Structure and relationships of the Trichomycteridae
(first edition of the original thesis presented in 1973)*

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A major objective of this work is to define monophyletic groups of siluriforms on the basis of advanced characters. A majority of the species formerly assigned to the Trichomycteridae (commonly known as the parasitic catfishes) has been examined, and a general search among siluriform groups has been conducted for characters that are advanced within the Siluriformes as a whole, within previously defined subgroups of siluriforms, and within the Trichomycteridae. Evidence is given for excluding a number of species from the Trichomycteridae (i.e., *Nematogenys*, *Phreatobius*, cetopsids). The remaining species form a monophyletic group, sharing characters advanced for the Siluriformes, and found only in the Trichomycteridae. Several of these are newly discovered characters - the prootic, sphenotic and pterosphenoid bones forming a single bone: dorsohyal and interhyal lacking: sensory canal lacking from the preopercular bone. A new hypothesis of the relationships of the Trichomycteridae is established on the basis of additional advanced characters shared by them and other catfish groups (Callichthyidae, Loricariidae, Astroblepidae and an undescribed loricarioid species). These advanced characters are: 1.) the development of a fully encapsulated Weberian apparatus; 2.) the loss of the claustrum and intercalarium; 3.) the presence of integumentary teeth on the opercular bones (secondarily lost in astroblepids). *Nematogenys inermis* is proposed as the closest relative of the monophyletic group formed by trichomycterids loricariids and their relatives. This is based upon the discovery of integumentary teeth on the pectoral fin of *Nematogenys*. Loricarioids are the only catfishes found to have integumentary teeth. An additional advanced character linking *Nematogenys* with other loricarioids is its almost fully encapsulated Weberian apparatus. A full set of Weberian ossicles, however, excludes *Nematogenys* from inclusion among other loricarioids. This scheme of loricarioid relationships differs from previous ones in that cetopsids and bunocephalids are excluded, and *Nematogenys* is proposed as the sister group of all other loricarioids. Advanced characters within the Trichomycteridae are distinguished by comparing trichomycterids with their relatives, and with other catfish groups. Six monophyletic groups are thus defined on the basis of these advanced characters, and an hypothesis of the relationships among them is proposed. Advanced characters within each group are distinguished by comparison of each group with its relatives and with other groups. The relationships among the genera and species of each group are inferred from analysis of these advanced characters. The proposed sister group relationships among loricarioid catfishes leads to hypotheses of the evolutionary trends that have occurred among these fishes. It is hypothesized that integumentary teeth developed first on the pectoral fin in the common ancestor of all loricarioids. Opercular teeth, and perhaps also a fully armored condition, later developed in the common ancestor of trichomycterids and loricariids. Teeth were lost from the pectoral fin in the common ancestor of the Trichomycteridae. Armor and teeth were lost from the head, body and opercular bones in astroblepids, and perhaps also in trichomycterids. The common ancestor of all loricarioids had a full set of Weberian ossicles and partially encapsulated swimbladder vesicles. Loricarioids other than *Nematogenys* lost the claustrum and intercalarium, and developed the fully encapsulated Weberian apparatus. The Weberian capsule was independently reduced in size and modified into a vase shape in the Astroblepidae and Trichomycteridae. The common ancestor of all trichomycterids is hypothesized to be a non-parasitic species, although several of the advanced characters of the family can be considered advantageous to a parasitic fish. Several new and significant features of an undescribed species of loricarioid are discussed. These features indicate that this species is the sister group of the Loricariidae and Astroblepidae together. New classifications are proposed which express the relationships within the Loricarioidei and within the Trichomycteridae.

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Introduction and historical review

An overall objective of this work is to define natural (*i.e.*, monophyletic in the sense of Hennig, 1966) groups of siluriforms. The group with which this study is mainly concerned is the family Trichomycteridae. A majority of the species formerly assigned to this family has been examined, and a general search among many catfish groups has been conducted for characters that are advanced within the Siluriformes as a whole and within previously defined subgroups of siluriforms, and that are found only among trichomycterids. The characters that are advanced for siluriforms were determined by comparison of representatives of cypriniforms and as many catfish groups as possible, and by reference to the literature.

The specific aims of this work are: 1) to produce a theory of the phylogenetic relationships of the Trichomycteridae and of the included genera; 2) to produce a classification of trichomycterids and their relatives which reflects the proposed relationships: 3) to reconstruct the evolutionary history of trichomycterids consistent with the proposed relationships.

Members of the order Siluriformes occur in almost all of the freshwaters of the world. Marine representatives are confined to the continental shelf regions. The vast majority of the estimated 2,000 living species (Cohen, 1971, Bailey and Lundberg pers. com.) are tropical. Definite siluriform fossils are known from the Palaeocene (Casier, 1960), but Frizzell (1965) describes possible catfish otoliths from the Cretaceous of South Dakota. The siluriforms, together with the remainder of the Ostariophysi, the Cypriniformes (minnows, characins and their relatives) and Gonorynchiformes, form the major vertebrate element in the freshwaters of the world.

As the vast number of species and truly remarkable diversity of catfishes was unfolded by earlier workers the taxonomic rank of the group was raised, and the number of subtaxa also increased. Gunther (1864) placed all catfishes in a single family, the Siluridae, but divided it into numerous subgroups. Various authors since have raised to family rank several of Gunther's subgroups which they considered to be the most distinctive or diverse. This of course resulted first in the recognition of the most distinctive groups. For example, the family Aspredinidae (banjo-cats) was recognized by Cope (1872) because he believed, erroneously, that its members lacked an opercular bone. The less obviously distinctive catfish groups, from both the Old and New World remained in the old family Siluridae more or less by default, not because of any conviction of the workers that this was a natural group (*e.g.*, Bleeker, 1863; Gill, 1872).

Most of the new families tended to be defined on the basis of geographical as well as biological considerations. That is, geographic proximity as well as overall biological similarity (mostly anatomical) have been considered evidence for relationship between species, and for placing them in the same higher taxon. Few of these newly established families contained both Old and New World forms. The establishment of taxonomic groups at least partially on the basis of their geographic distributions was further promoted by the regional nature of the work in catfish systematics. An outstanding example is the work of Eigenmann and Eigenmann (1890), who studied South American catfishes almost exclusively, and established several families without considering (at least in print) the possibility of including Old World forms. In fairness to Eigenmann and others both before him and since, it must be remembered that it is difficult even today to obtain adequate comparative material of such a large, diverse and widespread group of fishes.

The tendency to keep catfish subgroups confined to either the Old or New World has become well established chiefly due to the work of Regan (1911). This short paper is probably the single most important work in catfish anatomy and classification, and has served as a baseline for all future work on siluriform higher categories, as did Gunther's work previously. Regan gives a comprehensive osteological definition for the Siluriformes, which he considers a suborder, and for each of the 23 families he recognizes, as well as keys to their included genera. The coordinate anatomical data given for each family, mostly from the syncranium, makes this work especially valuable. The categories he established and many of his anatomical diagnoses have remained largely unaltered, in spite of the many new forms described since.

Most of the families established since Regan's and Gunther's work either have been based upon material unavailable to them, or are their subgroups elevated to family rank. This elevation of their subgroups has usually been done on the basis of a degree of difference, not because the worker believed a particular subfamily to be more closely related to some other family or group of families (*e.g.*, Hora, 1936; Weber and de Beaufort, 1913; Eigenmann, 1925). Very few of Regan's families have subsequently been established to be polyphyletic groups.

Regan raised to family status most of the subgroup established in the old "catch-basket" family Siluridae by Bleeker (1858, 1863) and Eigenmann and Eigenmann (1890). This left Regan's Siluridae as a distinct and probably monophyletic group of the Old World fishes including the European catfish, *Silurus glanis*. However, many of Regan's familial separations and his concepts of interfamilial relationships were apparently based largely upon geographic considerations. Consequently at least two of the former silurid subgroups, Regan's Pimelodontidae (New World) and Bagridae (Old World) cannot be completely distinguished, and appear to form "catch-baskets" for groups that do not clearly belong in any of his other families. Regan states (P.572) "Since the two groups (Pimelodontidae and Bagridae) are large, varied and geographically distinct, and seem to form the starting point for the evolution of most of the siluroids of South America and Asia and Africa respectively, it seems best to recognize them as distinct families." No fewer than five of his families are described as being "closely related" to the Bagridae. Regan (1922) still believed that most if not all of the other Old World families may be regarded as derived

from the Bagridae. He also stated that the Pimelodontidae may be regarded as ancestral to several of the other South American families.

Regan's work implies that South American catfishes and Old World catfishes each form a monophyletic group. This implication, although it may be true, is not supported by Regan's evidence, nor has a case been made for this by other workers since. Nevertheless, this implication has been tacitly accepted by almost all who have since been concerned with catfish relationships. Very few workers have fully considered the possibility that some South American groups may be more closely related to some Old World groups than to other South American groups.

Berg's (1940) classification added a few families to those recognized by Regan, making a total of 28. 6 Berg, however, went a step further and divided them into two superfamilies, one, the Diplomystoidae, for the monotypic Diplomystidae (*Diplomystes papillosus*) and the other, the Siluroidae, for all other catfish families. The Diplomystidae was first established by Eigenmann and Eigenmann (1890), who singled out *Diplomystes* as the most primitive living catfish. Regan (1911), whom Berg followed closely, further established the primitive position of this family, and Berg's classification was evidently meant to reflect this.

The 31 siluriform families recognized by Greenwood *et al*. (1966) were largely those of Berg and Regan, but no superfamily divisions were included. Chardon's (1968) classification of catfishes, based on a detailed and extensive comparative study of the Weberian apparatus, groups 31 families into eight suborders (including one for the Diplomystidae) and 15 superfamilies. Some of his higher categories contain families from both the New and Old Worlds. In his dendrogram (p. 241) these groups appear to be represented as natural groups, but this is not always consistent with statements in his text (see below, p. 64). Nevertheless, Chardon's classification best represents siluriform inter-family relationships as presently understood.

Bleeker, P. 1858
    Order Siluri
        Family Siluroidei
            Subfamily Sisorichthyoidei
            Subfamily Callichthyoidei
            Subfamily Bagrichthyoidei
            Subfamily Alichthyoidei
            Subfamily Silurichthyoidei
            Subfamily Plotosichthyoidei
        Family Aspredinoidei
        Family Loricarioidei
        Family Heterobranchoidei

Bleeker, P. 1863
    Family Loricarioidei
        Subfamily Plecostomiformes
        Subfamily Loricariaeformes
    Family Callichthyoidei

    Family Siluroidei
        Subfamily Sisoriformes
        Subfamily Bagriformes
        Subfamily Astroblepiformes
        Subfamily Trachelyopteriformes
        Subfamily Trichomycteriformes
        Subfamily Siluriformes
        Subfamily Ailiaeformes
        Subfamily Malapteruriformes
    Family Aspredinoidei
        Subfamily Asprediniformes
        Subfamily Bunocephaliformes
    Family Chacoidei
        Subfamily Chacaformes
        Subfamily Plotosiformes
    Family Hetrobranchoidei
        Subfamily Heterobranchiformes
        Subfamily Saccobranchiformes

Gill, Th. 1872 (Gunther's (1864) subgroups in parentheses)
    Order Nematognathi
        Family Hypophthalmidae Cope
        Family Trichomycteridae (Opisthopterae)
        Family Siluridae
        Family Chacidae (Chacina)
        Family Plotosidae (Plotosina)
        Family Clariidae (Clarina)
        Family Callichthyidae (Hypostomatina)
        Family Argiidae (Hypostomatina in part)
        Family Loricariidae (Hypostomatina in part)
        Family Sisoridae (Hypostomatina)
        Family Aspredinidae (Aspredinina) Cope

Eigenmann, C.H. and R.S. Eigenmann 1890
    Family Bunnocephalinae
        Subfamily Bunocephalinae
        Subfamily Platystacinae
    Family Diplomystidae
    Family Siluridae
        Subfamily Tachisurinae
        Subfamily Callophysinae
        Subfamily Pimelodinae
        Subfamily Doradinae
        Subfamily Auchenipterinae
        Subfamily Ageneiosinae
    Family Hypophthalmidae
    Family Pygididae
        Subfamily Cetopsinae
        Subfamily Pygidinae
        Subfamily Stegophilinae
    Family Argiidae
    Family Loricariinae
        Subfamily Loricariinae
        Subfamily Hypoptopominae
        Subfamily Plecostominae
    Family Callichthiidae

Regan, C.T. 1911
  Diplomystidae
  Ariidae
  Doradidae
  Plotosidae
  Siluridae
  Bagridae
  Amiuridae
  Amblycepidae
  Sisoridae
  Amphiliidae
  Chacidae
  Schilbeidae
  Clariidae
  Pangasiidae
  Synodontidae
  Malopteruridae
  Pimelodidae
  Helogenidae
  Hypophthalmidae
  Trichomycteridae
  Bunocephalidae
  Callichthyidae
  Loricariidae

Berg, L.S. 1940 (Reprinted 1965)
Suborder Siluroidei
  Superfamily Diplomystoidae
  Family Diplomystidae
  Superfamily Siluroidae
  Family Ariidae (Tachysuridae)
  Family Doradidae
  Family Auchenipteridae (Trachycorystidae)
  Family Ageniosidae
  Family Plotosidae
  Family Siluridae
  Family Bagridae (Porcidae, Mystidae, including Cranoglanidae)
  Family Doiichthyidae
  Family Amiuridae
  Family Amblycipitidae (Amblycepidae)
  Family Akysidae
  Family Sisoridae (Bagariidae)
  Family Amphiliidae
  Family Chacidae
  Family Schilbeidae (Pangasiidae)
  Family Saccobranchidae (Heteropneustidae)
  Family Clariidae
  Family Olyridae
  Family Synodontidae (Mochocidae)
  Family Malapteruridae (Malopteruridae)
  Family Pimelodidae
  Family Helogenidae
  Family Hypophthalmidae
  Family Trichomycteridae (Pygidiidae, Cetopsidae)
  Family Bunocephalidae (Aspredinidae)

Family Callichthyidae
Family Loricariidae (Argidae, Astroblepidae)

Gosline, W.A. 1945
  Family Diplomystidae
  Family Ariidae
  Family Ameiuridae
  Family Doradidae (Auchenipterinae)
  Family Ageneiosidae
  Family Pimelodidae
  Family Helogeneidae
  Family Hypophthalmidae
  Family Cetopsidae
  Family Pygidiidae
  Family Bunocephalidae
  Family Callichthyidae
  Family Loricariidae
  Family Astroblepidae

Chardon, M. 1968
  Order Siluriformes
    Suborder Diplomystoidei
      Family Diplomystidae
    Suborder Siluroidei
      Superfamily Helogeneoidei
        Family Helogeneidae
      Superfamily Siluroidae
        Family Siluridae
      Superfamily Amblycipitoidae
        Family Amblycipitidae
    Suborder Malapteruroidei
        Family Malapteruridae
    Suborder Bagroidei
      Superfamily Bagroidae
        Family Bagridae
        Family Pimelodidae
        Family Ictaluridae
        Family Ariidae
        Family Olyridae
      Superfamily Plotosidae
        Family Plotosidae
      Superfamily Schilbeidae
        Family Schilbeidae
      Superfamily Pangasioidae
        Family Pangasiidae
      Superfamily Chacoidae
        Family Chacidae
      Superfamily Doradoidae
        Family Mochokidae
        Family Auchenipteridae
        Family Doradidae
        Family Ageneiosidae
      Superfamily Sisoroidae
        Family Amphiliidae
        Family Sisoridae
      Superfamily Akysoidae

Family Akysidae
Superfamily Clarioidea
 Family Uegitglanididae
 Family Clariidae
 Family Heteropneustidae
Suborder Cetopsoidei
 Family Cetopsidae
Suborder Hypopthalmoidei
 Family Hypophthalmidae
Suborder Loricarioidei
 Superfamily Aspredinoidae
  Family Aspredinidae
 Superfamily Trichomycteroidae
  Family Trichomycteridae
 Superfamily Loricarioidae
  Family Astroblepidae
  Family Loricariidae
  Family Callichthyidae

The members of the family Trichomycteridae were first designated as a higher taxonomic category, the subfamily "Trichomycteriformes" in the family Siluroidei by Bleeker (1863). This family contained seven other subfamilies, and was evidently a "catch-basket" group for Bleeker, containing both Old and New World groups that he probably did not believe were closely related to any of his other five families.

The Trichomycteridae was first recognized as a family by Gill (1872). Eigenmann and Eigenmann (1888, 1890) and Eigenmann (1918) used the name Pygidiidae. (Tchernavin (1944, pp. 244-245) gave a thorough review of the history of the names *Trichomycterus* and *Pygidium*, which leaves no doubt that the proper name for the family is Trichomycteridae rather than Pygidiidae.) Both Regan (1911) and the Eigenmanns included the cetopsids in the Trichomycteridae. Cetopsids are also South American freshwater catfishes, known especially for their parasitic habits, as are trichomycterids. Members of both families are referred to by local inhabitants as "candiru", meaning pest. The parasitic habits of these fishes were reviewed by Eigenmann (1918), Gudger (1930), and Kelly and Atz (1964).

Eigenmann's (1918) monograph on the trichomycterids reviewed all of the species known at the time. He divided the family into six subfamilies Nematogenyinae, Pygidiinae (Trichomycterinae), *Pareiodon*tinae, Stegophilinae, Vandelliinae and Tridentinae. Cetopsids were excluded, but *Phreatobius* and *Nematogenys* were included. Both Eigenmann and Regan considered *Nematogenys inermis* to be the most primitive trichomycterid, and Eigenmann (1927) recognized a separate family, Nematogenyidae, for this species.

Myers (1944), also using the name Pygidiidae, included *Nematogenys* in the Trichomycteridae as the Nematogenyinae and *Phreatobius* as the Phreatobiinae. He established an additional subfamily, the Glanapteryginae.

Gosline's (1945) catalogue gave 136 species of trichomycterids, divided among 27 genera. He recognized

the same subfamily divisions as Myers (1944).

Myers and Weitzman (1966) described a new subfamily, the Sarcoglanidinae, and expressed doubt about *Nematogenys* being a trichomycterid. They also examined specimens of *Heptapterus*, a pimelodontid, which Reichel (1927), in his monograph on the anatomy of *Phreatobius cisternarum*, considered *Phreatobius* to most closely resemble. Myers and Weitzman concluded that *Heptapterus* is a pimelodontid and not a trichomycterid, and that *Phreatobius*, the only member of the Phreatobiinae, should be excluded from the Trichomycteridae. Specimens of *Phreatobius*, however, were not available to Myers and Weitzman (1966) or to Myers (1944).

Since the work of Eigenmann (1918) the only other significant synthesis done at the level of genus and species has been the work of Tchernavin (1944) and Miranda-Ribeiro (*e.g.* 1947, 1951).

Trichomycterids are typically small, slender, eel- like fishes with a depressed head and a compressed body. The mouth is subterminal or fully ventral, and in some (generally the parasitic forms) the lips form a ventral sucking disc. The species with the smallest over-all body size is *Tridens melanops* (*e.g.* M.C.Z. 8137, standard length 20 mm., head width 2 mm., head depth 1 mm., body width 1 mm., body depth 1.5 mm.). (These specimens have not been confirmed to be adults, but they are the only known specimens of the species.) Others (*e.g. Miuroglanis platycephalus*) have a shorter standard length, 17 mm. Trichomycterids generally range in size from about 30 mm to 150 mm in standard length. The Trichomycterinae are the largest, with museum specimens of *Trichomycterus dispar* observed to be 350-400 mm in standard length. Another member of this subfamily, *Eremophilus*, is fished commercially in Colombia.

Trichomycterids lack the well-developed pectoral and dorsal spines typical of most catfishes. The dorsal fin of trichomycterids is also distinctive in being located posteriorly.

Little is known of their life history. All species are found in fresh water and most are found inshore and in small backwaters. They are secretive and nocturnal, as are most catfishes. Aquarium observation by Dr. S. H. Weitzman (pers. comm.) of *Tridentopsis* confirms this. In general, trichomycterids tend to inhabit holes and other cavities in the substrate, or bury themselves in the gravel or sandy bottom.

Members of the Trichomycterinae are among the very few fishes found in the high Andean streams (Eigenmann, 1918, and G. Smith, pers. comm.), and in this habitat they range further south than any other South American freshwater fishes (to latitude 470 30', Eigenmann, 1918). The family also ranges through South America in the lowlands, and *Trichomycterus* extends as far north as Panama. The family is found on both sides of the Andes.

The primary distinguishing feature of trichomycterids is the presence of teeth (also referred to as spines or prickles) on the side of the head (opercular bones). These structures are absent, however, in some species.

Table 1. Classification of the Trichomycteridae.

Classification of Eigenmann (1918), as modified by Myers (1944) and Gosline (1945), with additional groups described since	Present reference of taxon
Trichomycterinae	Trichomycterinae
Eremophilus	*Eremophilus*
Hatcheria	*Trichomycterus*
Pygidium	*Trichomycterus*
Rhizosomichthys	*Rhizosomichthys*
Scleronema	*Scleronema*
Sarcoglanidinae	Sarcoglanidinae
Malacoglanis	*Malacoglanis*
Sarcoglanis	*Sarcoglanis*
Glanapteryginae	Glanapteryginae
Glanapteryx	*Glanapteryx*
Pygidianops	*Pygidianops*
Typhlobelus	*Typhlobelus*
Stegophilinae	Stegophilinae
Acanthopoma	*Acanthopoma*
Apomatoceros	*Apomatoceros*
Haemomaster	*Haemomaster*
Henonemus	*Stegophilus*
Homodiaetus	*Homodiaetus*
Ochmacanthus	*Ochmaaanthus*
Parastegophilus	*Parastegophilus*
Pareiodon	*Pareiodon*
Pleurophysus	*Pleurophysus*
Pseudostegophilus	*Pseudostegophilus*
Schultzichthys	*Schultzichthys*
Stegophilus	*Stegophilus*
Pareiodontinae	Stegophilinae
Pareiodon	*Pareiodon*
Tridentinae	Tridentinae
Miuroglanis	*Miuroglanis*
Tridens	*Tridens*
Tridensimilis	*Tridensimilis*
Tridentopsis	*Tridentopsis*
Vandelliinae	Vandelliinae
Branchioica	*Branchioica*
Parabranchioica	*Branchioica*
Paracanthopoma	*Paracanthopoma*
Paravandellia	*Paravandellia*
Plectrochilus	*Plectrochilus*
Vandellia	*Vandellia*
Nematogenyinae	Nematogenyidae
Nematogenys	*Nematogenys*
Phreatobiinae	Pimelodentidae
Phreatobius	*Phreatobius*

Methods and Materials

Cleared and alizarin stained specimens were prepared according to the enzyme technique of Taylor (1967). When additional clearing was necessary, specimens were also treated with carbon tetrachloride using the procedure of Miller and Van Landingham (1969). Specimens were disarticulated by heating in a weak potassium hydroxide solution, or by the technique of Ossian (1970). Methylene blue was used to stain for cartilage. Radiographs were also made.

Fin ray counts were made on alizarin clearings, radiographs or both. All detectable splints and segmented rays were counted, without regard to the number of pterygiophores. In those catfish without a pungent pectoral spine the first pectoral ray was counted along with the others. Principal caudal ray counts are given as the numbers of branched rays plus one simple ray in the upper and lower lobes separated by a slash (*e.g.* 6/7).

The number of vertebrae was determined from counts on alizarin preparations. Counts from radiographs were used to supplement this data, or when no alizarin preparations were available. The number of vertebrae given includes those in the Weberian complex (assumed to be five in trichomycterids, see Chardon, 1968 and p. 58 below), plus the first preural and the first ural vertebrae, which in catfishes form a single compound centrum (Lundberg and Baskin, 1969).

Measurement of relative eye size was made with an ocular micrometer. The methods of measuring other characters are given as an integral part of the description and analysis of the character itself, and will thus not be repeated here.

Drawings were made with the aid of a camera-lucida.

The generic and specific names recognized here, unless otherwise specified, are those recognized by Myers (1944), Gosline (1945) and Tchernavin (1944). Table 1 gives the generrecognized in the present work.

Abbreviations of Institutions

AMNH American Museum of Natural History. ANSP Academy of Natural *Sciences* of Philadelphia. BM(NH) British Museum (Natural History). CAS California Academy of Science. FMNH Field Museum of Natural History IU Indiana University Museum (now at CAS). MCZ Museum of Comparative Zoology. NMV Naturhistorisches Museum, Vienna. RNH,L Rijksmuseum van Natuurlijke Historie, Leiden. SIO Scripps Institute of Oceanography. SMF Senckenberg Museum. UMMZ University of Michigan Museum of Zoology. USNM United States National Museum. ZMA Zoological Museum Amsterdam.

Material Examined

Siluriformes-Trichomycteridae: *Apomatoceros alleni* Eigenmann: ANSP 109804, CAS-IU 15500 (type); *Branchioica phaneronema* Miles: MCZ 35874; *Branchioica magdalenae* Miles: BM(NH) 1947-7-1:203-208; *Branchioica bertoni* Eigenmann: SMF 8905, BM(NH) 1956,11.14 1-20, 1946-4-18:1-6, 1950-12.20:1, 1956-11-14:1-20, 1933-12-31:1-10; *Branchioica* sp. USNM 124880, SMF uncatalogued; *Eremophilus mutisii* Humboldt: AMNH 7072, UMMZ 179261; *Glanapteryx anguilla* Myers: CAS-IU 17700 (type); *Haemomaster venezuelae* Myers: AMNH uncatalogued, CAS-lU 17706, MCZ 31579; *Homodiaetus anisitsi* Eigenmann: CAS-lU 10155; *Homodiaetus maculatus* Steindachner: ANSP 93977, CAS-lU 13960, CAS-lU 13962, FMNH 58526, USNM 94126, BM(NH) 1935-9-9:13-14, 1913-1-1:18-19; *Malacoglanis gelatinosus* Myers and Weitzman: CAS-SU 50754 (type), 50755; *Miuroglanis platycephalus* Eigenmann and Eigenmann: MCZ 8172 (type); *Nematogenys inermis* Guichenot: ANSP 84197, 84198,NMV 45 333, USNM 84343, MCZ 7737, 8291 (type), MCZ 9839, USNM(IUM) 15060; *Ochmacanthus flabelliferus* Eigenmann: USNM 191585; *Ochmacanthus reinhardti* Steindachner: AMNH 27693, ANSP uncatalogued (Catherwood): *Ochmacanthus* sp. ANSP uncatalogued (Catherwood); *Parabranchioica teaguei*

Devincenzi and Vaz-Ferreira: BM(NH) 1944.3.3.10; *Pareiodon microps* Kner: BM(NH) 1926-10-27:270-273, NMV 45 486 (type), 45 487, CAS 18522, MCZ 46683; *Plectrochilus erythrurus* Eigenmann: ANSP 113932, 79163, USNM 167871, 120134; *Plectrochilus machadoi* Miranda-Ribeiro: ANSP uncatalogued (Catherwood); *Plectrochilus* sp. AMNH uncatalogued (Field No. B64-24), UMMZ uncatalogued, USNM 191600; *Pseudostegophilus nemurus* Gunther: AMNH 27553, AMNH uncatalogued, ANSP uncatalogued (Catherwood), USNM uncatalogued; Gunther: BM(NH) 1938.12.17; *Pygidianops eigenmanni* Myers: CAS 11121; *Rhizosomichthys totae* Miles: USNM 120130, 120129, BM(NH)

1947.7-1:202; *Sarcoglanis simplex* Myers and Weitzman: CAS-SU 50189; *Scleronema angustirostrus* Devincenzi and Teague: BM(NH) 1944.6.20:1; *Stegophilus insidiosus* Reinhardt: BM(NH) 1875.5.22.1 (type), FMNH 58532, NMV 44 733 (type); *Stegophilus intermedius* Eigenmann and Eigenmann: NMV 44 734, AMNH 20884, ANSP uncatalogued (Catherwood), FMNH 58087, USNM-IU 15499, 15707, 15708, 13958, USNM-IU uncatalogued, USNM uncatalogued, MCZ 9842 (type); *Trichomycterus amazonicus* Steindachner: SMF 9020; *Trichomycterus areolatus* Valenciennes: AMNH 963, MCZ uncatalogued; *Trichomycterus barbouri* Eigenmann: MCZ 29314, UMMZ 66334; *Trichomycterus bogatense*
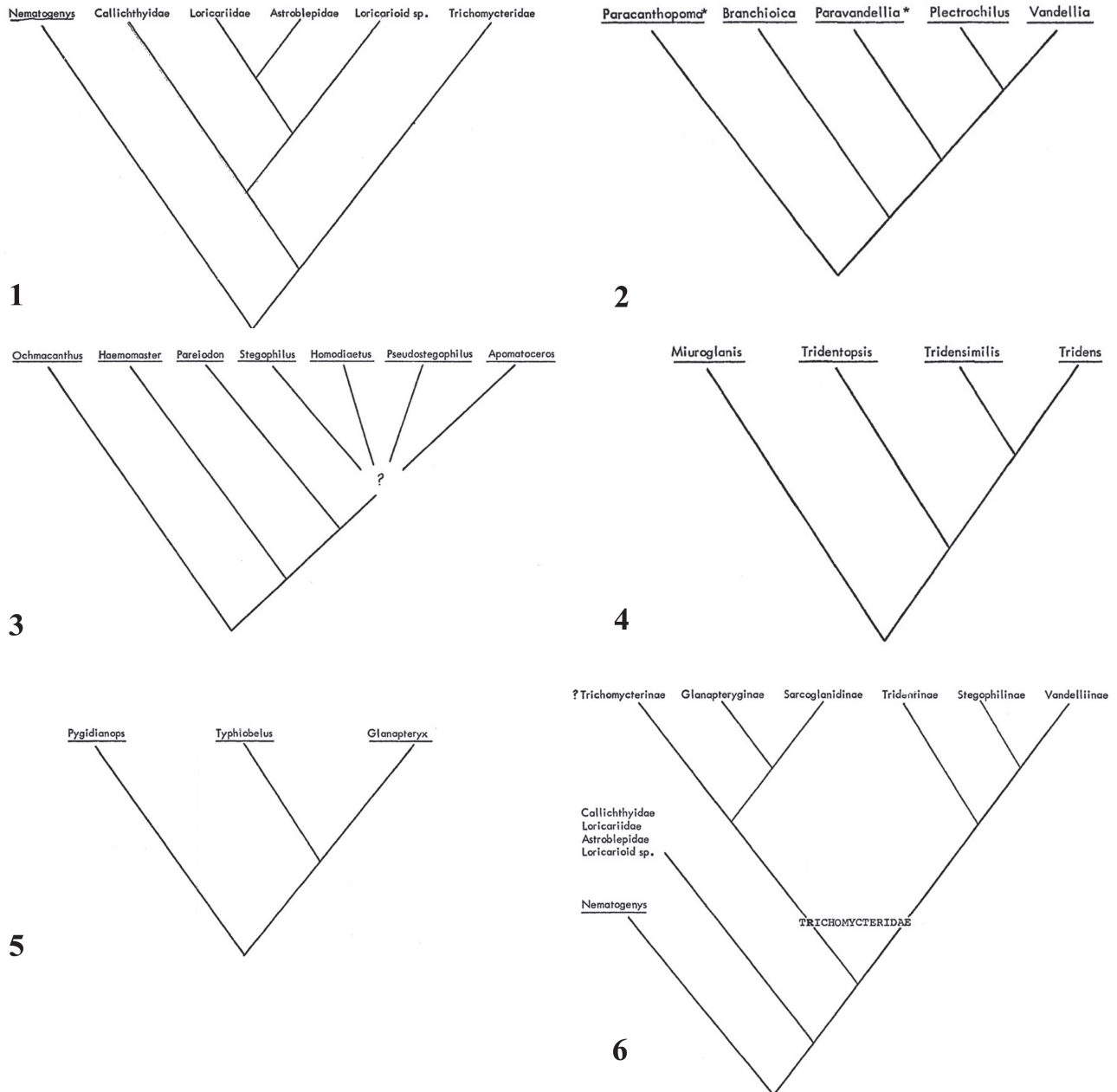
Fig. 1. Relationships within the loricarioidei. **Fig. 2.** Relationships among the genera of the Vandelliinae. An asterisk (*) indicates that no specimens of that genus were examined. **F ig. 3.** Relationships among the genera of the Stegophilinae. The question mark indicates relative uncertainty as to the relationship. **Fig. 4.** Relationships among the genera of the Tridentinae. **Fig. 5.** Relationships among the genera of the Glanapteryginae. **Fig. 6.** Relationships among the subfamilies of the Trichomycteridae. A question mark indicates relative uncertainty about the monophyletic status of a group.

Eigenmann: AMNH 7170; *Trichomycterus borellii* Boulenger: BM(NH) 1906-5-31:42-53; *Trichomycterus boylei* Nichols: AMNH 17271; *Trichomycterus brasiliensus* Reinhardt: MCZ 7734, 7735, 8303-4, 8306; *Trichomycterus caliense* Eigenmann: UMMZ 145747; *Trichomycterus conradi* Eigenmann: RNH,L uncatalogued; *Trichomycterus cordovense* Weyenbergh: BM(NH) 1911-11-25:1-10; *Trichomycterus guianense* Eigenmann: AMNH 9657, MCZ 32121-2-3, SMF 9018; *Trichomycterus retropinnae* Regan: RNH, L 24727; *Trichomycterus rivulatus* Valenciennes: AMNH 20351, AMNH uncatalogued, UMMZ 66324, 66341, 145061, 185310, MCZ 3963, 29296; *Trichomycterus spilosoma* Regan: BM(NH) 1914-5-18:50; *Trichomycterus spagazzinii* Berg: BM(NH) 1906-6-31:54-61; *Trichomycterus striatus* Meek and Hildebrand: USNM HL-177, UMMZ 182553; *Trichomycterus taenia* Kner: BM(NH) 1910-7-11:111-114; *Trichomycterus vermiculatus* Eigenmann: AMNH 9084, 9081; *Trichomycterus zonatus* Eigenmann: AMNH 9082; *Trichomycterus* sp. AMNH 17271, MCZ uncatalogued; *Tridens melanops* Eigenmann and Eigenmann: MCZ 8137, USNM 120296; *Tridensimilis venezuelae* Schultz: MCZ 37292, USNM 121291; *Tridentopsis pearsoni* Myers: CAS-IU 17277, USNM 204058, 204057, USNM uncatalogued, AMNH 13982; *Tridentopsis tocantinsi* La Monte: AMNH 20926, 13967 (type), SIO 69-160; *Typhlobelus ternetzi* Myers: CAS 11118 (type), 11119; *Vandellia cirrhosa* Cuvier and Valenciennes: AMNH 9663; *Vandellia gigantia*: BM(NH) 1897-12-1:232; *Vandellia gracillicauda*: MCZ 27572; *Vandellia hasemani* Eigenmann: AMNH uncatalogued; *Vandellia* sp. AMNH (Field No. B64-24).

The following siluriform material was examined in some detail as alizarin preparations.
Astroblepidae: *Astroblepus longifilis* (Steindachner): AMNH 11582; *Astroblepus whymperi*: MCZ 31512; *Astroblepus* sp. AMNH 20873. Bunocephalidae: *Chamaigenes filamentosus* (Cuvier and Valenciennes): ANSP uncatalogued; *Bunocephalus* sp. MCZ 46132, 46133; *Dupouyichthys sapito* Schultz: USNM 121073. Callichthyidae: *Hoplosternum thoracatum* (Cuvier and Valenciennes): AMNH 11580; *Callichthys callichthys* (Linnaeus): ANSP 53358-64; *Corydoras aeneus* Gill: AMNH 21772, USNM uncatalogued. Cetopsidae: *Hemicetopsis amphiloxus* Eigenmann: USNM uncatalogued; *Hemicetopsis candiru* (Spix): MCZ 8138; *Hemicetopsis plumbeus* Steindachner: USNM 194180, UMMZ 66316; *Hemicetopsis* sp. RNHL uncatalogued. Diplomystidae: *Diplomystes papillosus* (Cuvier and Valenciennes): ANSP 84193, MCZ 8290, USNM uncatalogued, NMV 20308, 46664. Hypophthalmidae: *Hypophthalmus edentatus* Spix: AMNH 4089; Loricariidae: *Ancistrus cirrhosus* (Valenciennes): ANSP 67790-95; *Ancistrus* [*Ancistrus*] sp. AMNH 20861; *Loricariichthys* sp. AMNH uncatalogued; *Otocinclus affinis* Steindachner: AMNH 22310; *Plecostomus* sp. ANSP 99907, 22409. Loricarioid sp. UMMZ (uncatalogued).

In connection with the present study alizarin clearings and/or alcohol specimens of all siluriform families recognized by Greenwood *et al.* (1966) were also examined, except the Chacidae, Cranoglanididae and Olyridae.

Advanced siluriform characters of the Trichomycteridae

The following are the advanced siluriform characters found in all, or most, trichomycterids. A discussion of each character is given, in which the following points are mentioned, as required: 1) a description of the character, 2)

the evidence for its being an advanced siluriform character, 3) the corresponding primitive condition, 4) exceptions or variations in its occurrence within the Trichomycteridae, 5) the occurrence of similar, and possibly homologous characters in other siluriforms. Unless otherwise stated, the condition in *Nematogenys* is primitive relative to that in trichomycterids.

Some of the advanced siluriform characters listed occur only in trichomycterids. These characters can thus be used as evidence to define the Trichomycteridae as a monophyletic group. Other advanced siluriform characters listed occur in at least a similar form in some other catfishes. These other catfishes are more closely related to trichomycterids than to remaining siluriforms. The evidence concerning the relationships of the Trichomycteridae to other catfish groups is discussed in the next section of this work.

1) Prootic, sphenotic and pterosphenoid form a single bone (figs. 9, 16).

In trichomycterids no lines of separation can be found between the pterosphenoid, sphenotic and prootic bones. This appears to be a case of fusion rather than loss of bones. The prootic and sphenotic portions of this compound bone are clear, having the typical relations to the surrounding bones, foramina and sensory canals. The hyomandibular facet is in the typical position. The pterosphenoid portion, although reduced, is also distinguishable as an antero-dorsal projection of the compound bone forming a portion of the dorsal border of the anterior trigemino-facialis foramen.

These three bones are separate in all other catfishes, and their unique consolidated condition in trichomycterids is probably an advanced condition for siluriforms. In many catfishes all three participate in forming the facet for the hyomandibular. The functional significance of their consolidated condition in trichomycterids may be strengthening support for the hyomandibular, which is involved in the support and manipulation of the toothed opercular and interopercular banes (see p. 36).

