts in the position of the ethmoidal commissure in *Diplomystes chilensis*. Within ostariophysans they have been described for cyprinids and cobitids (Fig.41; Lekander 1949: figs.11, 20, 24, 26, 28, 36; Satô 1955). They are present also in gonorynchiforms and characiforms; e.g., fields of numerous, small superficial neuromasts (Fig.41) are present in large specimens of *Chanos* and *Hoplias*.

A rostral fork replacement of the infraorbital canal is also known from esocoids (Pehrson 1944, Nelson 1972), gymnarchids (Pehrson 1945), salmonids (Pehrson 1944) and from a few advanced teleosts such as perciforms (Jakubowski 1963, 1966b) and gadids (Jakubowski 1967). Among Recent advanced actinopterygians a rostral fork replacement line as a canal is found in *Amia* (Allis 1889), *Elops* (Arratia 1987b), and clupeomorphs (Wolfhart 1937, Nelson 1984). The rostral fork replacement line occurring in a canal in amiids and primitive teleosts and the superficial line of neuromasts in advanced teleosts are homologous. The superficial line of neuromasts forming the rostral fork replacement of the infraorbital canal in teleosts may be present as an irregular field of neuromasts, or the neuromasts may be aligned in a row. These patterns may turn out to be useful as systematic tools when their distribution within teleosts is better known.

3) Antorbital line. – A short line formed by a few large neuromasts is found in *Nematogenys* (Fig.7B) and in a few individuals of *Diplomystes camposensis* (Fig.5B). They are commonly absent in *Trichomycterus areolatus* and *Hatcheria*. They were not observed in "*Trichomycterus*" *mendozensis*. Antorbital lines are also known from cyprinids (Satô 1955; present paper) and cobitids (Lekander 1949). According to Satô (1955) the neuromasts forming the antorbital line in cyprinids are innervated by the ramus buccalis. They also are present in gonorynchiforms (e.g., *Chanos*) and characiforms (e.g., *Hoplias*).

4) Infraorbital line or ventral infraorbital line. – A long neuromast line that follows the path of the infraorbital sensory canal forms the infraorbital line in certain siluroids (e.g., in *Nematogenys*: Fig.7A and in *Plotosus anguillaris*: Lekander 1949). A rudimentary line as a continuation of the posterior section of the infraorbital

sensory canal is present in adult *Trichomycterus areolatus* (Fig.11B). The infraorbital line is also known from cyprinids (Lekander 1949, Satô 1955), gonorynchiforms (e.g., *Chanos*), and characiforms (Fig.42).

5) Supraorbital accessory line. – A field of neuromasts irregularly distributed is present in *Nematogenys* (Fig.7B), and in other ostariophysans such as *Cyprinus* (Fig.41; Satô 1955) and *Hoplias* (Fig.42). It is uncertain if the field of neuromasts positioned above the frontal and sphenotic bones in *Hoplias* is also part of the supraorbital accessory line. It is absent in *Diplomystes, Trichomycterus areolatus, "Trichomycterus" mendozensis*, and *Hatcheria*.

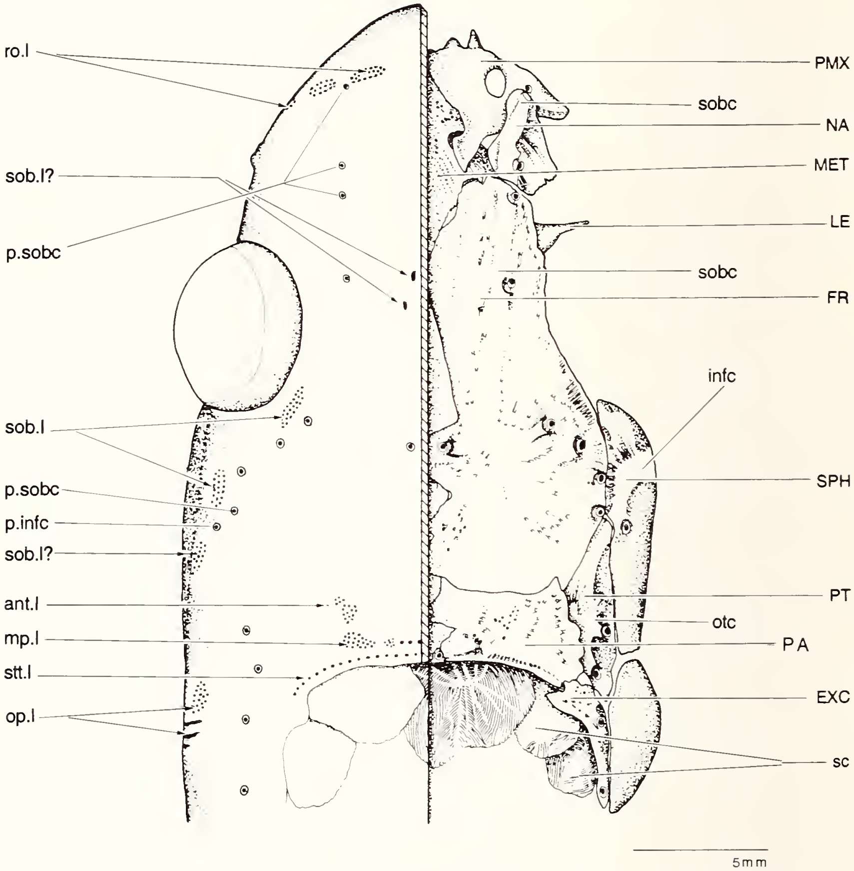

Fig.42: Distribution of superficial pit lines and fields of neuromasts (left) in *Hoplias malabaricus* (Bloch) and their relationship to cranial bones (right).
ant.l: anterior pit line; EXC: extrascapular bone; infc: infraorbital canal; FR: frontal bone; LE: lateral ethmoid; MET: mesethmoid; mp.l: middle pit line; NA: nasal bone; op.l: opercular lines (dorsal); otc: otic canal; PA: parietal bone; p.infc: pores of infraorbital canal; PMX: premaxilla; p.sobc: pores of supraorbital canal; PT: pterotic; ro.l: fork replacement of supraorbital canal; sobc: supraorbital canal; sob.l?: supraorbital accessory line?; sob.l: supraorbital fields of neuromasts; SPH: sphenotic; stt.l: supratemporal accessory line; sc: scales.

6) Anterior pitline. – The anterior pit line formed by a few large neuromasts is known in catfishes such as *Diplomystes chilensis* (Fig.4B), *Nematogenys inermis* (Fig.7B), *Trichomycterus areolatus* (Fig.11B), *Ameiurus melas* and *A. catus, Ictalurus punctatus*, and *Rhamdia sapo*. This pit line is present on the anterior part of the parietal bone in cyprinids (Fig.41; Lekander 1949) and characiforms (e.g., *Hoplias*: Fig.42). In cyprinids and characiforms the anterior pit line is usually represented by fields of numerous superficial neuromasts which are not clearly distinguishable from those of the middle pit line.

The anterior pit line of Recent siluroids commonly is not incised in bone; the same condition is observed in other ostariophysans such as Recent gonorynchiforms, cypriniforms, and characiforms, as well as other Recent teleosts such as *Elops*, clupeomorphs (e.g., *Chirocentrus*), esocoids (e.g., *Esox*), and salmonids (e.g., *Oncorhynchus*). The anterior pit line is incised in the parietal bone in the fossil ostariophysan *Chanoides* (Patterson 1984), and possible in the fossil siluroids *Hypsidoris* (interpretation of figure 1B by Grande 1987) and *Andinichthys* (Gayet 1988, labelled it as parietal

Fig.43: Dorsal view of the posterior part of the cranium of two ostariophysans illustrating the groove for the anterior pit line (indicated by an arrow) in (A) *Carassius auratus* (Linnaeus) and (B) *Bagre marinus* (Mitchill). Scales equal 5 mm.

branch on page 834). An anterior pit line incised in bone is occasionally present in Recent ostariophysans such as *Carassius* (Fig.43A), some specimens of *Hoplias*, and some species of Ariidae, Bagridae (Fig.43B), and Callichthyidae.

The anterior pit line is known from a variety of Recent teleosts such as elopids, esocoids, osmerids (Nelson 1972), cyprinids (Lekander 1949), characiforms (Fig.40), siluroids (Figs.8B, 20B, 27B, 33B; Allis 1904, Satô 1955, Arratia 1987a), salmonids (Disler 1960), gymnarchids (Pehrson 1945), and perciforms (Disler 1960, Jakubowski 1966b).

7) Middle pitline. – A small middle pit line formed by a few elongate neuromasts (two, three, or four) is transversely placed on the parieto-supraoccipital bone, posterior to the anterior pit line in siluroids such as some armored siluroids (Pollard 1892), in *Ictalurus* (Herrick 1901), *Silurus* (Allis 1904), *Diplomystes chilensis* (Fig.4B), *D. camposensis* (Fig.5B), *Nematogenys* (Fig.7B), and *Rhamdia* (Fig.10A).

A line of neuromasts in the position of the middle pit line may run in a groove. For instance, in fossil primitive teleosts (e.g., *Leptolepis, Tharsis*, and *Leptolepides*: Nybelin 1974, Patterson 1975; *Varasichthys*: Arratia 1984), in the fossil catfishes *Andinichthys* and *Incaichthys* (Gayet 1988, 1990, Arratia & Gayet in press) and in extant teleosts such as some armored siluroids (Pollard 1892), and in some species of ariids, callichthyids, pimelodids and occasionally in salmonids. The middle pit line runs in a groove on the parietal and pterotic bones in primitive fossil teleosts (Nybelin 1974, Patterson 1975, Arratia 1984). In most Recent teleosts, the middle pit line is superficially placed. The presence of the middle pit line in fossil teleosts is inferred based on the groove, but the middle pit line may have run superficially and not in a groove. In Recent salmonids, the middle pit line extends onto the parietal and pterotic bones but a groove is found only on the parietal. Among teleosts, the middle pit line is known from osteoglossomorphs, elopomorphs, esocoids (Nelson 1972; present paper), cyprinids (Lekander 1949, Satô 1955, Disler 1960), characiforms (Fig.42), siluroids (Figs.10, 17A; Herrick 1901), salmonids (present paper; in *Oncorhynchus keta*: Disler 1960), and gadids (Jakubowski 1967).