2) Dorsohyal lacking (fig. 85).

It seems clear that the presence of two proximal paired bones in the hyoid bar, the dorsal and ventral "hypohyals", is a condition primitive for teleosts, and that the phyletic trend within various teleost groups has been toward the condition of a single bone, usually the ventral "hypohyal" (see Ridewood, 1904; McAllister, 1968; Nelson, 1969).

The primitive condition for Ostariophysi and for Siluriformes is also two hypohyals. As in teleosts generally (Ridewood, 1904) and in catfishes the ventral "hypohyals" are the larger ones and they articulate medially. In trichomycterids and several other siluriform families (Loricariidae, Astroblepidae, Amphiliidae, Sisoridae and "Loricarioid sp.") there is but a single hypohyal ossification. This is probably the ventral hypohyal only, as there is no sign of its being a compound ossification and no catfish is known to have the hypohyals even partially co-ossified.

In none of these families has a separate dorsal hypohyal cartilage been found, nor has such a cartilage been found in any teleost here investigated, including *Elops* and *Hiodon*. In those teleosts which have them, the dorsal and ventral hypohyals are separate ossifications in a single cartilage. This condition is probably the primitive one for teleosts and for siluriforms.

In *Nematogenys inermis* the dorsal hypohyal is reduced to a tiny calcified remnant.

3) Interhyal lacking (figs. 45, 85).

Typically in teleosts the interhyal has a cartilaginous contact with the distal end of the hyomandibular and symplectic where it acts as a pivot for the lower portion of the hyoid arch, and connects the latter with the suspensorium (McAllister, 1968). In trichomycterids the hyoid bar is invariably well developed, even in forms with very weakly developed branchial arches (*e.g.*, *Vandellia*). It may be involved in the manipulation of the strongly toothed opercular and interopercular bones, as indicated by the well-developed, complex articulation of the postero-hyal ("epihyal") with the interopercular bone. The lack of an interhyal in trichomycterids may be related to this specialized function of the hyoid bar.

Other siluriforms that lack an interhyal are "Loricarioid sp.", the Loricariidae and their naked relatives the Astroblepidae. Callichthyids, another group of armored catfishes, believed to be related to loricariids, have an interhyal, as does *Nematogenys*.

Additional siluriforms lacking an interhyal are the Amphiliidae, Amblycipitidae and Sisoridae (*Bagarius*). These Old World families, as well as the New World Loricariidae and Astroblepidae, are fishes which use the substrate for attachment and locomotion in a fast-water environment or out of the water (Hora, 1922; Eigenmann, 1918; Johnson, 1912). The consolidation of the hyoid bar by the loss of the interhyal, and loss of the dorsal hypohyal in some (see p. 37), may be functionally related to these specialized habits. Some non-parasitic trichomycterids, *e.g.*, *Trichomycterus*, have also been reported to use the substrate for locomotion in fastwater (Eigenmann, 1918). Whether the lack of an interhyal in each of these families is due to their common ancestry, or is independently developed in some as a response to similar functional requirements must at present be resolved on the basis of other evidence.

4) Patch of close set integumentary teeth on interopercle; similar patch on posterior extension of opercle (figs. 41-54).

Arguments are given below (p. 57) that the presence of integumentary teeth, found in trichomycterids and some other catfish groups, is an advanced character for catfishes, and that the closest relatives of trichomycterids are those catfishes with integumentary teeth. Simply the presence of integumentary teeth therefore cannot be considered evidence relating trichomycterids among themselves.

Trichomycterids however, have integumentary teeth only on the opercular and interopercular bones, while all other catfishes (including *Nematogenys*) with integumentary teeth have them at least on the pectoral spine. Most of these other catfishes have integumentary teeth also on the opercular bones and elsewhere (see. p. 61). Only in trichomycterids, do they occur as a distinct patch of closely set teeth on the postero-ventral edge of the interopercle and on a posterior extension from the postero-dorsal corner of the opercle. This arrangement of the integumentary teeth in trichomycterids, and especially the posterior extension of the opercle, can be considered evidence that trichomycterid form a monophyletic group. Even those trichomycterid species without integumentary teeth (*i.e.*, the monotypic genera *Glanapteryx*, *Pygidianops* and *Typhlobelus*) have this posterior extension of the opercle, and appear to have secondarily lost the teeth. *Apomatoceros alleni*, which has interopercular teeth, but no opercular ones, has what appears to be a small posterior extension (cf. figs. 49, 50).

5) Preopercular bone lacking sensory canal (figs, 41-54).

In most siluriforms, including *Diplomystes*, the preopercular sensory canal extends from the temporal canal on the skull roof (in the pterotic) into the preopercular bone. In trichomycterids this sensory canal ends in the soft tissue, a short distance from the temporal canal opening and dorsal to the preopercular bone.

The preopercular bone of trichomycterids, and of catfishes generally, is firmly and immovably connected to the side of the suspensorium. The lack of a sensory canal in this region may be an additional specialization related to the probable use of the opercular teeth in locomotion and feeding (parasitism).

6) Rictal barbel present in upper lip (figs. 62-66).

All siluriforms have at least a single pair of barbels, the maxillary barbels, one barbel on each side of the mouth in the upper lip. The maxillary barbel has a core of cartilage- like material[2], which in cleared specimens can be traced to an origin at the tip of the maxillary bone.

All trichomycterids have an additional pair of barbels, the rictal barbels, at the corner of the mouth in the upper lip, just beneath the base of the maxillary barbels. They are invariably shorter than the maxillary barbels. In cleared specimens the core of the rictal barbel can be traced into the flesh of the upper lip just ventral to the maxillary bone. It originates from the ventro-medial edge of this bone. The trichomycterid rictal barbel may represent a modified branch or subdivision of the maxillary barbel, which is found more distally in some bunocephalids and in "Loricarioid sp."

Callichthyids also have a barbel at the corner of the mouth, just ventral to the maxillary barbel, which also has been designated as a rictal barbel (Gosline, 1940). This appears to be a different structure from the rictal barbel of trichomycterids. Its core can be traced into the lower lip, to the symphysial region of the dentary. This "rictal" barbel of callichthyids may be a modified mental barbel.

7) Supraoccipital crest lacking (*cf.* figs. 7, 9, 32, 33).

In catfishes and in most other ostariophysians a supraoccipital crest is present as a median posterior projection. In catfishes it often extends to the base of the dorsal fin spines, and in conjunction with nuchal plates, contributes to the support of the dorsal spines. In trichomycterids the postero-dorsal edge of the supraoccipital bone is smoothly rounded, lacking any hint of a median posterior projection. This may be an advanced siluriform condition, associated with the posterior position of the dorsal fin, and lack of a dorsal fin spine, which are probably, also advanced characters of the Trichomycteridae (see p. 45).
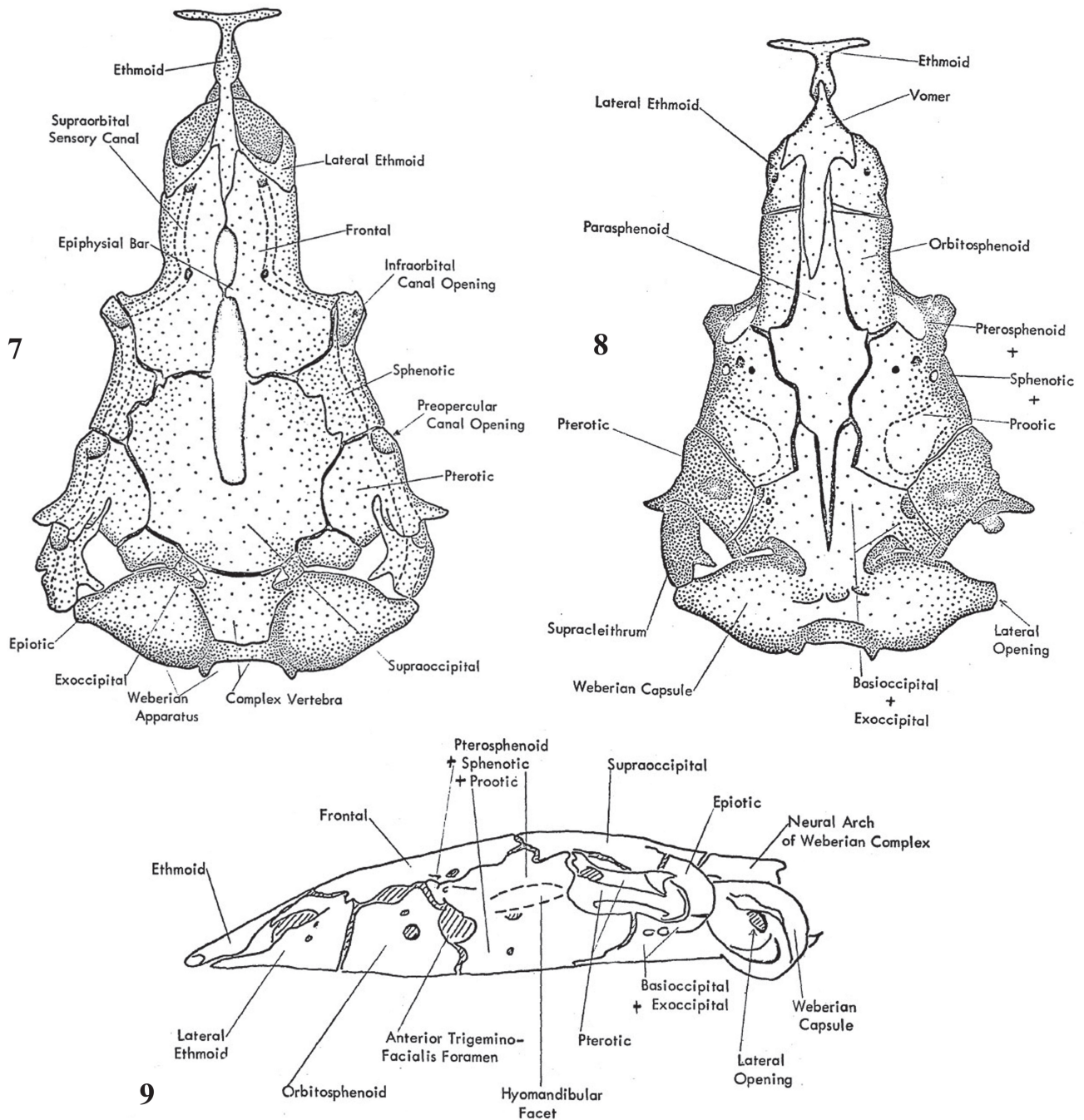
Fig. 7. Neurocranium and Weberian apparatus of *Trichomycterus rivulatus* (AMNH 20351), dorsal view, 8.5x magnification.
Fig. 8. Neurocranium and Weberian apparatus of *Trichomycterus rivulatus* (AMNH 20351), ventral view, 8.5x magnification.
Fig. 9. Neurocranium and Weberian apparatus of *Trichomycterus rivulatus* (AMNH 20351), lateral view of left side, 8.5x magnification.

Chardon (1968, pp. 177-179, figs. 164,165) reports the supraoccipital crest of *Trichomycterus* to be very little marked, and that the fused neural arches of the complex vertebra are joined to the supraoccipital forming a posterior extension of the occipital crest. I could find no hint of such a crest in any trichomycterid, which includes material of the species he examined (*Trichomycterus taenia*). The dorsal surface of the supraoccipital is smooth and round, without a hint of a median crest, and this bone is completely separated from the neural arches by a well-developed synchondral joint. It is possible that this discrepancy (compare my figs. 7, 9) could be due to his specimens being larger.

8) Epural lacking.

Within the Siluriformes there is a repeated trend toward consolidation of the caudal skeleton by fusion or loss of parts (Lundberg and Baskin, 1969), as is the case in teleosts generally (see *e.g.*, Patterson, 1968, Monod, 1968). Catfishes normally have a single epural bone in the caudal skeleton. Characoids, other ostariophysans and other teleosts usually have one or more epurals. Among catfishes loricariids and astroblepids have the epural partially fused to the uroneural and hypural elements. At least one aspredinid, *Agmus*, has such a condition also. Within both plotosids and chacids (*Chaca*) an epural is lacking in some, but present, although very much reduced, in others. (See Lundberg and Baskin, 1969, fig. 6).

The Trichomycteridae are the only Siluriform group in which the epural is consistently lacking. The only exceptions to this are the presence of a half-size epural in one of twelve specimens of *Trichomycterus rivulatus*, and the presence of a full neural spine on the first preural vertebra in one specimen of *Vandellia cirrhosa*.

9) Adipose fin lacking.

The adipose fin is probably a primitive character for the Euteleostei, present in some members of all of the major groups (Greenwood, *et al*., 1966; Rosen and Patterson, 1966), but has been independently lost several times within these groups. It is present in most Salmoniformes, and non-cyprinoid Ostariophysi and in primitive neoteleosts. Within the Siluriformes alone the adipose fin appears to have been lost several times, and its appearance is variable within some families, and perhaps even within some genera or species.

Among trichomycterids a possible adipose fin is present in but two species, forming the subfamily Sarcoglanidinae, known from only three specimens. It is consistently absent in all other trichomycterids. Myers and Weitzman (1966) have considered the possibility that the ridge of tissue anterior to the caudal fin on the caudal peduncle, supported by the often numerous caudal procurrent rays, is part of an adipose fin. There is little evidence to favor this theory. In the Sarcoglanidinae the adipose fin is long, but not associated with the procurrent rays.
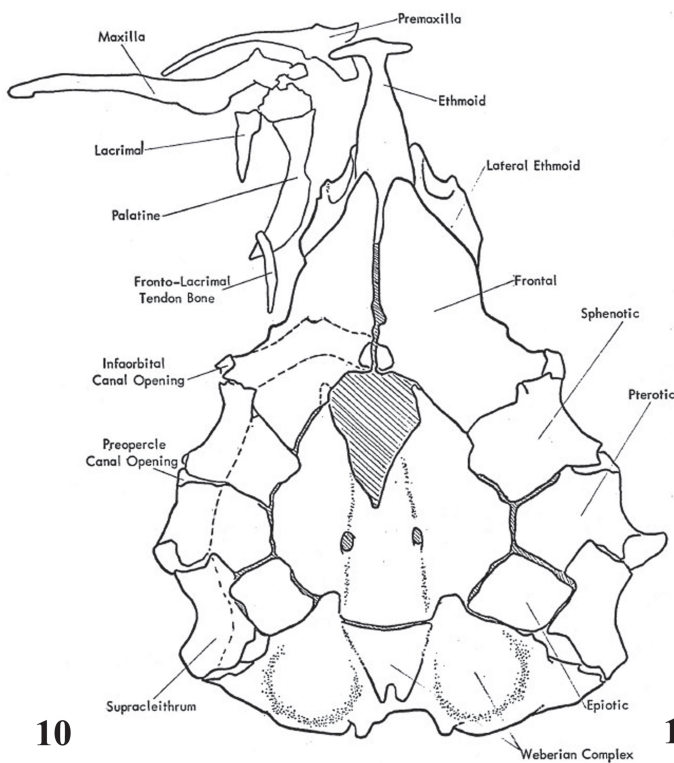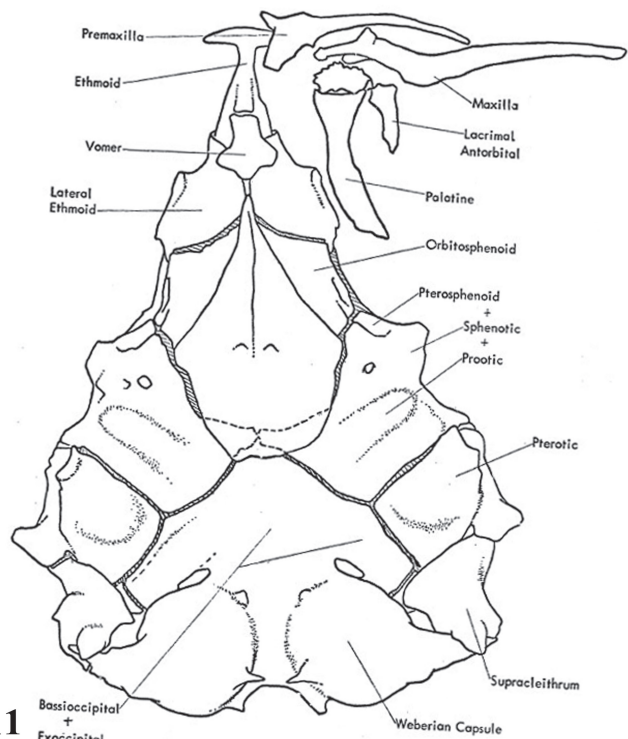
Fig. 10. Neurocranium and associated structures of *Malacoglanis gelatinosus* (CAS-SU 50755), dorsal view 25x magnification.
Fig. 11. Neurocranium and associated structures of *Malacoglanis gelatinosus* (CAS-SU 50755) *I* ventral view 25x magnification.

10) Dorsal fin rays unmodified, origin of dorsal on posterior half of body, posterior to origin of pelvic.

Diplomystes and most siluriform families have the dorsal fin in an anterior position just behind the head. The first two rays are modified into a spine and locking device supported by pterygiophores fitting between the bifurcate neural spines of the anterior vertebrae (see p. 55 and fig. 38). If *Diplomystes* is considered to be the sister group of all other catfishes, then it is possible that this condition of the dorsal fin is the primitive condition for catfishes. It is also possible that those catfishes which lack this condition of the dorsal fin have lost it, and secondarily developed an unmodified dorsal fin in a posterior position, as is found in characoids.

Most of these catfishes with the characoid condition have retained some of the modifications of the dorsal fin, usually bifurcate neural spines of the anterior vertebrae and expanded distal ends of the anterior pterygiophores. A

few trichomycterids have retained a slight bifurcation of the anterior neural spines, indicating that the typical catfish spine and locking device was present in their ancestors.

11) The first pectoral ray articulates only with the scapulo-coracoid, and forms neither a spine nor a locking device.

The typical condition for catfishes, found in *Diplomystes* and most others, is the modification of the first pectoral ray into a pungent spine, which forms a friction locking device in its articulation with the cleithrum (see description in Alexander, 1965). In characoids (*Brycon*) the first ray is stout, unbranched and articulates directly with the scapula. In catfishes a partial articulation with the scapula is retained. If *Diplomystes* is considered to be the sister-group of all other catfishes, this modification of the pectoral fin can be considered the primitive condition for catfishes.
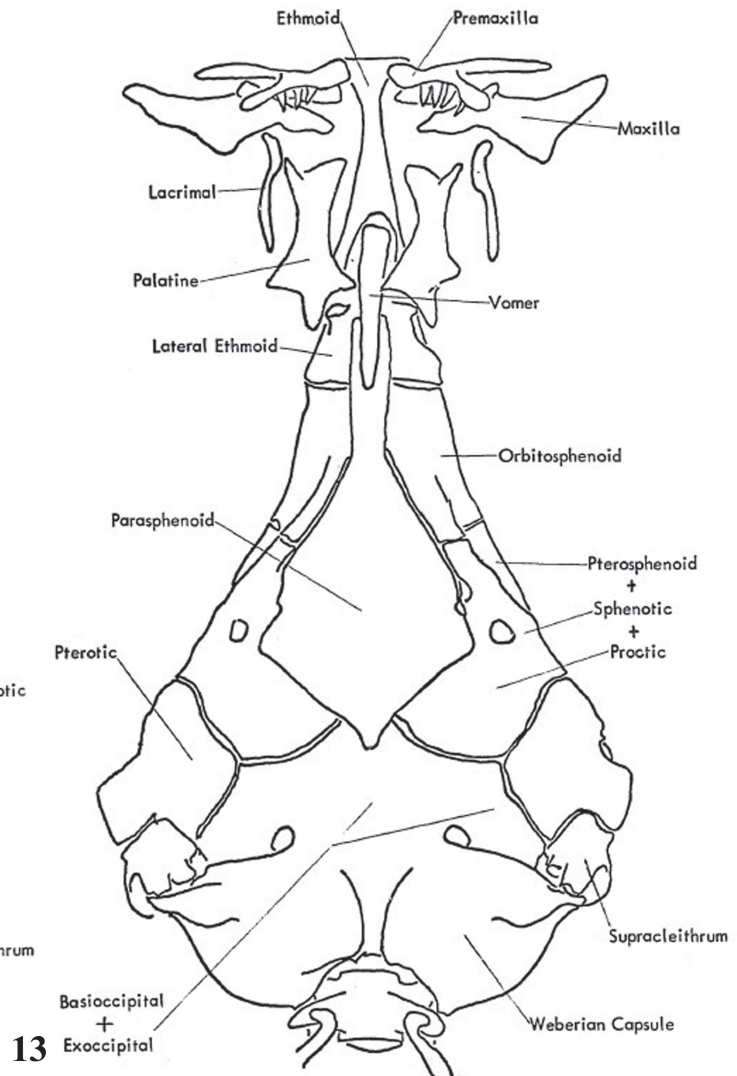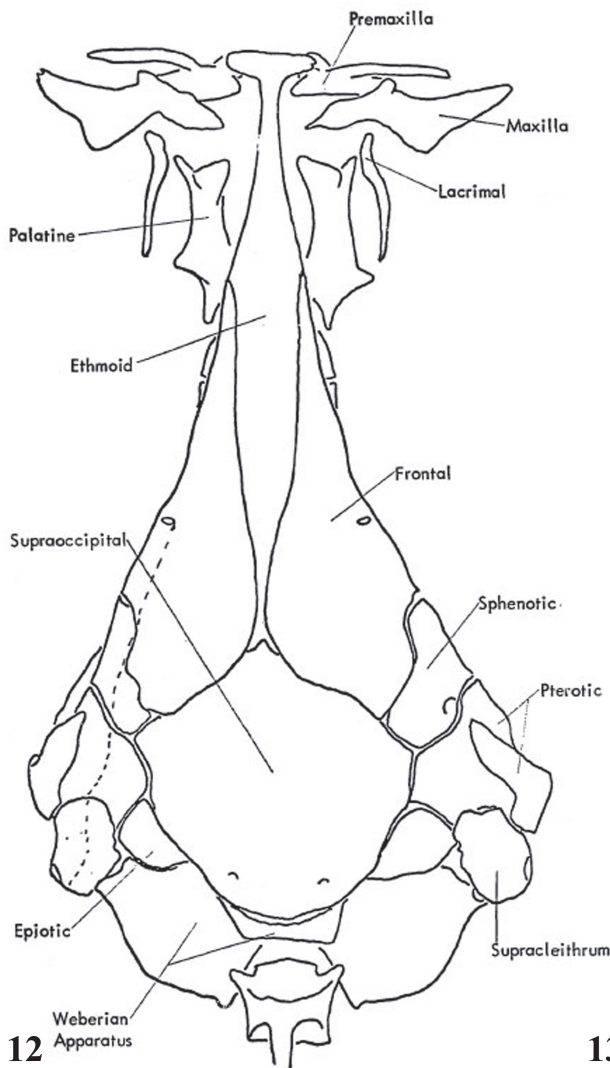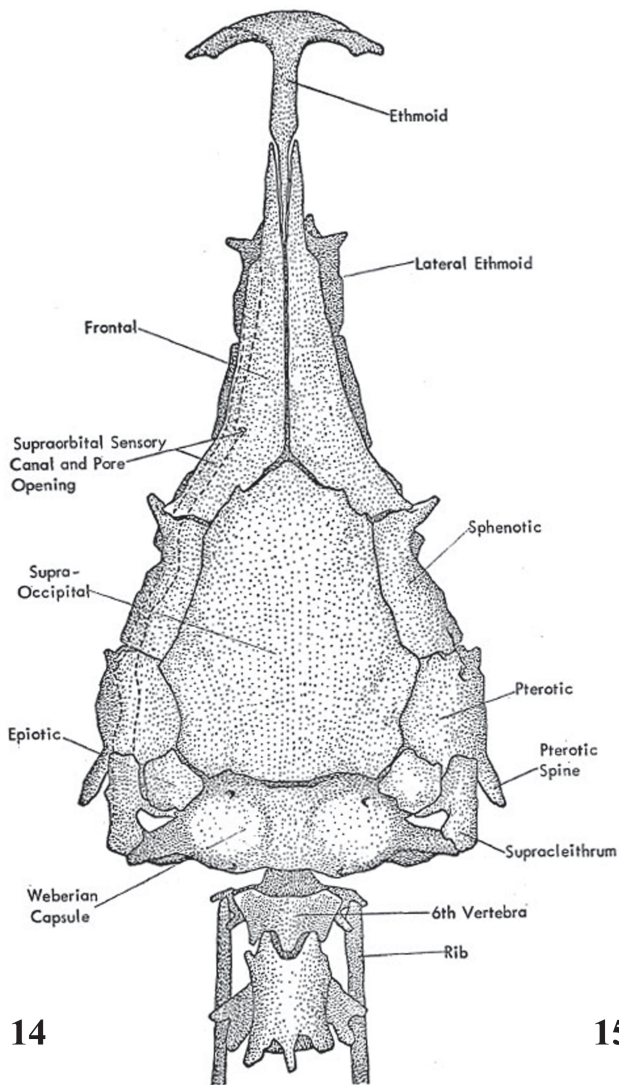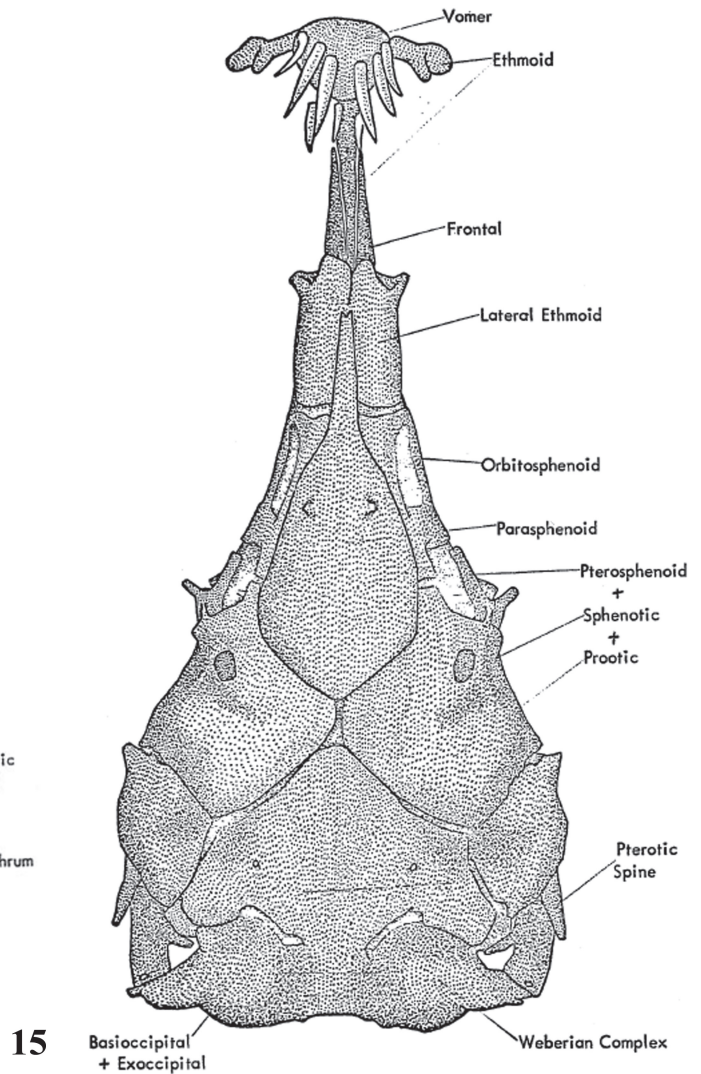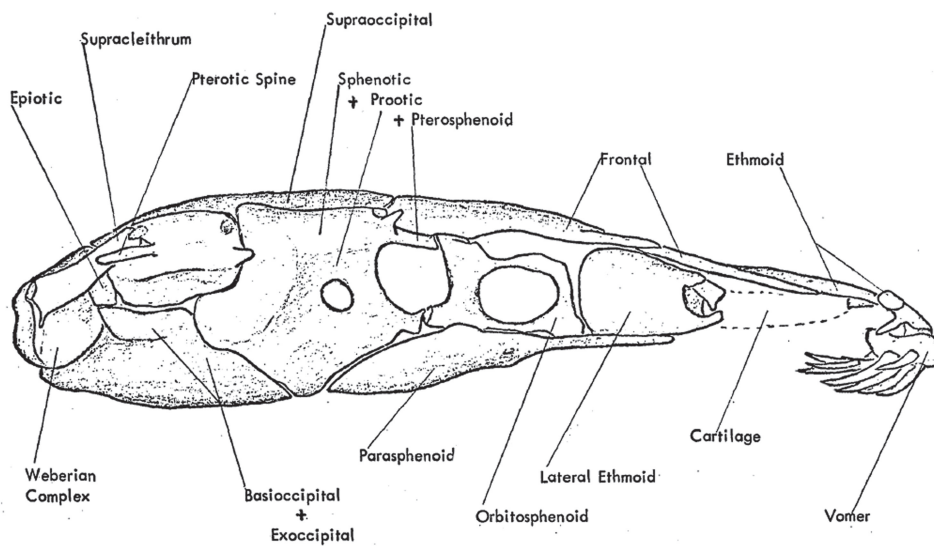

Fig. 12. Neurocranium and associated structures of *Pygidianops eigenmanni* (CAS 11121), dorsal view, 40x magnification,
Fig. 13. Neurocranium and associated structures of *Pygidianops eigenmanni* (CAS 11121), ventral view, 40x magnification,
all premaxillary teeth present are shown.

Fig. 14. Neurocranium and Weberian apparatus of *Vandellia cirrhosa* (AMNH 20497), dorsal view, l5x magnification, vomer not shown. **Fig. 15.** Neurocranium and Weberian apparatus of *Vandellia* sp. (AMNH uncatalogued), ventral view, 20x magnification. **Fig. 16.** Neurocraniurn and Weberian apparatus of *Vandellia* sp. (AMNH uncatalogued), lateral view, 20x rnagnification.

This spine and lock has apparently been independently lost or reduced in several groups (Trichomycteridae, *Nematogenys*, Helogeneidae, Astroblepidae, Cetopsidae). In these groups the spine is weakly developed and has little or no articulation with the cleithrum. In all of these cases, however, some spine-like modifications of the first pectoral ray have been retained (*e.g.*, Astroblepidae and *Helogenes*-lepidotrichia united proximally, unbranched; Cetopsidae-lepidotrichia united and proximal half unsegmented). The lack of a pungent spine and locking device can thus be considered an advanced character wherever it occurs in siluriforms.

Trichomycterids have carried this trend further than any other catfishes. The first ray articulates only with the scapula-coracoid (as in cetopsids and *Helogenes*), its lepidotrichs are united only at the base, are segmented but unbranched, and retain only very much reduced processes for muscle attachment. These features can be considered evidence that a pectoral spine and lock of the typical siluriform type was once present in the ancestry of trichomycterids. This can also be considered indirect evidence that the ancestry of trichomycterids included species in which the coracoids met in the midline and the cleithra had strong, broad contact. This is because of the probable need for a reinforced pectoral girdle supporting the spine, which may serve in defense to resist crushing forces (Alexander, 1965).

In *Nematogenys* there is no lock and only a minor articulation of the spine with the cleithrum, but the spine is fairly well developed, more so than any of the other groups with a reduced spine and lock. The lepidotrichs are fused and bear spine-like processes (barbs), but the distal half of the spine is segmented and poorly ossified. The proximal end of the spine has well developed processes for articulation and muscle attachment (fig. 82).

12) Scapulo-coracoids very small, not meeting in the midline (figs. 71-81).

It is probable that the primitive condition for siluriforms is to have the cleithra and coracoids meeting in the ventral midline, with the coracoids forming the abductor bridge (Alexander, 1965; and see pp. 54-55). This condition is present in *Diplomystes*, and most other catfish groups have developed in addition, a horizontal lamina of the coracoid that forms an interdigitating suture with its fellow in the midline. This strengthening of the shoulder girdle may be functionally associated with the development of a pectoral spine and locking mechanism (see below and Alexander, 1965). In many other ostariophysans the cleithra and coracoids meet in the midline (Weitzman, 1962; Roberts, 1969). Alexander (1965) refers to the ventro-medial portion of the coracoids that meet in the midline as the hypocoracoids.

In trichomycterids the cleithra meet only in a narrow junction at their antero-medial ends. The coracoids do not meet at all. The scapulo-coracoid of trichomycterids is confined to a more dorsal position, postero-lateral to the cleithrum. In *Trichomycterus* it has a small ventral extension

that appears to represent the hypocoracoid portion, but it does not even approach the ventral midline. The lack of a median juncture between the coracoids also occurs in the Hypophthalmidae, Siluridae, some Schilbeidae (see Regan, 1911; but see Tilak, 1963), Helogeneidae, Cetopsidae, Astroblepidae, and *Nematogenys*.

Even if the lack of a coracoid juncture is a primitive rather than an advanced condition for siluriforms, the extremely reduced scapulo-coracoid of trichomycterids, smaller by far than in other ostariophysans, is probably an advanced siluriform character.

In *Nematogenys* the coracoids also lack a median juncture, but they extend much further ventro-medially, on the postero-ventral surface of the cleithrum, than in any trichomycterid. The condition in *Nematogenys* (fig. 74) is intermediate between that of typical catfishes (*e.g.*, *Diplomystes*, cf., figs. 75, 77, 780 and trichomycterids, and in this character *Nematogenys* is closer to trichomycterids than are any other catfishes.

These 12 advanced siluriform characters are considered evidence that the genera here included in the Trichomycteridae form a monophyletic group, not including *Nematogenys*, *Phreatobius* or cetopsids.
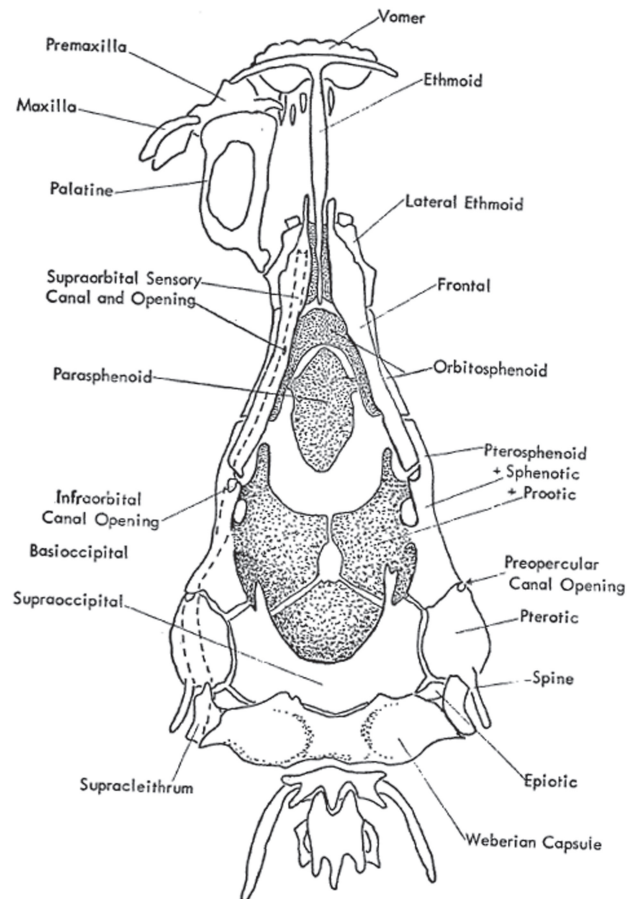

Fig. 17. Neurocranium and associated structures of *Branchioica bertoni* (SMF 8905), dorsal view, 20x magnification.

RELATIONSHIPS OF THE TRICHOMYCTERIDAE

Traditionally trichomycterids have been considered members of the order Siluriformes. They are found here to have all of the characters listed below which Regan (1911) and others consider diagnostic of catfishes, and advanced for the Ostariophysi.

In the search for the sister group of the Trichomycteridae attention was therefore concentrated upon other siluriforms, although the possibility of trichomycterids being related to Cypriniformes was also considered.

Definition of the Siluriformes

The following is a list of the characters that define siluriforms. They are all advanced characters for the Ostariophysi, and can be considered primitive for Siluriformes (*i.e.*, present in the common ancestor of all catfishes). Unless otherwise noted, these characters were designated by Regan (1911) as defining siluriform ostariophysans.

1) Symplectic bone absent;
2) Intermuscular bones absent;
3) Subopercular bone absent;

4) Separate parietal bones absent in adult (see also Bamford, 1950);
5) Cycloid scales absent;
6) Dermosphenotic and autosphenotic co-ossified (Lundberg, pers. com. and pers. obs.);
7) Infrapharyngobranchials 3 and 4 support the single pair of upper pharyngeal tooth plates (Nelson, 1969);
8) Parhypural and hypurals 1 and 2 co-ossified with PUl+Ul (Lundberg and Baskin, 1969);
9) Number of caudal rays in lower lobe equal or greater than number in upper lobe (Lundberg and Baskin, 1969);
10) Parapophyses ankylosed with centra;
11) Pelvic radials absent (Lundberg, pers. com. and pers. obs.);
12) Basihyal absent (pers. obs.);
13) Supraorbital bone absent (pers. obs.);
14) A maxillary barbel operated by maxillary and palatine bones (see Eaton, 1948 for description);
15) Scapula, coracoid and mesocoracoid (when present) forma single bone, the scapulo-coracoid;
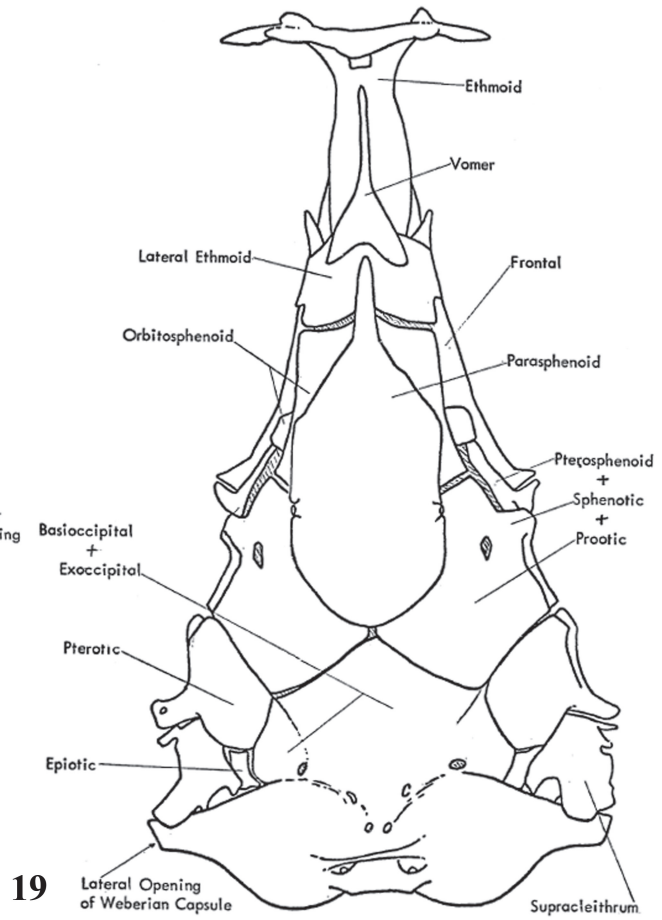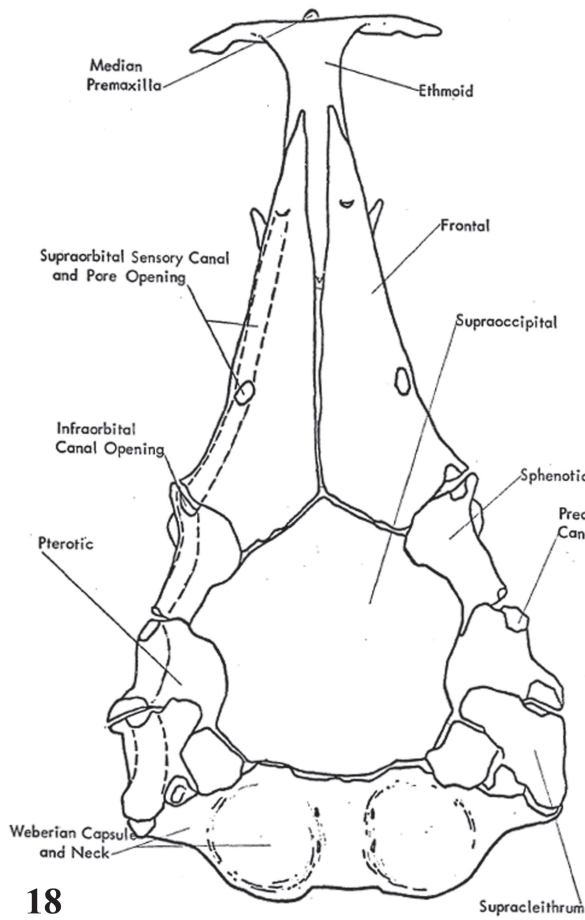16) Lateral cutaneous area present, a thin part of the body wall just lateral to the swimbladder (Alexander, 1964);

Fig. 18. Neurocranium and Weberian apparatus of *Ochmacanthus reinhardti* (AMNH uncatalogued), dorsal view, 19x magnification. **Fig. 19.** Neurocranium and Weberian apparatus of *Ochmacanthus reinhardti* (AMNH uncatalogued), ventral viev, 19x magnification.

17) Vertebrae #2, 3, and 4 or more fused to form the complex vertebra of the Weberian apparatus;

18) Parapophyses placed high on the anterior vertebrae (Alexander, 1964);

19) Parapophyses of complex vertebra are those of the 4th vertebra, and form a broad lamina of bone over the swimbladder;

20) Swimbladder with anterior section only, partially divided by a septum and grooved (or constricted) dorsally around complex vertebra (Alexander, 1964).

All of these characters are specializations found probably in all siluriforms, and may be hypothesized to be present in the common ancestor of all catfishes. A few are found also in some cypriniforms, but most of these are characters which are part of trends in teleosts generally, such as ankylosis of the parapophyses with the centra and the lack of intermuscular bones and cycloid scales.

Among catfishes, one family, the Diplomystidae, stands out as having more primitive siluriform characters than any other catfish (Lundberg and Baskin, 1969). All other catfishes can thus be considered a monophyletic group, with *Diplomystes* as its sister group.

This hypothesis of relationships leads to the inference that the common ancestor of all catfishes had, in addition to the characters listed above, the following features. All of these characters can be considered primitive for the Siluriformes because they are found in *Diplomystes* and in almost all of the other catfish families.

The references cited after each character give a description and the distribution of the character among siluriforms.

1) The first pectoral ray modified into a spine with a distinctive friction locking mechanism (for description, Alexander, 1965);

2) Mesocoracoid present (Regan, 1911);

3) Cleithra and hypocoracoids meet in the ventral midline and hypocoracoids form an interdigitating symphasis (Tilak, 1963; Starks, 1930);

4) First and second dorsal fin rays modified into a spine and unique locking device (Alexander, 1965);

5) Pterygiophores supporting dorsal fin fit between bifurcate neural spines of anterior vertebrae (Alexander, 1965; Lamoral and Millard, 1967);

6) Parapophyses of complex vertebra are those of the 4th vertebra only, and form a broad, horizontal sheet of bone over the anterior end of the swimbladder on each side (Alexander, 1965; Chranilov, 1929; Regan, 1911);

7) Body naked, without true scales or bony plates;
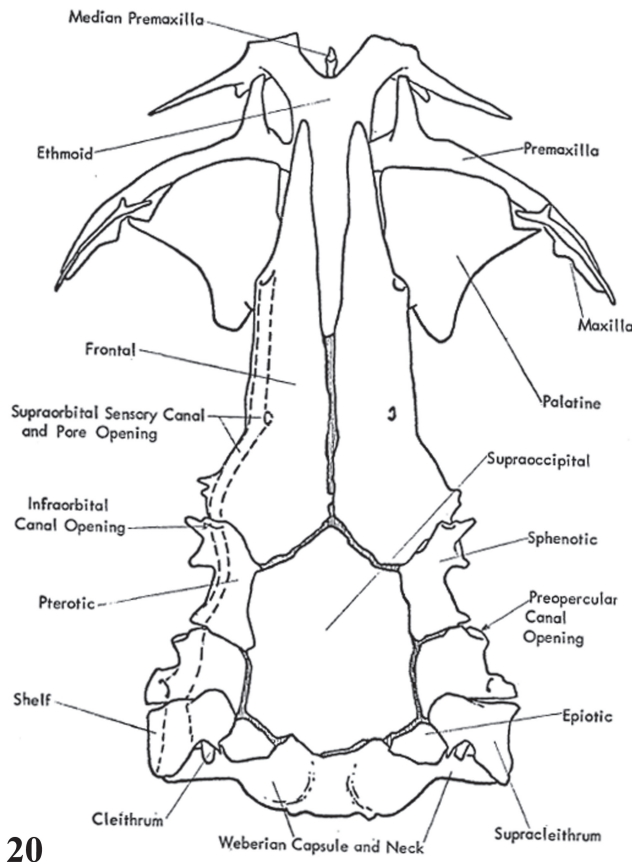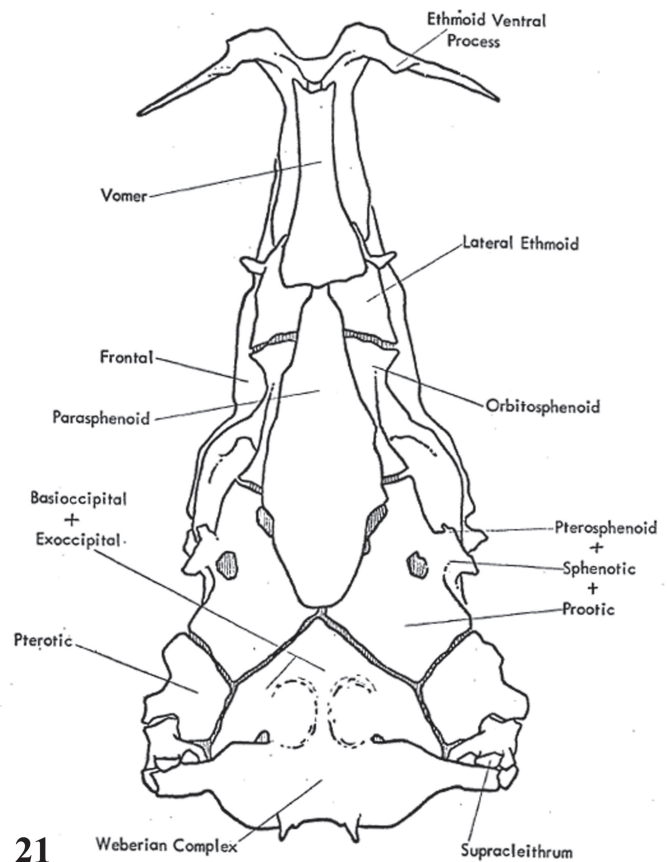
Fig. 20. Neurocranium and associated structures of *Haemomaster venezuelae* (AMNH uncatalogued), dorsal view, l7x magnification. **Fig. 21.** Neurocranium and Weberian apparatus of *Haemomaster venezuelae* (AMNH uncatalogued), ventral view, l7x magnification.

In most cases in which a catfish has a different condition of one or more of these seven characters, there is evidence that the condition is a modification of the primitive condition. This evidence is based on data from the characters themselves. For example, in those catfishes which lack the pectoral spine and locking mechanism the first pectoral ray and the pectoral girdle are modified in such a way as to indicate that this is a secondary reduction of the spine and locking device (see pp. 46-50). The secondary loss of the pectoral spine and lock can be considered advanced characters within the Siluriformes.

The alternative interpretation is that the condition found in these groups represents an incipient stage in the evolution of the spine and lock, rather than a reduction. It has been the consensus, however, among those who have studied catfishes, that the closest relatives of groups which lack these modifications associated with the pectoral and dorsal fins are groups which have them. This alternative interpretation is therefore the less acceptable one because it requires the spine and lock to have been independently evolved several times within the Siluriformes.

The Advanced Characters of the Trichomycteridae and Their Relatives.

The advanced characters given below as primary evidence of trichomycterid relationships are characters which can be considered advanced within the Siluriformes based upon the following assumptions:
1) the Siluriformes form a monophyletic group;
2) the sister group of the Siluriformes is another group of ostariophysans, either the characoids, the minnows or 'both.

It is not necessary to assume that the Diplomystidae are the sister group of all other catfishes in order to produce an argument that the characters given below are advanced. The Diplomystidae has, however, the proposed primitive condition of these characters. Therefore, an assumption that the Diplomystidae are the sister group of all other siluriforms makes it more probable that these characters are advanced.

Integumentary Teeth

Among catfishes teeth on the outside surface of the body, not associated with the jaws or any other oro-pharyngeal structures, are found only in trichomycterids, callichthyids, loricariids, astroblepids, and in Loricarioid sp. and *Nematogenys inermis*. These teeth have been referred to by various workers as dermal teeth, denticulations, prickels,
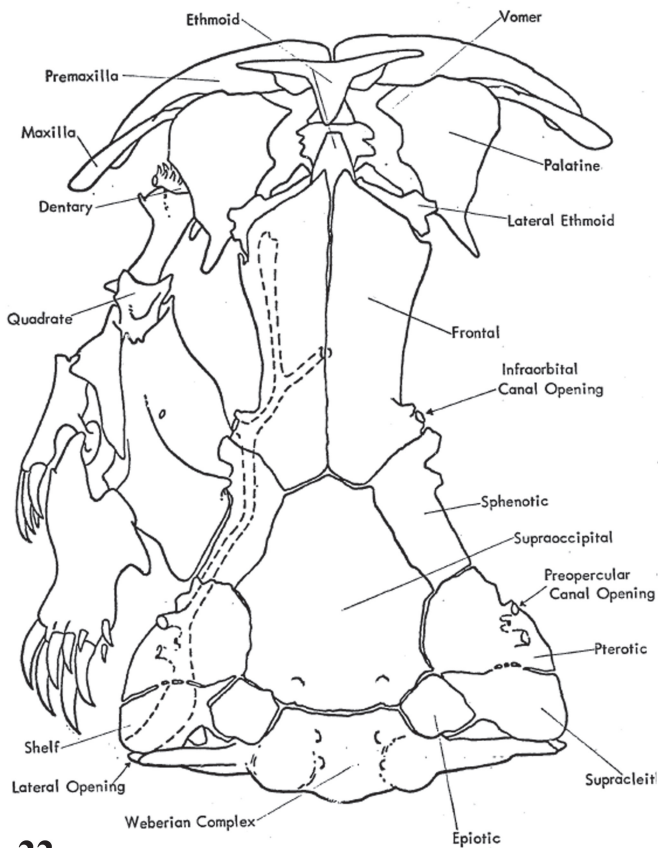
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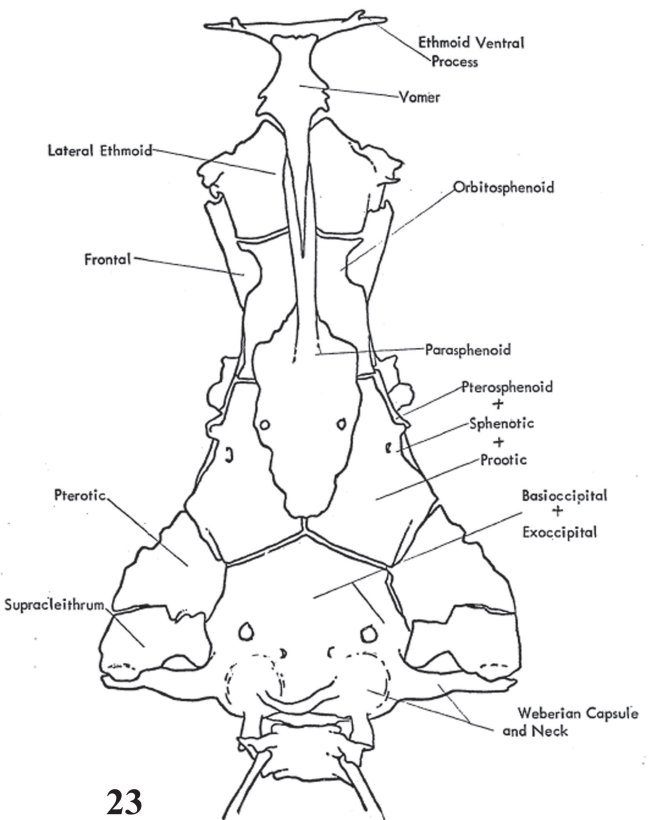
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Fig. 22. Neurocranium and associated structures of *Pareiodon microps* (BM(NH) 1926-10-27:270-273), dorsal view, 8x magnification. **Fig. 23.** Neurocranium and Weberian apparatus of *Pareiodon microps* (BM(NH) 1926-10-27:270-273), ventral view, 8x magnification.

barbs, spines and denticles. The term "integumentary teeth" is used here at the suggestion of Dr. Paul F.A. Maderson, who pointed out (pers. com.) that this term expresses the fact that these teeth are in the skin on the external surface of the body, rather than oro-branchial teeth associated with the jaws, palate and other visceral arches. The term "integumentary teeth" also avoids the implication in the term "dermal teeth" that these structures are of dermal rather than ectodermal origin.

Integumentary teeth of some loricariids, callichthyids and *Nematogenys* have been studied histologically by Peyer (1922) and Bhatti (1938) and found to be the same as jaw teeth of these and other actinopterygians, i.e., calcified conical structures with a pulp cavity surrounded by dentine capped with enamel, and attached to a bony base by connective tissue (Hans Peter Schultze, pers. com.; Kerr, 1960;). The integumentary teeth of astroblepids, trichomycterids and Loricarioid sp. have not been investigated in detail histologically, but my preliminary histology and gross observations of alizarin stained specimens indicate that these are the same as the integumentary teeth of other catfishes. The integumentary teeth of these catfishes have

been confused with the hook-like or "tooth-like" bony processes found often on the pectoral and dorsal spines of catfishes, which are outgrowths from each bony segment of the modified fin rays (Reed, 1924). The hooks on the sides of the body of many doradid catfishes, which have also been confused with teeth, are bony extensions of the plates of bone in the skin associated with the lateral line canal (Bhatti, 1938).

The question of the origin of integumentary teeth remains open. They may have reached the outside surface of the body by spreading of oro-branchial teeth onto the external surface. (Some characoids, the Xenurobryconini, have jaw teeth extending distinctly outside the mouth [Myers and Böhlke, 1956].) Integumentary teeth may also have developed as an independent expression of the potential of dermis, epidermis, and ectomesenchyme to interact and produce teeth, or tooth-like structures (i.e., enamel and dentine over lying bone). The differences between the teeth of actinopterygians and tetrapods, described by Kerr (1960), and the various kinds of enamel and dentine described in early vertebrates by Orvig (1951, 1957, 1967), could be an indication that at least
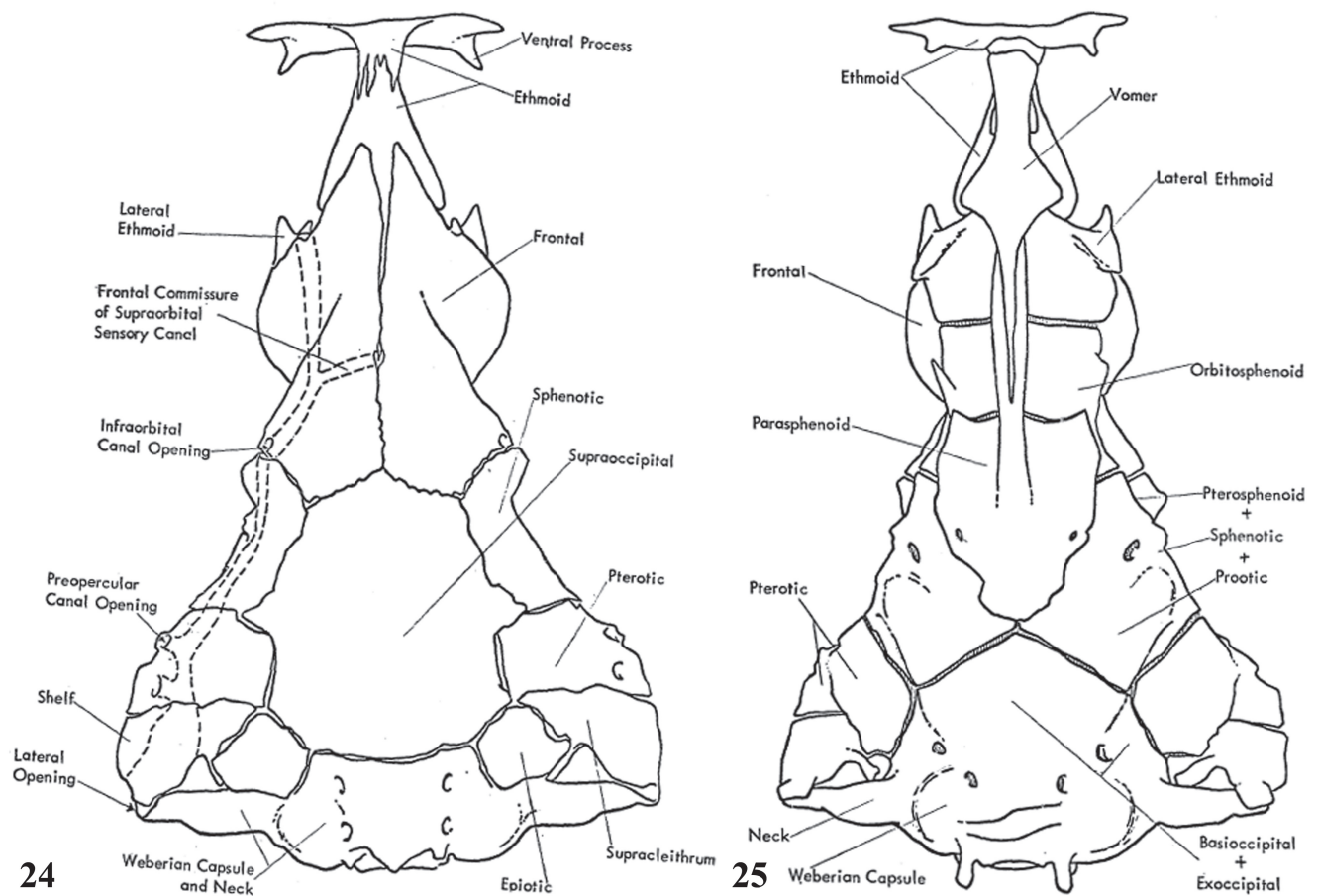

Fig. 24. Neurocranium and Weberian apparatus of *Pseudostegophilus nemurus* (AMNH uncatalogued), dorsal view, l2x magnification. **Fig. 25.** Neurocranium and Weberian apparatus of *Pseudostegophilus nemurus* (AMNH uncatalogued), ventral view, 12x magnification.

some teeth have evolved independently in at least some of these groups. The investigation of such a potential for tooth development, as yet undefined, is beyond the scope of the present work. The subject of such tissue interactions has been reviewed by Moss (1968), Orvig (1967), and Jarvik (1959). Siluriforms would make excellent experimental animals for the investigation of the potential for tooth development, which will be the objective of future studies.

That some such potential exists in vertebrates for the production of integumentary teeth, or tooth-like structures, is indicated by the occurrence of these structures in a wide variety of vertebrates (see Orvig, 1951, 1957). The presence of integumentary teeth or tooth-like structures in most agnathan groups and some gnathostome groups makes it possible to hypothesize that common ancestors of gnathostomes and agnathans (i.e., the Vertebrata) had enamel, dentine and bone on the external surface of the body. The distribution of such tissues among teleostomes, however, indicates that they were not actually present on the external surface of the body in the common ancestors of either the Teleostei, the Euteleostei[4] the Otophysi[5]

the Ostariophysi, or the Siluriformes. This leads to the hypothesis that the common ancestor of each of these groups retained same potential, as yet undefined, for the development of integumentary teeth, and that this potential has become expressed independently in those teleosts which actually have them. The actual presence of integumentary teeth can thus be considered an advanced character for teleosts and for siluriforms, and may indicate that the catfishes with these teeth form a monophyletic group.

The distribution of integumentary teeth in these catfishes is as follows: Trichomycteridae - posterior-dorsal corner of opercle, posterior and ventral edge of interopercle; *Nematogenys* - pectoral spine; Callichthyidae and Loricariidae - all fin rays including spine in adipose fin; on bony plates covering virtually the entire surface of the body (and head in loricariids), on external surface of skull bones, including opercular bones; Astroblepidae all fin rays, including spine in adipose; Loricarioid sp. - anterior-most rays (or spines) of all fins, dermal bony plates on body and head, some skull bones, including opercular bones, and posterior process of coracoid.
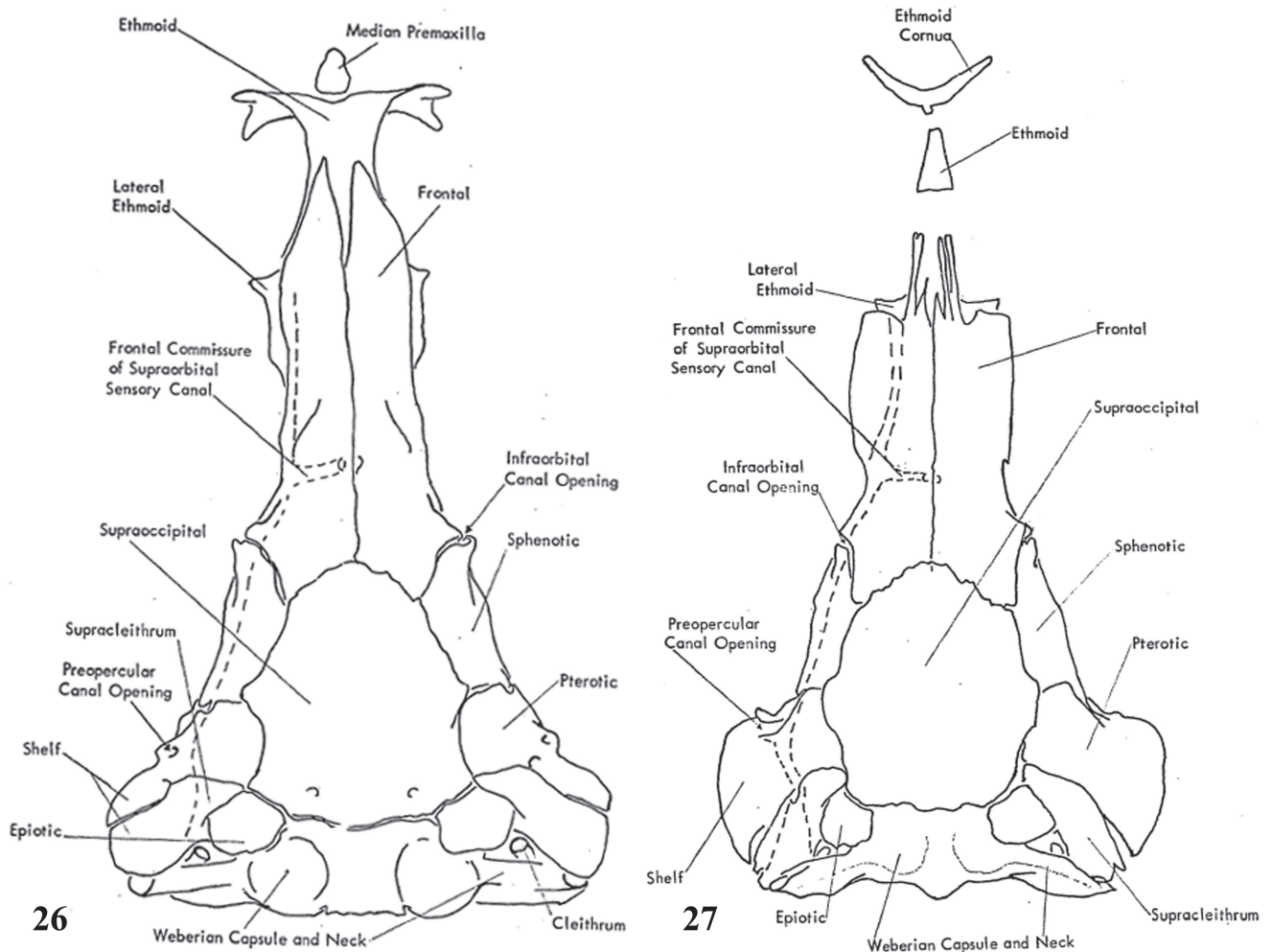

Fig. 26. Neurocranium and Weberian apparatus of *Stegophi1us intermedius* (USNM-IU 15499), dorsal view, 9x magnification.
Fig. 27. Neurocranium and Weberian apparatus of *Apomatoceros alleni* (ANSP 109804), dorsal view, 7x magnification.

In most callichthyids, loricariids, astroblepids and in Loricarioid sp. and *Nematogenys* the integumentary teeth are about the same size and shape *(i.e.,* small, pointed and conical) wherever they occur on the animal (Notable exceptions are the large recurved teeth on the rostral plate of Loricarioid sp. and the large hook-like teeth anterior to the opercular bone of *Ancistrus*). Trichomycterids often have some of the integumentary teeth larger than others, and recurved.

Only trichomycterids have integumentary teeth found only on the postero-lateral edge of the opercular and interopercular bones. They may be numerous, as in *Trichomycterus* (fig. 41) and most members of the family, or small and very few, as in *Sarcoglanis* and *Malacoglanis* (fig.42). They occur on these bones as a distinct patch of closely set teeth, and those on the opercular bone are always found at the postero-dorsal corner, at the end of a posterior extension of the bone. Integumentary teeth are lacking in *Glanapteryx*, *Pygidianops* and *Typhlobelus*, monotypic genera known only from a very few specimens. In all catfishes with integumentary teeth, except the trichomycterids, there are pointed, conical teeth on the pectoral spine. Therefore it is possible to hypothesize that this is the primitive condition for these groups of catfishes, and that teeth on the opercular bones and elsewhere is a more advanced condition. The lack of teeth on the pectoral spine would therefore be an advanced character for catfishes with integumentary teeth, an advanced character which is evidence that trichomycterids form a monophyletic group. This conclusion is based however, on the previous conclusion (*i.e.*, that catfishes with integumentary teeth form a monophyletic group), and thus cannot be considered primary evidence for relating trichomycterids among themselves.

The presence of integumentary teeth on the opercular bones in trichomycterids, Loricarioid sp., callichthyids and loricariids indicates that this was the condition in the common ancestor of these fishes. It is thus possible to hypothesize that the teeth on the opercular bones were independently lost in astroblepids, which are the closest relatives of loricariids (see discussion of relationships p.154), and in *Glanapteryx*, *Pygidianops* and *Typhlobelus* (see discussion p.162).

Weberian Apparatus

Other advanced features of the Trichomycteridae bearing upon their relationships to other catfish groups concern the parts of the Weberian apparatus. This structural complex is the subject of a recent comparative study by Chardon (1968), in which he gives detailed and coordinate anatomical data (most osteological) for almost every catfish family. Some inconsistencies unfortunately make the use of certain of his data and conclusions difficult. Data given in one part of his work is sometimes ignored when not consistent with
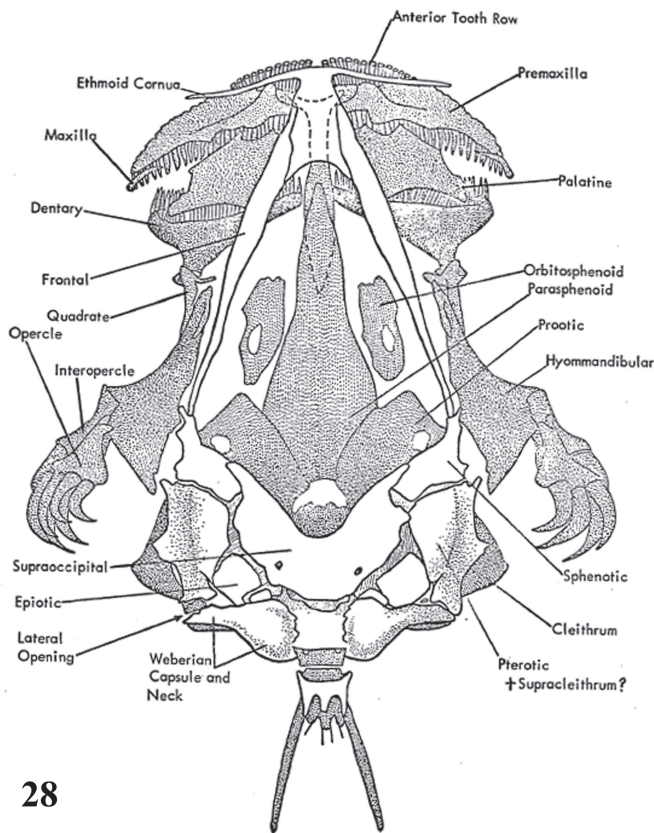
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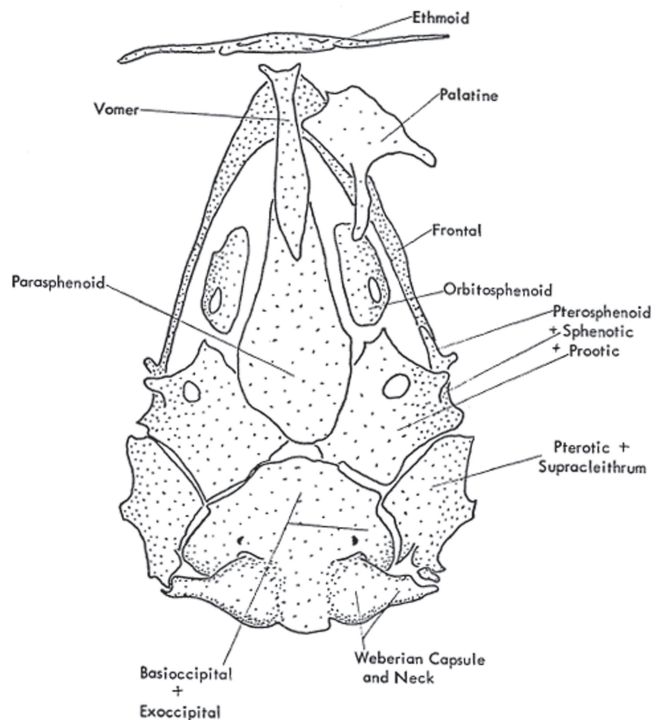
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Fig. 28. Syncranium of *Tridensimilis venezue1ae* (USNM 121291), dorsal view, 25x magnification. **Fig. 29.** Neurocranium and associated structures of *Tridensimilis venezuelae* (USNM 121291), ventral view, 25x magnification.

the data or conclusions in a later part. For example, the Chacidae are said to have the anterior point of the sacculus reduced to a tubercule as in the Aspredinidae (Chardon, 1968, pp. 156, 175 and cf. figs.149, 163), but where this same condition is used as evidence relating aspredinids to groups without the anterior point (i.e., trichomycterids, loricariids, etc. pp. 210, 235) the condition in chacids is ignored. Also, some errors, and inconsistencies between different figures of the same animals, lead one to use the data with care. For example, in two figures of *Trichomycterus taenia* (figs. 164-165) one correctly shows a clear suture between the neural arch of the complex vertebra and the supraoccipital, while the other shows no such suture. The text says (p. 179) that

the fused neural arches are joined in front to the supra- and exoccipitals, and form a prolongation of the occipital crest. The degree to which the Weberian complex is joined to the skull is used later by Chardon (p. 210) as evidence of relationship. Another error is Chardon's claim of finding well developed parietal bones in *Diplomystes*. These are not known to occur consistently in any adult siluriform (see Bamford, 1948; Alexander, 1965, p. 124), and I could not find a hint of parietals in any of the five specimens of *Diplomystes papillosus* I have examined. A comparison of Chardon's two figures (15 and 16, p. 29) of the skull roof of the same *Diplomystes* specimen show inconsistencies in the shapes and positions of bones.
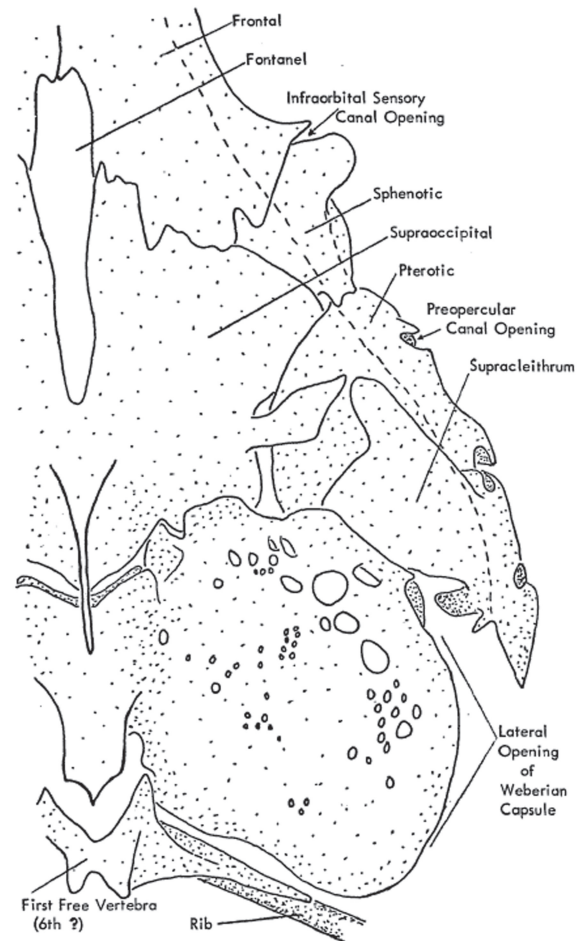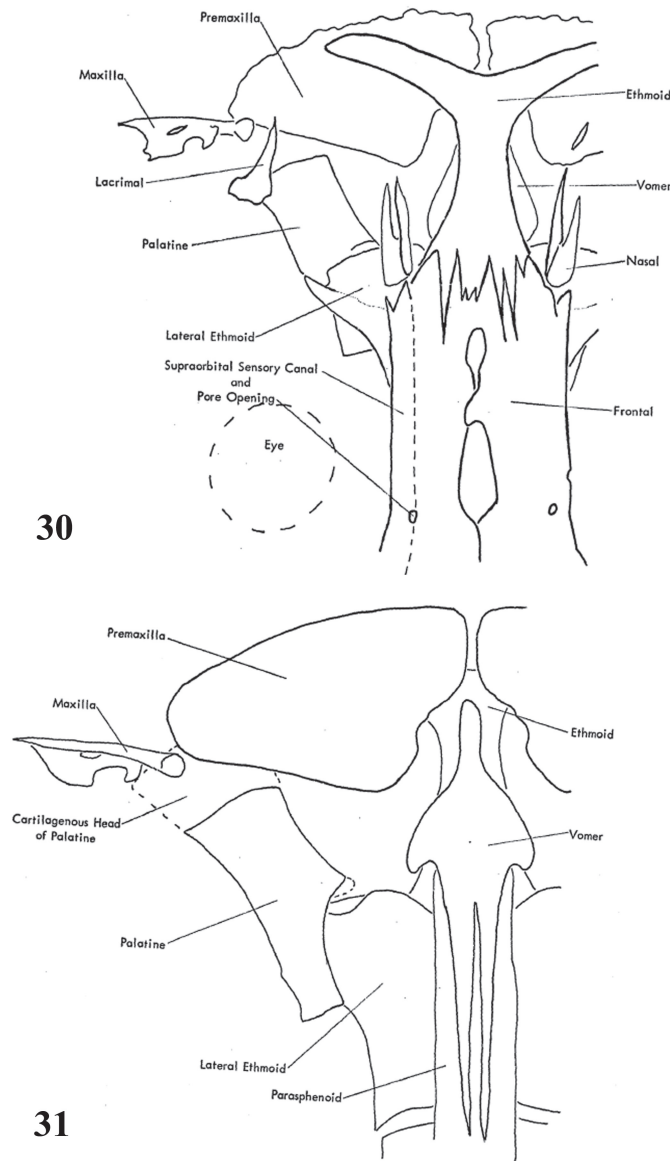

Fig. 30. Anterior portion of skull of *Nematogenys inermis* (MCZ 9839) 7x magnification, dorsal view. **Fig. 31.** Anterior portion of skull of *Nematogenys inermis* (MCZ 9839), ventral view, 7x magnification, premaxillary teeth not shown. **Fig. 32.** Weberian apparatus and posterior portion of neurocraniurn of *Nernatogenys inerrnis* (MCZ 9839), dorsal view, 9x rnagnification, not all the holes in the Weberian apparatus are shown.