8) Supratemporal accessory line. – The supratemporal accessory line is commonly formed by one elongate neuromast in *Diplomystes chilensis* and *D. camposensis* (Figs.4B, 5B), *Nematogenys* (Fig.7B), *Trichomycterus areolatus* (Fig.11B), *Ameiurus catus* (Fig.10C), and *Rhamdia sapo* (Fig.10A). This line occurs in the position of the series of superficial neuromasts which accompany the supratemporal canal in gonorynchiforms, cypriniforms (Fig.41; Lekander 1949, Satô 1955), and characiforms (Fig.42). Small fields of free neuromasts are placed in front of the supratemporal accessory line and supratemporal commissure on the parietals, and occasionally extending onto the pterotics in the primitive cypriniforms *Opsariichthys* and *Zacco*. Recent siluroids lack the supratemporal canal but some of them retain the supratemporal accessory line of neuromasts.

The supratemporal accessory line is known from a few teleosts such as cyprinids (Fig.41; Atoda 1936, Lekander 1949, Satô 1949, 1955), characiforms (Fig.42), siluroids (Figs.4B, 5B, 7B, 11B), gadids (Jakubowski 1967), and perciforms (Jakubowski 1966b). Although the supratemporal accessory line present in primitive siluroids is commonly formed by one to three elongate superficial neuromasts lying on or in front of the extrascapular bone, there is no reason to doubt that this structure is homologous with the long neuromast line present in cyprinids and characiforms. Studies on many teleosts are needed to interpret the evolution of this structure within teleosts.

9) Opercular lines. – Short superficial neuromast lines or fields of superficial neuromasts are present on the opercular region in some siluroids (e.g., *Nematogenys, Trichomycterus areolatus*). Dorsal and ventral opercular lines are known in cypriniforms (Lekander 1949, Satô 1955).

10) Dorsolateral line or trunk lines of neuromasts. – Superficial neuromasts may be aligned in different lines:

(1) A line dorsally placed on the flank, extending between the occiput and the origin of the dorsal fin dorsal trunk line; e.g., in *Ictalurus* (Herrick 1901), in *Parasilurus* (Satô 1955), in *Nematogenys*: Fig.7B, and in *Trichomycterus*: Fig.11A.

(2) A subdorsal trunk line placed between the dorsal trunk line and middle trunk line: e.g., in *Parasilurus* (Fig.44: Satô 1955), in *Nematogenys* (Fig.7A), and in *Trichomycterus areolatus* (Fig.11A).

(3) A ventral trunk line placed below the middle trunk line: e.g., in *Parasilurus* (Fig.44: Satô 1955), in *Nematogenys* (Fig.7A), and in *Trichomycterus areolatus* (Fig.11A): this line was named horizontal body line in *Parasilurus* by Satô (1955).

(4) In addition, accessory trunk lines or numerous superficial neuromasts may be irregularly distributed all over the flank, e.g., in *Ictalurus* (Herrick 1901), in *Nematogenys* (Fig.7A), and in *Trichomycterus areolatus* (Fig.11A). In large individuals of *Rhamdia sapo*, superficial neuromasts, not organized in lines, are distributed on the flank.

The trunk lines seem to be formed by a series of neuromasts very regularly placed along the body in *Parasilurus* (Fig.44). Such regularity has not been observed in *Nematogenys* and trichomycterines.

Dorsal trunk lines and trunk accessories were described for cyprinids by Srivastava & Srivastava (1968): they also are present in characiforms, e.g., *Hoplias*. In the latter, the dorsal trunk lines are formed by fields of numerous small, superficial neuromasts.

Lines of neuromasts are commonly present in ostariophysans, except for gymnotoids. The lines of neuromasts are highly variable in composition of neuromasts, throughout

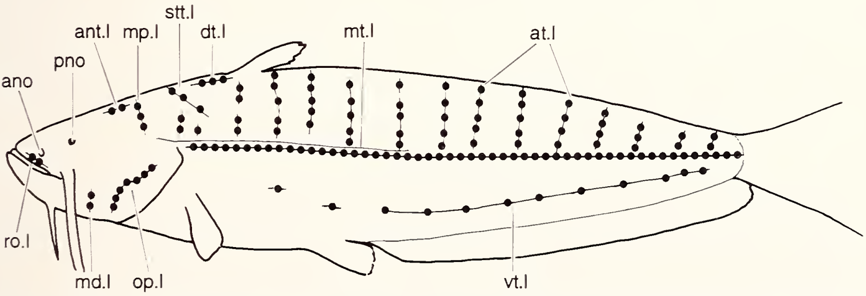

Fig.44: Diagram of *Parasilurus asotus* Linnaeus in lateral view showing the distribution of the neuromast lines in an individual of 250 mm length (modified from Satô 1955).
ano: anterior nasal opening; ant.l: anterior pit line; at.l: accessory trunk line; dt.l: dorsal trunk line; md.l: mandibular line (dorsal?); mp.l: middle pit line; mt.l: middle trunk line; op.l: opercular line (dorsal and ventral); pno: posterior nasal opening; ro.l: rostral line (= fork replacement of supraorbital canal?); sdt.l: subdorsal trunk line; stt.l: supratemporal accessory line; vt.l: ventral trunk line.

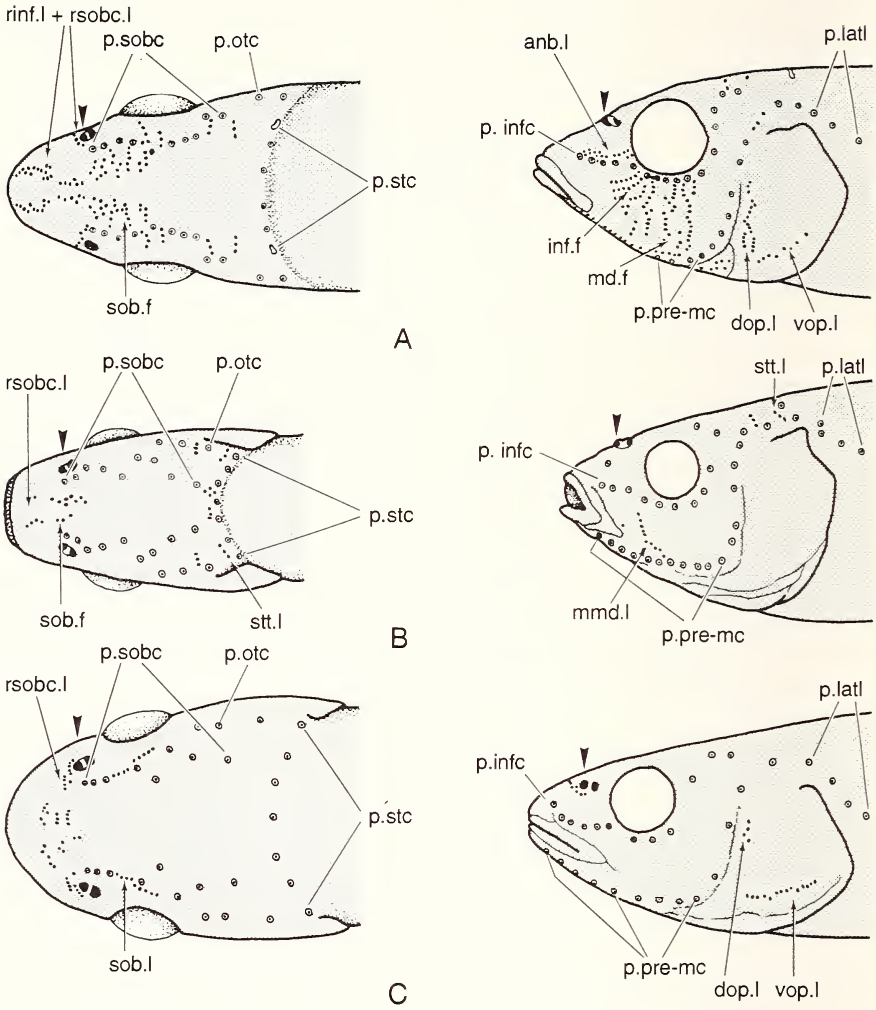

Fig.45: Diagram of cyprinid heads showing the distribution of neuromast lines in dorsal (left) and lateral (right) views of (A) *Cyprinus carpio*, (B) *Carassius auratus*, and (C) *Leuciscus hakuensis* (slightly modified from Satô 1955). Arrowheads point to nostrils.
anb.l: antorbital line; dop.l: dorsal opercular line; inf.f: infraorbital field of neuromasts; md.f: mandibular field of neuromasts; mmd.l: median mandibular line; p.infc: pores of infraorbital canal; p. latl: pores of main lateral line; p.otc: pores of otic canal; p.pre-mc: pores of preoperculo-mandibular canal; p.sobc: pores of supraorbital canal; p.stc: pores of supratemporal canal; rinf.l caudal fork replacement line of infraorbital canal; rsobc.l: rostral fork replacement of supraorbital canal; sob.l: supraorbital accessory line; sob.f: supraorbital field of neuromasts; stt.l: supratemporal accessory line; vop.l: ventral opercular line.

ontogeny, and among individuals of similar length. In addition, there are strong differences in presence or absence and composition of the lines among closely related ostariophysan genera. For instance, Satô (1955) concluded that *Cyprinus carpio, Carassius auratus*, and *Leuciscus hahuekensis* have well-developed canal systems, but there are considerable differences in the development of the neuromast lines (Fig.45A-C) which are faintly developed in *Carassius* and *Leuciscus*. Among catfishes the neuromast lines are very well developed in *Parasilurus* (Fig.44) and in *Nematogenys* (Fig.7B), and less developed in diplomystids and ictalurids.

The function of the superficial neuromasts seems to be similar to the neuromasts of the lateral line canals (Herrick 1901, Dijkgraaf 1962, Flock 1971), that are mechanoreceptive and respond to close-range vibratory stimuli (≥ 200 Hz) and with disturbances that originate either close to the fish or from its own movements (Denton & Gray 1988). It is widely recognized that natural stimuli to the neuromasts are:

(1) "Local pressure gradients produced by a fish's own swimming movements.