Within the Siluriformes, and to some extent in other ostariophysans, there has been a trend toward the consolidation and reduction of the Weberian apparatus, and reduction of the swimbladder to a pair of separate lateral vesicle enclosed in bony capsules. This has been described in detail, most recently by Chardon (1968) and Alexander (1964, and 1965). The Trichomycteridae have this trend highly developed, as indicated by the following advanced characters of their Weberian apparatus and associated structures;

1) No ductus pneumaticus (Chardon, 1968);

2) Swimbladder divided into a pair of completely separate lateral vesicles;

3) Parapophyses of the 4th vertebra (and perhaps 5th, Chardon, 1968: Alexander, 1964) form a complete capsule around each swimbladder vesicle, only open laterally;

4) Lateral opening of capsule constricted;

5) Claustrum and intercalarium lacking, tripus lacks transformator process;

6) First vertebra incorporated into complex vertebra;

7) Fifth vertebra fused with complex vertebra;

8) Superficial ossification on ventral surface of complex vertebra (Alexander, 1964) extends over joint with basioccipital;

9) Loss (presumably) of the ventral process of the exoccipital, which in other ostariophysans separates the sinus impar from the foramen magnum (Chardon, 1968).

All of these features were recorded by Chardon (1968) in *Trichomycterus taenia*. I have found numbers 3, 4, 6, 7 and 8 in gross dissection in all trichomycterid groups examined. However, in order to determine some characters with confidence, such as the composition of the complex vertebra and capsule, and the lack of a connection between the swimbladder vesicles, additional study of serial sections and developmental series is necessary. (For example, Chardon finds no connection between the swimbladder vesicles in loricariids including *Plecostomus punctatus*, but Alexander [1964] finds a tiny duct between them in *Plecostomus plecostomus* by using serial sections.) Numbers one, five and nine have been checked and confirmed only in *Trichomycterus*. Number two has not yet been adequately checked by me in any trichomycterid.

Each of these nine characters is found fully or almost fully developed in at least some other catfish families, and numbers 1, 2, 5, 6, and 7 are found in several groups from both the New and Old World. Since these characters all involve the loss or
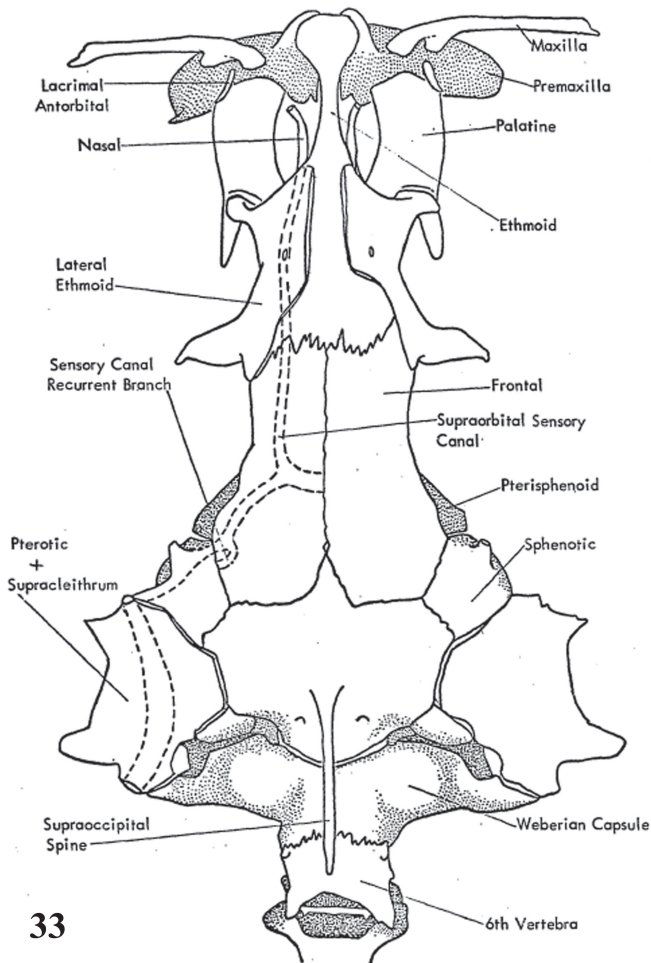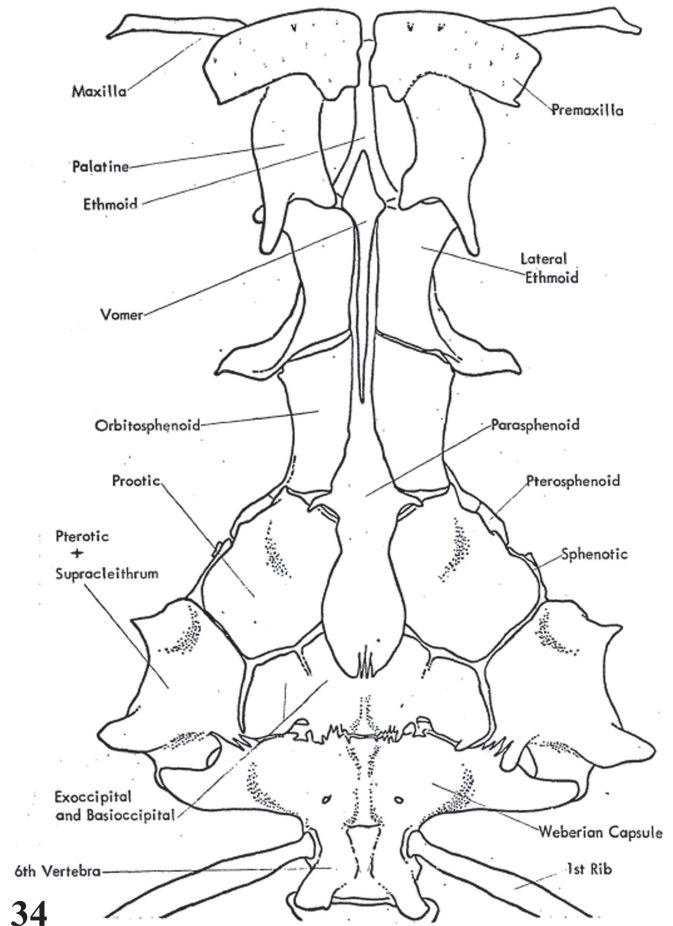
Fig. 33. Neurocranium and associated structures of *Astroblepus longifilis* (AHNH 11582), dorsal view 10x rnagnification.
Fig. 34. Neurocranium and associated structures of *Astroblepus longifilis* (AMNH 11582), ventral view lOx magnification.

reduction of structures there is little or no direct evidence available (i.e., from the structures themselves) indicating that they have evolved in the same way, or independently. Alexander (1964) using serial sectioning finds that the swimbladder capsule of the Clariidae is formed by the extension of a ventral process from the complex vertebra as well as from parapophyses of the 4th and 5th vertebrae. (Chardon believes that the 5th vertebra is not involved.) He finds that in *Plecostomus* (a loricariid) and *Hoplosternum* (a callichthyid) the ventral process does not contribute to the formation of the capsule, which is formed only by parapophyses of the 4th vertebra. The composition of the capsule in these and other catfishes, especially the role of the 5th parapophyses, remains problematic, as Alexander points out *(see* also Chranilov, 1929). (The use of developmental series in conjunction with serial sections will probably help resolve this problem.) Alexander interprets the mode of capsule formation in *Clarias*, in which the capsule is incomplete in his material, as primitive relative to that of Plecostomus and *Hoplosternum*. In very large clariid specimens however, (skull length 400 mm.) the capsule is complete, although sutures are visible. In these specimens (in contrast with Plecostomus and *Hoplosternum*) the ventral process forms part of the capsule. This indicates that a complete capsule can form differently in different catfish groups.

In addition to the Trichomycteridae, the only other catfish groups with all nine of the advanced characters listed above (except perhaps number two, completely separate lateral swimbladder vesicles) are the Callichthyidae, Loricariidae and Astroblepidae. It is the consensus of virtually everyone who had studied siluriform family interrelationships, including myself (and see p. 75), that these three families form a monophyletic group, and that the Loricariidae

and Astroblepidae are sister groups. Not all of these nine advanced characters are found in all three of these families. Loricariids and callichthyids have wide lateral opening of the capsule, which is the primitive condition, found also in *Nematogenys*. Astroblepids have a small lateral opening, as in all trichomycterids. Astroblepids also share a further advanced condition, found only in some trichomycterids (the Vandelliinae-group, see p. 145). This is a neck-like constriction of the lateral portion of the swimbladder capsule, between the lateral opening and the more medial swimbladder vesicle. In loricariids the wide lateral opening of the capsule is covered by an expanded supracleithrum (the post-temporal of Alexander, 1964).

Another of the nine advanced characters, number eight, (superficial ossification extending over the joint with the basioccipital), is lacking in astroblepids but found in loricariids and callichthyids. It is thus possible to hypothesize that this character (number eight) and number four (constricted capsule openings) were independently evolved in trichomycterids, but that the remaining nine advanced characters (except perhaps number two) were present in the common ancestor of trichomycterids and a group consisting of the Astroblepidae, Loricariidae and Callichthyidae.
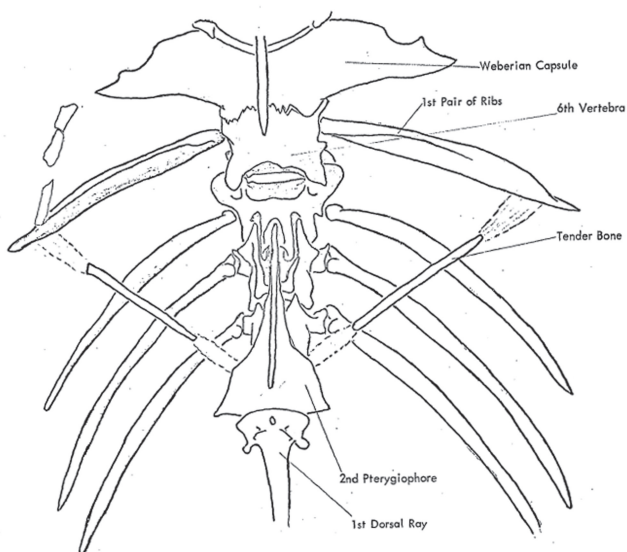

Fig. 35. Dorsal fin, anterior vertebrae and associated structures of *Astrob1epus longifi1us* (AMNH 11582), dorsal view, 12x magnification.
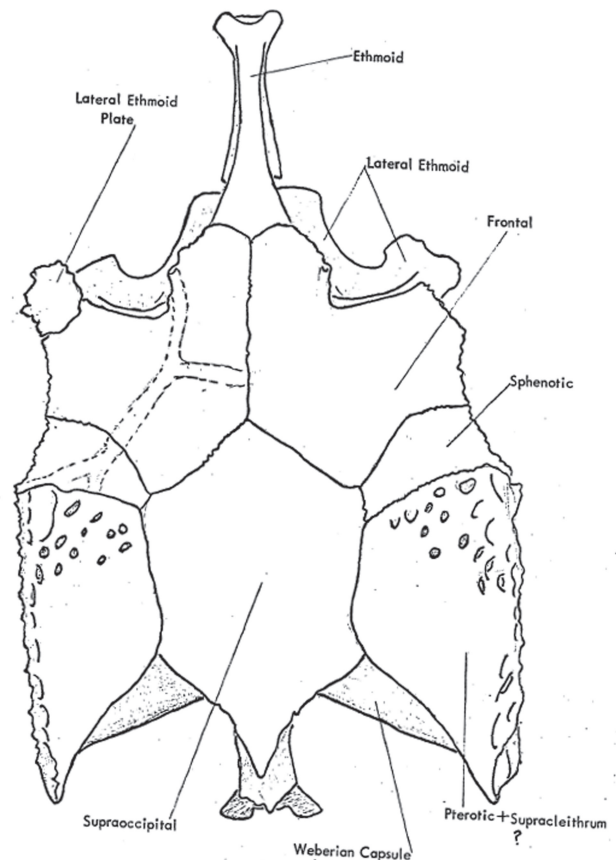

Fig. 36. Neurocranium and Weberian apparatus of *Otocinclus affinis* (AMNH 22310), dorsal view, 12x magnification, integurnentary teeth and right lateral ethrnoid plate rernoved.

Chardon (1968) points out that the monotypic Hypophthalmidae strongly resembles the Trichomycteridae, and his description indicates that *Hypophthalmus* lacks only characters four, seven, and nine (constricted capsule opening, fifth vertebra fused with the complex vertebra and loss of the ventral process of the exoccipital). My preliminary observations, however, do not agree with his. He places great emphasis on the supposed joining of the trichomycterid and hypophthalmid capsule with the cranium (i.e., epiotics and exoccipitals). In trichomycterids the anterior wall of the capsule abuts against these bones, but is not joined or fused with them, as his figure 167 shows. In *Hypophthalmus* the situation is much more complex than he represents *it*. The capsule itself appears to be surrounded almost completely by additional ossification, which is made up dorsally of what is probably a medial extension of the supracleithrum fused with the complex vertebra, and ventrally of lateral extensions of the complex vertebra and its superficial ossification. I agree with Chardon's conclusion in keeping this highly specialized filter-feeding catfish separate taxonomically until the significance of its peculiar anatomy (Wright, 1885) is better understood.

It is, as Chardon points out, difficult and often misleading to use as evidence of relationship characters which are parts of an overall trend that has apparently occurred independently more than once within the siluriforms. Nevertheless, the high degree of resemblance, in terms of advanced characters, between the Trichomycteridae and the Astroblepidae, and to a slightly lesser extent the Loricariidae and Callichthyidae, cannot be ignored. These characters, fortunately, represent apparent extremes of the consolidation trend described above, and can thus be used as evidence that these families form a monophyletic group.

Chardon (1968) concludes that this group also includes the Aspredinidae (=Bunocephalidae). On the basis of Chardon's description and my own observations, aspredinids have only character nine (loss of the ventral process of the exoccipital), and lack a claustrum (part of number five). The former condition is, according to Chardon, found among catfish only in these families. If *it* is indeed an advanced character, as is possible, it may be considered evidence of relationship. However, none of the other advanced characters listed by Chardon as evidence of the aspredinid relationship with these other four families (Trichomycteridae, Callichthyidae,
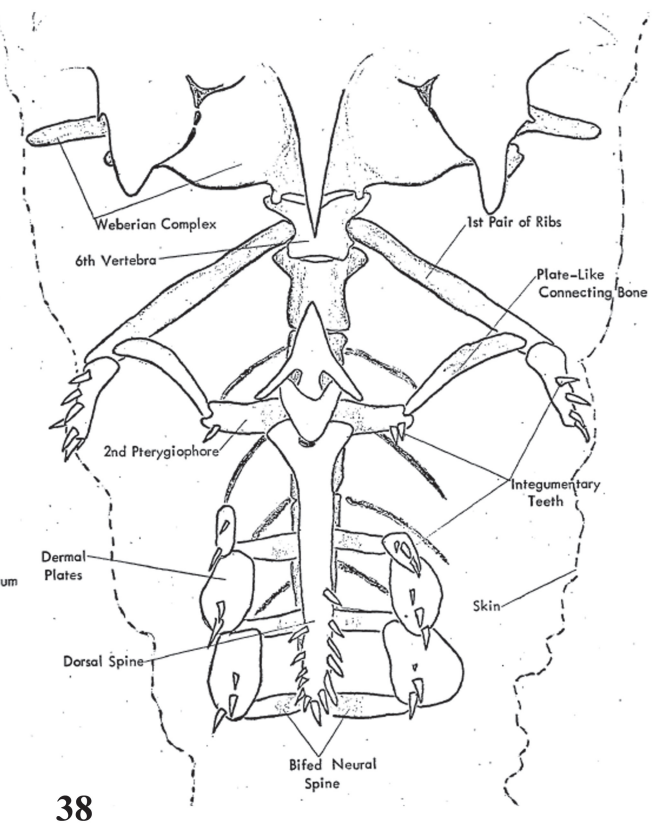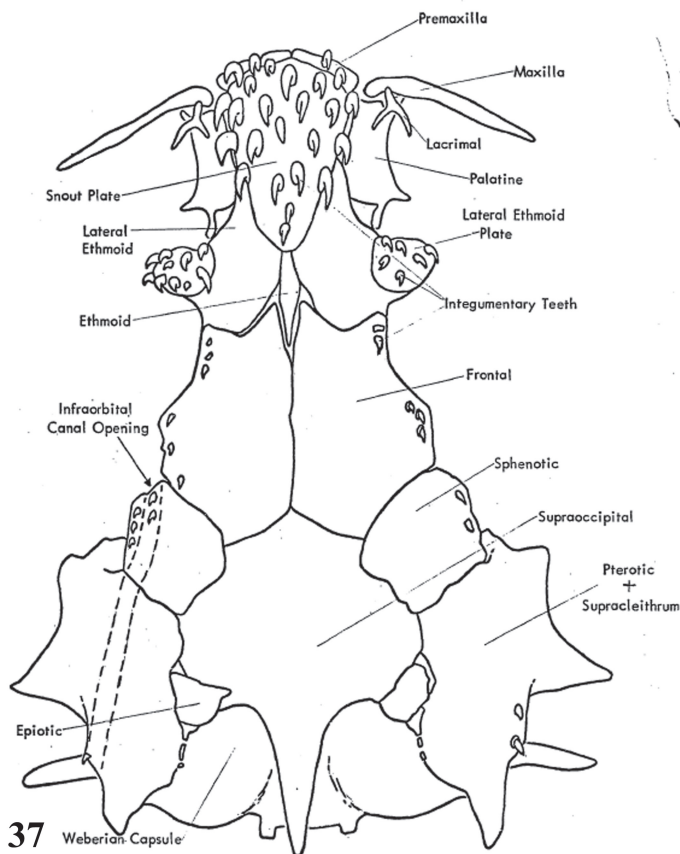

Fig. 37. Neurocranium and associated structures of Loricarioid sp. (UMMZ uncatalogued), dorsal view, 30x magnification.
Fig. 38. Dorsal fin, anterior vertebrae and associated structures of Loricarioid sp. (UMMZ uncatalogued), dorsal view, 30x magnification.

Loricariidae and Astroblepidae) are unique to this group. One character he lists, the presence of bony plates in the skin *(i.e.,* armor), is not found at all in aspredinids, although armor has been recorded erroneously in this group (Schultz, 1944; Myers, 1942).

The Weberian apparatus of *Nematogenys* (fig. 32) is more primitive than that of trichomycterids, astroblepids, loricariids and callichthyids with respect to the nine characters listed above. There is no separate first vertebra, both it and the fifth are probably incorporated into the complex vertebra, which is not fused with the cranium. The swimbladder capsule appears to be formed by the parapophyses of the 4th and perhaps the 5th vertebrae, and by lateral extensions from at least one pair of ventral processes from the complex vertebra. Its anterior wall is formed by the ventral arm of the supracleithrum and by the posterior surface of the cranium. There is a wide lateral opening. There is a complete set of Weberian ossicles and the tripus bears a transformator process. The sinus impar is separated from the foramen magnum. The swimbladder capsule resembles that of callichthyids and loricariids in having numerous fairly large holes in the walls. Trichomycterids, astroblepids and some other groups have what appear to be numerous very tiny holes, but this has not yet been investigated in detail. The participation of the cranium and supracleithrum in the anterior wall of the capsule, as in callichthyids and perhaps also loricariids, may also be an advanced condition relating *Nematogenys* to these groups. Further work is necessary, especially on the Weberian apparatus of *Nematogenys*, before such phylogenetic conclusions can be made with confidence.

Until the composition of the swimbladder capsule and complex vertebrae of trichomycterids is known in more detail, and comparable data is available for other groups, these characters may be considered as evidence of relationship among those catfishes that have them, even in only a partially developed state. The conception that these consolidation trends have occurred independently several times among catfishes is largely based upon the presence of these consolidated structures in families which have not been considered to be closely related, and in families that also contain species with little or no consolidation (*e.g.*, sisorids). The concept that some families with a consolidated Weberian apparatus are not
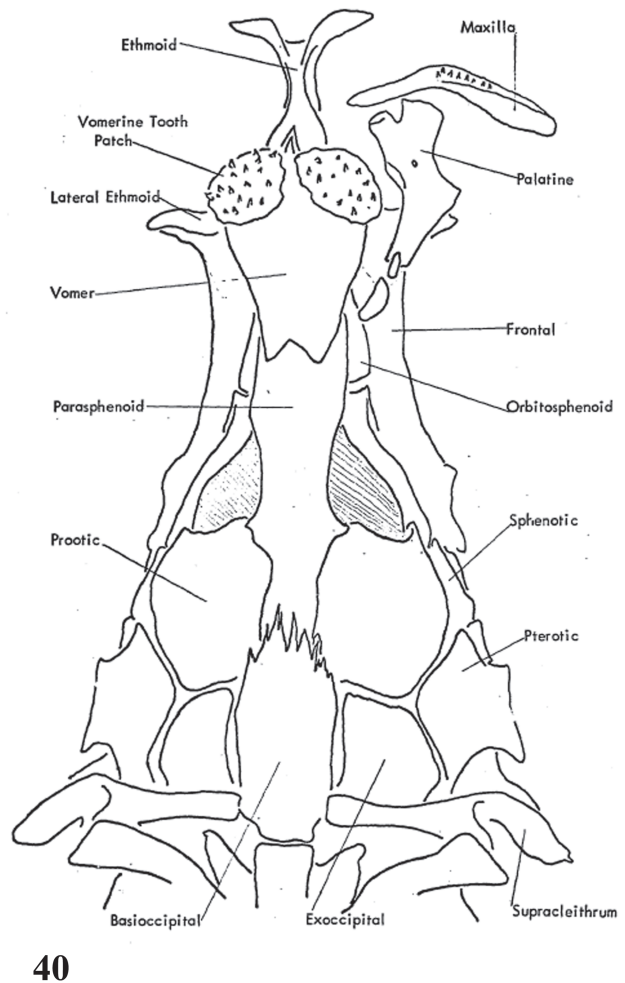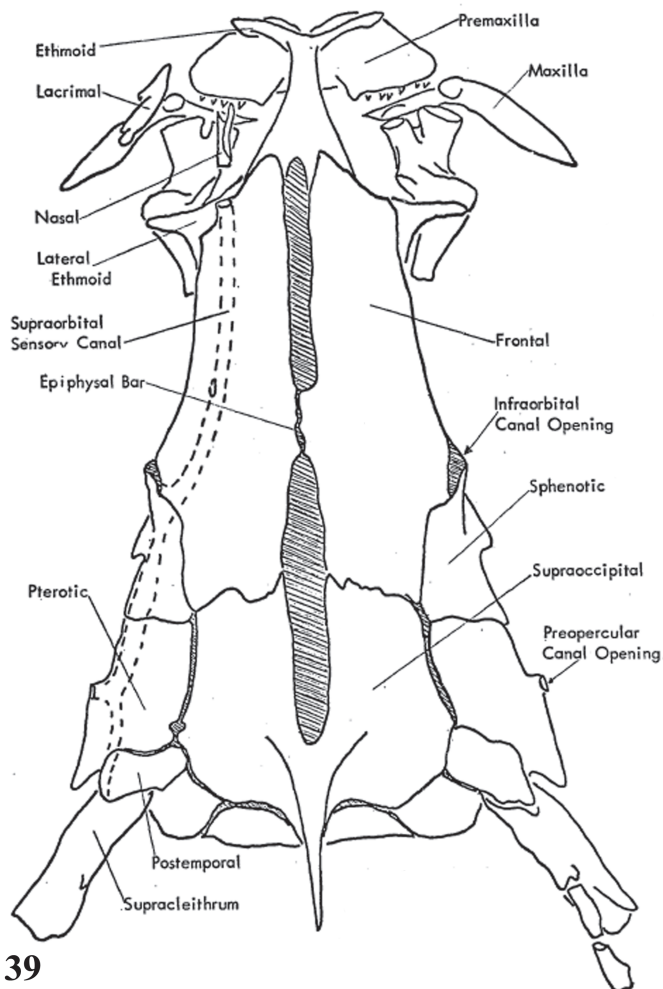

**Fig. 39.** Neurocranium and associated structures of *Diplomystes papillosus* (ANSP 84193), dorsal view, 7x magnification.
Fig. 40. Neurocraniurn and associated structures of *Diplornystes papillosus* (ANSP 84193), ventral view, 7x rnagnification.

closely related is at least partially based upon the occurrence of some in the Old World and others in the New World. There is very little good evidence on the comparative composition of the consolidated Weberian apparatus in various catfish families, and possible relationships between Old and New World families must be reconsidered.
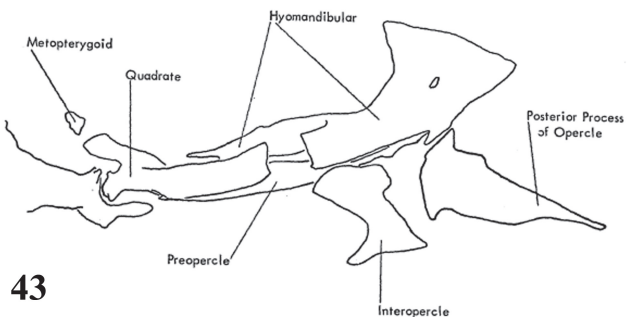
The advanced features described above from the Weberian apparatus and integumentary teeth indicate that the Trichomycteridae, Callichthyidae, Loricariidae, Astroblepidae, Loricarioid sp. and *Nematogenys* form a monophyletic group. Peyer (1922) also places these groups together, into a group
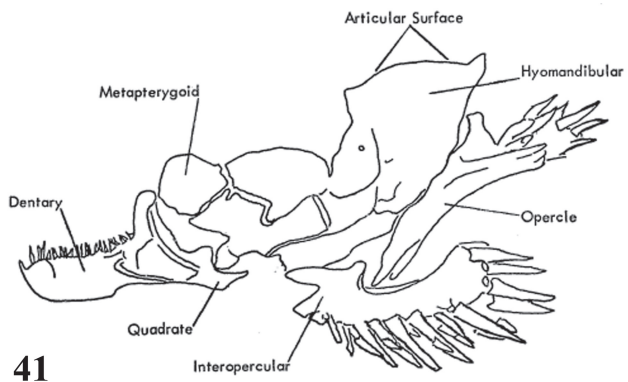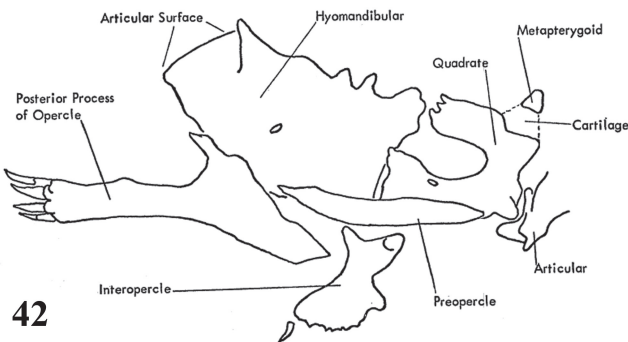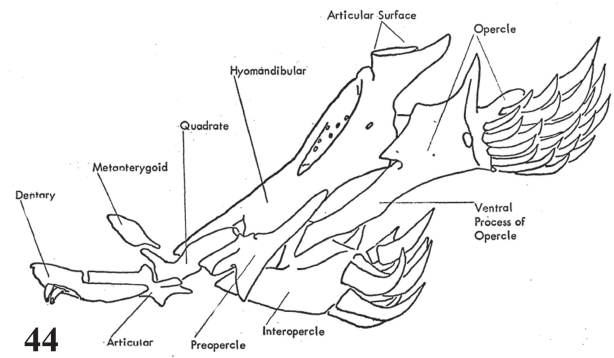

Fig. 41. Opercu1ar apparatus and suspensorium of *Trichomycterus rivu1atus* (AMNH 20351) lateral view. **Fig. 42.** Opercular apparatus and suspensorium of *Malacoglanis gelatinosus* (CAS-SU 50755), lateral view of right side, 30x magnification. **Fig. 43.** Opercu1ar apparatus and suspensorium of *Pygidianops eigenmanni* (CAS 11121), lateral view of 1eft side, SOx magnification.
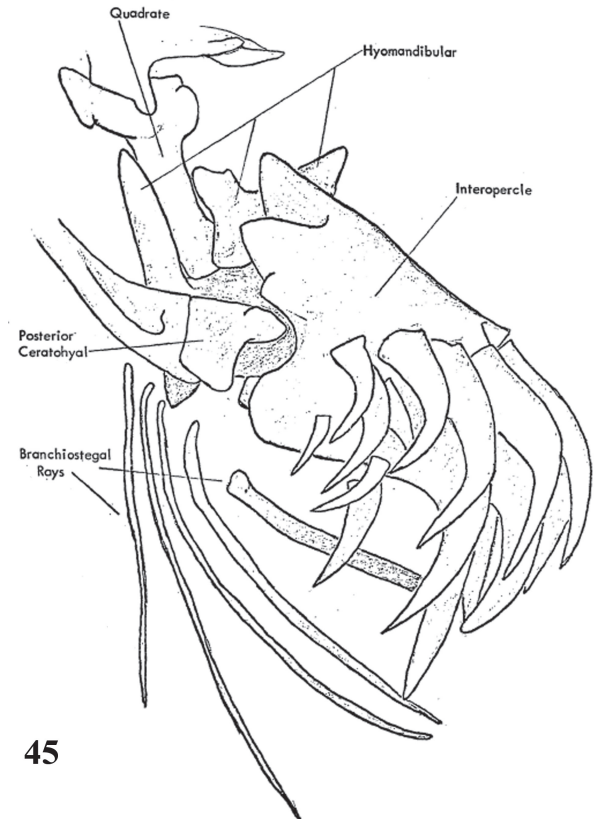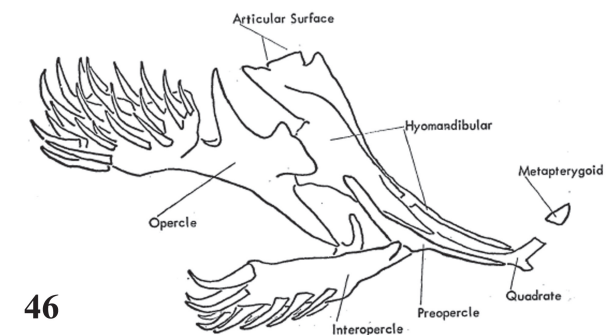
Fig. 44. Opercular apparatus and suspensorium of *Plectrochilus* sp. (AMNH uncatalogued), lateral view of left side, 25x magnification. **Fig. 45.** Opercu1ar apparatus and associated structures of *Vande11ia* sp. (AMNH uncata1ogued), ventral view of 1eft side, SOx magnification. **Fig. 46.** Opercular apparatus and suspensorium of *Branchioica bertoni* (SMF 8905), lateral view of right side, 0x magnification.

he designates as the suborder Loricarioidei. He bases this conclusion on the integumentary teeth and the pattern of fin ray segmentation in these fishes. His conclusion differs from mine only in his inclusion of cetopsids and *Nematogenys* in the Trichomycteridae. He did not examine astroblepids. Eigenmann (1888) evidently also believes these groups to be related, since he states (p. 684) that "The relationships of the American families may be seen from the following key:". In this key the following families are together: Hypophthalmidae, Pygidiidae (=Trichomycteridae, including Cetopsids and *Nematogenys*), Argeidae (=Astroblepidae), Loricariidae, Callichthyidae. This is based in large part on data from the Weberian apparatus. The similar views of Chardon (1968) have already been discussed.

The advanced characters of the Weberian apparatus discussed above also indicate that the closest relatives of the Trichomycteridae are a group consisting of the armored catfishes and their relatives (callichthyids, loricariids, astroblepids and Loricarioid sp.). The closest relative of these two groups together is *Nematogenys* (fig. 1; which shares some of the advanced features of the Weberian apparatus and has, in addition, integumentary teeth. The Loricarioidei of Peyer (1922) could thus be emended to include all of these catfishes, but not cetopsids (fig. 1).

The evidence concerning the relationships of Loricarioid sp. is given on p. 150. That concerning the relationships between the loricariids, astroblepids and callichthyids is given by numerous authors (*e.g.*, Regan, 1911; Alexander, 1964, 1965; Chardon, 1968; Sheldon, 1937; Eigenmann, 1888). Their consensus is that the Astroblepidae are probably most closely related to the Loricariidae (but see Eigenmann, 1888, p. 649). My preliminary observations are consistent with this interpretation, but the evidence will not be critically reviewed here (but see p. 154).

RELATIONSHIPS WITHIN THE TRICHOMYCTERIDAE SUBFAMILIES

The Trichomycteridae have previously been divided into nine subfamilies (see Myers, 1944, and p. 24 above). Evidence is given in the preceding sections (p. 35 and p. 57) for the exclusion of the Nematogenyinae and Phreatobiinae from the family Trichomycteridae. The evidence concerning the status for the remaining seven subfamilies is discussed below. They are each defined in terms of their advanced characters, and the evidence is given for each character being advanced within the family Trichomycteridae. It is hypothesized that the common ancestor of the family had the corresponding primitive condition of each character. It is also hypothesized that the common ancestor of each subfamily had all of the advanced characters defining the subfamily.

All of the genera examined for each subfamily have all of the advanced characters defining that subfamily, unless otherwise noted, and for each subfamily, the genera recognized are listed along with the type species.

Trichomycterinae

The subfamily Trichomycterinae as used here is essentially that described by Eigenmann (1918), plus a few genera described since that time. Unfortunately, no evidence has been found to indicate that the genera included form a monophyletic group. Evidence given below (p.158), however, indicates that they are all more closely related to a
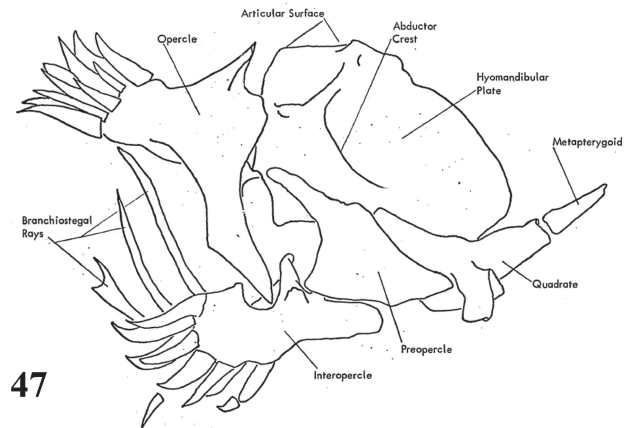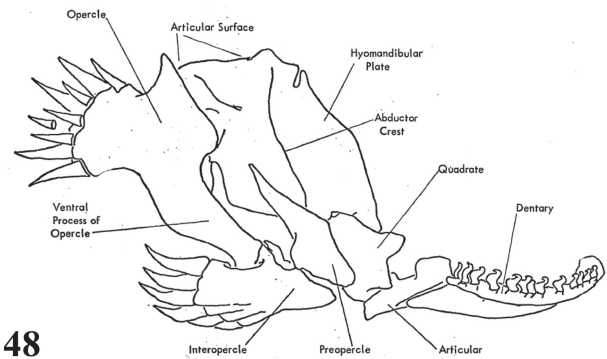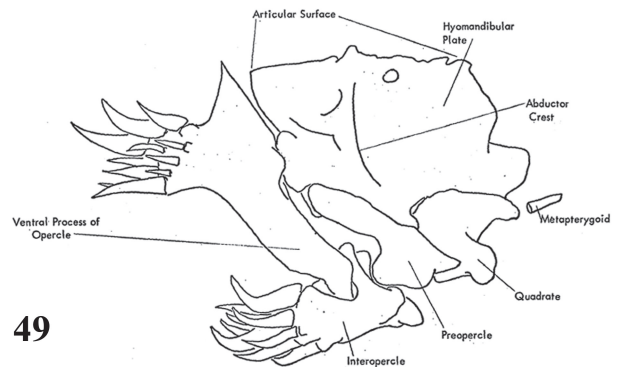
Fig. 47. Opercular apparatus and suspensorium **of** *Ochmacanthus reinhardti* (AMNH uncatalogued), lateral view of right side, 30x magnification. **Fig. 48.** Opercular apparatus and suspensorium of *Pareiodon microps* (BM(NH) 1926-10-27:270-273) , lateral view of right side, 10x magnification. **Fig. 49.** Opercular apparatus and suspensorium of *Pseudostegophilus nemurus* (AMNH uncatalogued), lateral view of right side, l5x magnification.

monophyletic group consisting of the Sarcoglanidinae and Glanapteryginae than to any other fishes. In the present work the Trichomycterinae will be treated as a monophyletic group for the sake of convenience, but it must be remembered that some of the included genera may be more closely related to these other two subfamilies than to the other genera of Trichomycterinae.

Myers (1944), Eigenmann (1918) and others have used the name *Pygidium* instead of *Trichomycterus* and consequently used the subfamily name Pygidiinae and the family name Pygidiidae. Tchernavin (1944) has clearly shown that *Trichomycterus* is the valid name for the genus. Tchernavin also considers *Hatcheria* a synonym of *Trichomycterus*.

Genera recognized:

Eremophilus, Humboldt, 1811, (type species by original designation, *Eremophilus mutisii* Humboldt).

Rhizosomichthys, Miles, 1943, (type species by original designation, *Rhizosomichthys totae* (Miles)).

Scleronema, Eigenmann, 1918, (type species by original designation, *Scleronema operculatum* Eigenmann).

Trichomycterus, Valenciennes, 1846, (type species by original designation, *Trichomycterus punctulatus* Valenciennes).

The Vandelliinae

Genera recognized by Myers (1944):

Branchioica, Eigenmann, 1918, (type species by original designation, *Branchioica bertoni* Eigenmann).

Paracanthopoma, Giltay, 1935, type species by original designation, *Paracanthopoma parva* Giltay).

Paravandellia, Miranda-Ribeiro, 1912, (type species by original designation, *Paravandellia oxyptera* Miranda-Ribeiro).

Parabranchioica, Devincenzi and Vaz-Ferreira, 1939, (type species by original designation, *Parabranchioica teaguei* Devincenzi and Vaz-Ferreira).

Plectrochilus, Miranda-Ribeiro, 1917, (type species by original designation, *Plectrochilus machadoi* Miranda-Ribeiro, 1917).

Vandellia, Cuvier and Valenciennes, 1846, (type species by original designation, *Vandellia cirrhosa* Cuvier and Valenciennes).