(2) Mechanical disturbance of the lateral line system caused by distortion in the fish's tissues arising from its movements.

(3) Local pressure gradients produced by external sources (e.g., by neighboring animals in mid-water, by disturbances at the surface, or by the flow of water around rocks in streams)." (Denton & Gray 1988:595).

It has been proposed that fishes with a reduced head canal pattern, canal segments containing neuromasts are replaced by lines of superficial neuromasts (Satô 1955, Webb 1989a). This condition may be true for certain fishes, but at least not for the trichomycterids (Figs.11B, 12B). Among the catfishes studied, adult *Nematogenys inermis* has all patterns of neuromast lines mentioned above and its cephalic sensory system is complete; in addition, it has small fields of neuromasts (three to five) on the head between the nasal openings, on the cheek, and isolated superficial papillate neuromasts all over the head. Adult *Trichomycterus areolatus* has lesser pit lines than *Nematogenys*, and it has lost the preopercular and mandibular canals. "*Trichomycterus*" *mendozensis* commonly has no pit lines and its cephalic sensory canal is reduced (Fig.12B). *Nematogenys inermis, Trichomycterus areolatus*, and "*T.*" *mendozensis* present isolate superficial papillate neuromasts irregularly distributed on the body.

Epidermal papillae and skin surface

The skin surface in catfishes may be smooth (e.g., in *Arius* and *Galeichthys*) or papillose under the examination with a stereoscope microscope or even under the naked eye (e.g., in *Diplomystes* aff. *chilensis*). Numerous catfishes have a papillate surface all over the body or only in certain regions; the papillate or verrucose surface is due to the presence of epidermal papillae. Epidermal papillae correspond to regions of thickened squamous epithelium covered by the cuticle. Epidermal papillae may have a smooth surface (e.g., in *Diplomystes* spec.; Fig.20A, D, E) or bear numerous micropapillae on its entire surface (e.g., in *Trichomycterus areolatus*; Figs.36B, C, 37D). However, there are differences in the size of the micropapillae, being comparatively large in *Diplomystes* (Fig.20A, B), and very small in *Trichomycterus areolatus* (Figs.36B, C, 37D) and *Hatcheria*.

Epidermal papillae may bear receptors or not. Papillae bearing one taste bud per papilla is the condition usually found in *Nematogenys* (Figs.30B, C, 32A, B), *Trichomycterus areolatus* (Figs.36B-D, 37B), and other loricarioids (Ono 1980, Ovalle & Shinn 1977). Epidermal papillae bearing numerous taste buds per papilla are found in *Diplomystes* (Fig.20E). Papillae bearing more than one superficial papillate neuromast are present in *Diplomystes* (Fig.23A) and in *Trichomycterus areolatus* (Fig.16A) and "*Trichomycterus*" *mendozensis* (Fig.38A, B).

The presence of epidermal papillae on the palatal region was considered a characteristic feature of the primitive families Diplomystidae and Nematogenyidae, and its absence was reported for the Trichomycteridae, Astroblepidae, and Loricariidae (Howes 1983). In contrast, we found epidermal papillae and taste buds in the palatal region of trichomycterines, *Astroblepus*, and *Loricaria*. *Astroblepus* has a low number of epidermal papillae in comparison to loricariids and trichomycterines. The presence and distribution of epidermal papillae is variable among members of the same family. For example, all trichomycterines have numerous well-developed epidermal papillae in the gular and branchiostegal regions like those in *Nematogenys* and *Diplomystes*; however, papillae do not occur in other trichomycterids, e.g., the sarcoglanidines (de Pinna 1988). Epidermal papillae on the body of adult *Trichomycterus areolatus*, *T. chiltoni*, and *T. roigi* are scarce in difference to *T. boylei* (Arratia & Menu Marque 1984) and *Nematogenys*. Skin completely covered with large, elongate epidermal papillae on body and adipose fin is characteristic of *Diplomystes chilensis* and *D.* aff. *chilensis*, or short, blunt papillae in *D. camposensis*, whereas large papillae are missing or are very few in *Diplomystes* spec.

Epidermal papillae develop during ontogeny in the catfishes examined (e.g., *Diplomystes camposensis, Nematogenys inermis, Trichomycterus areolatus, "Trichomycterus" mendozensis*, and *Hatcheria macraei*). Among the catfishes examined, males of "*T.*" *mendozensis* have more papillae than females. Whether this is a sexually dimorphic condition is difficult to decide because it is difficult to quantify how many more papillae are in males than in females.

The growth of conical dermal papillae inside the epidermal papillae that reach the skin surface and can emerge over the surface (Fig.26A, B), was only observed in large individuals of *Nematogenys* and it is not a sexual dimorphic character since the condition is present in adult males and females.

The epidermal cells covering the skin surface in the catfishes studied (e.g., diplomystids and loricarioids) are intrincately patterned with microridges (Figs.16B, 20B, C, 24B, 26A, B). Similarly complex patterns are known from the loricariids *Ancistrus, Farlowella*, and *Otocinclus* (Ono 1980: figs.21, 31, 35). The ictalurid *Ameiurus nebulosus* has the epidermal surface densely covered by villus-like microridges (Reutter 1978: fig.1b, c). "The fish skin is subjected to at least two types of stresses, because of its watery environment: 1) osmotic pressure gradients between the cells and the water and (2) physical forces not only from the water itself but from other environmental hazards, for example rocks. In addition, disease organisms such as fungi, bacteria, and water-worm parasites have easy acces to the skin" (Hawkes 1974:147). The specialized microridges on the epidermal surface have been considered adaptation to these stresses (Yamada 1968, Hawkes 1974) in fishes. According to Hawkes (1974) and Reutter (1978), the microridges present in the gill epithelium and surface epidermis possible serve to enlarge the respiratory surface (gill and cutaneous respiration, respectively). The microridges also aid in holding mucous secretions to the skin surface and in initiating wound closure by contraction of their basal microfilaments (Bereiter-Hahn 1971).

The complex, dense pattern of microridges found in the catfishes studied, which live mainly in the hazardous environment provided by the torrential Andean rivers, is supposed to give some mechanical defense; probably they aid in holding mucus secretion to the skin surface as shown for other fishes by van Oosten (1957), Hawkes (1974), and Reutter (1978).

Cells bearing protrusion

Cells with domed protrusion (Figs.20C, 27A) were observed on the skin surface of the dorsal part of the head in *Diplomystes* spec. and *D. camposensis* but not in *Diplomystes* aff. *chilensis*. Similar cells were also observed in the dorsal region of the head in *Nematogenys, Trichomycterus areolatus* (Fig.14C) and *Hatcheria*, and just behind the head in *Galeichthys peru ianus*. Brush-like protrusions (Fig.38B) are found in "*Trichomycterus*" *mendozensis*. Cells bearing protrusion have been reported in teleosts other than siluroids, e.g., *Agonus* (Whitear & Mittal 1986: pl. IVd-g). "It is supposed that the central protrusion marks especially active secretion of cuticular material" (Whitear & Mittal 1986: 558).

Unicellular unculi

Unicellular unculi, or unicellular horny projections, or unculi arising from single cells are known from numerous ostariophysans such as gonorynchiforms, cypriniforms, characiforms, and catfishes (see Roberts 1982, for a survey of the literature). Among the catfishes they are known in members of the families Akysidae, Amphiliidae, Aspredinidae, Loricariidae, Mochokidae, Sisoridae (Roberts 1982), and they are also present in Nematogenyidae and some Trichomycteridae (see above). They have different shapes and different positions among ostariophysans. For example, they are found on the upper lip in the gonorynchiforms *Chanos, Kneria*, and *Phractolaemus* (Thys van Audenaerde 1961, Roberts 1982), on the jaws in some cyprinids such as *Barilius* and *Garra* (Rauther 1928, Minzenmay 1933) and on the cuticular spines in the mouth of *Garra* (Leydig 1895), near the corner of the mouth in the catfish *Synodontis* (Wiley & Collette 1970), on the labial papillae of the loricarioid catfish *Hypostomus (= Plecostomus*; Rauther 1911), on oral papillae of loricariids (Ono 1980), on the ventral surface of the outer pectoral fin-ray of amphiliid and sisorid catfishes (Hora 1922, Bell-Cross & Jubb 1973), and on the thoracic adhesive organ of some sisorids (Hora 1922, Saxena 1961).

According to Ferri (1982, based on *Pimelodus maculatus*) the unculiferous cells as well as the keratinized cells of amphibians and reptiles (Matoltsy & Huszar 1972) originate from cells where keratohyalin granules are absent. However, keratinized cells of fishes (Mittal & Whitear 1979) and of tetrapods (Matoltsy & Huszar 1972) are enveloped by a modified plasma membrane which thickens from the inside of the cell by deposition of an amorphous material. Unculiferous cells do not have the thickened envelope.

Unicellular unculi are present in most ostariophysans, but they are unknown in gymnotoids and non-ostariophysan teleosts. Among siluroids, unicellular unculi have not been found in catfishes such as *Diplomystes* and ictalurids. Among the loricarioids, they are present in *Nematogenys* and certain trichomycterines (e.g., *Hatcheria macraei*) as elongate projections (Fig.33D) positioned just behind the skin covering the cleithrum. In other loricarioids, unicellular unculi or brush-like projections termed epidermal brushes by Ono (1980) are present near the mouth (Ono 1980, Roberts 1982). Unculiferous plaques are present in *Pimelodus* (Fig.39A); the entire surface is covered by unculiferous plaques or tubercles in sisorids (e.g., *Bagarius bagarius*) and akysid catfishes (Roberts 1982).

Although the function of the unicellular unculi is unclear, they have been hypothetized as having a protective function against microorganisms and parasites (Mittal & Bannerjee 1974, Roberts 1982). The unicellular unculi present in *Nematogenys* and certain trichomycterines, just posterior to the pectoral girdle may also have similar function, protecting the branchial cavity of microorganisms and parasites. Ono (1980:139) suggested that the brush-like unculi found on the oral papillae in certain loricariids serve as protective devices for the taste buds and as abrasive surfaces for substrate scraping during feeding. Hora (1922) suggested that unculi on the ventral surface of paired fins and thoracic organs of sisorids facilitate clinging or adherence on the surface of rocks and stones. According to Roberts (1982:55) unculi seem to have been especially important in the diversification of cyprinoid feeding habits and in the adaptation of bottom-dwelling cyprinoids and siluroids to swift-water habitats.

The unicellular unculi are different from the structures named multicellular horny tubercles by Roberts (1982) or breeding tubercles by Wiley & Collette (1970, Collette 1977); breeding tubercles are known from many teleosts.

Goblet cells

Goblet cells (Figs.17A, B, 28B, 35A, B) are present in the epidermis of all catfishes examined, but their number and distribution vary along the body and between species. They are comparatively fewer in *Diplomystes* than in *Nematogenys* and trichomycterids. Few goblet cells are on the maxillary barbels of *Diplomystes*, whereas they are numerous in *Nematogenys*; trichomycterids have fewer goblet cells in the barbels than *Nematogenys*. *Ictalurus punctatus* has goblet cells "in all regions of the body but are especially abundant in the oral cavity" (Grizzle & Rogers 1979:40). *Ameiurus nebulosus* has a few goblet cells on the barbels (Reutter 1978:55). A similar condition seems to be present in the epidermis of the maxillary barbel of *Ictalurus punctatus* as illustrated by Grizzle & Rogers (1979: figs.126, 127). Van Oosten (1957) showed that mucus is one of the most important protective substances associated with fish skin. The number of goblet cells is often inversely related to the presence or absence of scales in fishes (Oosten 1957). Most catfishes with naked skin have numerous goblet cells, however *Bagarius bagarius* has few goblet cells (Mittal & Munshi 1970), a fact that could be associated with the thick and shark-like skin in *Bagarius*, which is completely covered by unculiferous plaques.

According to the present evidence, it is risky to decide whether a pore corresponds to a goblet cell or to a sunk pit-organ by only using SEM microscopy. The histological cross sections show that goblet cells and some deeply sunk ampullary organs may have apertures of similar diameter; therefore they can be confused.

Club cells or alarm substance cells

Fright reaction is displayed by gonorynchiforms and most other ostariophysans (Pfeiffer 1960, 1967, 1977). Frisch (1938, 1941a) first described the fright reaction in a cyprinid fish and proposed that it was due to an alarm substance produced by injured skin. The alarm substance was associated with specialized club cells present in the epidermis of all fish species which revealed the fright reaction (Pfeiffer 1960); the association between club cell and alarm substance was further confirmed by Pfeiffer (1963a), and others.

Table 5: Presence (+) or absence (-) of club cells and of fright reaction in certain siluroids listed alphabetically. ?: unknown condition.

Family Species	Club cell	Fright reaction	Source
Ariidae			
Ariidae spp.	+	?	Pfeiffer 1970
Tachysurus spec.	+	?	Pfeiffer 1970
Asprenidae			
Bunocephalus bicolor	–	–	Pfeiffer 1963b
Bagridae			
Auchenoglanis occidentalis	+	?	Pfeiffer 1970
Bagrus bayard	+	?	Hussaini & Lufty 1958
Chrysichthys auratus	+	?	Hussaini & Lufty 1958
Rita rita	+	+	Mittal & Munshi 1969
Clariidae			
Clarias spp.	+	?	Hussaini & Lufty 1958, Pfeiffer 1963b, 1967, Thins & LeGrain 1973
Diplomystidae			
Diplomystes spec.	+	+	present paper
Diplomystes camposensis	+	+	present paper
Doradidae			
Doras spinosissimus	+	?	Pfeiffer 1963b
Ictaluridae			
Ameiurus nebulosus	+	+	Pfeiffer 1960
Ictalurus punctatus	+	?	Grizzle & Rogers 1979
Loricarioidei			
Callichthys spec.	+	?	Batti 1938
Corydoras paleatus	+	+	Pfeiffer 1960
Loricaria filamentosa	–	–	Pfeiffer 1963b, 1967
Nematogenys inermis	+	+	present paper
Otocinclus affinis	–	–	Pfeiffer 1963b, 1967
Parastegophilus maculatus	+	?	Pfeiffer 1970
Plecostomus spec.	–	–	Batti 1938,
		+	Pfeiffer 1963b, 1967
Pseudostegophilus spec.	+	?	Pfeiffer 1970
Trichomycterus areolatus	+	+	present paper
"Pimelodidae"			
Microglanis parahybae	+	+	Pfeiffer 1963b
Pimelodella gracilis	+	+	Pfeiffer 1963b
Pimelodus spec.	+	?	Madeiros et al. 1970
Plotosidae			
Copidoglanis spp.	+	?	Pfeiffer 1970

There are a few histochemical and structural studies of alarm substance cells (e.g., Madeiros et al. 1970, Henrikson & Matoltsy 1968, Mittal & Munshi 1969, 1970, Pfeiffer et al. 1971, Bianchi 1975, Yoakim & Grizzle 1982, Whitear & Mittal 1983). The cytoplasma of the club cells of the channel catfish and other ostariophysans is filled with a fine, homogeneously dispersed fibrilar material (Pfeiffer et al. 1971, Yoakim & Grizzle 1982).

Cells with alarm substance and fright reaction are known from seven catfish species and the presence of club cells from about fifteen catfish families (Pfeiffer 1977: Tab.1; Tab.5 herein). The present paper reveals the presence of a high quantity of alarm substance cells (Figs.17A, B, 18A, 19A, D, 25B) all over the epidermis in diplomystids. However, the number of cells varies along the body in catfishes. For instance, many club cells (Figs.17A, 34A, B) are present in the maxillary barbel of *Diplomystes* and *Trichomycterus areolatus*, a few club cells are in *Nematogenys* (Fig.29A, C), but *Ameiurus* and *Ictalurus* lack club cells in the epidermis of the barbels (Reutter 1978, Grizzle & Rogers 1979).

Frisch (1938, 1941a, b) suggested that the fright reaction is characteristic of fishes exhibiting schooling behavior and is considered an important insurance against predation (Pfeiffer 1977). The catfish species examined do not exhibit schooling behavior, but they live in small groups among and below the stones (e.g., *Trichomycterus areolatus, Hatcheria macraei*; Arratia & Menu Marque 1981, Arratia 1983b), or stones and gravel (e.g., "*Trichomycterus*" *mendozensis*), or between the gravel (e.g., *Bullockia*; Arratia et al. 1978), or among the stones or cavities on the ground or "walls" of deep rivers (e.g., *Nematogenys*; Arratia 1983b). The alarm substance in these fishes communicates the presence of danger to individuals of the same species that live more or less close to each other.

Recently, Whitear & Mittal (1983) suggested that the primary function of the club cells is protective and that the recognition of specific pheromones in ostariophysans is a secondary phenomenon. Oxner (1905) considered that the appearance of club cells in damaged epidermis might indicate a supportive function. Observations in goldfishes suggested that the club cells become confluent when the outer epidermis is severely damaged forming a protective layer over the deeper part of the epidermis (Whitear & Mittal 1983). *Diplomystes, Nematogenys*, and *Trichomycterus areolatus* have permanently many layers of club cells in the epidermis of the body, suggesting supportive and protective functions of the club cells.

As observed in a series of experiments (observ. by G. Arratia, A. Chang & H. Díaz), *Trichomycterus areolatus* marks its territory and defends it when other individuals of its species are introduced in the aquarium, but it does not reacts similarly when fishes of other catfish species (e.g., *Nematogenys inermis*), or non-catfish species (e.g., *Basilichthys australis, Cheirodon pisciculus, Percilia gillissi, Percichthys melanops*) are introduced in the aquarium (similar results were described for ictalurids by Todd et al. 1967, Todd 1971). During the series of experiments, individuals of *T. areolatus* were left in separate aquaria for a few days; each individual usually was hidden below stones, imitating its natural environment in the "dead zone" of the river. Then, another individual of the same species was introduced in the aquarium. The aggressive reaction against the intruder was almost instantaneous. The fish moved out of its territory, approached the intruder and adopted an aggressive position with the pectoral fins, and opercular region expanded laterally. Usually the fish used its opercular and interopercular teeth to attack the intruder. We think that the reaction showed by individuals of *T. areolatus*, recognizing other congeners, is explained by the presence of specific pheromones. If this is true, then the pheromones are not only produced by injured skin, but also by normal skin. We do not know whether this function recognizing co-specific individuals is associated with the club cells or not.

Taste buds

Taste cells are primarily contained in pear-shaped taste buds, though cells purported to be isolated taste buds have been suggested by Reutter (1974) and Lane & Fox (1982). Some fishes are characterized by having numerous external taste buds. In addition, some fishes have chemoreceptors which may be solitary receptors resembling gustatory cells (Fox et al. 1980).

Taste buds occur on the lips, chin, surface of head, and on the entire body, especially on the barbels and fins in some siluroids. They also are present in the mouth, palatal, and gill regions. The distribution and quantity of taste buds are variable with age and also vary between adult siluroid species. Ictalurids such as *Ictalurus natalis, I. punctatus*, and *Ameiurus melas* have many taste buds all over the body (Bardach & Atema 1971, Grizzle & Rogers 1979, Reutter 1978); a large quantity of taste buds are reported from *Ameiurus nebulosus*, e.g., 175,000 taste buds in the mouth-gill region (Atema 1971) in an individual of 22 cm length. Taste buds are present all over the body in loricariids; all fins "are all covered with dermal spines which are found in association with the taste buds" (Ono 1980:144). In contrast, many taste buds are found on the barbels, and in the oral, gular, and branchiostegal regions of diplomystids (Arratia 1987a, present paper), *Nematogenys*, and *Trichomycterus areolatus*. Taste buds are scarce on body and fins in these forms.