Seven generic names have been proposed for various members of the Vandelliinae. Material representing five of these is available for the present study. Of these five, *Vandellia*, *Plectrochilus* and *Branchioica* are recognized. The only specimen of *Parabranchioica* available is a co-type
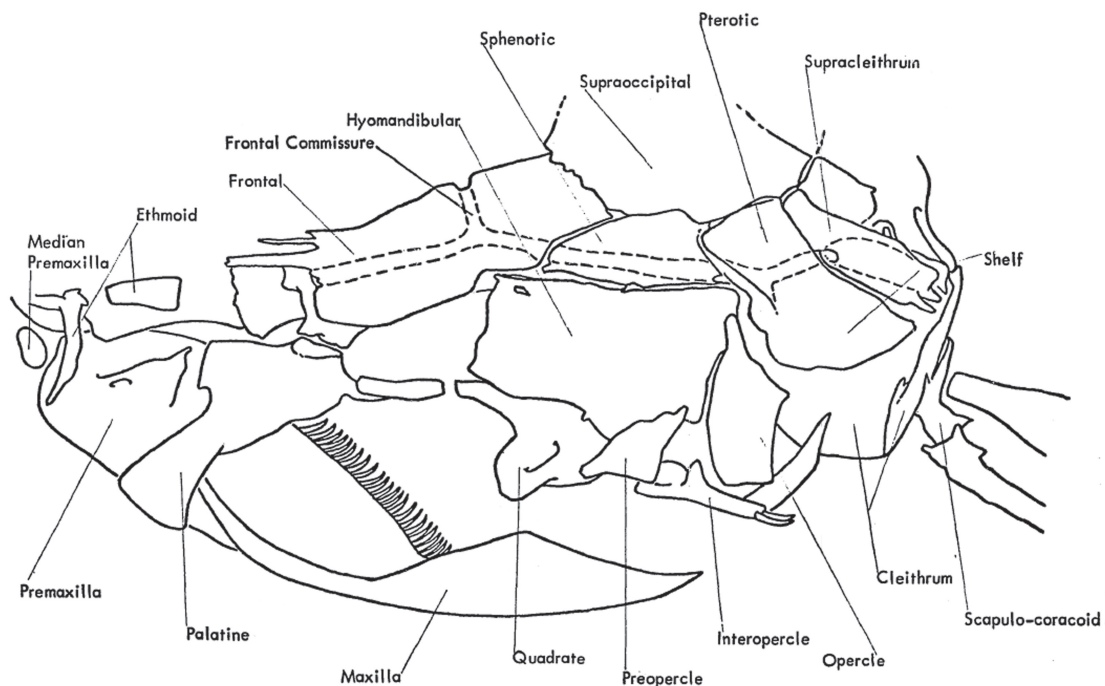

Fig. 50. Syncranium of *Apomatoceros alleni* (AlIJSP 109804), dorso-lateral view of left side, 7x magnification, lower jaw and anterior tooth rows not shown.

of the type species, *P. teaguei*, and it is not distinguishable from *Branchioica*. The *Urinophilus* material available is indistinguishable from that of *Plectrochilus*, and I agree with Myers (1944) in considering the former a synonym of *Plectrochilus*.

Material of *Paravandellia* and *Paracanthopoma* was not available to me. Eigenmann (19l8), however, believed that *Paravandellia* might turn out to be the same as *Branchioica* when material is examined more closely, because he thought that teeth might be found on the mandibles of *Paravandellia*. It is unlikely, however, that these two genera are the same, because the mandibular teeth of *Branchioica* are large, well developed and easily seen. The small size (22 mm.) however, of the only specimen of *Paravandellia* reported (Miranda-Ribeiro, 1912) is characteristic of *Branchioica*. The anatomical differences (*e.g.*, vertebra number, and see p. 91) between *Branchioica* and these other vandelliines make it unlikely that *Branchioica* are young of these other genera. The significance of the lack of small (i.e., less than about 40 mm.) *Vandellia* and *Plectrochilus* from collections is not known.

On the basis of Giltay's (1935) description, *Paracanthopoma* is apparently distinct from other vandelliines, because its branchiostegal membrane is free from the isthmus. Giltay considered it to be between the Vandelliinae and the genus *Acanthopoma* of the Stegophilinae. Myers (1944) in his key to trichomycterid genera placed it in the Vandelliinae, but the only clearly advanced character indicating this is the separation of the mandibles. Giltay's illustration indicates that *Paracanthopoma* is more heavily bodied than other vandelliines, as are the stegophilines. Its small size (25 mm.) is suggestive of *Branchioica*.

Myers' (1944) key also states that *Branchioica* is the only vandelliine with "A large claw-like tooth at the end of each maxillary…" (p. 598), and that all other genera (other than *Paracanthopoma*) lack this tooth. The bone in question is the premaxilla, not the maxilla, and in all of the Vandelliinae examined here this bone bears claw-like teeth (see below).

Another problem encountered in previous descriptions of vandelliines is the confusion between the teeth of the vomer and those of the premaxilla. The single set of teeth on the vomer in the middle of the upper jaw has been often called premaxillary teeth, while those on the premaxilla were thought to be maxillary teeth (see for example Eigenmann, 1918).
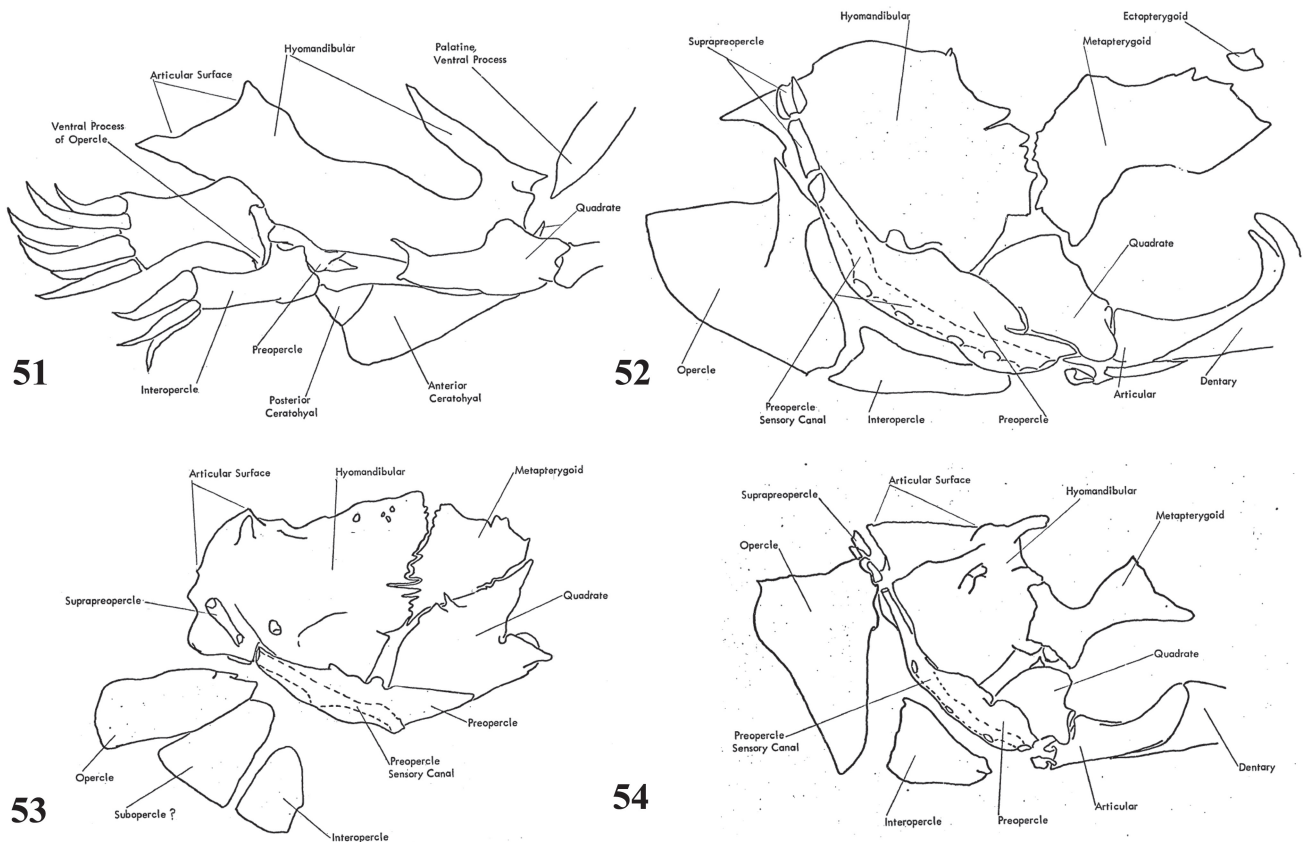
Fig. 51. Opercular apparatus and suspensorium of *Tridensimilis venezuelae* (USNM 121291), lateral view of right side, 60x magnification. **Fig. 52.** Opercular apparatus and suspensorium of *Nematogenys inermis* (MCZ 9839), lateral view of right side, lOx magnification. **Fig. 53.** Opercu1ar apparatus and suspensorium *Astroblepus longifilis* (AMNH 11582), lateral view of right side. l5x magnification. **Fig. 54.** Opercular apparatus and suspensorium of *Diplomystes papillosus* (ANSP 84193), lateral view of right side, 8x magnification.

Advanced Characters of the Vandelliinae

1) Vomer in middle of upper jaw (figs. 15, 16, 17, 56-58).

The strongly toothed vomer is the most anterior bone in the skull. It is located directly beneath the ethmoid, cornua, between the premaxillae, and its anterior edge extends slightly beyond the ethmoid. In *Vandellia* and *Plectrochilus* it is approximately oval shaped, the width being slightly greater than the length. In *Branchioica* the vomer is wider and slightly

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Fig. 55. Snout and upper jaw bones of *Trichomycterus rivulatum* (AMNH 20351), dorsal view, right side, 20x magnification. **Fig. 56.** Upper jaw bones and associated structures of *Plectrochilus* sp., (AMNH uncatalogued), 30x magnification, dorsal view, left side.

constricted in the middle, giving it a sort of bilobed shape (fig. 58). In this way it resembles the toothed portion of the vomer of Diplomystes, which bears two distinct patches of teeth (fig. 40).

In all other siluriforms, and at least some other ostariophysans, the vomer lies at least partially under the lateral ethmoids, and its posterior extension contacts the parasphenoid. This posterior extension is completely lacking in the Vandelliinae. The wide portion of the vomer, normally in ostariophysans found beneath the lateral ethmoids, has apparently extended forward in the Vandelliinae, and the posterior extension is lost.

The primitive condition for catfishes is probably that found in *Diplomystes*, in which the wide portion is completely beneath the lateral ethmoids and there is a pair of vomerine tooth patches, each of which can be disarticulated intact from the vomer. The posterior extension in *Diplomystes* is sutured to the anterior end of the parasphenoid, and there is a shorter anterior extension, giving the bone an overall crucifix-like shape. *Trichomycterus* also has this primitive condition, except that it lacks vomerine teeth. A possible intermediate condition is found in some other trichomycterids (Tridentinae and some Stegophilinae) in which the wide portion is completely anterior to the lateral ethmoids and the posterior end is not sutured to the parasphenoid. In one stegophiline, *Ochmacanthus*, the vomer is entirely anterior to the parasphenoid.

The only other catfishes with a median toothed bone in the upper jaw are the Stegophilinae (see discussion p. 99). This bone in stegophilines, the "median premaxilla", is probably not formed from any part of the vomer because these catfishes have abnormal, well-developed vomer. An alternative interpretation, however, is that the vomer in the Vandelliinae has actually been lost, and that the toothed bone described here as the vomer is actually the median premaxilla of the Stegophilinae. Research into the development of these bones and the associated soft anatomy may yield some direct evidence bearing on the homologies of these structures. Also, if independent evidence indicates that the Vandelliinae and Stegophilinae are sister groups this alternative interpretation would be equally possible. The relationships of these subfamilies remains problematic (see discussion p. 148).

2) Vomer Toothed (figs. 15, 16).

The vomer bears several large recurved teeth oriented posteriorly. These form a single tooth patch extending for the entire width of the vomer. Vomerine teeth are lacking in all other trichomycterids. The vomerine teeth found in *Diplomystes* and some other siluriforms are usually a pair of patches. Alexander (1965) states that the pair of tooth plates attached to the vomer of *Diplomystes* have been shown by Bamford (1948) to be dermopalatines. Bamford, however, examined only *Galiechthys*, in which neither the palatine nor the vomer bear teeth.

If the Vandelliinae has secondarily developed teeth on the vomer, this secondary development can be considered an advanced character for the family.
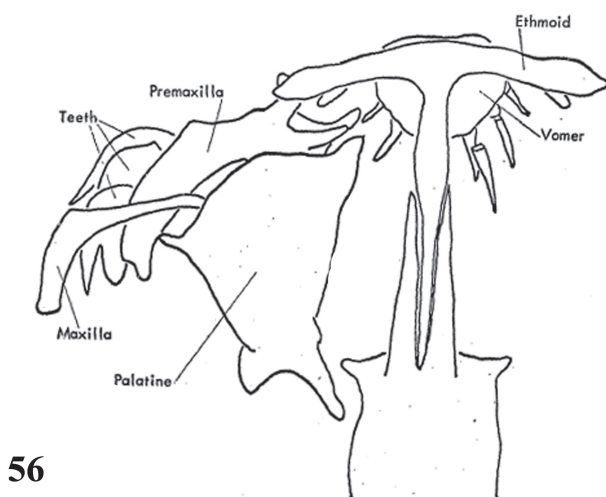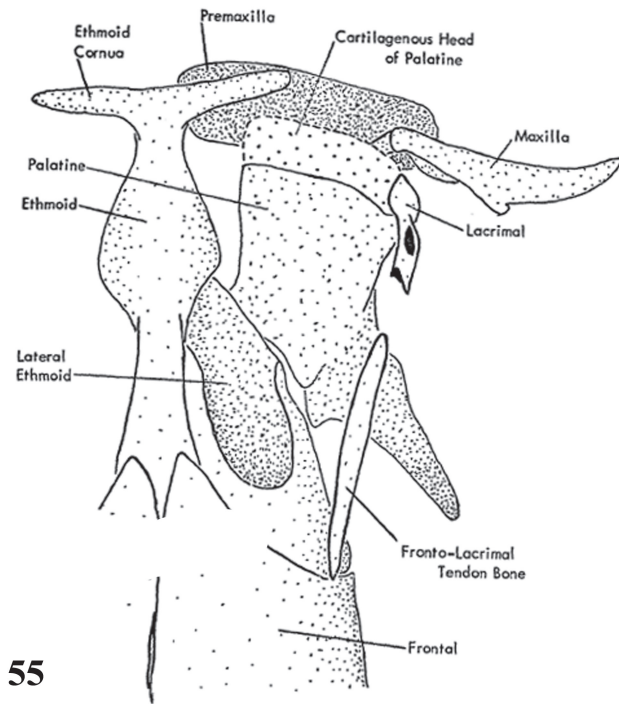
3) Claw-like teeth on distal end of premaxilla, enclosed in a pocket of skin (figs. 57, 58, 60, 63).

The premaxillae extend laterally beyond the corner of the mouth, and claw-like teeth on their distal ends are oriented laterally, on the sides of the head, with their tips pointed posteriorly. One or more of these teeth are covered by a fold of skin forming a pocket from which they can be extended. The claw-like shape of these teeth appears to develop from an outgrowth at the base of the tooth. This outgrowth forms a huge posterior expansion below and parallel to the sharply recurved tip of the tooth (fig. 60). This form and arrangement of the teeth may be an advanced condition, perhaps unique among fishes, and probably functions to secure a position for these parasitic fishes on or in their hosts.

4) Dentaries well separated in midline (figs. 57-58).

In siluriforms and trichomycterids generally the dentaries are strongly connected in the midline, although there is no suture between them as is found in characoids. In the Vandelliinae, however, the mandibles are widely separated. They are connected only by the soft flesh of the lower lip.
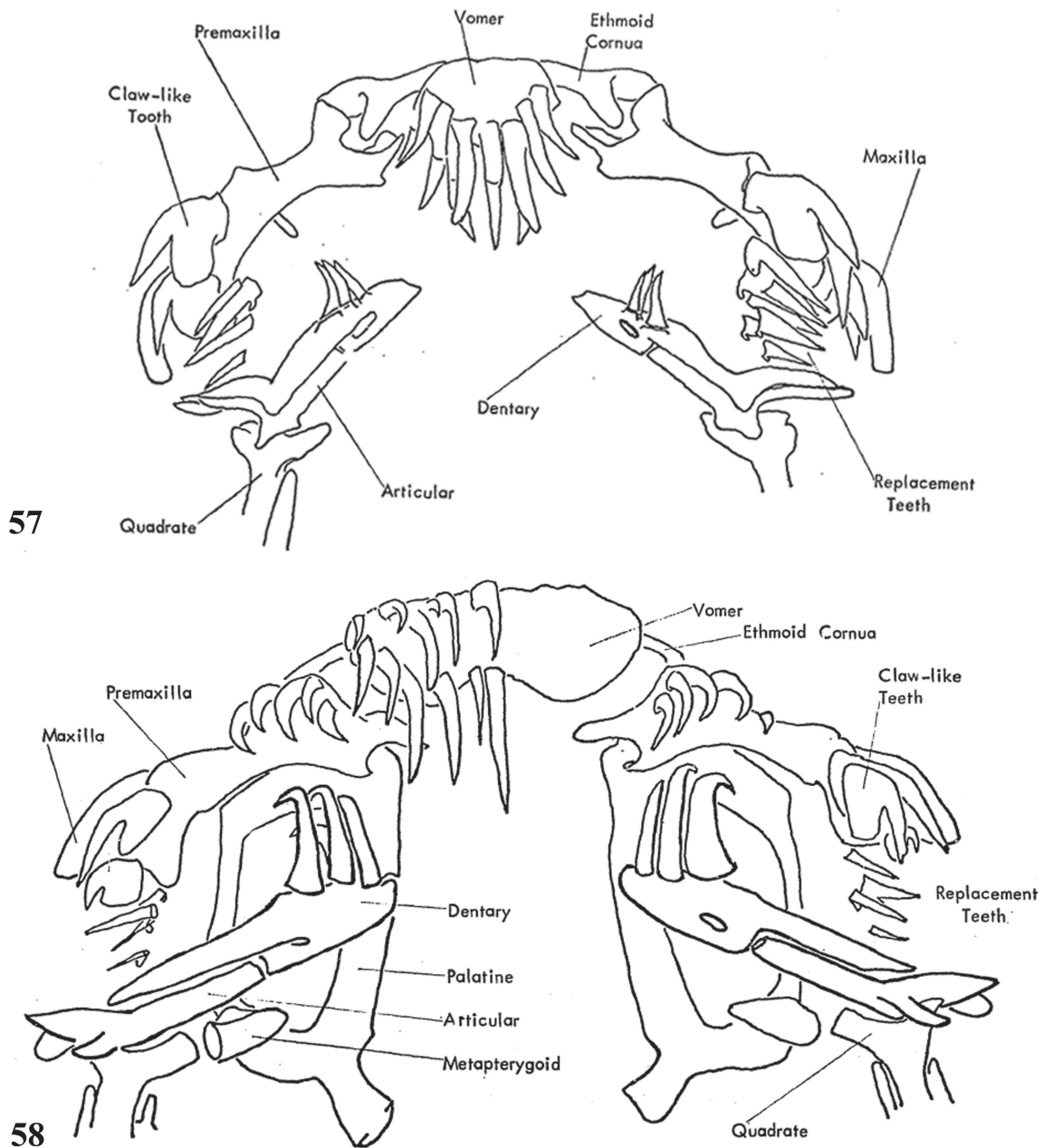

Fig. 57. Jaws and associated structures of *Plectrochilus* sp. (ANNH uncatalogued), ventral view, 30x magnification. **Fig. 58.** Jaws and associated structures of *Branchioica bertoni* (SMF 8905), ventral view, SOx magnification, teeth on left side of vomer not shown.

5) Pterotic process (figs. 14-17).

At the posterior-lateral edge of the pterotic bone there is a finger-like or spine-like process. It extends lateral to the supracleithrum, and ends posteriorly about even with the posterior edge of the epiotic. Various other trichomycterids (*e.g. Trichomycterus*, Stegophilines), catfishes (*e.g. Diplomystes*), and teleosts have various lateral extensions of the pterotic, but none of the catfishes examined has a distinct finger-like process such as is found in the Vandelliinae.

6) Pharyngeal teeth and fifth ceratobranchial lacking (fig.85).

The fifth ceratobranchial is lacking completely. Not even a cartilaginous rudiment is present. The only other actinopterygians known to lack this bone are eels (Nelson, 1969, and pers. comm.). In all other teleosts it is present, and in most it bears teeth.

Pharyngeal teeth on the fifth ceratobranchial of teleosts are generally used for feeding on solid material. All of the Vandelliinae for which the feeding habits are known feed on blood. This may make pharyngeal teeth superfluous. With the loss of these pharyngeal teeth the fifth ceratobranchial, which in all other catfishes bears these teeth, may also become superfluous. The lack of pharyngeal teeth and fifth ceratobranchials may even be an advantage to a fish feeding on blood. The Stegophilinae, the only other trichomycterids known to be parasitic, have relatively small fifth ceratobranchials with few teeth relative to most other trichomycterids and their relatives (cf. figs. 83-86).

7) Hypobranchials two and three lacking (fig. 85).

In the Vandelliinae hypobranchial one is ossified, but no other hypobranchials are present, even as cartilage. In all other catfishes at least three pairs of hypobranchial elements are present, either as cartilage or bone. The only apparent exception to this is *Typhlobelus ternetzi* of the Glanapteryginae, but the single alizarin preparation available has not been stained for cartilage.

8) Infrapharyngobranchial four unossified.

The fourth infrapharyngobranchial, which in all other catfishes is the ossified support for the upper pharyngeal tooth plate, is here unossified.

9) Upper pharyngeal tooth plate toothless.

The infrapharyngeal tooth plate is ossified but lacks teeth.

Fig. 60. Premaxillary bone and teeth of *Vandellia cirrhosa* (AMNH 20497). A. ventral view of left side, teeth in place, 30x magnification. B. Teeth shown in A separated from bone, 1- fully developed, 2 and 3 - replacement teeth, magnification 60x.
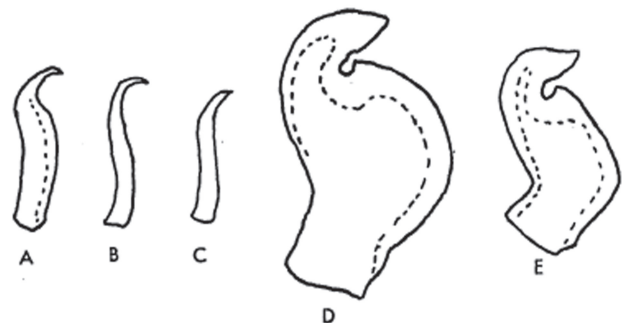
Fig. 61. Jaw teeth of (A) *Ochmacanthus reinhardti* (AMNH 27693), (B) *Haemomaster venezuelae* (AMNH uncatalogued), (C) *Tridentopsis pearsoni* (USNH-IU 17277), (D) and (E) *Pareiodon microps* (BM(NH) 1926-10-27: 270-273); all 60x magnification; B, C, and E from premaxilla (E from distal end of premaxilla, other *Pareiodon* premaxillary teeth similar to D); A and D from dentary.
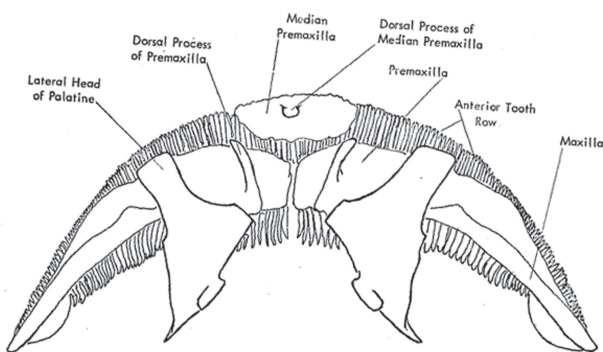

Fig. 59. Upper jaw of *Pseudestegophilus nemurus* (AMNH uncatalogued), dorsal view, 13x magnification, only the anterior and posterior most tooth rows are shown.
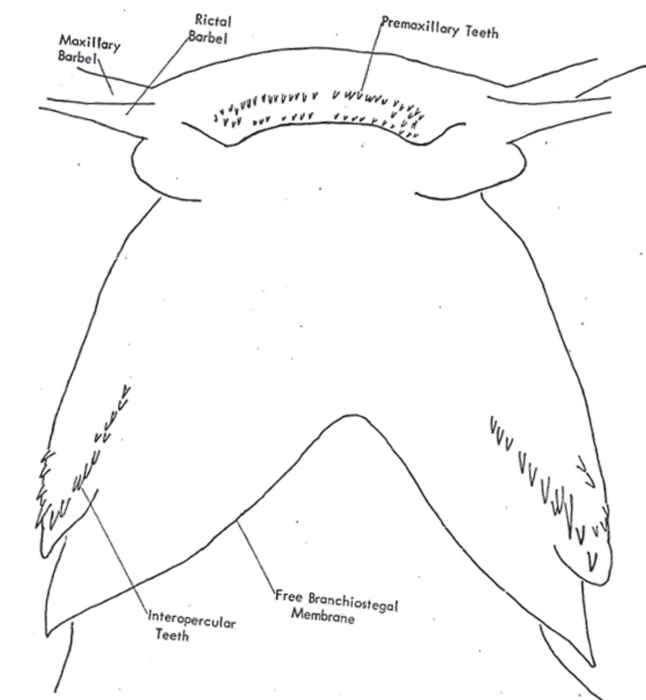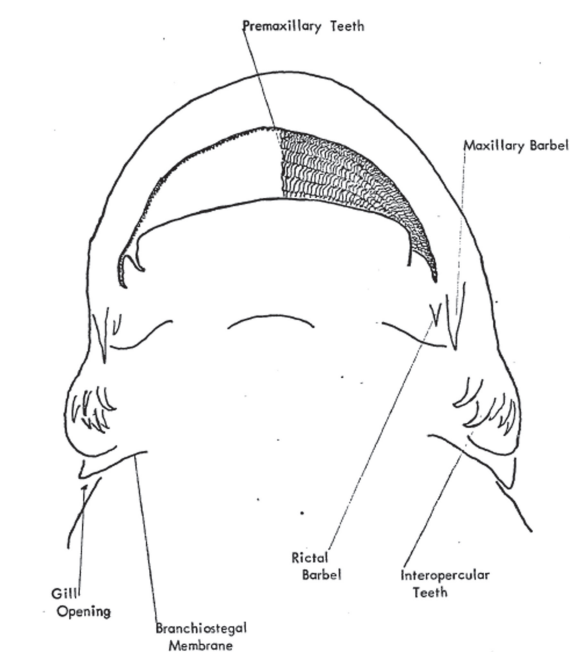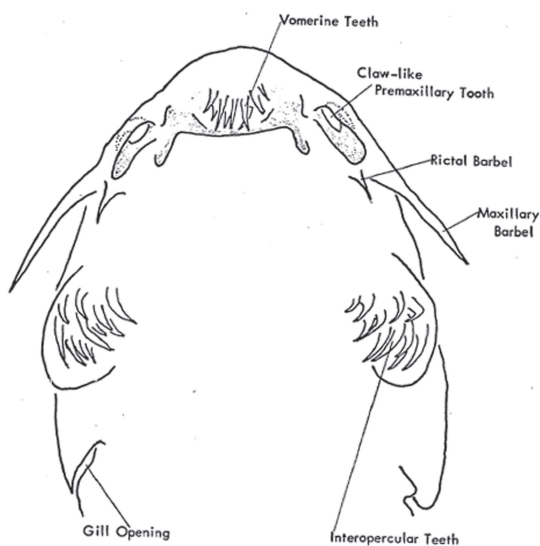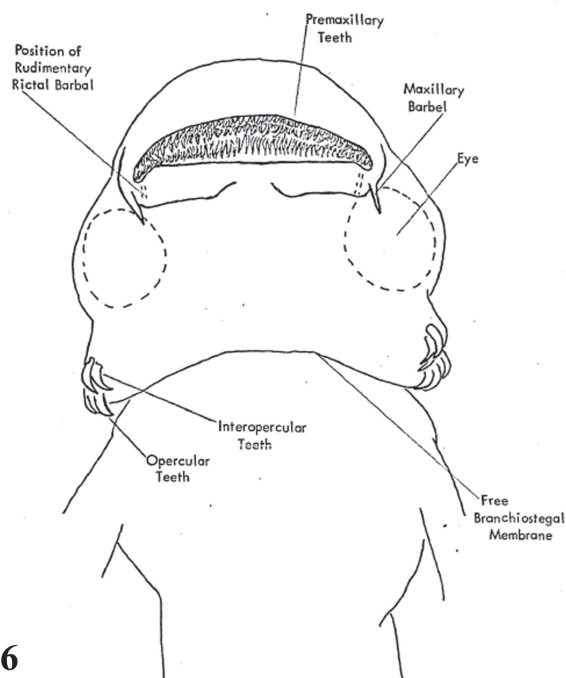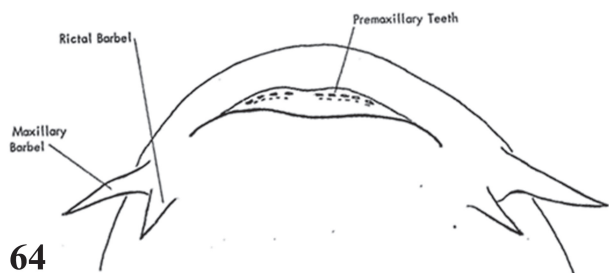
Fig. 62. Head of *Trichomycterus striatum* (USNM 182553), ventral view, 10x magnification, not all premaxillary and interopercular teeth are shown. **Fig. 63.** Head of *Plectrochilus* sp. (UMMZ uncatalogued),ventral view, l2x magnification, distal end of premaxillary tooth indicated by dotted outline, covered by fold of skin. **Fig. 64.** Head of *Pareiodon microps* (MCZ 46683), ventral view, 7x magnification. **Fig. 65.** Head of *Pseudostegophilus nemurus* (AMNH uncatalogued), ventral view, 7x magnification, premaxillary teeth shown on left side only, one row of teeth anterior to the premaxilla shown on both sides, no lower jaw teeth shown. **Fig. 66.** Head of *Tridensimilis venezuelae* (USNM 121291), ventral view, 17x rnagnification.
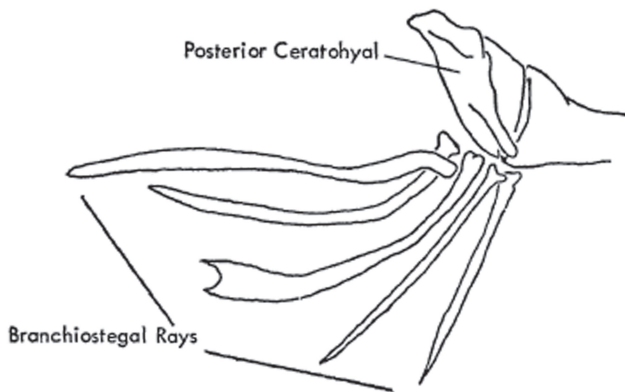
Fig. 67. Branchiostegal rays of *Haemomaster venezuelae* (AMNH uncatalogued), lateral view, right side, 25x magnification.

These teeth are present in all other siluriforms examined (see also Nelson, 1969, p. 492). This character, as well as the lack of a fifth ceratobranchial and the other reduced features of the gill arches described here may also be functionally related to the sanguisugous food habits of these fishes.

10) Feeding parasitically on the blood of other vertebrates.

All of the genera are known to feed on the blood from the gills of other fishes (see Kelly and Atz, 1964, for review). Almost all of the known specimens of *Branchioica* were found attached to the gills of large fishes. *Plectrochilus* has been found in a wound on the body of an alligator, so it is possible that blood is gotten from places other than the gills by at least some Vandelliinae. There is no evidence, however, that any feed on anything other than blood.

11) Mesocoracoid absent.

The mesocoracoid, a primitive feature of catfishes and teleosts generally, is present in Trichomycterinae and probably also in the Stegophilinae. Its distribution among other trichomycterids is problematic (see discussion of the Stegophilinae, p.104), but the Vandelliinae is the only other trichomycterid group with an ossified scapulo-coracoid that definitely lacks a mesocoracoid. In this subfamily the pectoral radial articulates with a stout ventro-medial process of the scapulo-coracoid. This process could represent either the ventral portion of the ring-like extension found in the Stegophilinae, or the remnant of the hypocoracoid portion of the scapulo-coracoid (the horizontal lamina of Alexander, 1965, cf. figs. 75, 77).

**Relationships within the Vandelliinae**

The relationships are fairly clear among the Vandelliinae examined (fig. 2). *Vandellia* and *Plectrochilus* are probably more closely related to each other than either is to *Branchioica*. In fact these two genera may not be distinct. The only consistent difference between them is that *Plectrochilus* (= *Urinophilus*) has two or three small but fully developed recurved teeth on the dentary; *Vandellia* has none. They are tentatively recognized here as distinct genera, although it may turn out that the presence of these teeth varies within populations, as suggested by Myers (1944). There is some indication of this in a large series of *Plectrochilus* (or *Vandellia*) from Bolivia, in which some specimens appear to lack dentary teeth and others have them. A detailed analysis of this collection and of the species in these genera is not yet complete.

It is unlikely that the dentary teeth are lost through careless handling of specimens, because they are firmly attached to the bone and difficult to remove, at least in well preserved specimens. It is easy to overlook them, however, on unstained specimens. For this reason descriptions that report them absent cannot be trusted.
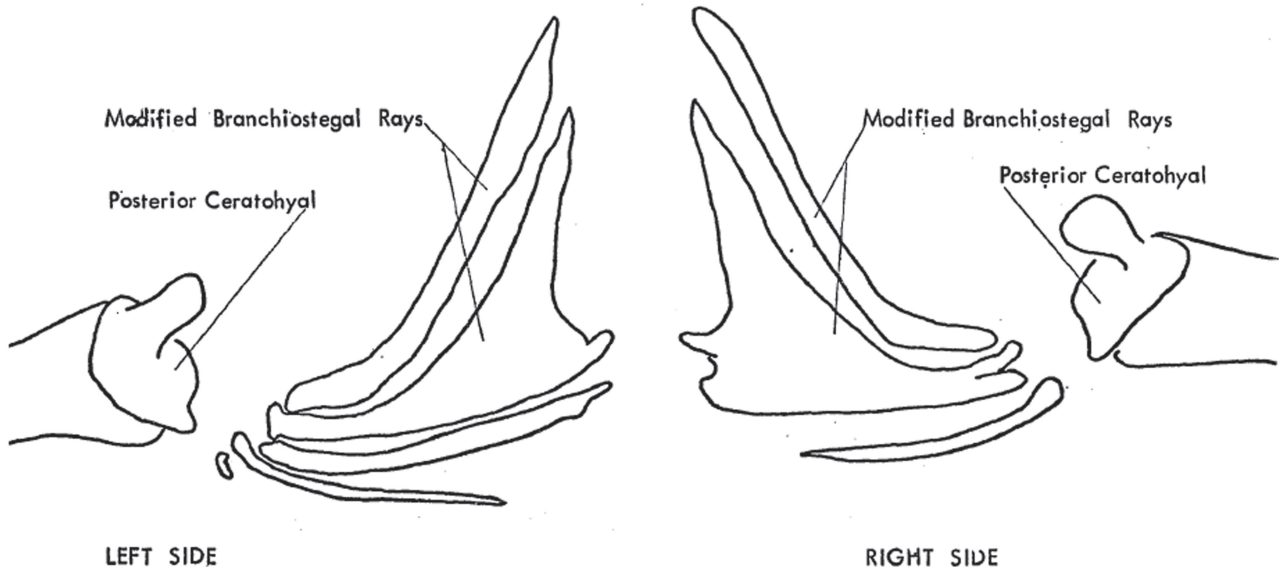
Fig. 68. Branchiostega1 rays of *Pareiodon microps* (BM(NH) 1926-10-27: 270-:273 , lateral view, 12x magnification.
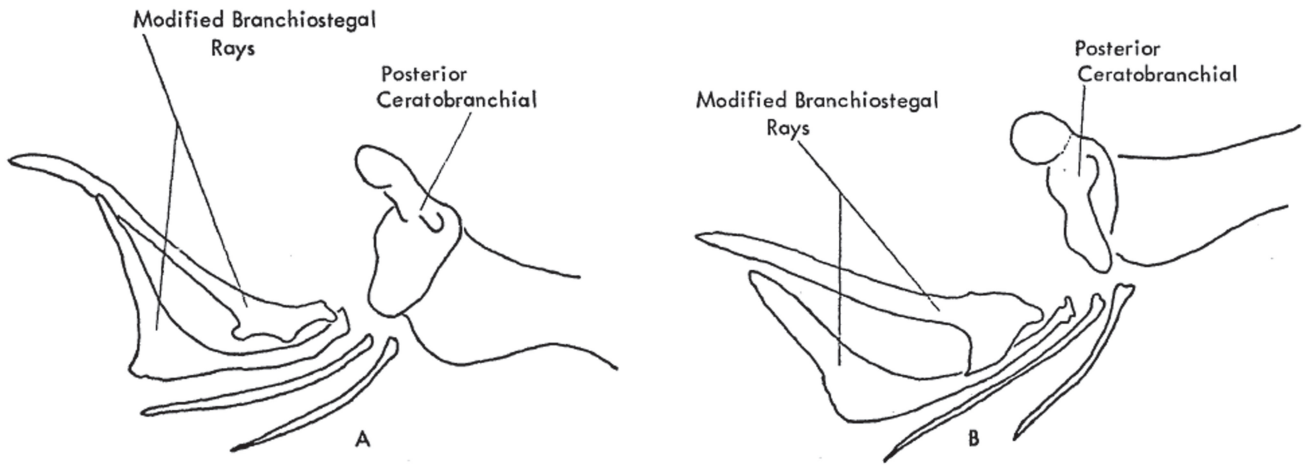
Fig. 69. Branchiostega1 rays of (A) *Pseudostegophi1us nemurus* (AMNH uncata1ogued) and (B) *Stegophi1us intermedius* (USNM-IU 15499), lateral view, right side, magnification (A) 15x, (B) 12x.
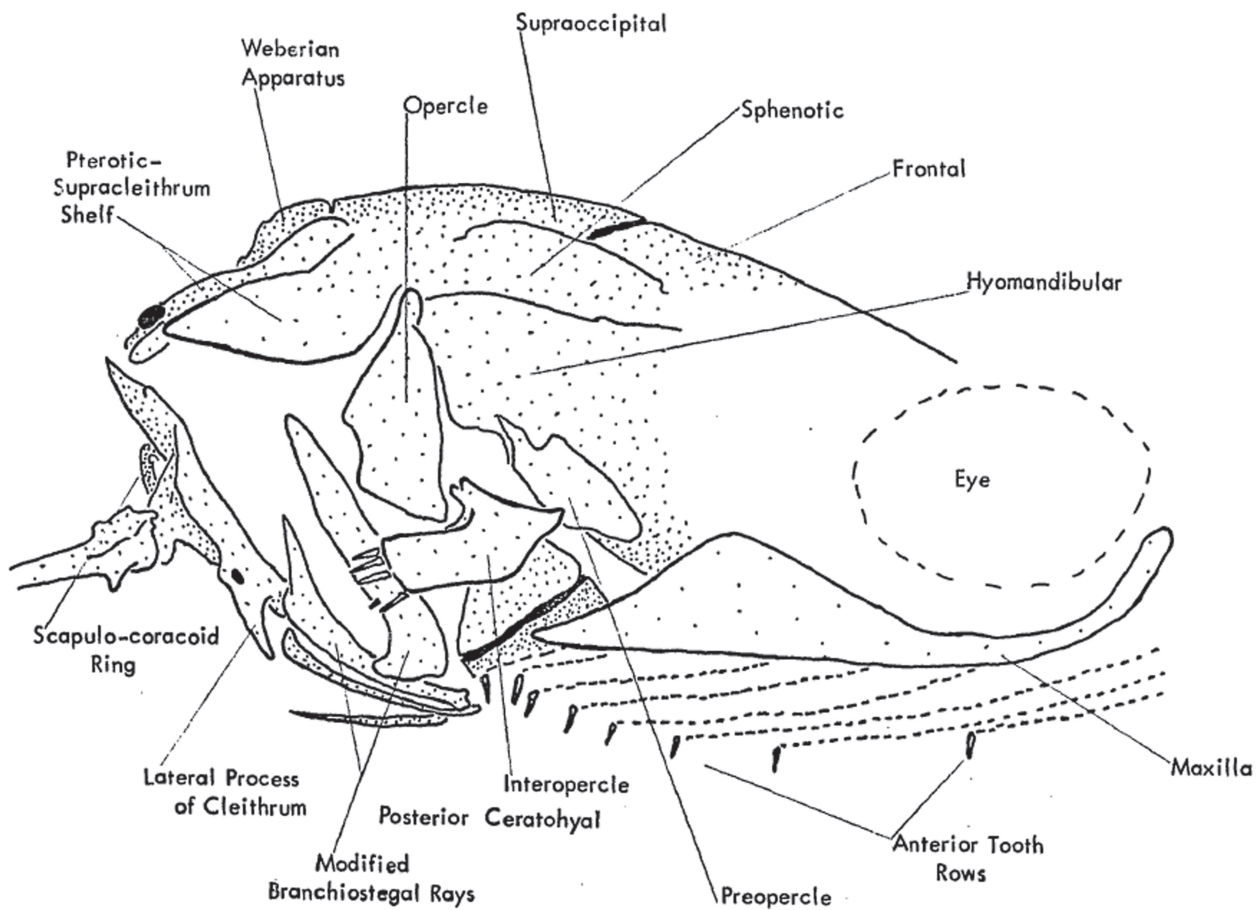
Fig. 70. Portions of the syncranium of *Apomatoceros alleni* (ANSP 109804), lateral view of right side, 7x magnification, approximate position of anterior tooth rows (in the upper lip anterior to the premaxilla) shown by broken lines, only the posterior-most tooth in each row is shown.
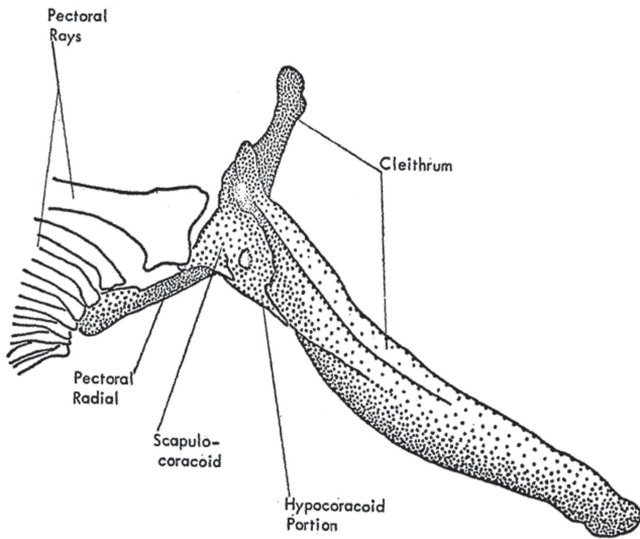
Fig. 71. Pectoral girdle of *Trichomycterus rivulatum* (AMNH 20351), lateral view, right side, 25x magnification.

Vandellia and *Plectrochilus* share the following advanced trichomycterid characters not found in *Branchioica*.

1) More than 55 vertebrae.

Branchioica has 48-52 vertebrae, while *Vandellia* and *Plectrochilus* have 60 and 60-65 respectively.

2) Proximal end of premaxilla forked around the ethmoid cornua (figs. 56-58).

There are two processes on the proximal end of the premaxilla in *Vandellia* and *Plectrochilus* (figs. 57). An anterior one extends lateral to the forked ethmoid cornua, and a medial one extends medial to the end of the ethmoid. Together these two processes fit around the forked end of the ethmoid cornua. The portion of the premaxilla of *Branchioica* that bears the proximal set of recurved teeth could represent the primitive condition of the anterior process in *Vandellia* and *Plectrochilus*. In *Branchioica* (fig. 17) the ethmoid is not forked (presumably a secondary condition, see below p. 152) and the premaxilla does not articulate with the ethmoid as in *Vandellia* and *Plectrochilus*. The premaxilla of these both genera also articulates with the antero-medial edge of the palatine, but in *Branchioica* this articulation is much better developed. The corner of the palatine fits into a
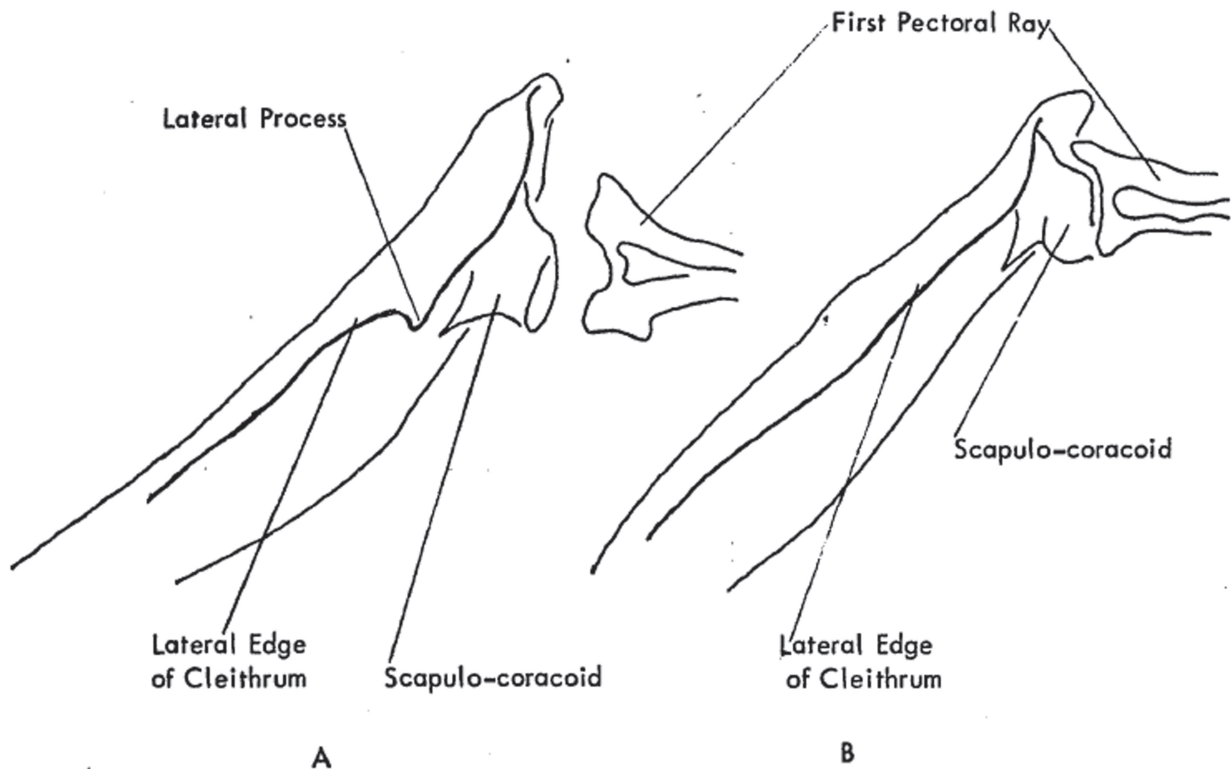
Fig. 72. Pectoral girdle of (A) *Haemomaster venezulae* (AMNH uncatalogued) and (B) *Ochmacanthus reinhardti* (AMNH 27693), lateral view1 of left side, 25x magnification.
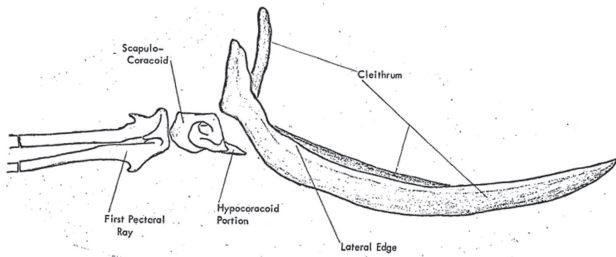
Fig. 73. Pectoral girdle of *Vandellia cirrhosa* (AMNH 9663), lateral view, right side, 25x magnification.

deep notch, or fork, in the proximal end of the premaxilla. The relatively greater development of this articulation is an advanced character of *Branchioica* relative to the condition in other vandelliines. Thus a forked, or notched, proximal end of the premaxilla has apparently evolved independently in *Branchioica* and in other vandelliines. The function of these complex articulations is most probably involved with the manipulation of the claw-like teeth at the distal end of the premaxilla.

3) Interopercular teeth oriented more posteriorly (figs. 41-54).

In *Vandellia* and *Plectrochilus*, as compared with *Branchioica*, the interopercular bone is shorter, the toothed portion is almost entirely on the posterior edge and the teeth all point more posteriorly than ventrally. *Branchioica* is similar to the primitive condition for the family, as found in *Trichomycterus*, in which most of the interopercular teeth are oriented ventrally (cf. figs. 44-46).

Fig. 75. Pectoral girdle of *Trichomycterus rivulatum* (UMMZ 66324), posterior view, 11.5x magnification.

4) Fewer than four dentary teeth, confined to the lateral part of the bone (figs. 57- 58).

Branchioica has at least six teeth on each dentary, extending to the medial edge of the bone. They are distinctly larger (about equal to the largest vomerine teeth), and more strongly recurved that those of Plectrochilus, in which the mandibular teeth are smaller than those on the vomer.

5) Premaxillary teeth all claw-like and confined to the distal portion of the bone (figs. 56-58).

In addition to these claw-like teeth *Branchioica* has several recurved teeth at the proximal end of the premaxilla, opposing the mandibular teeth. These teeth are apparently also present in *Paravandellia*. If mandibular teeth are truly lacking in *Paravandellia* then this genus could be considered distinct from *Vandellia* and *Plectrochilus*, but more closely related to them than to *Branchioica*.

Fig.74. Pectoral girdle of *Nematogenys inermis*, (MCZ 9839), lateral view, left side, 8x magnification.
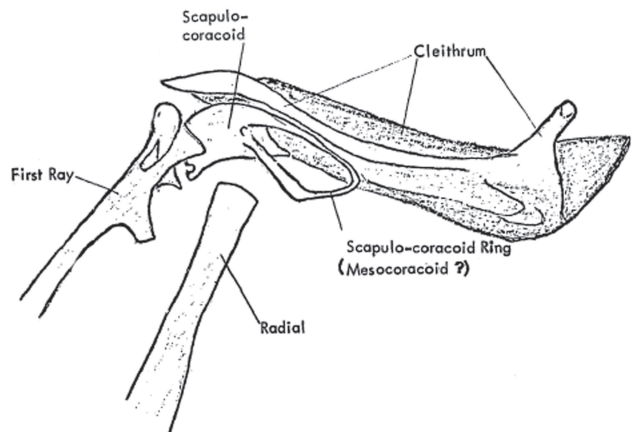
Fig. 76. Pectoral girdle of *Ochmacanthus reinhardti* (AMNH 27693), postero-dorsal view, 30x magnification.

Paracanthopoma parva is more primitive than other vandelliines, if it is indeed a member of this subfamily, is having its branchiostegal membrane free from the isthmus, and being heavier bodied than other vandelliines. This species can thus be tentatively considered as the sister group of all other vandelliines (fig. 2).

The Stegophilinae

Pareiodon microps, recognized by Myers (1944) as a monotypic subfamily *Pareiodon*tinae, shares a number of advanced characters with the Stegophilinae. The closest relative of *Pareiodon* appears to be a group consisting of only part of the Stegophilinae (see fig. 3 and discussion in this section below). Therefore, in order to retain the Stegophilinae as a monophyletic group, *Pareiodon* is here included as a member of the Stegophilinae and the *Pareiodon*tinae is not recognized.

The stegophiline genera recognized by Myers (1944) and by Gosline (1945), but not available to me, have been uncritically recognized here. I a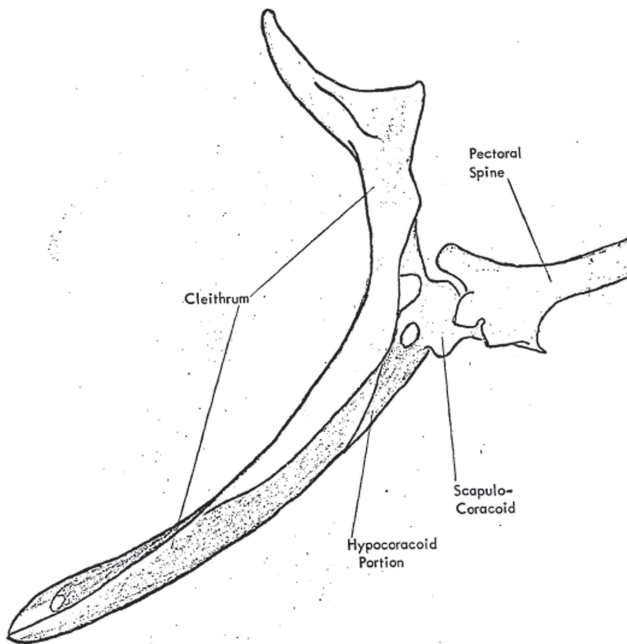gree with Miranda-Ribeiro (1951) in his placing of *Henonemus* in the synonymy of *Stegophilus*, but I would recognize *Homodiaetus* as distinct from *Ochmacanthus*. Type material of *Ochmacanthus* was not available for study, however.

Genera recognized:
Acanthopoma, Lütken, 1892, (type species by original designation, *Acanthopoma annectens* Lütken).
Apomatoceros, Eigenmann, 1922, (type *species* by original designation, *Apomatoceros alleni* Eigenmann).
Haemomaster, Myers, 1927, (type species by original designation, *Haemomaster venezuelae* Myers).

Homodiaetus, Eigenmann and Ward, 1907, (type species by original designation, *Homodiaetus anisitsi* Eigenmann and Ward).
Ochmacanthus, Eigenmann, 1912, (type species by original designation, *Ochmacanthus flabelliferus* Eigenmann).
Parastegophilus, Miranda-Ribeiro, 1946, (type species by original designation *Stegophilus maculatus* Steindachner).
Pareiodon, Kner, 1855, (type species by original designation, *Pareiodon microps* Kner).
Pleurophysus, Miranda-Ribeiro, 1918, (type species by original designation, *Pleurophysus hydrostaticus* Miranda-Ribeiro).
Pseudostegophilus, Eigenmann and Eigenmann, 1889, (type species by original designation, *Stegophilus nemurus* Gunther).
Schultzichthys, Dahl, 1960, (type species by monotypy, *Schultzichthys gracilis* Dahl)
Stegophilus, Reinhardt, 1859, (type species by original designation, *Stegophilus insidious* Reinhardt).

Advanced Characters of the Stegophilinae

1) Mouth opening a wide crescent-shaped disc (figs. 59, 62-66).
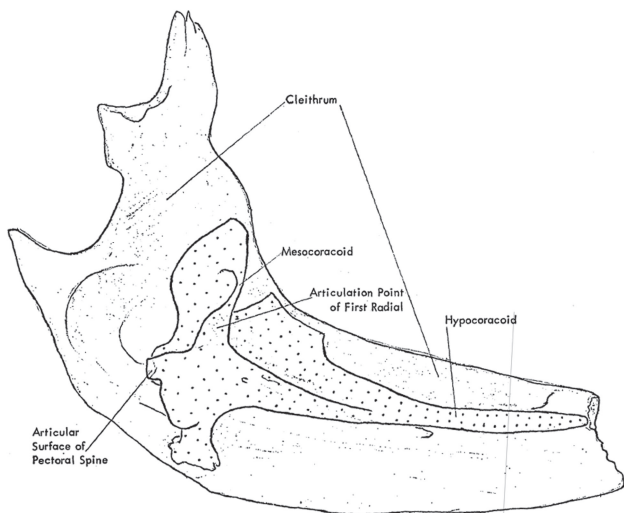
Fig. 71. Pectoral girdle of *Diplomystes papillosus* (MCZ 2890), postero-ventral view of left side, 7x magnification, scapulo-coracoid stippled.
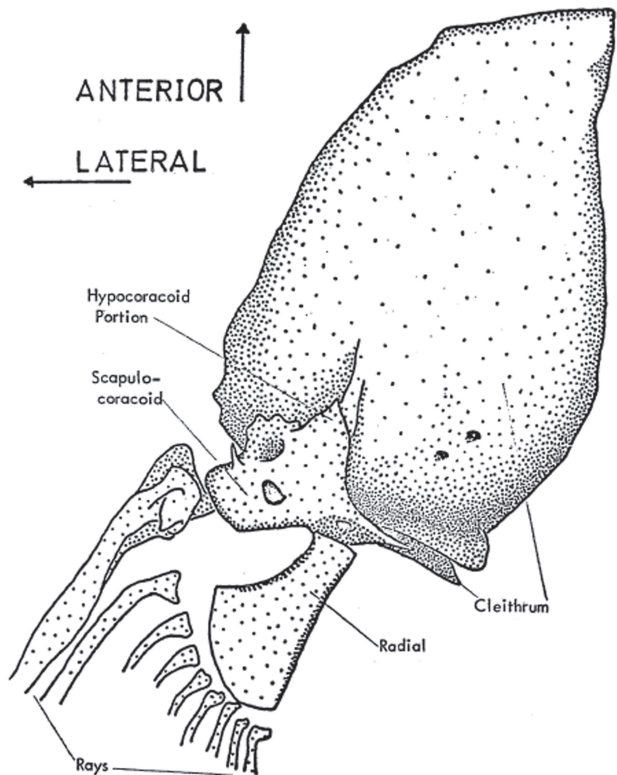
Fig. 72. Pectoral girdle of *Trichomycterus rivulatum* (AMNH 20351), ventral view, right side.

The primitive condition for trichomycterids, and for catfish as a whole, is a transverse, subterminal mouth. Some catfish groups have developed a completely ventral mount with the lips modified into a sucking disc (*e.g.*, loricariids and astroblepids). Among trichomycterids a fully ventral mouth is found in the Tridentinae, Vandelliinae and Glanapteryginae. Only in the Stegophilinae (except *Pareiodon*) does the mouth opening form a ventral, crescent-shaped disc, with the corners of the mouth extending well posterior to the anterior edge of the lower lip.

The width of the mouth (the distance between the extreme corners of the mouth opening) is greater in stegophilines, (except *Pareiodon*) than any other trichomycterids. This width is much more than the greatest neurocranium width. In *Pareiodon* the mouth is about equal to the neurocranium width, as in the Tridentinae. It is narrower still in other trichomycterids, except perhaps *Scleronema* (not examined, but see Tchernavin, 1944).

Correlated with the wide, crescent-shaped mouth opening in stegophilines, the distance between the lateralmost teeth of both the upper and lower jaws is also more than the maximum width of the neurocranium. Also, the lateral-most premaxillary teeth are situated directly lateral to the dentary teeth, and at least the tips of these premaxillary teeth are posterior to the dentary teeth. In stegophilines other than *Ochmacanthus*, *Haemomaster* and *Pareiodon* some of the lateral premaxillary teeth are completely posterior to the dentary teeth, and point more medially than posteriorly.

2) Median premaxilla (figs. 18, 20, 26, 50, 59).
All stegophilines except *Pareiodon* have a single median toothed bone in the middle of the upper jaw, just anterior and medial to the premaxillae, and anterior to the toothless vomer. The median premaxilla is a fairly thin plate-like bone lying just beneath the ethmoid cornuae, and it has a dorsal
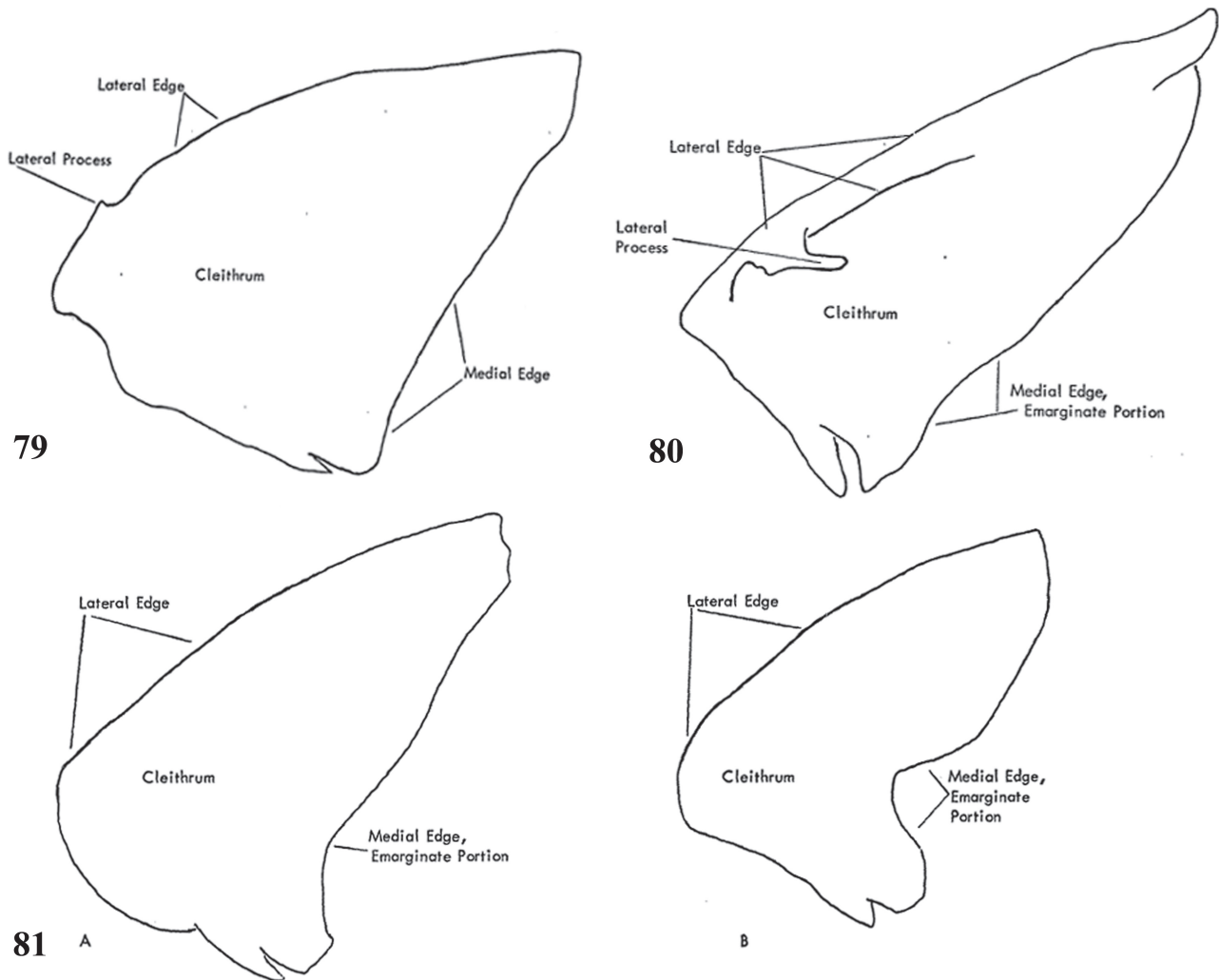
Fig. 79. Pectoral girdle of *Haemomaster venezulae* (CAS-IU 17706), diagramatic outline of ventral view, right side, 25x magnification. **Fig. 80.** Pectoral girdle of *Pareiodon microps* (BM(NH) 1926-1027:270-273), ventral view, right side, 12x magnification. **Fig. 81.** Pectoral girdle of (A) *Stegophilus intermedius* (USNM-IU 15499) and (B) *Pseudostegophilus nemurus* (AMNH uncatalogued), diagramatic outline of ventra1view, right side, both 13x magnification.

part that extends up directly in front of the ethmoid (lacking in *Apomatoceros*). This makes the median premaxilla the anterior most bone in the skull. The ventral surface of the median premaxilla is completely covered with teeth that are essentially the same as the teeth on the premaxilla and those in the upper lip anterior to the premaxilla. All of these teeth are arranged in distinct transverse rows (see p. 153), and the teeth on the median premaxilla form an integral part of these rows. Another similarity between the premaxilla and the median premaxilla is that the thickness and degree of development of the bones tends to be correlated. In those species with a rather thick well-developed premaxilla the median premaxilla is also thick (i.e., *Ochmacanthus reinhardti*), whereas in other species both bones are much thinner. In *Apomatoceros alleni* both are extremely thin sheets of bone.

The evolutionary origin of the median premaxilla is obscure. The only other catfishes with a median toothed bone in the upper jaw are the Vandelliinae. In the Vandelliinae, however, this median bone is probably the vomer (see discussion, p. 84). Stegophilines have a well-developed vomer, which lacks teeth.

The median premaxilla of stegophilines could be formed from detached medial portions of the premaxillae.

Fig. 82. Pectoral spine of a juvenile *Nematogenys inermis* (USNM 84343), ventral view of right side, 20x magnification, cartilage stippled.

Developmental evidence, presently unavailable, could substantiate this. It is also possible that the median premaxilla is formed by the fusion and development of the bases of the teeth found free in the upper lip anterior to the premaxilla in most stegophilines and one tridentine. In the stegophilines examined the bases of these teeth tend to be joined to each other. The anterior edge of the premaxilla appears to be formed from the bases of the anteriormost premaxillary teeth.

3) Fontanel closed (figs. 18, 20, 22, 24, 26, 27).

An open fontanel is present in most catfishes, including *Diplomystes*, cetopsids and *Nematogenys*. Among trichomycterids it is present in all the Trichomycterinae, Sarcoglanidinae, Tridentinae, and in *Branchioica* and *Typhlobelus*. Therefore the best hypothesis is that the presence of an open fontanel is the primitive condition for trichomycterids, and the lack of this fontanel in all stegophilines is evidence that they are related.

4) Pterotic-supracleithral shelf (figs. 18, 20, 22, 24, 26, 27).

A number of catfish groups have an extension of the pterotic lateral to the other parts of the neurocranium (*e.g.*, *Diplomystes*, ictalurids, cetopsids, astroblepids, Loricarioid sp. [see p .185]), and this condition may well be primitive for catfishes. This lateral extension bears the sensory canal, and represents a dermal portion of the pterotic. There is usually little or no development of the pterotic lateral to the sensory canal. The sensory canal continues posteriorly into the supracleithrum, where it also occupies the lateral edge of the bone.

Among trichomycterids only the stegophilines have the supracleithrum extending laterally just as far as the pterotic, and with both forming a shelf of bone lateral to the sensory canal. In most stegophilines a broad thin shelf of bone extends laterally from the dorsal surface of both bones. The line between the pterotic and the supracleithrum is at about the middle of the shelf, so each bone forms about an equal part.

The shelf is poorly developed in *Haemomaster* and especially in *Ochmacanthus* (figs. 18, 20). It is possible that this degree of shelf development is a primitive condition for trichomycterids, because it is similar to the condition found in some species of *Trichomycterus* (*e.g.*, *T. rivulatum*), and perhaps also in the Tridentinae and in *Nematogenys*. If this is the case, the condition of the shelf in *Ochmacanthus* and *Haemomaster* may not be considered evidence that these two genera are related to other stegophilines.

5) Hyomandibular plate well developed (figs. 47-50).

The antero-medial edge of the hyomandibular is made up of a broad plate-like sheet of bone, which extends anterior to the articular facet of the hyomandibular with the sphenotic. The levator arcus palatini muscle originates on this portion of the hyomandibular. A crest of bone, for the origin of the adductor mandibulae, marks the posterior and lateral extent of this muscle origin in many trichomycterids.
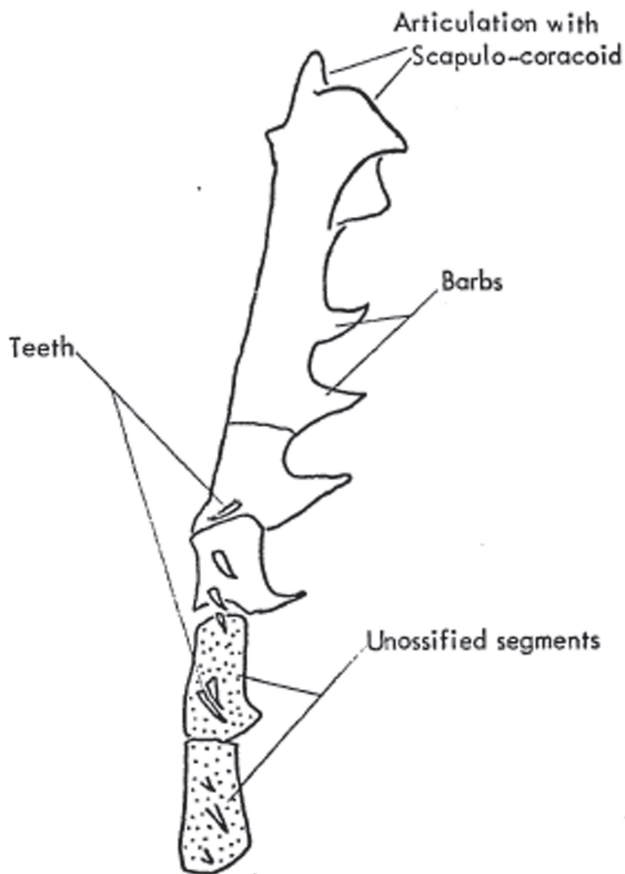
This hyomandibular plate is developed to at least some degree in most catfish groups, and the primitive condition for siluriforms is possibly that found in *Diplomystes* (fig. 54), *Nematogenys* (fig. 52), and astroblepids. In these groups a broad anterior extension of the hyomandibular, which may represent the hyomandibular plate of stegophilines, forms a suture with the metapterygoid. The metapterygoid also contacts the medial edge (or extension) of the quadrate.

The condition in *Trichomycterus* can be considered primitive for the family (fig. 41). Here there is a broad anterior part of the hyomandibular plate that extends along the dorso-medial edge of the quadrate, and contacts the metapterygoid. A small vertical part extends along the anterior edge of the main body of the hyomandibular. In the Stegophilinae the entire space between these two portions of the hyomandibular is

filled by the hyomandibular plate (cf. figs. 41, 47-50), but there is no contact with the metapterygoid. In *Pareiodon*, however, this plate is little more developed than in *Trichomycterus*. The well-developed hyomandibular plate of stegophilines, (especially the condition in *Ochmacanthus*), can equally well be considered the retention of a primitive condition (such as the condition in *Nematogenys*), or an advanced condition derived from a condition like that in *Trichomycterus*. This antero-medial portion of the hyomandibular is variously modified or absent in other trichomycterid groups, and a more detailed analysis will be necessary before the uncertainty can be resolved.

6) Scapulo-coracoid ring (=mesocoracoid?) (figs. 75-78).

All stegophilines have a small scapulo-coracoid with a
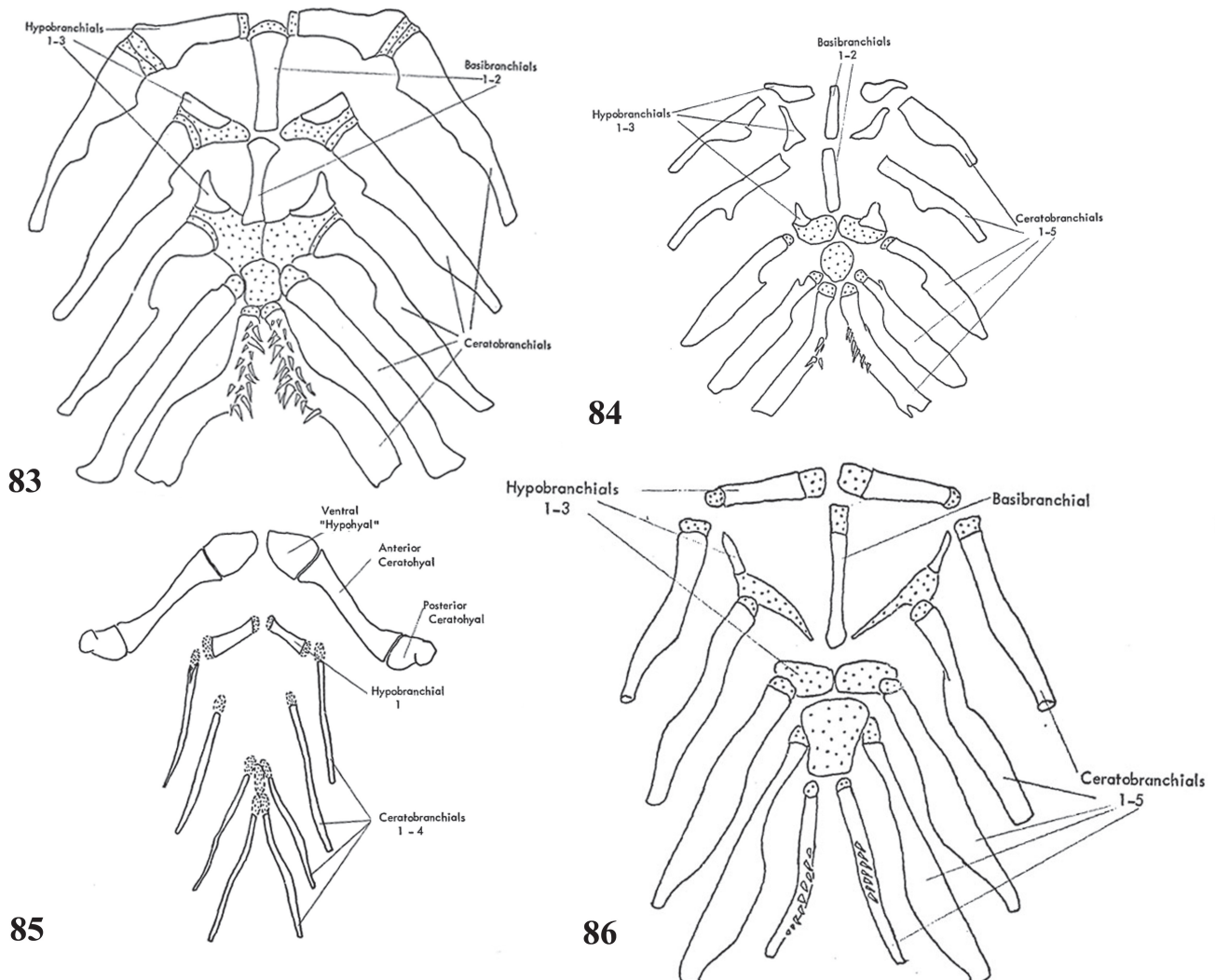
Fig. 83. Gill arches of *Trichomycterus rivulatum* (AMNH 20351), dorsal view, ventral parts, 20x magnification, cartilage stippled. **Fig. 84.** Gill arches of *Pygidianops eigenmanni* (CAS 11121), dorsal view, ventral parts, 60x magnification, cartilage stippled. **Fig. 85.** Hyobranchial apparatus of *Vandellia chirrosa* (AMNH 9663), dorsal view of ventral parts, 20x magnification, cartilage stippled. **Fig. 86.** Gill arches of *Pareiodon microps* (BH (NH) 1926-10-27: 270-273), dorsal view, ventral parts, 12x magnification, cartilage stippled.

very thin, delicate ring of bone extending medially (fig. 76). The cartilaginous proximal end of the more medial pectoral radial (the only one in most species) articulates with the ventral edge of this ring where the ring meets the body of the scapulo-coracoid. The presence of this ring on the scapulo-coracoid could be an advanced condition. It may, however, be at least partly formed by the mesocoracoid.

The presence of a mesocoracoid, fused with the scapulocoracoid, is the primitive condition for catfishes (Regan, 1911; Alexander, 1965). In *Diplomystes* it forms a thin bridge of bone on the posterior medial face of the scapula coracoid (fig. 77). The mesocoracoid has apparently been lost independently in a number of catfish groups (Regan, 1911; Tilak, 1963). It is present, however, in *Nematogenys*, and in loricariids, astroblepids, and callichthyids (Regan, 1911). Among trichomycterids, in at least the Trichomycterinae, there is a large opening in the scapulo-coracoid which is probably bordered by the mesocoracoid medially. In all of these fishes the more medial pectoral radials articulate with the bone forming the ventral edge of this opening. Also, in those catfish groups with a mesocoracoid, adductor muscles of the pectoral spine pass through the opening surrounded partially by the mesocoracoid (Alexander, 1965). A preliminary investigation of *Trichomycterus* and stegophilines indicates that the opening found in these fishes also is occupied by muscles inserting on the pectoral fin rays.