Maxillary barbels covered by taste buds are found in the trichomycterids *Trichomycterus areolatus* (Fig.36A, B), "*Trichomycterus*" *mendozensis*, and *Hatcheria macraei*, as well as in *Corydoras* (Ovalle & Shinn 1977: fig.3) and ictalurids (Reutter 1978, 1982, Grizzle & Rogers 1979); thus the entire barbel is a taste organ. In other siluroids, such as diplomystids and nematogenyids, many taste buds (Figs.23A, 26C) are concentrated at the base of the maxillary barbel and in the upper lip. Numerous taste buds (alone or associated with brush-like unculi) are present in the oral papillae of the fleshy lips in loricariids (Ono 1980).

The distal tip of the maxillary barbel in diplomystids and nematogenyids has few taste buds or none; however, the barbel is used to touch the bottom and other individuals, so it is possible that its tip has mechanoreceptive or chemoreceptive abilities although no specific receptor for these functions has been identified. Herrick (1903b) and Olmsted (1920) showed experimentally that an ictalurid bullhead becomes aware of food only after touching it with its barbels; similar results were obtained by Parker (1922) and Satô (1937) in other teleosts with barbels (e.g., cyprinids). Blinded bullheads made reaching movements with the maxillary barbels when they were close to a taste substance according to Bardach et al. (1967). The barbels in bullheads are more sensitive to mechanical than to chemical stimulation according to Hoagland (1933), Tateda (1961), and Bardach et al. (1967).

One taste bud (TBI or TBII) on each epidermal papilla is commonly found on barbels, lips, and body of *Nematogenys* (Figs.30B, C, 31A-C) and other loricarioids (Ovalle & Shinn 1977, Ono 1980). The papilla bearing the taste bud is a large conical evagination arising over the skin surface in these fishes. *Nematogenys* has mainly taste buds of type II, whereas the trichomycterines and *Corydoras* have taste buds of type I (present paper, Ovalle & Shinn 1977: fig.6).

Earlier SEM studies reported that fish taşte buds fall into three categories (TBI-IIIs) based on their external surface (Reutter at al. 1974). In the present study, we found large taste buds located at the surface of the skin in the maxillary barbel of *Diplomystes* (Figs.20D, 23D, E) and *Nematogenys* (Fig.30C, D). These taste buds do not correspond to any of the types described by Reutter et al. (1974). *Diplomystes* aff. *chilensis* presents in addition to the unclassified taste buds, TBIIs in the middle and distal regions of the barbel. *Trichomycterus areolatus* and "*Trichomycterus*" *mendozensis* has mainly unclassified taste buds: Ovalle and Shinn (1977) described TBII in the barbel of *Corydoras*. Only one small TBIII was found in the adipose fin of *Diplomystes* spec.: no similar structure was observed in *Diplomystes* aff. *chilensis*. Whether differences in size and shape of the taste buds are associated with functional differences is beyond the scope of the present study.

Solitary cells

Solitary chemosensory cells (Fig.39B) were only observed in *Galeichthys peru ianus* within the studied siluroids. "Solitary chemosensory cells are not all alike, either morphologically or in their responses" (Whitear & Kotrschal 1988:365). Because skin structures of most catfishes remains undescribed, the taxonomic and evolutionary meaning of the solitary cells in certain siluroids cannot be interpreted yet.

Ampullary organs

The ampullary organs show great morphological diversity (see Szabo 1974). According to Zakon (1988) electroreceptors may be naturally classified as either ampullary or tuberous on morphological and physiological grounds. Among teleosts, a few of them are electroreceptive; for instance, the Siluroidei and Gymnotoidei possess ampullary receptors, but specialized tuberous receptors and weakly electric organs are found only in the gymnotoids (Zakon 1988: fig.32.5). Among gymnotoids, two different tuberous organs are identified: 1) The pulse-type found in *Hypopomus*, *Gymnotus*, and *Rhamphichthyes*. 2) The wave-type found in *Sternopygus* and *Eigenmannia* (see Zakon 1988, for references).

The structure of the ampullary organs has been investigated in a variety of catfishes such as *Clarias*, *Heteropneustes*, *Rita*, *Mystus* (Lahiri & Kapoor 1957, Srivastava & Seal 1980), *Ictalurus* (Herrick 1901, Müllinger 1964), *Kryptopterus* (Wachtel & Szamier 1969), *Parasilurus* (Satô & Katagiri 1969), *Plotosus* (Friedrich-Freksa 1930, Szabo 1972), *Silurus* (Jakubowski 1987), and *Sorubin* (Gelinek 1978).

The ampullary organs in teleosts are diminutive, being not more than 100 microns long and barely penetrating the epidermis, and with a few cells. They have 20 receptor cells in the catfish *Kryptopterus* (Zakon 1988). The canal is filled with a jelly that, in the marine catfish *Plotosus*, contains high levels of ion potasium in the ampullary lumen (Okitsu et al. 1978). In contrast to most teleosts, the ampullae in *Plotosus* have long canals and a large number of receptor cells (Obara 1976). The freshwater catfishes examined show differences in the structure of the ampullary organs, with short canals in diplomystids and nematogenyids and long canals in *Trichomycterus areolatus*. The distribution of the electroreceptors on the body is only known from a few catfishes, e.g., *Kryptopterus*.

Ampullary organs were first described for *Ameiurus (= Ictalurus) melas* by Herrick (1901). They vary in quantity and distribution within siluroids. For instance, they are found on the whole external surface of the body of *Ictalurus punctatus* but are most abundant on the head (Grizzle & Rogers 1979). The presence of ampullary organs varies among diplomystids. In *Diplomystes* spec. they are abundant on the head, mainly around the oral surface and base of the maxillary barbel, but also close to the main lateral line and adipose fin; in contrast, there are many on the papillae of the adipose fin in *Diplomystes* aff. *chilensis*. The distribution and size of ampullary organs (Fig.21A-D) on the adipose fin in *Diplomystes* spec. (a few and large) and *Diplomystes* aff. *chilensis* (numerous and small) seem to be characteristic of these species. A few ampullary organs (Figs.34B, 35A, B) are in *Trichomycterus areolatus* and many in "*Trichomycterus*" *mendozensis* (Fig.38A); they seem to be absent in *Corydoras* (M. Whitear, pers. comm.). It is unclear whether the "multiampullary" organs which open outside through a common canal are present in diplomystids or not. "Multiampullary" organs have been described in *Silurus glanis* by Jakubowski (1987: fig.1) and "paired" organs in *Parasilurus* (Satô & Katagiri 1959) and in *Clarias* (Srivastava & Seal 1980).

"Canal length of ampullary organs varies significant between fresh and marine forms and can be explained as an adaptation for increasing sensitivity (Bennet 1971, Szabo et al. 1972, Kalmijn 1974)." (Zakon 1988:820). Teleosts, contrary to elasmobranchs, are supposed to have shorter canals, and most freshwater teleosts are supposed to have high skin resistance and a low internal resistance to aid in osmoregulation; therefore they are considered as isopotential and the ampullae can be referenced to the same potential by protruding through the epidermis (Kalmijn 1974). The diplomystids and loricarioids examined here are freshwater, however they show differences in the length of the canals, e.g., short in diplomystids and nematogenyids, long in *Trichomycterus areolatus*.

The ampullary organs possess electroreceptors (Dijkgraaf 1962, Bennett 1971, Zakon 1988). Ampullary receptors are specialized to detect low frequency to DC electric fields primarily of biological origin as the biopotentials produced by preys, and are used for locating prey and for orientation (Kalmijn 1974, Himstedt et al. 1982, Zakon 1988). As shown above, catfishes vary in the presence, quantity, and distribution of ampullary organs. It is interesting that closely related fishes differ in the quantity of ampullary organs, therefore the capacity for electroreception within closely related catfishes differs (e.g., *Diplomystes* spec. and *Diplomystes* aff. *chilensis*, *Nematogenys inermis* and *Trichomycterus areolatus*).

FINAL COMMENTS AND CONCLUSIONS

Systematic Considerations

Lateral line system

1) The sensory canals, tubules, and pores show great diversification among siluroids. The sensory canals may be simple (the generalized condition) or they may ramify through ontogeny (e.g., pimelodines, *Arius*, *Plotosus*); the latter corresponds to a derived condition among catfishes. This character favors a close relationship between certain "pimelodids" and ariids than to other catfishes (Fig.1).

2) Complete cephalic sensory canals and a complete main lateral line correspond to the generalized conditions in siluroids and are interpreted as plesiomorphic character states. Loss of sections of canals (e.g., portion of supraorbital canal between nasal and frontal bones or of complete canals) and appearance of new sensory branches are interpreted as derived conditions in siluroids. For instance:

2.1. The lack of the supratemporal canal is a siluroid synapomorphy by comparison with other ostariophysans; the appearance of a new branch, the pterotic branch of the postotic canal is another siluroid synapomorphy (Fink & Fink 1981, Arratia 1992, Arratia & Gayet in press). The loss of the parietal branch of the supraorbital canal and the loss of the pterotic branch of the postotic canal are hypothetized as synapomorphies of loricarioids.

2.2. A supraorbital canal running in the frontal bone is the common condition in siluroids; however, the canal is missing in some trichomycterids such as "*Trichomycterus" mendozensis, Glanapteryx* and *Listrura*.

2.3. A complete infraorbital canal represents the plesiomorphic condition in siluroids; the presence of a fragmented infraorbital canal or its complete absence correspond to derived character states. Numerous tubules branching from the main infraorbital canal is interpreted as the primitive condition in siluroids including *Nematogenys*; in contrast, the reduction of the canal to its anterior and posterior sections is a derived condition characterizing most trichomycterids with the exception of copiodontines.

2.4. The antorbital branch of the infraorbital canal is present in catfishes such as diplomystids, nematogenyids, and in copiodontines among trichomycterids (our interpretation of de Pinna 1992: fig.17). The antorbital branch is missing in other trichomycterids (the condition is unknown in *Trichogenes*).

2.5. The absence of the mandibular canal and the absence of most of the preopercular canal is a synapomorphy of trichomycterids (modified from Baskin 1970). The short dorsal portion of the preopercular canal of trichomycterids has different lengths among groups and is absent in some species (e.g., *Trichomycterus areolatus*). A detailed investigation of this canal and its pores could be useful to clarify the limits of the genus *Trichomycterus*. The same situation is with the infraorbital and supraorbital canals, which are reduced or completely lost in different trichomycterids, however, a detailed investigation of the sensory canals within *Trichomycterus* has never been done. [Arratia (manuscript in prep.) is studying the *Trichomycterus* species of southern South America, including the lateralis system.]