The condition in the stegophilines, compared to that in *Trichomycterus*, could represent a terminal stage in the reduction of the mesocoracoid (cf. figs. 75, 76). Among the remaining trichomycterids the Vandelliinae definitely lack the mesocoracoid (fig. 73). In the Tridentinae the scapulo-coracoid is unossified, in the Glanapteryginae it is apparently lacking altogether, and in *Malacoglanis* the mesocoracoid may be absent but the specimens available make this determination difficult. Thus, if the scapulocoracoid ring in the Stegophilinae is a mesocoracoid, as may well be the case, its presence may be considered a primitive character for the family. The rather unique condition of the mesocoracoid here however, forming the "scapulo-coracoid ring", may be considered an advanced condition, found in no other catfishes examined.

Relationships within the Stegophilinae

The Stegophilinae can be divided into two groups (fig. 3), one including only *Ochmacanthus*, and the other including the remaining six genera examined: *Haemomaster*, *Pareiodon*, *Pseudostegophilus*, *Stegophilus*, *Homodiaetus*, and *Apomatoceros*. The latter group, which will be referred to as the *Haemomaster*-group, is united by the following three advanced characters.

1) Cleithrum with a lateral process (figs. 70-74, 79-80).

In all stegophilines the lateral edge of the cleithrum, just lateral to the scapulo-coracoid, is a posteriorly directed flange of bone. This condition is found in other ostariophysans, and in most catfishes, including *Nematogenys* and other loricarioids, but in no other trichomycterids. This may

be considered a primitive condition for trichomycterids, retained only in stegophilines. In *Ochmacanthus* this flange is unmodified. In all other stegophilines it is modified into a finger-like process. *Haemomaster*, however, has this process only very slightly developed. Even this slight development of the lateral process can be used as evidence that *Haemomaster* is more closely related to the remaining stegophilines than to *Ochmacanthus*.

2) Weberian capsule with a well-developed neck-like constriction (figs. 14-29).

In all trichomycterids the lateral opening of the Weberian capsule is much smaller in diameter than the capsule itself. In at least some members of the Vandelliinae, Tridentinae and Stegophilinae the lateral portion of the capsule, between the opening and the swimbladder vesicle itself, is constricted into a narrow neck about the same diameter as the opening. The primitive condition for the family is like that in the Trichomycterinae, Glanapteryginae, Sarcoglanidinae, in which this constriction is very weakly developed, if at all.

Branchioica (a vandelliine) and *Ochmacanthus* have this constriction little more developed than *Trichomycterus* (cf. figs. 7, 17, 18), indicating that this may be the primitive condition for the Stegophilinae. If this is the case, then the more advanced condition, in which the length of the neck-like constriction is about equal to or greater than the diameter of the capsule, evolved independently in the Tridentinae and Stegophilinae. All of the stegophilines in the *Haemomaster*-group have the advanced condition, with the neck longer than that of *Ochmacanthus*. In *Haemomaster* the neck is least well developed.

3) Rows of teeth free in the upper lip, anterior to the premaxilla (figs. 28, 59, 70).

These anterior tooth rows, described on p. 153 below, are an advanced condition for trichomycterids. They are present, however, in five of the seven genera of the Stegophilinae examined (lacking in *Ochmacanthus* and *Pareiodon*) and in at least one of the Tridentinae. They could thus be considered evidence that the Stegophilinae and Tridentinae are sister groups (see discussion p. 148). The anterior tooth rows would thus be a primitive condition for the Stegophilinae (and for the Tridentinae), and independently lost in *Ochmacanthus*, *Pareiodon* and some of the Tridentinae.

The present hypothesis of relationships (see p. 148) indicates, however, that these tooth rows were evolved independently in these two subfamilies, and lost only in *Pareiodon*. The presence of these tooth rows is thus an advanced condition for the Stegophilinae.

Relationships within the *Haemomaster*-Group

Within the *Haemomaster*-group *Pareiodon*, *Pseudostegophilus*, *Stegophilus*, *Homodiaetus* and *Apomatoceros* share seven advanced characters not found in *Haemomaster*. These five genera will be referred to as the *Pareiodon*-group.

More than the usual amount of evidence (and effort) is needed here to establish this as a monophyletic group including *Pareiodon* because, as pointed out above, *Pareiodon* lacks some very striking characters found in all or most other stegophilines (*e.g.*, median premaxilla, anterior tooth rows in the upper lip, several rows of teeth on the premaxilla, wide crescent shaped ventral mouth). All of these characters are part of the mouth. The advanced characters that *Pareiodon* shares with other stegophilines, as described above, and especially those it shares with the other genera in the *Pareiodon*-group are also distinctive, numerous and come from several different parts of the animal. The most economic hypothesis is therefore the one put forth here: that *Pareiodon* has secondarily lost the advanced characters of the mouth and jaws.

4) Pterotic-supracleithral shelf better developed than in other stegophilines (figs. 22, 24, 26, 27, 50, 70).

In these five genera the shelf extends further to the side, than in other stegophilines, beyond the edges of the other neurocranial bones. The shelf is more pronounced because the anterior edge extends out more sharply from the side of the skull. It is also longer and involves more of the pterotic. In *Apomatoceros* most of the shelf is formed by the pterotic, whereas in *Haemomaster* most of it is formed by the supracleithrum. The shelf is also wider, most of the greater width being accounted for by development of the bone lateral to the sensory canal. In *Ochmacanthus* and *Haemomaster* the sensory canal is near the edge of the pterotic; in *Apomacanthus* most of the pterotic is lateral to the sensory canal.

Another striking feature of the shelf in these five genera is that the edge is distinctly convex. In *Ochmacanthus* and *Haemomaster* it is approximately straight or slightly indented.

5) Cleithrum emarginate (figs. 78-81).

In *Pseudostegophilus* the dorsal portion of the medial edge of the cleithrum is distinctly indented. The other members of the *Pareiodon*-group also have this emargination, but it is less distinct. No other trichomycterids have this condition.

6) Single median sensory pore (in the skin) from an epiphysial commissure of the supraorbital sensory canal (figs. l8, 20, 22, 24, 26, 27, 50).

In *Diplomystes*, *Nematogenys*, *Trichomycterus* and several other catfish groups medial extensions of the frontal bones meet across the cranial fontanel, over the epiphysial bar. Approximately opposite this bar, and between the eyes, sensory pores open from the supraorbital sensory canal in the lateral edges of the frontal bone. Externally, this appears as a pair of 3ensory pores in the skin, approximately between the eyes. This is the primitive condition for catfishes, and for trichomycterids.

In all of the Stegophilinae the fontanel is closed. In *Ochmacanthus* and *Haemomaster* the supraorbital sensory pores are paired. In the *Pareiodon*-group the supraorbital sensory canal on each side gives off a medial branch which meets, or nearly meets, the one from the opposite side in the midline. Thus only a single median sensory pore is found in the skin in these catfishes, except in *Homodiaetus* anisitsi and *Stegophilus* insidiosus in which a pair of pores is found very close together. No pore at all could be found here in the skin of Apomatoceros. Both species of the Sarcoglanidinae, also have a single median pore in the skin. This has evidently developed independently in this group.

7) Last two branchiostegal rays distinctly larger than the others (figs. 67-69).

The last two branchiostegal rays, which are also the most dorsally situated, are longer and thicker than the more anterior rays. They are also larger than the corresponding rays in *Haemomaster* and *Ochmacanthus*. These two rays in the *Pareiodon*-group may be compound, having developed by the fusion of two or more existing rays. This fusion is indicated by the double head and double tip on the second from the last ray. In *Pareiodon* there are four separate rays on the left side. On the right side one of these appears to be partially fused with the second from the last ray (fig. 68).

8) Caudal fin forked.

The primitive condition for trichomycterids is a truncated or slightly emarginated caudal fin, as is found in *Haemomaster* and most other trichomycterids. *Pareiodon*, *Pseudostegophilus* and *Apomatoceros* have strongly forked caudal fins. In *Stegophilus* and *Homodiaetus* the caudal fin is less strongly forked, but still more so than in the primitive condition.

9) Preopercular sensory canal joins the temporal canal in the pterotic bone (figs. 7, 17, 22, 24, 26, 27, 32, 33).

In most catfish groups, including *Diplomystes* and *Nematogenys*, these two sensory canals meet in the middle of the pterotic, so this can be considered the primitive condition for catfishes. In astroblepids, Loricarioid sp. and all trichomycterids other than the *Pareiodon*-group they meet at the anterior edge of the pterotic (or between the pterotic and the sphenotic). In the *Pareiodon*-group they meet in a more posterior part of the pterotic, as in the primitive condition for catfishes. The most parsimonious hypothesis, however, is that this condition has been secondarily arrived at in these stegophilines. It is therefore an advanced condition for trichomycterids, and for the Stegophilinae.

10) Lateral edge of the cleithrum with a distinct finger-like process (figs. 70, 80).

The lateral process of the cleithrum, described above (p.197) as an advanced character of the *Haemomaster*-group, is developed in the *Pareiodon*-group into a distinct finger-like process.

Relationships within the *Pareiodon*-Group

Within the *Pareiodon*-group four genera, *Pseudostegophilus*, *Stegophilus*, *Homodiaetus* and *Apomatoceros*, share advanced characters not found in *Pareiodon*. These are referred to as the *Stegophilus*-group.

11) Palatine bone with an extremely large antero-lateral head (figs. 20, 22, 50, 59).

This palatine head extends anteriorly beyond (and over the maxilla almost to the anterior edge of the premaxilla. The maxilla articulates with the side of this antero-lateral head.

12) The hyomandibular plate larger than in other stegophilines, and articulating with the orbitosphenoid (figs. 47-50).

The hyomandibular plate extends further anterior and dorsal than in other stegophilines. Its dorsal edge meets orbitosphenoid and the pterosphenoid portion of the compound prootic. This extends the hyomandibular articulation forward from its normal position on the sphenotic part of the compound prootic to include also the pterosphenoid portion and the orbitosphenoid. No other trichomycterids have the hyomandibular articulation extending this far forward.

A satisfactory scheme of relationships among these four genera in the *Stegophilus*-group has not yet been developed.

The Tridentinae

The Tridentinae is the only trichomycterid subfamily with sufficient material available at present for a critical evaluation of all the genera and species. A synonymy is therefore given below, to the level of species.

Genus *Miuroglanis* Eigenmann and Eigenmann

Miuroglanis Eigenmann and Eigenmann, 1889, p. 55 (type species, by original designation, *Miuroglanis platycephalus* Eigenmann and Eigenmann).
Miuroglanis platycephalus Eigenmann and Eigenmann
Miuroglanis platycephalus Eigenmann and Eigenmann, 1889, p. 56, (original description; Jutahy [Brazil]; type, M.C.Z. No. 8172).

Remarks: The monotypic genus *Miuroglanis* was described by Eigenmann and Eigenmann (1889) on the basis of a single 17 mm. specimen collected by the Thayer Expedition, M.C.Z. No. 8172. In his 1918 monograph Eigenmann reported (p. 371) that a recent search in the M.C.Z. failed to locate the type. The specimen examined by the present author was found in 1968 in the M.C.Z. type collection. It was labeled as the type of *Miuroglanis platycephalus*. The catalogue number, size of specimen and locality (Jutahy, Brazil) are all the same as given in the type description. However, Mrs. M. Dick, of the M.C.Z., informs me that this may not be the type specimen because Dr. Borodin had replaced missing types with specimens that fit their description.

The specimen of *Miuroglanis* in question agrees with the Eigenmanns' type description in most respects. Three characters, however, cast doubt on its authenticity, the dorsal fin origin just slightly anterior to the anal origin, the eye small relative to that of *Tridens* and the lack of pelvic fins. In the type description of *Miuroglanis* Eigenmann and Eigenmann (1889) state, "Origin of the dorsal little behing that of the anal." They could easily have been mistaken, since the specimen is poorly preserved and the first dorsal ray is preceded by a fold of skin.

He also states that the eye is large, but gives no other reference to its size relative to any body part, or to any other species.

The eye of the type specimen could be considered large for trichomycterids, and is certainly large relative to that of *Pareiodon*, the species listed just before the description of *Miuroglanis* in the 1889 paper. The eye of all other tridentines is distinctly larger, but it was not until later papers that Eigenmann placed *Miuroglanis* in this group. In the 1889 paper it is listed at the end of the paper, after the stegophilines and *Pareiodon*. Eigenmann and Eigenmann (1889) probably believed it to be related to these species, since it was their practice to list related species together.

No mention is made of the pelvic fins in the type description. If their absence had been noticed it probably would have been mentioned. It is possible, however, that it was not noticed, since the specimen is small and in poor condition. It is also possible that their absence was noticed, but considered an abnormality of this single specimen.

The specimen in hand is thus considered to be the actual type specimen described by Eigenmann and Eigenmann (1889).

Genus *Tridentopsis* Myers

Tridentopsis Myers, 1925, p. 84 (type species, by original designation, *Tridentopsis* pearsoni Myers).
Tridentopsis brevis (Eigenmann and Eigenmann)
Tridens brevis Eigenmann and Eigenmann, 1889, p. 54 (original description; Tabatinga [Amazonas; type, M.C.Z. No. 8160).
Tridentopsis brevis Myers, 1925, p. 86.
Tridensimilis brevis Schultz, 1944, p. 269.
Tridentopsis tocantinsi La Monte
Tridentopsis tocantinsi La Monte, 1939, pp. 1-2 (original description; aquarium material reported from Rio Tocantins, Brazil; type, A.M.N.H. No. 13967).
Tridentopsis pearsoni Myers
Tridens brevis (misidentification, not of Eigenmann and Eigenmann) Pearson, 1924, *pp.* 17-18, (description, adults, locality).
Tridentopsis pearsoni Myers, 1925, *pp.* 84-86 (original description, based on *Tridens* brevis of Pearson, 1925, not of Eigenmann and Eigenmann; Lake Rogoagua, Bolivia; holotype, C.A.S. (I.U.) No. 17664).

Remarks: Eigenmann (1918) suggests that brevis may not be congeneric with *Tridens melanops*, the type species of the genus described in 1889 to include both species. He also reports that the holotype, and only known specimen of brevis, is missing. There is thus no specimen or figure available, and the description is scanty. I nevertheless agree with Myers' (1925) interpretation that brevis is more closely related to *Tridentopsis* pearsoni than to melanops, rather than Schultz's interpretation of brevis being most closely related to *Tridensimilis venezuelae*. This is because brevis is described as having "six or more" opercular teeth, the anal fin origin "very little" anterior to the dorsal origin, and the first pectoral ray "greatly produced." Both *Tridens* and *Tridensimilis* have six or fewer opercular teeth and the anal origin distinctly anterior to the dorsal origin. *Tridentopsis* pearsoni is the only one of the Tridentinae with an elongate first pectoral ray.

Genus *Tridens* Eigenmann and Eigenmann

Tridens Eigenmann and Eigenmann, 1889, p. 53 (type species, by original designation, *Tridens melanops* Eigenmann and Eigenmann).
Tridens melanops Eigenmann and Eigenmann
Tridens melanops Eigenmann and Eigenmann, 1889, p. 53, (original description; Ica [Brazil - Peru boundary], 27 types, M.C.Z. No. 8137).
Remarks: Figured by Eigenmann 1918, plate XLIII, figs. 1-2.

Genus *Tridensimilis* Schultz

Tridensimilis Schultz, 1944, *pp.* 266-267 (type species, by original designation, *Tridensimilis venezuelae* Schultz).
Tridensimilis venezuelae Schultz
Tridensimilis venezuelae Schultz, 1944, pp. 267-268, plate 6, C (original description; Rio Negro below mouth of Rio Yasa, Maracaibo Basin, [Venezuela] *;* holotype, U.S.N.M. No. 121290).

Advanced Characters of Tridentinae

1) Fontanel expanded (fig. 28).

Most of the skull roof consists of a membrane-covered opening, the fontanel. The very narrow frontal bones form the edge of the skull roof and, along with the sphenotics, they form the lateral borders of the fontanel. The anterior fontanel border is formed by the posterior edge of the ethmoid, which separates the frontals anteriorly. The posterior border of the fontanel is formed by the supraoccipital. The fontanel length is about two-thirds of the length of the entire cranium (distance from the posterior edge of the supraoccipital to the anterior edge of the ethmoid). The fontanel width is equal to at least four fifths of the greatest cranium width (distance between the edges of the pterotic).

The primitive condition for the Trichomycteridae appears to be the presence of a much narrower fontanel, bordered only by the frontals and supraoccipital. It is divided into two

by a bridge formed by the frontal bones, over the epiphysial bar. The combined length of these two openings is no more than half the cranium length. This primitive condition occurs in *Trichomycterus* (fig. 7), and similar conditions occur in other siluriforms, cypriniforms and related teleost groups. An expanded fontanel, similar to that in the Tridentinae, occurs in one genus of the Vandelliinae, Branchio*ica* (see p. 155).

2) Maxillary bone very small (fig. 28).

The tridentines have the smallest and most weakly ossified maxilla in the family. It is just a tiny, barely ossified sliver of bone, lying behind the distal end of the premaxilla. The maxillary length is less than one tenth the length of the entire cranium.

3) Eyes exposed ventrally (fig. 66).

In all tridentines the eye is laterally placed, so as to be partially visible in ventral view. This condition occurs in only one other trichomycterid *species, Haemomaster* venezuelae, a stegophiline.

4) Opercular and interopercular tooth patches juxtaposed (figs. 51, 66). These tooth patches are separately movable, since they are on separate bones in all trichomycterids. In the tridentines, these tooth patches are separated by less than the width of either one of them. In *Miuroglanis* they give the appearance of forming a single continuous tooth patch. In *Tridens melanops* the size and number of teeth is .reduced, and the interopercular teeth point more ventrally than in other tridentines. Consequently, the space between tooth patches may appear to be greater than the width of the tooth patch in some specimens, especially if some teeth are missing.

The primitive condition of this character, found in all other trichomycterids, is for the space between tooth patches to be more than the width of the opercular patch. In most groups, it is also more than the width of the interopercular patch, but in the Trichomycterinae the interopercular patch is much more extensive, and is approximately equal to the distance between patches.

All these distances are measured at the base of the teeth where they contact the bone. The width is simply the greatest measurement of the tooth patch. This is usually a dorsal-ventral line, but will, of course, vary according to the orientation of the bones. The distance between patches is from the ventral edge of the opercular patch to the dorsal edge of the interopercular patch.

In almost all cases, this character can be distinguished on uncleared specimens, simply by eye, without actually measuring distances. The juxtaposition of these tooth patches is perhaps functionally related to the depressed condition of the head.

5) Opercular bone with a short ventral process (fig. 51).

The opercular bone of trichomycterids is approximately the shape of a backwards and upside-down L. The tooth patch is on the dorsal portion. The ventral portion, which is at least

as long as—the width of the tooth patch, extends down into a depression in the interoperculum. In the Tridentinae this ventral portion is about half as long as the width of the tooth patch.

6) Origin of dorsal fin just above or posterior to anal origin.

The anal origin has been reported to be anterior to the dorsal fin origin in all tridentines, based on observations of uncleared specimens. In *Tridens* and *Tridensimilis* the anal origin is clearly anterior, in *Tridentopsis* slightly anterior, but in the single known specimen of *Miuroglanis* is questionable. In all other trichomycterids with dorsal and anal fins, the dorsal fin origin is distinctly anterior to the anal origin.

The position of the dorsal fin can be best determined using x-rays or alizarin preparations. In this way, the position of the anterior-most splint can be best determined. These splints, however, are quite often variable or weakly developed. The best way to measure the relative positions of these fins in trichomycterids is by the positions of the pterygiophores relative to the vertebral column. The origins are defined as being at the vertebra whose neural spine is the first one anterior to the first pterygiophore. Using this criterion, the dorsal fin origin of *Miuroglanis* is one vertebra anterior to the anal origin. Externally, however, the origins appear virtually same. All other tridentines have the dorsal origin at least two vertebrae posterior to the anal origin.

7) Hyomandibular with distal process (fig. 51).

A process extends from the distal, medial edge of the hyomandibular. It starts as a broad medial extension, in a dorsal and sli9htly anterior direction. In a short distance, it curves sharply to a posterior direction, becomes distinctly narrower, and extends dorsally medial to the eye.

This distinctive process, not found in any other trichomycterid, may be an extension of the broad, plate like hyomandibular region found in some other trichomycterids (*e.g.*, Trichomycterinae and Stegophilinae) and in various other catfish families (see discussion p. 102).

8) Anal rays 15 or more.

Most Tridentinae have 18 to 22 anal rays. Only one, *Miuroglanis*, has 15. No other trichomycterid has more than 12, and most have 8 to 10, which is the primitive condition for the family.

Relationships within the Tridentinae

Within this subfamily three of the four included genera, *Tridens*, *Tridensimilis* and *Tridentopsis*, form a monophyletic group (fig. 4) which will be referred to as the *Tridens*-group. It is defined by the following characters, which are advanced for the subfamily. *Miuroglanis*, the only other member of the subfamily, is primitive in each of these characters, relative to the *Tridens*-group.

1) The *Tridens*-group has a greater number of anal rays, 18-22, whereas *Miuroglanis* has but 15.

2) The origin of the anal fin is anterior to the dorsal origin, with the anterior-most anal pterygiophore two vertebrae anterior to the dorsal pterygiophores.

3) The ventral exposure of the eye is at least as great, or greater than the dorsal exposure.

4) The eye is distinctly larger in the *Tridens*-group than in *Miuroglanis*.

All four of these characters are certainly advanced for the Trichomycteridae as a whole, as well as for the Tridentinae. Other tridentine characters are not so clearly interpreted. For example, *Miuroglanis* has gill openings restricted to a small lateral opening just in front of the pectoral fin, with the free posterior edge of the gill membrane restricted to the area just over L29 the gill opening. This is also the condition in the Vandelliinae and Stegophilinae (see p. 149), and is an advanced feature for trichomycterids. The subfamilial relationships proposed here (p. 148 and fig. 6), however, leads to the hypothesis that this advanced condition *(i.e.* the restricted gill opening and the lack of a free posterior edge of the branchiostegal membrane) was present in the common ancestor of the Vandelliinae and Stegophilinae, and independently developed in Miuro9lanis. (See also discussion on p. 148.)

The lack of a pelvic fin in *Miuroglanis* may be considered evidence that it is the closest relative of *Tridens melanops*, because the latter has the smallest pelvic fin, with the fewest rays (three) of any member of the Tridentinae, or related subfamilies. This also, however, is a less parsimonious interpretation of the data, especially considering the apparently independent loss of pelvics at least twice in more distantly related groups within the Trichomycteridae *(i.e.,* Trichomycterinae and Glanapteryginae), and in other siluriform and teleost groups.

Relationships Within the *Tridens*-group

Within the *Tridens*-group, *Tridensimilis venezuelae* is more closely related to *Tridens melanops* than to *Tridentopsis*. This conclusion is based on their sharing of the following characters, which are advanced for the *Tridens*-group, and for the Tridentinae. Both *Tridentopsis* and *Miuroglanis* are primitive with respect to these characters.

1) Fewer opercular teeth.

Tridensimilis has six and *Tridens* three, whereas *Tridentopsis* and *Miuroglanis* have at least 10-15.

2) Rictal barbel not visible externally (fig. 66).

In a cleared specimen of *Tridensimilis* the rudiment of the rictal barbel is visible as only the core of the barbel, extending from the maxilla into the lip. In the original description of *Tridens melanops* (Eigenmann and Eigenmann, 1889), it is stated, "…barbels minute, scarcely evident." (p.53), and Schultz (1944 states in a key p.266),

"…2 maxillary barbels present but minute". The only published figures of *Tridens melanops* (Eigenmann, 1918, plate XLIII, figs. 1-2) show but a single maxillary barbel on each side of the mouth, and I could find only these on uncleared paratypes. In *Tridentopsis* and *Miuroglanis* the rictal barbel is clearly visible, and equal to at least half the eye length.

3) Eyes face more ventrally than dorsally (fig. 66).

In *Tridens* and *Tridensimilis* the ventral aspect of the eye is clearly greater than the dorsal aspect. In *Tridentopsis* this is about equal.

4) Weberian capsule with an elongate neck (figs. 28, 29).

The lateral opening of the Weberian capsule, beneath the lateral cutaneous area, is at the end of a distinct neck-like constriction of the capsule, leading from the more medial, rounded portion of the capsule containing the ossicles and swimbladder. Other tridentines lack this neck-like constriction of the Weberian capsule. The interpretation of this neck as an advanced character for the Tridentinae is problematic (see discussion p. 146).

5) Anal fin origin three or more vertebrae anterior to dorsal origin.

In *Tridens* the anal fin origin is nine vertebrae anterior to the dorsal origin, in *Tridensimilis* three, and in *Tridentopsis* two. The greater number of vertebrae is an advanced character, and although the difference between *Tridensimilis* and *Tridentopsis* is small, it is consistent.

The Sarcoglanidinae

Genera recognized:

Malacoglanis, Myers and Weitzman, 1966, (type species by original designation, *Malacoglanis* gelatinosus Myers and Weitzman).

Sarcoglanis, Myers and Weitzman, 1966, (type species by original designation, *Sarcoglanis* simplex Myers and Weitzman).

Advanced Characters of the Sarcoglanidinae

Myers and Weitzman (1966) described this subfamily on the basis of three specimens, representing two new genera and species. Their descriptions are based mostly upon external characters, although an alizarin clearing was made of the single *Malacoglanis* paratype. With the aid of radiographs and this single alizarin preparation I am able to add some information to their descriptions. Most of this is internal osteological data on *Malacoglanis* only, and can thus only be used as evidence bearing on the relationships of the subfamily to other trichomycterids. The evidence that these two species form a natural group must come from characters that can be observed in both species, and most of these are by necessity external because *Sarcoglanis* simplex is known only from the holotype.

Myers and Weitzman list ten characters that the subfamily is "…especially characterized by" (p. 278). The following six of these "…set these fishes apart from all Trichomycteridae previously known."

l) "compact, little elongate body form" and 2.) "very large, relatively deep head."

Neither of these characters have been quantitatively analyzed here for trichomycterids. My observations, however, confirm that all other trichomycterids have more elongate bodies and more compressed heads than *Sarcoglanis*. This distinction is less clear in *Malacoglanis*.

Osteological characters examined here also tend to confirm this difference in body shape. The Sarcoglanidinae have fewer vertebrae (37-38) than any other trichomycterids, probably an advanced condition. The cranium of *Malacoglanis* is wider and deeper than other trichomycterids, also an advanced condition.

This compact external appearance of the body is due partly to the adipose organ (see below, p. 136), a thick band of tissue extending around the body to the ventral surface in the pectoral region. This structure is larger in *Sarcoglanis* than in *Malacoglanis*, and is an advanced character for the family.

3) "long adipose fin..."

The only other trichomycterids with a structure similar to an adipose fin are *Pygidianops* and *Typhlobelus* of the Glanapteryginae. If this is an advanced character for trichomycterids (see p. 44), it may be evidence that these two subfamilies are related.

4) "extremely large, broad pectoral fins, their length far greater than that of large head tips of pectoral rays not filamentous hut all of tips project far beyond membrane."

The pectoral fins of sarcoglanidines are definitely longer than those of any other trichomycterids, and this is probably an advanced character.

5) "upper jaw toothless; dentary teeth uniserial, long, cylindrical, conical and hooked inward at tip"

The lack of premaxillary teeth is an advanced character, as Myers and Weitzman point out (p. 284), found in no other trichomycterid and probably in no other catfish. The single alizarin stained specimen of *Typhlobelus* (Glanapteryginae), however, has but one small tooth on each premaxilla. One of the two remaining specimens of this species may lack such teeth altogether, but radiographs do not show this clearly.

Both glanapterygines and vandelliines have uniserial dentary teeth similar to those of sarcoglanidines. The primitive condition for the family is probably a patch of numerous, straight, conical teeth on each mandible, as is found in Trichomycterinae, and most catfishes. The dentary teeth of vandelliines are more strongly hooked inward, and those of the Glanapteryginae less so than in the Sarcoglanidinae. Thus, the condition of the dentary teeth as described by Myers and Weitzman cannot be used as evidence for relating *Sarcoglanis*

and *Malacoglanis* to each other any more closely than to vandelliines or glanapterygines.

6) "a conspicuous, sac-like, fat-filled, adipose organ on each side immediately above pectoral fins."

This pectoral adipose organ is a unique advanced character of the Sarcoglanidinae, as Myers and Weitzman 136 point out. It is possible that it is a modification of the axillary gland, which i5 well developed in most trichomycterids, especially in the stegophiline, *Ochmacanthus*. In *Sarcoglanis* there is a pore at the posterior edge of the adipose organ. It does not appear to be a sensory pore, and it is similar to the axillary pore found behind the pectoral base in all other trichomycterids. In *Malacoglanis* a number of pores are found over and around the adipose organ, but most of these appear to be sensory pores, and none could be clearly identified as the pore of an axillary gland. No dissection has been made since only the holotypes are available.

The Glanapteryginae

Glanapteryx, Myers, 1927, (type species by original designation, *Glanapteryx anguilla* Myers).
Pygidianops, Myers, 1944, (type species by original designation, *Pygidianops* eigenmanni Myers).
Typhlobelus, Myers, 1944, (type species by original designation, *Typhlobelus* ternetzi Myers).

Advanced Characters of the Glanapteryginae

1) Dorsal fin absent.

No trace of dorsal fin rays or pterygiophores is present in any member of this subfamily. *Pygidianops* and *Typhlobelus* have a narrow, translucent membrane along the back from the nape to the caudal fin, but this does not appear to represent the vestige of a dorsal fin. A similar membrane occurs in the Sarcoglanidinae (see below p. 163).

2) Pectoral rays one or none.

The pectoral fin of *Pygidianops* consists of only a single, rather short ray, fully divided. No trace of a pectoral appendage is found in *Typhlobelus*. *Glanapteryx* has tiny flaps of tissue that Myers (1927) interprets as pectorals "…reduced to useless *inconspicuous* fleshy flaps." (p. 129). No trace of fin rays could be found in these pectoral flaps, even with the use of radiographs. Staining or dissection was not attempted, since only the holotype is known.

3) Opercular and interopercular teeth absent (fig. 43).

No sign of opercular or interopercular teeth is found in any members of the Glanapteryginae. This is interpreted as a loss of these teeth (see p. 40), and is thus an advanced character within the Trichomycteridae. As such, it can be considered evidence for a relationship between the Glanapteryginae and other trichomycterids in which these teeth are either reduced or partially lacking *(i.e.,* Sarcoglanidinae, see p. 156). Opercular

and interopercular teeth like these do not occur in any other catfishes.

4) Fewer than seven anal rays, none segmented or branched.

All other trichomycterids have at least seven anal rays, some of which are segmented and branched. Some subfamilies have as few as eight, and the Sarcoglanidinae have seven. Both the Sarcoglanidinae and the Glanapteryginae are known from but a few specimens, so additional material may reveal overlap between these two groups in the number of anal rays, and between these two groups and others.

The lack of segment at *ion* and branching in the anal rays of *Pygidianops* and *Typhlobelus* is probably unique among trichomycterids and their relatives. This is probably part of a trend toward the loss of the anal fin, because *Glanapteryx* lacks this fin altogether.

5) Principle caudal rays 5/6 or fewer.

A trend within the Siluriformes as a whole has been toward a reduction in the number of caudal rays, from an apparently primitive condition of 9/9 (Lundberg and Baskin, 1969). The primitive condition for trichomycterids is 6/7. The Glanapteryginae is the only subfamily in which all members have fewer than 6/7 caudal rays. (One of the two *Ochmacanthus* species examined, *O. flabelliferus*, subfamily Stegophilinae, has 5/6 principle caudal rays).

As is the case with the number of anal rays, the difference between the Glanapteryginae and other subfamilies is sufficiently small that additional overlap will probably be found. The trend, nevertheless, is clear, and differences are sufficiently consistent between subfamilies to use the low number of caudal rays in *Pygidianops* (5/6), *Typhlobelus* (4/5) and *Glanapteryx* (3/3?) as evidence that they form a monophyletic group.

6) Pelvic fins minute or absent.

Glanapteryx has a pair of tiny flaps of tissue at the anterior edge of the anus. These are probably vestigial pelvic fins, as Myers (1927) suggests. As in the similar pectoral flaps of this species, no fin rays could be detected by Myers or myself.

Both of the remaining species of this subfamily lack pelvic fins completely. Pelvic fins are also absent from one species of the Tridentinae, *Miuroglanis* platycephalus, and at least two species of the Trichomycterinae (Miranda-Ribeiro, 1949).

Relationships within the Glanapteryginae

Pygidianops and *Glanapteryx* do not share any advanced characters that are not also found in *Typhlobelus*. Therefore the question of the relationships within this subfamily can be reduced to the question of whether *Typhlobelus* is more closely related to *Pygidianops* or to *Glanapteryx*.

Typhlobelus shares two advanced characters with *Pygidianops*. One is the absence of pelvic fins. (In *Glanapteryx* they are small but present.) The other character is the absence of functional eyes. In *Glanapteryx* the eyes are

small but appear functional, the primitive condition for the Trichomycteridae. *Pygidianops* has no external evidence of eyes, and in *Typhlobelus* there is only a small spot of dark pigment. No other trichomycterids are known to lack functional eyes.

Typhlobelus shares with *Glanapteryx* three characters that are apparently advanced for the subfamily. One is a high number of vertebrae. *Pygidianops* has 45, approximately the primitive number for the whole family. *Typhlobelus* has 60 and *Glanapteryx*, 84. (Only one other trichomycterid group has this many vertebrae, the Vandelliinae, which has from 48 to 67,) The second character is the lack of pectoral rays. *Typhlobelus* lacks any external trace of a pectoral fine *Glanapteryx* has a small pair of fleshy flaps, in which no rays could be detected. Since no stain could be used, several small rays could be present, which would reduce or negate the importance of this character. *Pygidianops* has one fairly long rayon each side. The third character shared by *Typhlobelus* and *Glanapteryx* is a reduced number of principle caudal rays. Since alizarin clearing of *Pygidianops* and *Typhlobelus* are available the number of '-rays (5/6 and 4/5 respectively) was accurately determined. The caudal fin of *Glanapteryx* is very small, weakly ossified, lacking distinct lobes (i.e., rounded) and has several relatively well developed procurrent rays. This makes reliable principle ray counts difficult at best because only radiographs can be used. Nevertheless, if the count of 3/3 found in *Glanapteryx* is correct, it is evidence of relationship with *Typhlobelus*, because no other trichomycterids have fewer than 5/6 caudal rays.

The tentative conclusion reached here (fig. 5) is that *Typhlobelus* and *Glanapteryx* are each others closest relatives. This is because they share more advanced characters with each other than either does with *Pygidianops*. Also, one of the advanced characters shared by *Typhlobelus* and *Pygidianops*, the lack of the pelvic fin, is also found in some other trichomycterid groups. A consequence of the conclusion that *Typhlobelus* and *Glanapteryx* are sister groups is that loss of pelvic fins and the reduction of the eyes evolved in parallel in *Typhlobelus* and *Pygidianops*.

RELATIONSHIPS AMONG TRICHOMYCTERID SUBFAMILIES

The six trichomycterid subfamilies defined above are divided into two monophyletic groups. One, the Trichomycterinae group, consists of the Trichomycterinae, the Glanapteryginae and the Sarcoglanidinae. The other, the Vandelliinae-group, consists of the Vandelliinae, the Tridentinae and the Stegophilinae (including the *Pareiodon*tinae).

The Vandelliinae-group

Advanced Characters of the Vandelliinae-group

The following advanced trichomycterid characters are found in all or most of the Vandelliinae, Tridentinae, Stegophilinae.

1) Absence of the lacrimal bone.

All other trichomycterids except some glanapterygines (*Typhlobelus* and perhaps *Glanapteryx*) have a well-developed lacrimal, as does *Nematogenys* and the other relatives of the Trichomycteridae.

2) Large eyes (the minimum eye length more than half of the snout length).

Catfishes generally have small eyes and this appears to be the primitive condition for the group (Alexander, 1965). All of the Vandelliinae-group except *Pareiodon* microps have eyes larger than those of other trichomycterids and their relatives. The best measure of the eye size in these fishes appears to be the eye length relative to the snout length. In all members of the Vandelliinae-group except *Pareiodon* the eye length is more than half the snout length, and in most it is about equal to the snout length. In all other trichomycterids and their relatives the eye length is one-third or less of the snout length. The very small size of the eye of *Pareiodon* (one-fourth the snout length) is probably a secondary condition.

3) Parasitic feeding habits of the Stegophilinae and Vandelliinae.

This includes the scale eating habit of *Apomatoceros alleni*, and perhaps other stegophilines. All of the *species* for which data is available in these two subfamilies have been reported to be parasitic. Kelly and Atz (1964) report that captive Vandellia would feed on nothing but blo0d directly from the gills of live gold fish.

The feeding habits of the Tridentinae in nature are unknown. However, Weitzman (pers. com.) observes that specimens in the aquarium appear to pursue characins (*Hyphessobrycon*) larger than themselves, but these same specimens would also take brine-shrimp or Daphnia. Until parasitism is discovered among the Tridentinae, parasitism can be used as evidence for a relationship only between the Stegophilinae and Vandelliinae.

4) Lateral opening of the Weberian capsule at the end of a neck-like constriction (figs. 45-51).

The primitive trichomycterid condition of the Weberian capsule (described on p. 65) is a sphere of bone with a small lateral opening beneath the lateral cutaneous area. Members of all three subfamilies of the Vandelliinae-group have the lateral portion of the capsule (between the lateral opening and the swim bladder vesicle) constricted like the long neck of a vase. Other members of each of these subfamilies have the primitive condition (i.e. the lack of this long neck), as do all of the Trichomycterinae-group. It is most probable that the common ancestor of the Vandelliinae-group had the primitive condition also. The occurrence of the advanced condition in members of all three subfamilies is evidence that they share some potential for this development, not present in the Trichomycterinae-group.

5) Lack of ossified third hypobranchials. (See discussion on page 159.)

Relationships within the Vandelliinae-Group

The relationships among the three subfamilies of the group remain problematic. The problem is whether the Stegophilinae are more closely related to the Vandelliinae or to the Tridentinae. Present evidence appears to favor the former alternative, but the evidence for each is given below.

The following five advanced trichomycterid characters are shared by all Vandelliinae and Stegophilinae:

1) Parasitic habits (see p. 146).

2) Maxillary and rictal barbels reduced (figs. 62-66).

In other trichomycterids the length of the maxillary barbel is much more than half the head length. This is also the ease in *Nematogenys*, Loricarioid sp. and callichthyids. In all stegophilines and vandelliines the maxillary barbel is less than half the head length, and in most members of these groups it is less than one-third.