3) A complete lateral line extending near to or lateral to the hypural plate, partially enclosed in ossicles and giving off numerous short tubules which open through the skin by pores, represents the plesiomorphic condition in siluroids. Among loricarioids, a lateral line reaching close to the dorsal fin, partially enclosed by ossicles, and with about 10 pores is present in *Nematogenys*. According to de Pinna (1992) copiodontines have a complete lateral line, without ossicles; tubules and pores were not mentioned. Most trichomycterines and other advanced trichomycterids share an atrophied lateral line partially enclosed by ossicles and with a few tubules and pores. The condition is unknown in *Trichogenes*. According to the available information it seems more parsimonious to interpret the condition of the lateral line in copiodontines as a specialization of this subfamily. The athrophy of the lateral line may be a synapomorphy of the Trichomycteridae without Copiodontinae, or of trichomycterids without Copiodontinae and *Trichogenes*.

4) Seven or eight pores of the supraorbital canal are present in diplomystids (Figs.4B, 5B), similar to the condition found in primitive characiforms (Fig.3C). In many other catfish groups the supraorbital canal has six pores (Lundberg 1982, present paper). Five pores are normally present in ictalurids (Lundberg 1982). The condition varies among "pimelodids", e.g., six pores in *Rhamdia*, four in *Heptapterus*, and many pores in *Parapimelodus*. Although some catfishes may have the same number of pores (e.g., five) not always the same pores are present. For instance, most catfishes have pores 1, 2, 3, 6 and 8 in the supraorbital canal (by comparison with diplomystids); however, *Noturus* has the second pore of the supraorbital canal fused with the first pore of the infraorbital canal (Taylor 1969, Lundberg 1982). In contrast, pore 2 of the supraorbital canal in *Heptapterus* is fused with the second pore of the infraorbital canal. Commonly, the right and left supraorbital canals are separated from each other in siluroids. However, some catfishes present both canals joined at the midline (e.g., *Clarias*; some loricarioids, e.g., *Trichomycterus metae*).

5) The presence of two (e.g., *Trichomycterus nigricans, T. areolatus, T. rivulatus*) or only one median (e.g., *Trichomycterus metae*) pore associated to branches 6 of the supraorbital canal should be carefully investigated among members of *Trichomycterus* to clarify the limits of the genus. Number and position of pores vary among catfishes and need to be carefully studied to understand their phylogenetic meaning within siluroids and their value as taxonomic tools. The same is true for pores of other canals.

6) In general, the main sensory canal and its secondary branches and pores seem to be potentially significant in taxonomic and phylogenetic studies in siluroids.

Superficial neuromasts

1) Superficial neuromasts, isolated, in lines, or fields, are variably present in siluroids. Lines formed by a few (one to three commonly), large neuromasts are characteristic of siluroids (also noted by Lekander 1949) among ostariophysans (compare Figs.4B, 5B, 7B, 10A-D, 41, 42).

2) Numerous small superficial neuromasts grouped in lines or as fields are present in gonorynchiforms, cypriniforms, and characiforms. Primitive catfishes (e.g., diplomystids) have a few, large neuromasts, therefore the pit lines are formed by one or three neuromasts, commonly. Pit lines formed by a few large neuromasts is another synapomorphy of siluroids.

3) The presence of the fork replacement of the supraorbital canal, fork and caudal replacements of the infraorbital canal, anterior and middle pit lines, and supratemporal accessory line is considered here the plesiomorphic condition in siluroids by comparison with other ostariophysans and more primitive teleosts. The absence of some or of all pit lines in some adults of Diplomystidae may be considered as autapomorphic for some species.

4) Pit lines such as fork replacement of the supraorbital canal, rostral replacement of the infraorbital canal, supraorbital accessories, anterior, middle, supratemporal accessories, antorbital and infraorbital, and field of neuromasts in catfishes and other ostariophysans follow the pathway of the sensory canals (Figs.4B, 5B, 7B, 11B, 13). They are interpreted here as homologues to those present in other teleosts.

5) In most Recent ostariophysans the neuromast lines do not lie in a groove on the underlying bone; however, in some fossil and Recent ostariophysans some pit lines are

incised in bone (Fig.43A, B; Patterson 1984, Gayet 1988, Arratia & Gayet in press). Since the presence of pit lines incised in bone is a feature that appears in distant lineages, it should be interpreted as new appearances characteristic of each taxon, e.g., †*Chanoides*, *Carassius*, †*Andinichthys*, *Bagre*, etc.

6) The presence of all pit lines and richness in field of neuromasts and isolated neuromasts all over the body may be a specialization of Nematogenyidae to compensate that the fish is blind or almost (the skin covering the eye has melanophores). The presence of all pit lines and numerous fields of neuromasts may also be interpreted as primitive among loricarioids following the proposed phylogenies by Howes (1983), Schaefer (1987), and de Pinna (1992); therefore the absence of some pit lines, or of all pit lines, would correspond to derived character states among loricarioids.

7) The absence of pit lines in gymnotoids and its complete absence or reduction in certain diplomystids (e.g., in *Diplomystes*) may be another character shared by both groups. Still, the absence of pit lines in gymnotoids is a synapomorphy of this group among ostariophysans. The development of the pit lines in different catfish groups should be studied in detail because this could be another potential character useful to characterize clades.

Skin

1) A scaleless skin is a characteristic of siluroids (Fink & Fink 1981); still some of them develop an armored skin of bony plates or unculiferous plaques; these structures represent different derived character states within siluroids.

2) The soft or papillate skin is also a useful feature characterizing some catfish clades. The skin of large *Nematogenys*, with large papillae each bearing a conical dermal papilla emerging over the surface (Fig.28A, B) seems to be an autapomorphy of Nematogenyidae. The external aspect of the skin, perforated by numerous pores of ampullary organs (Fig.38A) seems to be characteristic of "*Trichomycterus*" *mendozensis*.

3) The general micromorphology of the epidermis and dermis has the same pattern in most catfishes studied here and in others known from the literature. Commonly, well developed outer, middle, and basal layers of cells are distinguished in the epidermis; in contrast, *Nematogenys* seems to miss the middle layer of epidermal cells (Figs.28B, 29A-E). In addition, *Nematogenys* is unusual also in that the dermis does not intrude the epidermis (Fig.29A-C) as it does in other catfishes examined, therefore the taste buds and other receptors are not placed in well-developed evaginations of the dermis. Melanophores, a protective cellular element of the skin, are unevenly distributed in the epidermis, dermis, and hypodermis in the diplomystids and trichomycterids studied, but they are restricted to the dermis and subjacent layers (Figs.28B, 29A-C) in *Nematogenys*. Although other elements of the epidermis as the goblet cells are variably present along the body in different catfishes, at present there is not enough information to understand the differences in distribution of these cells among catfish groups.

4) Unicellular unculi are present in the skin of most ostariophysan groups; still they are unknown in gymnotoids and non-ostariophysan teleosts. Among ostariophysans the information is still not available in primitive cypriniforms (e.g., *Opsariichthys* and *Zacco*) and primitive characiforms (e.g., *Xenocharax*). Among siluroids, unicellular unculi have not been found in catfishes such as diplomystids and ictalurids. Since uni-

cellular unculi have not been searched in most catfish families, their phylogenetic interpretation cannot be addressed properly. Still, the presence of unicellular unculi can be interpreted as an ostariophysan character because they have not been found in non-ostariophysan fishes. The apparent absence of unicellular unculi in gymnotoids and diplomystids can be interpreted as a synapomorphy shared by these groups and its presence in certain more advanced catfishes with specialized unculi or unculiferous plaques, as characters of these subgroups. Among the loricarioids, they are present at least in *Nematogenys* and some trichomycterines (e.g., *Hatcheria macraei*) as elongate projections (Fig.33D) positioned just behind the skin covering the cleithrum. In other loricarioids, unicellular unculi or brush-like projections termed epidermal brushes by Ono (1980) are present near the mouth (Ono 1980, Roberts 1982).

5) The presence of alarm substance cells is a synapomorphy of ostariophysans (Fink & Fink 1981); they are present in most ostariophysans with the exception of gymnotoids (Pfeiffer 1963b). Among gonorynchiforms, *Kneria* and *Phractolaemus* present both the club cells and the fright reaction (Pfeiffer 1967), but the information about the fright reaction is not available yet for other gonorynchiforms. Most cypriniforms, characiforms, and catfishes present both the club cells and the fright reaction. Therefore, it could be more appropriate to consider both the presence of alarm substance cell and the fright reaction an ostariophysan synapomorphy, than presence of club cells alone, because the presence of club cells and alarm substance is not always associated with fright reaction. For instance, the characiforms *Anoptichthys antrobius* and *A. jordani* and serrasalmids have club cells but no fright reaction can be detected (Schutz 1956, Thinés & LeGrain 1973, Pfeiffer 1963b, 1967). Considering the distribution of the club cells and the fright reaction among ostariophysans, the loss of both features are considered synapomorphies of Gymnotoidei.

6) The presence of alarm substance cells in diplomystids as well as in other catfishes confirms it as a primitive condition for catfishes. However, they are missing in some catfishes, e.g., *Bunocephalus* does not have club cells and fright reaction (Pfeiffer 1963b; Tab.5). Among the loricarioids, the presence of alarm substance cells and fright reaction in *Nematogenys* and trichomycterines represents the primitive character state and their losses in loricariids such as *Loricaria, Otocinclus*, and *Hypostomus* (Pfeiffer 1963b, 1967; Tab.3) derived character states.

7) The structure of the cytoplasma of the club cells of the channel catfish and other ostariophysans seems to be unique among teleosts. It is filled with a fine, homogeneously dispersed fibrilar material (Pfeiffer et al. 1971, Yoakim & Grizzle 1982), a feature that seems to be a synapomorphy of ostariophysans (Yoakim & Grizzle 1982). The club cell cytoplasma of other fishes does not reveal such fibrilar organization (Henrikson & Matoltsy 1968, Downing & Novales 1971, Whitear 1986).

8) The phylogenetic meaning in the pit-organs and taste buds of different catfishes is unclear. Their presence cannot be explained as result of adaptations to the environment since fishes living in similar environments differ in presence of pit-organs and taste buds (see above). Still those features can be used phylogenetically.

8.1. It can be hypothetized that the absence of pit lines on the head of "*Trichomycterus*" *mendozensis* represents the advance condition by comparison to primitive loricarioids (e.g., *Nematogenys*).

8.2. Some pit lines (e.g., supraorbital accessory line, ventral infraorbital line, and opercular lines) which are present in gonorynchiforms, cypriniforms, and characiforms are absent in diplomystids. They may be present in other catfishes (e.g., *Nematogenys*) and could be interpreted as new formations since they seem to be absent in gymnotoids also.

8.3. Among loricarioids, the presence of the supraorbital accessory line in *Nematogenys* may be interpreted as an autapomorphy of this taxon and its absence as a synapomorphy of more advanced loricarioids. In constrast one could consider that the presence of the pit line is a synapomorphy at the primitive level which is lost in more advanced forms.

8.4. The antorbital line present in *Nematogenys* and copiodontines (the condition is unknown in *Trichogenes*) has not been observed in other loricarioids. It is possible that this loss is another synapomorphy of more advanced loricarioids.

9) Among teleosts, the Siluroidei and Gymnotoidei possess ampullary receptors and share electroreceptive capabilities; as consequence, this feature was considered a synapomorphy shared by both groups (Fink & Fink 1981). However, there are morphological differences between both because specialized tuberous receptors and weakly electric organs are only found in the gymnotoids (Zakon 1988).

Environment *versus* Morphology

1) The catfishes here studied are benthic forms feeding mainly on prey living on the bottom, such as crustaceans. The preferred prey of *Nematogenys*, a typical habitant of the Potamon, and *Trichomycterus areolatus* and *"Trichomycterus" mendozensis* of the Rhitron, is the crustacean *Aegla lae is*, a common habitant of the austral Andean torrential rivers. That also seems to be true for the diplomystids investigated. Despite similarities in food, the skins of these fishes differ in the kind, number, and distribution of sensory structures. The differences just cannot be explained as a consequence of the environment, in particular to the variety of food (Meyer-Rochow 1981). It seems reasonable to assume that the character of the skin is genetically controlled and is the result of evolutionary processes which can be interpreted with additional information. It is also possible that under some environmental conditions the skin develops more or less receptors, within certain limits of innervation, as in other vertebrates.

2) According to Lowenstein (1957), fishes which are continuous swimmers or those living in torrential habitats possess well-developed canal systems, whereas bottom dwellers and sluggish forms usually have secondarily reduced canal systems. Lowenstein (1957) documented his conclusion on three fishes belonging to different teleostean subgroups, the cobitids *Misgurnus* and *Nemacheilus*, and the esocoid *Esox*; these fishes occupy different habitats and have different swimming capacities. Hoagland (1933) arrived at a similar conclusion while studying a catfish and a trout. Such a conclusion is not reached from closely related fishes described in this paper.

3) Comparing the acoustico-lateralis system of many centrarchids in correlation with their habitats, Branson & Moore (1962:88) concluded: "Thus a fish with a reduced lateral line system would not be adapted to live in a rigorous habitat or as a fast-swimming form since its lateral-line organs would quickly become overstimulated and cease to function". All catfishes studied are benthic forms of Andean torrential rivers; although all of them prefer to live in the "dead zone" of the rivers, all of them are able to leave the "dead zone" during feeding, breeding, attack from other aquatic forms,

etc. Of the three catfishes studied here, adult *Diplomystes* and *Nematogenys* prefer the Potamon of torrential rivers where the conditions are not so rigorous as in the Rhitron where *Trichomycterus* is commonly found. Adult *Diplomystes* and *Nematogenys* are similar in habitat and also habits, both are active during night, and the cephalic sensory canals of both fishes are more or less similar, but the main lateral line is long in *Diplomystes* and shorter in *Nematogenys*. The development of the superficial neuromasts, however, differs between these genera (compare Figs.4A, B, 7A, B). Trichomycterids lack part (e.g., *Trichomycterus areolatus*: Fig.11B) or almost the entire cephalic sensory canal system (e.g., "*Trichomycterus*" *mendozensis*: Fig.12B). Thus, the fish lacking part of the cephalic sensory canals and in addition, the lines of superficial neuromasts, should have other mechanisms to compensate such loss of sensory canals and superficial neuromasts and permit it to move from the "dead zone" to the fast running superficial waters of torrential streams. From present information we are unable to interpret the differences as an ecological adaptation as suggested by other authors for other fishes.

4) It has been suggested that "Correlation between sensor types and the habitat and lifestyle of fishes suggest that ambient noise levels provide a major selection pressure for the evolution of lateral line systems" (Coombs et al. 1988:586). Canal loss and replacement with superficial neuromasts have been associated with non-siluroid fishes living in relatively quiet water or having sedentary behavior (Dijkgraaf 1962, Marshall 1971, Merriles & Crossman 1973, Coombs et al. 1988). However, this is not true for the catfishes studied here. For instance, *Trichomycterus areolatus* and "*Trichomycterus*" *mendozensis* live in the quiet "dead zone" of the Rhitron of Andean torrential rivers, where the speed of the water is null, but both differ in the development of the cephalic sensory canal and of pit lines (compare Figs.11B, 12B). As a consequence, the capacity of mechanoreception would differ within catfishes, even among those closely related and/or those living in similar habitat (e.g., *Trichomycterus areolatus* and "*Trichomycterus*" *mendozensis*). A similar conclusion was reached by Satô (1955) after studying the lateralis system and pit lines in *Cyprinus carpio, Carassius auratus*, and *Leuciscus hakuensis* (Fig.45A-C).

5) *Trichomycterus areolatus* and "*Trichomycterus*" *mendozensis* are typical inhabitants of the Rhitron of Andean torrential rivers. Their cephalic sensory canals are reduced in comparison to those in *Diplomystes* and *Nematogenys*, and the main lateral line is atrophied; adult "*Trichomycterus*" *mendozensis* apparently lacks most superficial neuromast lines, but it has papillate superficial neuromasts unevenly distributed all over the body; adult *T. areolatus* has lines of superficial neuromasts in the head and body and papillate superficial neuromasts unevenly distributed on the flank. The fishes have a reduced lateral line on the body and are able to live in rigorous torrential rivers, in the "dead zone" of the Rhitron, a fact which reveals that closely related fishes have developed different forms of adaptations to their environments. How such morphofunctional mechanisms evolved is a question for which we do not have an explanation at present.

6) In conclusion, features of the skin and lateralis system are of systematic value, but the available information makes it difficult to interpret the adaptational meaning of the different kind of receptors, and other structures of the skin within ostariophysans and other teleosts. We agree with Northcutt (1989:70) that "continued behavioral, morphological and physiological studies are needed to sample the staggering array of diversity in teleost lateral lines" and receptors.

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ABSTRACT

Lateralis systems, neuromast lines, and skins of the freshwater benthic siluroids *Diplomystes, Nematogenys, Trichomycterus areolatus, "Trichomycterus" mendozensis* and *Hatcheria macraei* were examined by light and scanning microscopy. The lateralis system comprises the main lateral line, postotic, otic, supraorbital, infraorbital, preopercular, and mandibular canals in primitive catfishes (e.g., diplomystids). The absence of the supratemporal canal is a siluroid synapomorphy. An interrupted lateralis system loosing parts of the supraorbital, infraorbital, and preoperculo-mandibular canals is found in other catfishes

(e.g., trichomycterids). A rudimentary preopercular canal or its absence is a synapomorphy of trichomycterids. The lateralis system is formed by narrow simple tubules in primitive catfishes (e.g., diplomystids), whereas they are highly ramified in other catfishes (e.g., *Arius felis* and *Parapimelodus*). Variation in the structure of the sensory canals and in the presence of certain sensory tubules and pores seem to be diagnostic for different hierarchic levels of siluroids.

A few large superficial neuromasts may be aligned in rows in siluroids such as diplomystids (e.g., *Diplomystes chilensis), Arius, Ictalurus, Galeichthys, Bagre, Rhamdia, Nematogenys*, and certain trichomycterids (e.g., *Trichomycterus areolatus*); if so, they occupy the same position as the rostral, anterior, middle, and supratemporal accessory pit lines in other teleosts and they are interpreted as homologues. In addition, accessory supraorbital, antorbital, infraorbital, and opercular pit lines are present in *Nematogenys*. Trunk lines (dorsal, subdorsal, middle, ventral, and accessories) of large, elongate superficial neuromasts occur between the occiput and caudal fin in adult catfishes such as *Nematogenys, Ictalurus*, and occasionally in *Diplomystes*. The pit lines of primitive siluroids are characterized by one or a few elongate superficial neuromasts unlike those in gonorynchiforms, cypriniforms, and characiforms, which consist of fields of numerous, small superficial neuromasts.

There are important differences in the presence, distribution and size of epidermal papillae, goblet cells, club cells, and unicellular unculi; in the distribution and types of taste buds: and in the presence or absence of ampullary organs, superficial neuromasts, and solitary cells in the skin of these genera. These differences may be useful in systematics; evaluation of them in a phylogenetic context is not possible at present, due to scarce information in most siluroid families and in other ostariophysans.

Unicellular unculi are present in most ostariophysans, with the exception of gymnotoids and non-ostariophysan teleosts. They are known from at least eight catfish families, including Nematogenyidae and Trichomycteridae. They are unknown in diplomystids. Differences in structure and distribution of the unculi among catfish groups may be of taxonomic and phylogenetic value. The presence of alarm substance cells and fright reaction are ostariophysan synapomorphies. Diplomystids are characterized by numerous club cells on the whole epidermis of the body. Siluroids and gymnotoids possess electroreceptive capabilities; specialized tuberous receptors are found only in gymnotoids. Siluroids may have ampullary organs deeply sunk in the epidermis (e.g., *Trichomycterus areolatus*) or near to the epidermal surface (e.g., *Diplomystes*).

The siluroids examined (*Diplomystes, Nematogenys*, trichomycterines, and "*Trichomycterus" mendozensis*) are carnivorous, and their diets appear similar. Thus the differences in type and distribution of epidermal gustatory structures may function in ways other than for discrimination of particular prey species. Adult *Diplomystes* and *Nematogenys* are typical habitants of the Potamon of Andean torrential rivers; however, their skin differs strongly in the presence of gustatory receptors, ampullary organs, and mechanoreceptors. The skin also differs among diplomystid species. *Trichomycterus areolatus* and "*Trichomycterus" mendozensis* are typical habitants of the "dead zone" of the Rhitron and they differ strongly in the lateralis system and pit-organs. The adaptive and phylogenetic significance of these differences needs to be explored (or explained).

ZUSAMMENFASSUNG

Seitenliniensystem, Neuromast-Linien und die Haut der benthischen Süßwasserwelse *Diplomystes, Nematogenys, Trichomycterus areolatus, "Trichomycterus" mendozensis, Hatcheria macraei* sind mit Licht- und Rasterelektronenmikroskop untersucht worden. Das Seitenliensystem umfaßt bei primitiven Welsen (z.B. Diplomystiden) Haupt-, postotikalen, otikalen, supraorbitalen, infraorbitalen, praeoperkularen und mandibularen Kanal. Das Fehlen des supratemporalen Kanals ist eine Synapomorphie der Welse. Ein unterbrochenes Seitenliniensystem, wo Teile des supraorbitalen, infraorbitalen und praeoperkulomandibularen Kanals fehlen, tritt bei einigen Welsen auf (z.B. Trichomycteriden). Ein rudimentärer praeoperkularer Kanal oder sein Fehlen ist eine Synapomorphie der Trichomycteriden. Das Seitenliniensystem wird bei primitiven Welsen (z.B. Diplomystiden) von einfachen engen Röhrchen gebildet, während diese in einigen Welsen (z.B. *Arius felis* und *Pimelodus*) stark verweigt sind. Variationen in der Struktur der Seitenlinienkanäle und dem Vorhandensein bestimmter Seitenlinienröhrchen und -poren scheinen diagnostische Merkmale auf verschiedenen hierarischen Ebenen der Welse zu sein.

Wenige große oberflächliche Neuromasten können bei Welsen wie Diplomystiden (z.B. *Diplomystes chilensis), Arius, Ictalurus, Galeichthys, Bagre, Rhamdia, Nematogenys* und einigen Trichomycteriden (z.B. *Trichomycterus areolatus*) in Reihen angeordnet sein. Wo das der Fall ist, nehmen sie die gleiche Position ein wie die rostrale, vordere, mittlere und supratemporale akzessorische Grübchenlinie anderer Teleosteer; sie werden als ihnen homolog interpretiert. Zusätzlich ist die akzessorische supraorbitale, antorbitale, infraorbitale und operkulare Grübchenlinie bei *Nematogenys* ausgebildet. Die Linien des Körpers (dorsale, subdorsale, mittlere, ventrale und akzessorische) der großen, länglichen, oberflächlichen Neuromasten treten zwischen dem Hinterkopf und der Schwanzflosse bei erwachsenen Welsen wie *Nematogenys, Ictalurus* und gelegentlich *Diplomystes* auf. Die Grübchenlinien der primitiven Welse sind durch eine oder wenige längliche, oberflächliche Neuromasten gekennzeichnet, ganz im Gegensatz zu Gonorynchiformen, Cypriniformen und Characiformen, wo sie aus Feldern zahlreicher kleiner, oberflächlicher Neuromasten aufgebaut werden.

Es gibt bedeutende Unterschiede in Auftreten, Verteilung und Größe der epidermalen Papillen, Becherzellen, Kolbenzellen und einzelliger Unculi, in Verteilung und Typen der Geschmacksknospen und in Auftreten oder Fehlen von Ampullenorganen, oberflächlichen Neuromasten und solitären Zellen in der Haut dieser Gattungen. Diese Unterschiede können systematisch brauchbar sein. Eine Bewertung in phylogenetischem Sinne ist zur Zeit nicht möglich, da die Information für die meisten Familien der Welse und anderer Ostariophysen zu sporadisch ist.

Einzellige Unculi gibt es in den meisten Ostariophysen mit Ausnahme der Gymnotoiden und nicht-ostariophysen Teleosteern. Sie sind zumindest von acht Familien der Welse (Nematogenyidae und Trichomycteridae eingeschlossen) bekannt, nicht aber von Diplomystiden. Unterschiede in der Struktur und Verteilung der Unculi mögen taxonomische und phylogenetische Bedeutung für viele Gruppen der Welse haben. Das Auftreten von Zellen mit Alarmsubstanz und Schreckreaktion sind eine Synapomorphie der Ostariophysen. Diplomystiden sind durch zahlreiche Kolbenzellen auf der gesamten Körperepidermis gekennzeichnet. Welse und Gymnotoiden besitzen elektrorezeptive Fähigkeiten: spezialisierte röhrchenförmige Rezeptoren wurden nur in Gymnotoiden gefunden. Welse können Ampullenorgane haben, die entweder tief in der Epidermis (z.B. *Trichomycterus areolatus*) oder nahe der epidermalen Oberfläche liegen (z.B. *Diplomystes*).

Die untersuchten Welse (*Diplomystes, Nematogenys*, Trichomycterinen und *"Trichomycterus" mendozensis*) sind carnivor; sie sind in ihrer Nahrung einander ähnlich. Daher sollten die Unterschiede in Typ und Verteilung der epidermalen Geschmacksstrukturen auf eine andere Funktion als die Unterscheidung von bestimmten Nahrungsarten angepaßt sein. Erwachsene *Diplomystes* und *Nematogenys* sind typische Bewohner des Potamon der reißenden Flüsse der Anden; allerdings zeigt ihre Haut starke Unterschiede im Auftreten von Geschmacksrezeptoren, Ampullenorganen und mechanischen Rezeptoren. Die Haut unterscheidet sich ebenfalls zwischen den Arten der Diplomystiden. *Trichomycterus areolatus* und *"Trichomycterus" mendozensis* sind typische Bewohner der ruhigen (toten) Zone des Rhitron; sie unterscheiden sich stark im Seitenliniensystem und den Grübchenorganen. Die adaptative und phylogenetische Bedeutung dieser Unterschiede muß noch untersucht werden.

RESUMEN

El sistema canal sensorial, las líneas de neuromastos y la piel de los bagres bentónicos *Diplomystes, Nematogenys, Trichomycterus areolatus, "Trichomycterus" mendozensis* y *Hatcheria macraei* fue examinada con microscopia óptica y microscopia de barrido. El sistema canal sensorial incluye la línea lateral principal y los canales postótico, ótico, supraorbital, infraorbital, preopercular y mandibular. La ausencia del canal supratemporal se considera como una sinapomorfía de Silurodei. Un sistema canal sensorial interrumpido, perdiendo secciones de los canales supraorbital, infraorbital and preopérculo-mandibular se encuentra en otros bagres (ej.: tricomictéridos). La presencia de un canal preopercular rudimentario y la ausencia del canal mandibular es una sinapomorfía de tricomictéridos. El sistema canal sensorial está formado por canales simples y angostos en bagres primitivos (ej.: diplomystidos); los canales son altamente ramificados en otros bagres (ej.: *Arius felis* y *Parapimelodus*). La variación en la estructura de los canales sensoriales y en la presencia de ciertos túbulos sensoriales y poros parecen ser caracteres diagnósticos de niveles jerárquicos diferentes dentro de Siluroidei.

Los escasos neuromastos superficiales se pueden distribuir en forma linear en ciertos bagres tales como *Diplomystes, Ictalurus, Galeichthys, Bagre, Rhamdia, Nematogenys* y en ciertos tricomictéridos (ej.: *Trichomycterus areolatus*). Los neuromastos que se distribuyen en líneas (rostral, anterior, media y supratemporal o posterior) ocupan la misma posición de las líneas sensoriales o pitlines en otros teleósteos y son interpretados como estructuras homólogas. Además, líneas antorbital e infraorbital se encuentran consistentemente presentes en *Nematogenys*. Líneas corporales (dorsal, subdorsal, media, ventral y accesorias) constituidas por grandes neuromastos superficiales se presentan entre la parte posterior del cráneo y la aleta caudal en bagres adultos (ej.: *Nematogenys* e *Ictalurus* y ocasionalmente en *Diplomystes* y en *Trichomycterus*). Las líneas de neuromastos superficiales de bagres primitivos están constituidas por uno o escasos neuromastos alargados a diferencia de la condición presente en Caraciformes y Cipriniformes, en los cuales están formadas por campos de numerosos y pequeños neuromastos superficiales.

Hay diferencias importantes en la piel de las especies de esos géneros en cuanto a la presencia, la distribución y el tamaño de las papilas epidérmicas y en la presencia de diferentes elementos celulares tales como las células mucosas, células club y unculi unicelulares. Hay diferencias en la distribución y en los tipos de corpúsculos gustativos, en la presencia o ausencia de órganos ampulares o electroreceptores, en neuromastos superficiales y en

células solitarias. Los bagres estudiados (especies de *Diplomystes, Nematogenys, Trichomycterus, Hatcheria* y "*Trichomycterus*" *mendozensis*) son carnívoros y sus dietas son aparentemente similares. Por lo tanto, las diferencias en los tipos y distribución de corpúsculos gustativos debe funcionar de manera diferente que para la discriminación de presas particulares. Individuos adultos de *Diplomystes* y *Nematogenys* ocupan un ambiente similar: son típicos habitantes del Potamon de ríos andinos torrentosos. Sin embargo, sus pieles se diferencian en la presencia de corpúsculos gustativos, electroreceptores y mecanoreceptores. Además, la piel presenta variación interespecífica en *Diplomystes*. *Trichomycterus areolatus* y "*Trichomycterus*" *mendozensis* habitantes típicos del Ritrón de ríos andinos torrentosos, difieren en el sistema canal sensorial y en los diferentes receptores cutáneos. El significado adaptativo y filogénetico de esas diferencias necesita de mas investigaciones detalladas.

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