The rictal barbel in the Vandelliinae and Stegophilinae is but a tiny flap of tissue at the base of the maxillary barbel. Often it is barely distinguishable. Other trichomycterids and some tridentines have a well-developed rictal barbel, more than half the length of the maxillary barbel. In *Tridens*, however, the rictal barbel is minute and in *Tridensimilis* it is not distinguishable at all externally. On the basis of the relationships within the Tridentinae discussed on p. 128 (see fig. 4) the reduction of the rictal (and maxillary) barbel J.49 may be considered to have occurred independently in the Tridentinae. However, the hypothesis of relationships within the Tridentinae is in part based upon the assumption that the small size of the barbels is an advanced character for the Tridentinae.

There is also a significant possibility that the "reduced" condition of the rictal barbel may be primitive for the Tridentinae, and perhaps primitive for the whole family Trichomycteridae. Since the rictal barbel probably first developed in the common ancestor of the Trichomycteridae it may have first appeared as a very small structure, and the small or rudimentary condition could well be primitive rather than advanced. Although the presence of a well-developed rictal barbel in some tridentines, and the association of the smaller rictal barbel with the smaller maxillary barbel is evidence against this interpretation, there is little difference in parsimony between these two interpretations.

3) Gill opening restricted to a small lateral opening (figs. 62, 63, 65, 66).

This restricted condition of the gill opening (fig. 65) is present in all members of both subfamilies. It is also found in one tridentine, *Miuroglanis* (see discussion under number four below).

4) Branchiostegal membrane lacks a free posterior edge (figs. 62, 63, 65, 66).

One additional advanced character is found in all vandelliines and most stegophilines—the branchiostegal membrane is completely confluent with the skin of the gular region, so there is no free posterior edge in this region. The only free edge of the gill membrane *i50* is directly over the gill opening. In some species of stegophilines there is a slight fold of skin across the throat, but this feature may vary according to the preservation. In most species there is either a distinct free edge of the branchiostegal membrane, or no hint of one.

It appears that the development of this advanced character, (i.e., the lack of a free edge of the branchiostegal membrane) in the Vandelliinae-group is the next evolutionary step after the gill opening has become restricted to the lateral surface. One species of the Tridentinae, *Miuroglanis* platycephalus, also has a restricted gill opening and no free branchiostegal membrane across the throat, as is the case in the Vandelliinae and Stegophilinae. The remaining five species in the Tridentinae have the primitive condition, with the gill opening unrestricted ventrally and the normal free branchiostegal membrane. The fact that the intermediate condition (i.e., free membrane with a restricted opening, as in some stegophilines) does not occur in the Tridentinae may be an indication that the advanced condition in *Miuroglanis* has developed independently of that of the Vandelliinae and Stegophilinae.

An alternative hypothesis is that this advanced condition (or at least the restricted gill opening) was present in the common ancestor of the Vandelliinae-group. It would thus be an advanced character of this group, and evidence for the group being monophyletic. However, this alternative appears less acceptable because it requires that the primitive condition was redeveloped in the tridentines.

A third possibility may also be considered, that *Miuroglanis* is not a tridentine e Present evidence (see p. 122 above) does not favor this interpretation, but only one specimen of *Miuroglanis* is known. Additional material may help resolve this problem. At present, the common ancestor of the Vandelliinae-group can only be attributed with a potential to develop the advanced characters of the gill opening described above in *Miuroglanis*, stegophilines and vandelliines. This potential, when defined, may be evidence favoring the proposed relationship among these three subfamilies. At present, the actual presence of the restricted gill opening is evidence for the relationship between the Vandelliinae and Stegophilinae.

5) Ventral process on the end of each ethmoid cornua (figs. l5, 19, 2l, 23, 25, 29).

The primitive condition for catfishes and for trichomycterids is to have the ethmoid cornuae as simple lateral extensions of the anterior end of the ethmoid, over the premaxillae, as in *Trichomycterus* (fig. 55). Branchioica also has this primitive condition, but in Plectrochilus and Vandellia the ends of the cornuae are forked, and articulate

with the premaxillae. The ventral process on the ethmoid cornua of all stegophilines also is involved in articulation with the premaxilla, and may correspond to the ventral arm of the forked cornua of Vandellia and Plectrochilus. A ventral process may also be present in tridentines (fig. 29).

The advanced trichomycterid characters shared by the Stegophilinae and Tridentinae are the following:

1) Teeth of the dentary and premaxillary bones are arranged in distinct rows.

The rows are more numerous toward the midline, and those of the premaxilla extend to the extreme corner of the mouth.

2) Teeth are found anterior to the premaxilla, in the flesh of the upper lip.

Several stegophilines have this condition, but only one tridentine, *Tridensimilis venezuelae*. (*Miuroglanis* may also have such teeth but this cannot be clearly determined with only the holotype available.) In all the species with this condition the teeth anterior to the premaxilla are the same size and form as those on the premaxilla, and arranged in one or more distinct rows parallel to the premaxillary tooth rows. These teeth are probably premaxillary teeth that have lost their attachment to the bone. The premaxillary bone of tridentines and stegophilines (except *Pareiodon*) is quite thin, especially its anterior edge, which in some species is actually formed only by the contiguously arranged bases of the anterior-most teeth.

The condition found in *Tridens melanops* could represent an intermediate stage in the evolution of the free tooth rows. This species has all the teeth of the upper jaw attached to the premaxilla, but the anteriormost tooth row is on the edge of the very thin premaxilla. There is a wide space between this row and the more posterior ones. The anterior row could become free by the loss of the anterior portion of the premaxilla.

The presence of these free tooth rows, whatever their evolutionary origin, is an advanced condition for trichomycterids.

3) The premaxillary teeth of stegophilines are 'S' shaped in lateral view (fig. 61).

This also is the case in at least some of the jaw teeth (dentary and perhaps premaxillary teeth) of tridentines.

4) Mouth width greater than width of neurocranium (figs. 20, 28, 62-66).

The mouth of the Stegophilinae and Tridentinae is extremely wide relative to that of the remaining trichomycterids, *Nematogenys*, and other loricarioids. This can be expressed in various ways. One of the most striking is that the distance between the extreme corners of the mouth (where the upper and lower lips meet) is at least equal to the greatest width of the neurocranium *(*in the occipital region). The distance between the tips of the premaxillae is also at least equal to the greatest neurocranium width. Also, the extreme corners of the mouth extend laterally beyond the lower jaw bones.

In association with the wide mouth of stegophilines and tridentines, the jaw teeth extend laterally further than those of other trichomycterids. The toothed surface of the dentary extends beyond the edge of the neurocranium and the quadrate-articular joint. The premaxillary bone and teeth extend further laterally than the dentary bone and teeth.

In addition to these four characters shared by stegophilines and tridentines, one stegophiline, *Haemomaster*, has eyes more laterally placed than any other member of this subfamily. Its eyes are slightly visible on the ventral side. This arrangement of the eyes is a condition found elsewhere among trichomycterids in the Tridentinae. This apparent parallel development in these two groups could also be considered evidence that they are related.

There is also some evidence that the Tridentinae and Vandelliinae are sister groups. The Tridentinae and one of the three genera of the Vandelliinae, Branchioica, share a very distinctive character: the cranial fontanel is expanded, leaving the roof of the skull unossified. The remaining Vandelliinae and all the stegophilines have the skull roof completely ossified, and the fontanel closed. This is the only advanced character shared only by the Tridentinae and Vandelliinae. Evidence given above indicates that the closest relative of the Vandelliinae is the Stegophilinae; therefore, the unossified skull roof has developed independently in the Tridentinae and Branchioica. Differences found in the skulls of Branchioica and tridentines (figs. 17, 28) tend to confirm this. The sphenotics form a much greater portion of the fontanel's lateral margin in Branchioica, and in tridentines the sphenotics overlap the frontals. Also, the posterior portion of the ethmoid of tridentines is broad, and forms the anterior border of the fontanel. In Branchioica it is very narrow and fits between the anterior ends of the frontals, which form most of the anterior border of the fontanel.

All vandelliines have but one pair of ribs and tridentines have one to five pairs. Stegophilines have four to eight. Thus the Vandelliinae and Tridentinae have both carried the trend toward the reduction in the number of ribs further than any of the stegophilines. This cannot be considered very significant evidence for their relationship because this is a common trend that appears to have taken place within other trichomycterid subfamilies (i.e., Glanapteryginae).

The Trichomycterinae-Group

The Trichomycterinae-group (Trichomycterinae, Glanapteryginae and Sarcoglanidinae) is less well defined \ than the Vandelliinae-group, and it may turn out that it is not a monophyletic group. The only character of the Trichomycterinae-group that is clearly advanced for the family Trichomycteridae is the presence of a fronto-lacrimal tendon bone (fig. 55).

The fronto-lacrimal tendon bone is an ossification in a tendon which extends from the edge of the frontal bone to the lacrimal. Eigenmann (1918, pl. 40, p. 376) erroneously identified it as the nasal. It is found in no other siluriform examined, has no sensory canal associated with it, and lies just beneath the skin in a position similar to the supraorbital of characoids. It is probably not a supraorbital bone, which is a primitive condition for Ostariophysi, because no other siluriform has a supraorbital, and the supraorbital is not a tendon bone.

The fronto-lacrimal tendon bone is present in all species of the Trichomycterinae, and in *Malacoglanis* of the Sarcoglanidinae (probably also in *Sarcoglanis*, but radiographs do not show it clearly). *Typhlobelus* of the Glanapteryginae lacks the tendon, the tendon hone, and the lacrimal bone. This is probably a secondary loss of the tendon bone, since another member of the Glanapteryginae, *Pygidianops*, has a lacrimal with a long posterior extension, and this extension is attached to the edge of the frontal by a tendon. This long posterior extension on the lacrimal of *Pygidianops* (fig. 12) could represent the tendon bone fused to the lacrimal. Even if this is not the case, the presence of the fronto-lacrimal tendon in *Pygidianops* may be evidence that the Glanapteryginae is part of the Trichomycterinae-group.

The Trichomycterinae group of subfamilies also has a character found in few other catfishes, hypobranchials 1, 2, and j all ossified. This is a primitive feature for teleosts and for Ostariophysi. The only catfishes, other than these trichomycterids, that have three hypobranchials ossified are the Amphiliidae, but most catfishes have the third pair present as cartilage. The trend within teleosts (Nelson, 1969), siluriforms and trichomycterids appears to generally be toward a reduction in the number 159 of ossified hypobranchials, and some have lost the cartilaginous ones also. One species of the Trichomycterinae- group, *Typhlobelus*, has no detectable hypobranchial elements, while all of the other species (for which information is available) have three ossified pairs. *Diplomystes* and all of the relatives of trichomycterids have fewer than three ossified hypobranchials. This allows the possibility that the common ancestor of trichomycterids may have had but two ossified pairs and that the Trichomycterinae-group secondarily developed ossification in the third hypobranchial cartilages. If this is the case, these ossified third hypobranchials can be considered an advanced character for the Trichomycteridae.

This hypothesis, however, is not significantly less probable than the alternative, that three ossified hypobranchials is the primitive condition for trichomycterids and for their relatives, and that reduction has occurred in parallel within the Trichomycteridae (in *Typhlobelus* and in the Vandelliinae-group) and their relatives, and in all other catfishes except the Amphiliidae. If this alternative hypothesis is acceptable, the lack of ossified third hypobranchials would be an advanced condition for the Trichomycteridae. This advanced condition could then be considered evidence that the Vandelliinae-group forms a monophyletic group.

A similar problematic character of the Trichomycterinae-group is the presence of a nasal barbel, associated with the anterior nostril. The occurrence of such a nasal barbel is widespread and variable in catfishes. It is present in all members of the Trichomycterinae-group, l6l but in only one species of the Vandelliinae-group, *Tridentopsis* pearsoni. It is also present in *Nematogenys*, but in none of the other relatives of trichomycterids or in Diplomystes. As in the case of the hypobranchial bones, either the presence or the absence of the nasal barbel may be the advanced condition for the Trichomycteridae, although its presence in *T. pearsoni* tends to favor absence as the advanced condition. This question cannot be resolved confidently with the present data.

Relationships within the Trichomycterinae-Group

Within this group of three subfamilies, the Glanapteryginae and the Sarcoglanidinae are more closely related to each other than either is to the Trichomycterinae. This is indicated by the following advanced characters shared by these two groups.

1) Opercular and interopercular teeth reduced or absent (figs. 42-43).

None of the Glanapteryginae have any opercular or interopercular teeth. *Malacoglanis* has four small teeth on the opercle (fig. 42), and *Sarcoglanis* has two. There are no interopercular teeth in *Sarcoglanis*, and only four very small ones in *Malacoglanis* (only one of these is well calcified). One other trichomycterid, *Apomatoceros* alleni, a stegophiline, lacks opercular teeth and has but a few small interopercular teeth.

2) Opercular bone with a long posterior process.

In trichomycterids gene rally the tooth bearing portion of the opercular bone is apart of the posterior edge that is more or less extended posteriorly. In the Sarcoglanidinae this toothed posterior extension is much longer and narrower than in other trichomycterids. In the Glanapteryginae the opercle also has a long narrow posterior process which probably bore teeth in the primitive condition.

3) A dorsal membrane present.

Typhlobelus and *Pygidianops*, but not *Glanapteryx*, have a membrane extending along the back. It appears to contain some fat tissue, but this was not confirmed histologically. *Sarcoglanis* has a similar membranous fold anterior to the dorsal fin (the "predorsal fold" of Myers and Weitzman, 1966) and a possible adipose fin extending from the caudal to the dorsal. *Malacoglanis* also has a long adipose fin, but it is much lower and less distinct, and similar to the predorsal fold of *Sarcoglanis* and glanapterygines.

The similarity of the adipose fin of *Malacoglanis* and *Sarcoglanis* to the predorsal fold of *Sarcoglanis* and the dorsal membrane of *Typhlobelus* and *Pygidianops* indicates that both structures may be remnants of an embryonic fin fold. The adipose fin of the Trichomycterinae- group may therefore have

developed independently of the adipose fin of other catfishes and other Euteleosteans. The dorsal membrane, or predorsal fold, of these fishes may therefore be considered an advanced character for trichomycterids.

4) Anal rays fewer than 8.

The primitive number of anal rays for the family is about 10. The Trichomycterinae has 9-10, and one stegophiline, *Pareiodon*, has 8. The only groups with fewer anal rays are the Sarcoglanidinae with 7, and the Glanapteryginae with 6 or none. This reduced number of anal rays cannot be considered important evidence for their relationship, however, because of the small amount of reduction difference and small sample size.

5) Reduced number of premaxillary teeth.

The Trichomycterinae have numerous teeth on the premaxillary and dentary bones, and this appears to be the primitive condition for the family. Both the Glanapteryginae and the Sarcoglanidinae have but a single series of about 5 - 10 teeth in the lower jaw, and the sarcoglanidines have no teeth in the upper jaw. The single alizarin stained specimen of *Pygidianops* has four teeth on each premaxillary, and the only stained *Typhlobelus* has one tooth on the left side only. Radiographs of the additional specimens do not show more teeth in these species, but *Glanapteryx* appears to have at least as many teeth as *Pygidianops*. Unfortunately these fishes are too small for radiographs to give an accurate picture of tooth number.

TRENDS IN THE EVOLUTION OF LORICARIOID CATFISHES

The sister group relationships proposed in the present work lead to hypotheses of the conditions of the common ancestors of these sister groups. The criterion of parsimony is used for the reconstruction of these hypothetical common ancestors. The differences between 165 the hypothetical ancestral conditions and the actual conditions of the descendent species (*i.e.*, the members of the sister group) leads further to hypotheses of the trends that have occurred in the evolution of these species.

The presence of integumentary teeth on segments of the first pectoral ray in both *Nematogenys inermis* and in most members of its sister group (Trichomycteridae, Loricariidae, Astroblepidae, Loricarioid sp. and Callichthyidae) indicates that this was the condition in the hypothetical common ancestor of all loricarioids. An alternative hypothesis, that the common ancestor of all loricarioids had the fully armored condition (le., integumentary teeth on ray segments of all fins, on bony plates in the skin of the head and body, and on the opercular bones) is less acceptable because it requires that *Nematogenys* would have lost armor and retained only teeth on the first pectoral ray.

The question, however, of the condition of the common ancestor of all remaining loricarioids (the Trichomycteridae and its sister group) is unclear. Two alternative hypotheses are possible. One i8 that the common ancestor of remaining loricarioids developed the fully armored condition. This leads to the further hypothesis that the fully armored condition is retained in the line leading to the Loricariidae and its relatives, and that trichomycterids have lost the armor and teeth on the fins and body, retaining only the teeth on the opercular bones. It is thus possible that the teeth on the opercular bones of trichomycterids got there by spreading from the pectoral fin.

An alternative hypothesis, equally as possible as the first, is that the fully armored condition evolved only in the evolutionary line leading to the Loricariidae and its relatives. This leads to the further hypothesis that the armor and teeth on the body were lost only once, in the Astroblepidae. Also, the common ancestor of the Trichomycteridae would have lost integumentary teeth only from the pectoral fin, never having had the armored condition found in other loricarioids. This alternative hypothesis implies that the teeth on the opercular bones of trichomycterids developed there independently, rather than having spread from some other part of the fish. It is at present difficult to evaluate the hypothesis of spreading from one part to the body to another verses that of independent development on different parts of the body.

Three things are clear for both of the two alternative hypotheses. The first is that the common ancestor of trichomycterids and loricariids had integumentary teeth on at least the opercular bones and pectoral fin. Tb. second is that integumentary teeth have been lost from various parts of the body in different loricarioids independently (i.e., lost from at least the pectoral fin, and po&8ibly from the whole body, in the Trichomycteridae, and from the head, body and opercular bones in the Astroblepidae). The third is that the common ancestor of all loricarioids had at least a potential, as yet undefined, to develop integumentary teeth all over its external surface. The exact point in loricarioid evolution at which this potential became fully expressed i8 not presently clear.

A further consideration of the habits and relationships among trichomycterids may shed some light upon the selective advantage under which the opercular teeth evolved. This in turn may help to clarify whether these teeth evolved independently in the trichomycterid line, or were present in the common ancestor of trichomycterids and loricariids, and hence developed as part of an overall development of integumentary teeth, as found in the armored catfishes today.

Members of the Trichomycterinae are reported to use their opercular teeth to secure a position on the substrate of fast running Andean streams (Eigenmann, 1918). These teeth may also be used by members of parasitic subfamilies to maintain a position on or in a host. However, the proposed relationships among trichomycterid subfamilies (fig. 6) leads to the conclusion that parasitic habits evolved only once among loricarioids, in the common ancestor of the Vandelliinae and Stegophilinae. Hence the opercular teeth may be primarily an adaption for securing a position on the bottom, with attachment on or in a host being secondary.

It is also possible to hypothesize that the general trend within the Trichomycteridae has been toward a reduction, and in some cases a loss, of the opercular teeth. Opercular teeth are well developed in the Trichomycterinae, Vandelliinae, Tridentinae and most members of the Stegophilinae, indicating that this was also the ease in the common ancestor of the entire family. This hypothetical common ancestor of the Trichomycteridae may have had opercular teeth as numerous as those of the Trichomycterinae (fig. 46). If this is the case, a consistent trend toward reduction in the number of opercular teeth can be hypothesized to have occurred in the Tridentinae, Vandelliinae and Stegophilinae. In all but one of the species in these three subfamilies the remaining opercular teeth are prominent. The exceptional species, *Apomatoceros* alleni, has lost all teeth from the opercle and reduced the number OD the interopercle to four. A second, independent trend toward reduction has taken place in the sister group of the Trichomycterinae, the Sarcoglanidinae and Glanapteryginae.

Opercular teeth are very weakly developed in the former (fig. 42) and lacking altogether in the latter. Both the Sarcoglanidinae and Glanapteryginae have very few jaw teeth also (see discussion p. l64), so their lack of opercular teeth may be part of an over-all trend toward tooth reduction in these two subfamilies. The opercular teeth in the common ancestor of Trichomycteridae and Loricariidae: may well have been much like those in the Loricariidae and Callichthyidae. In the latter two families integumentary teeth are more or less uniformly distributed on the sides and edges of the opercle. The trend in the trichomycterid line would then be first toward the development of opercular teeth in distinct patches, restricted to the posterior and ventral edges of the opercular bones (see description p. 39). The tooth reduction trend within the family could thus be considered as a continuation of an over-all reduction of integumentary teeth and their: specialization for the various trichomycterid modes of life.

It can therefore be concluded that in the evolutionary history of loricarioids integumentary teeth developed first on the pectoral fin in the common ancestor of all loricarioids. Then the common ancestor of trichomycterids and loricariids developed teeth on at least the opercular bones. Pectoral fin teeth were later lost in the line leading to the Trichomycteridae. The fully armored condition was either developed in the sister group of the Trichomycteridae, or retained from the common ancestor of trichomycterids and loricariids. Astroblepids, and perhaps also trichomycterids, have lost armor and teeth from the head, body and opercular bones.

Several distinct trends can also be distinguished in the evolution of the loricarioid' Weberian apparatus. Among loricarioids only *Nematogenys* has a full set of Weberian ossicles. This is the primitive condition for catfishes as well as for loricarioids. Remaining loricarioids lack the claustrum and intercalarium, although the absence of these two bones has been confirmed in only a few species from each loricarioid group.

A consolidation of the vertebrae of the Weberian apparatus has also occurred. The common ancestor of all loricarioids can be hypothesized to have had a condition similar to that of *Nematogenys* — an incomplete capsule with a wide lateral opening (fig. 32), the complex vertebra formed by vertebrae one through five with the sixth vertebra free.

The common ancestor of remaining loricarioids can be hypothesized to have had a fully formed capsule of bone surrounding each of the two distinct lateral swimbladder vesicles, with these vesicles occupying most of the space enclosed by bone. In astroblepids and some trichomycterids the diameter of the swimbladder vesicle and bony capsule has become reduced. In these fishes the capsule has also become vase shaped (see description p. 147), with a neck portion extending laterally to just beneath the lateral cutaneous area. This entire trend, from the capsule with a wide lateral opening to the smaller vase shaped capsule with a small lateral opening at the end of a neck, has occurred both in the evolutionary line leading to the Astroblepidae and independently in the Trichomycteridae.

The common ancestor of all trichomycterids can be hypothesized to have had a condition similar to that of Trichomycterus, *Pygidianops* and Branchioica, with a large capsule but a small lateral opening with a short constriction of the capsule around the opening. A smaller capsule with a proportionally longer neck has apparently developed independently in the Tridentinae, Vandelliinae and Stegophilinae, since each of these subfamilies has members with the more primitive condition. This trend is carried to its extreme in the Stegophilinae, especially in the genera of the *Pareiodon*-group, in which the length of the neck has become greater than the diameter of the capsule enclosing the swimbladder vesicle. This trend is reversed in the Glanapteryginae, in which the neck is very indistinct (Pygidianops) or lacking (*Typhlobelus*).

The 12 advanced characters uniting the Trichomycteridae (see pp. 35-56) can be hypothesized to have developed in the common ancestor of the family. The most conspicuoU8 feature of this group of characters is the predominance of characters involving loss of a particular structure (*e.g.* adipose fin), or the failure to produce a particular modification (egg. pectoral and dorsal fin spines).

Among these advanced characters i8 the unmodified condition of the dorsal and pectoral fins (i.e., lacking spines and locking devices, see pp. 45-50). The conclusion that this represents a reduction or loss of the spines and associated structures leads to the additional hypothesis that the fully developed condition was present in both the common ancestor of all loricarioids and the common ancestor of the Trichomycteridae and Loricariidae, and that the reduced condition evolved independently in trichomycterids and in *Nematogenys*. These characters cannot be considered as having evolved as adaptations for a parasitic way of life because the present evidence indicates that parasitism evolved only in the Vandelliinae group of subfamilies, and that the common ancestor of all trichomycterids was not a parasite.

Some of these modifications, however, may have been advantageous to those trichomycterids which later evolved parasitic habits. For example, a fish such as Branchioica, which enters the gill chambers of other fishes, may find it disadvantageous to have a pectoral or dorsal fin spine when maneuvering to enter or leave a gill cavity. A fish such as Vandellia, which inserts its head into the gill chamber might find it an additional advantage to have the dorsal fin in a posterior position.

If this posterior position of the trichomycterid dorsal fin (on the posterior half of the body) can be considered as advanced character, as concluded above (p. 45), the even more posterior position of the dorsal fin in the Tridentinae, posterior to the anal fin origin, can be considered as a continuation of this trend. The complete lack of a dorsal fin in the Glanapteryginae may also be a continuation of th.is reduction trend.

It is also hypothesized that in the common ancestor of the Glanapteryginae the pectoral fin was reduced to a tiny flap of tissue with but a single ray, as in *Pygidianops*. Within the Glanapteryginae there i8 a trend toward the further reduction (*Glanapteryx*) and loss (*Typhlobelus*) of the pectoral fine The pelvic fins are also reduced in *Glanapteryx* and lacking in *Pygidianops* and *Typhlobelus*. The Glanapteryginae are all elongate fishes, and the loss of fins, especially pelvics, is a common feature of elongate teleosts generally.

The common ancestor of the Trichomycteridae is hypothesized also to have bad small eyes (one third of the snout length or less). Two trends in eye size have occurred within the family. One trend has been a decrease in the eye size in the Trichomycterinae-group. In the Trichomycterinae the eye is small, and in larger specimens of some species it tends to be covered with thickened skin and papillae (Tchernavin, 1944). In the Sarcoglanidinae the eye is as small as or smaller than in the Trichomycterinae. The eyes of the Glanapteryginae are smaller yet, less than one-tenth the snout length in *Glanapteryx*, reduced to only a dark pigment spot externally in *Typhlobelus* and indistinguishable externally in *Pygidianops*.

A second trend is an increase in the eye size (one-' half the snout length or more) in the common ancestor of the Vandelliinae-group. This group of subfamilies includes all the known parasitic species of the family. One species of the Stegophilinae which has not been reported to be a parasite, *Pareiodon* microps, has reversed this trend and reduced the eye diameter to less than one third the snout length.

Among the Stegophilinae several features of the skull and feeding apparatus show distinct evolutionary trends. One of these trends is the development of a wide crescent shaped mouth, which is partially developed in the Tridentinae and well developed in all stegophilines except *Pareiodon*. The similarities between the mouths of tridentines and stegophilines may, however, be independent developments, because the closest relative of the Stegophilinae is here proposed to be the Vandelliinae. In the Stegophilinae the mouth is wider and more crescent shaped than in the

Tridentinae, as indicated by the fact that in stegophilines the lateral-most premaxillary teeth in the upper lips are situated directly lateral to the dentary teeth (see pp. 98-99 and fig. 65). This crescent shape of the upper lip is even further developed in the *Stegophilus* group of the Stegophilinae, in which the posterior premaxillary teeth extend lateral and posterior to the dentary teeth. This mouth development is most extreme in *Apomatoceros* alleni, in which the premaxillary teeth in the upper lip (anterior tooth rows) extend back to the articulation of the posterior ceratohyal and interopercle (fig. 70). This trend has been reversed in *Pareiodon*, the closest relative of the *Stegophilus*-group. Sere the mouth opening is only slightly curved, and the upper lip is not wide and crescent shaped.

The *Stegophilus*-group is also distinctive among stegophilines in having an enlarged lateral head of the palatine, and a larger maxillary bone than other stegophilines. These osteological features may be functionally related to the operation of the wide mouth and lips.

An additional trend in the stegophiline feeding apparatus is the development of rows of teeth in the lip anterior to the premaxilla (anterior tooth rows, see pp. 97 and 136). This condition is most highly developed in *Haemomaster*, which has eight of these anterior tooth rows. *Pareiodon* has lost these teeth and has retained only the teeth attached to the premaxillary bone.

The shape of the jaw teeth of the Stegophilinae has evolved from the primitive conical shape found in Trichomycterus to a distinctly curved, almost S shape (fig. 61). An intermediate, somewhat less curved condition, is found in the Tridentinae and Vandelliinae. *Pareiodon* has developed this trend further yet. The curved proximal portion of the tooth is further modified into a narrow blade-like structure, separated from the distal, recurved cusp (top of the S) by a distinct notch.

An additional distinctive feature of the stegophiline jaws is the presence of a median premaxilla. This structure is present in all species of the subfamily except *Pareiodon*, in which it also has been lost (see discussion p. 99).

All the genera of stegophilines except *Pareiodon* have been reported to contain at least some parasitic species. The distinctive feeding apparatus and small eyes of *Pareiodon* may be an indication that its feeding habits are substantially different from those of other stegophilines, and that the large eyes of other stegophilines are related to their parasitic feeding habits.

Trends toward the reduction of the hyobranchial apparatus have also occurred throughout trichomycterid history. The common ancestor of the family can be hypothesized to have lost the dorsohyal and interhyal. The most marked reduction has taken place in the Vandelliinae, in which the common ancestor can be hypothesized to have lost all hypobranchials except the first pair, lost the anterior basibranchials, the ossified fourth infrapharyngobranchial, the teeth from the pharyngeal tooth plates and the fifth ceratobranchial and its associated teeth. This trend is carried further yet in one member of the Vandelliinae, *Branchioica*, in which the

fourth ceratobranchial is also lacking. This over-all reduction of the vandelliine gill arches may be functionally related to their SaDguisugou8 habits (see discussion p. 88). The Stegophilinae, which are also parasites and are here prop08ed as the sister group of the Vandelliinae, have an intermediate condition. The fifth ceratobranchial is smaller, relative to the first four ceratobranchials, than in other trichomycterids and other loricarioids.

CLASSIFICATION

A phylogenetic classification expressing the relationships of Trichomycteridae with other catfish groups, as proposed in the present work, could be as follows:

Suborder Loricarioidei
 Superfamily Nematogenyoidae
  Family Nematogenyidae
 Superfamily Loricarioidae
  Family Trichomycteridae
  Family Loricariidae
   Subfamily Callichthyinae
   Subfamily Loricariinae
    Tribe __ (including only Loricarioid sp.)
    Tribe Loricariini
     Subtribe Loricariina
     Subtribe Astroblepina

The following is a phylogenetic classification expressing the relationships within the Trichomycteridae as proposed in figure 6:

Family Trichomycteridae
 Subfamily Trichomycterinae
  Tribe Trichomycterini
  Tribe Glanapterygini
   Subtribe Glanapterygina
   Subtribe Sarcoglanidina
 Subfamily Vandelliinae
  Tribe Tridentini
  Tribe Vandelliini
   Subtribe Vandelliina
   Subtribe Stegophilina

APPENDIX

THE SIGNIFICANCE OF AN UNDESCRIBED LORI-CARIOID

It has been the consensus among ichthyologists, including myself, that the Callichthyidae, Loricariidae and Astroblepidae form a natural group, and that astroblepids may be more closely related to loricariids than to callichthyids (see above p. 75).

During the course of the present investigation the conclusion was reached that these three families form the sister group of the Trichomycteridae. This conclusion was based upon their sharing advanced characters of the Weberian apparatus, including fully encapsulated lateral swimbladder vesicles, and integumentary teeth. At this point in the investigation Dr. John Lundberg called to my attention a tiny undescribed catfish species collected by Dr. R.M. Bailey in Bolivia in 1965.

Dr. Bailey's undescribed catfish is referred to here as Loricarioid sp. It shares the following advanced characters with the group consisting of callichthyids, loricariids and astroblepids:

1) Dermal bony plates on the body, bearing integumentary teeth (fig. 38).
Separate, tooth bearing bony plates in the skin, not associated with the lateral line canal, are found among catfishes in callichthyids and loricariids only. Astroblepids, the closest relatives of the loricariids, are naked, which is the primitive condition for catfishes. Whether they have lost this armor, or never had such armor, remains an open question.

2) Integumentary teeth on all fins, and on skull bones (figs.37-38).
Nematogenys has integumentary teeth only on the pectoral spine. Only loricariids, astroblepids and callichthyids have these teeth on all the fins. Loricariids and callichthyids have integumentary teeth on the skull bones also, including the opercular bones. (The lack of these teeth on the skull bones of astroblepids could either be a primitive condition or a secondary loss.) The conclusion reached above (see discussion p. 57 and fig. 1), that *Nematogenys* is the sister-group of all other loricarioids, leads to the hypothesis that the presence of integumentary teeth on all fins and on the skull bones is an advanced condition within the Loricarioidei.

3) Complete bony capsules surrounding separate lateral swimbladder vesicles (figs. 33-38).
This condition occurs also in trichomycterids, and perhaps in some other catfish groups (see above, p. 64). Thus it cannot be used alone as evidence of relationship between Loricarioid sp. and the armored catfishes. A number of the additional advanced characters of the Weberian apparatus found in trichomycterids and their relatives (see above, p. 66) may be discovered in Loricarioid sp.

4) First pair of ribs (on the 6th vertebral much larger than others, and longitudinally compressed (figs. 35,38).

5) Supracleithrum at least partly covers the lateral opening of the Weberian capsule (figs. 33,36,37).
In callichthyids and loricariids the bone covering the lateral opening is probably the supracleithrum (Regan, 1911). In astroblepids and Loricarioid sp. the supracleithrum is apparently fused with the pterotic, and the posterior edge of this compound supracleithrum-pterotic bone partially covers the lateral opening of the Weberian capsule.

Loricarioid sp. also shares a number of additional advanced siluriform characters with loricariids and astroblepids, not found among callichthyids:

1) First pair of ribs with two heads articulating directly with the 6th vertebra.

This condition, described in Plecostomus by Alexander (1964), is found among the catfishes examined only in loricariids, astroblepids and Loricarioid sp. The rib has two distinct points of articulation with the vertebra, one high on the neural arch and the other directly below, in the middle of the cent rum.

2) Connecting bone between the distal end of the first rib and the second pterygiophore (figs. 35, 38).

In most catfishes, including these, the pterygiophores of the dorsal fin are modified for the support of the dorsal fin spine and the distal ends of the anterior pterygiophores extend laterally beneath the skin on each side of the fin. This is probably the primitive condition for catfishes.

In Loricarioid sp., loricariids and astroblepids, a bone extends beneath the skin from each of the lateral tips of the second pterygiophore to the distal portion of the first rib. In loricariids and Loricarioid sp. the connecting bone is plate-like. In astroblepids there is unossified tissue between the ends of this connecting bone and the rib and pterygiophore, and the connecting bone is a rod-like tendon bone. In callichthyids there is a muscle from the pterygiophore to the rib, but no bone.

3) Bicuspid teeth.

4) Snout with tooth-bearing bony plates (figs. 36-37).

Among catfishes, only the loricariids have tooth-bearing plates of bone on the snout. Loricarioid sp. also has a single median plate on the end of the snout, bearing large teeth. A pair of smaller tooth-bearing plates sutured to the dorso-lateral tip of the lateral ethmoid are also present in Loricarioid sp. and loricariids. These bones are lacking in astroblepids.

These shared advanced characters are evidence that Loricarioid sp. may be the sister group of the Loricariidae and Astroblepidae together. Although Loricarioid sp. more closely resembles the Loricariidae in two of these characters (nos. 2 and 4), Loricariidae and Astroblepidae still appear to be more closely related to each other than either is to Loricarioid sp. because they share the following advanced characters not found in Loricarioid sp.:

1) Mouth completely ventral, with lips expanded to form a sucking disc.

Callichthyids also have a ventral mouth, but no sucking disc. Loricarioid sp. has a simple, subterminal mouth, which is the primitive condition for catfishes.

2) Sixth vertebra sutured to the Weberian complex.

3) Lateropterygium present.

This is a large plate-like or spine-like bone embedded in the musculature of the body wall just over the place where the pelvic fin rays articulate with the pelvic girdle (Shelden, 1937). Its ventral end articulates with the girdle and first pelvic ray, indicating that it may be a modified pelvic splint or part of a ray. No other catfish has this structure.

The relationships of Loricarioid sp. proposed here make it possible to hypothesize that the common ancestor 188· of the Loricariidae and Astroblepidae had toothed armor on the body and head, and integumentary teeth on the skull and fin rays. This means that astroblepids have lost these characters, and retained only the integumentary teeth on the fin rays.

FOOTNOTES

[1]The ideas of various authors concerning the phylogenetic relationships within the Siluriformes can often only be inferred from their classifications. In the present work it is assumed that by placing species together in the same taxonomic category an author believed them to form a monophyletic group, unless the accompanying text or figures, such as dendrograms, indicate otherwise (*e.g.*, Eigenmann and Eigenmann, 1890). Of course such an assumption cannot be applied in the same sense to pre-Darwinian, or anti-Darwinian authors (*e.g.*, Agassiz). Their ideas of classification however will be treated in a similar manner, since their taxonomic insights should not be ignored. Many post-Darwinian workers still use the same criteria of overall similarity as evidence for phylogenetic relationship.

[2]This core material is stained by metholene blue. Alexander (1965) found that in *Cryptoperus* and Malopterurus it stained orange with Mallory's Triple, and contained neither cells nor fibers. He could not identify it histologically.

[3]One catfish family, the monotypic Hypophthalmidae, has a dorsal fin in a posterior position (origin at vertebra number 22) well behind the pelvic origin (vertebra number 13), but with a well-developed spine and lock. Both dorsal and pelvic fins, however, are on the anterior half of the body.

[4]The Cohort Euteleostei \l7as proposed by Greenwood *et al.* (1967) as equivalent to the Division III fishes of Greenwood *et al.* (1966).

[5]The Series Otophysi is used here in the sense of Rosen and Greenwood (1970) to include both the Cypriniformes and Siluriformes, which is included by them, together with the Series Anotophysi (including only the Gonorynchiformes), in the Superorder Ostariophysi.

[6]In the original description of *Tridentopsis* brevis, Eigenmann and Eigenmann (1889) states, "Opercle with a bunch of six or more spines."

SUMMARY

The major objective of this work is to define natural groups of siluriforms. The group with which this study is mainly concerned is the family Trichomycteridae (parasitic South American catfishes). A majority of the *species* formerly

assigned to this family have been examined, and a general search among many catfish groups has been conducted for characters that are advanced within the Siluriformes as a whole and within previously defined subgroups of siluriforms, and that are found only among trichomycterids.

Most of the characters are osteological. Cleared and alizarin-stained specimens were used wherever possible. Alizarin preparations of most siluriform families were examined.

The Trichomycteridae consists of a group of siluriform genera that have the following advanced siluriform characters:

1) Prootic, sphenotic and pterosphenoid form a single bone;

2) Dorsohyal lacking;

3) Interhyal lacking;

4) Patch of close set integumentary teeth on interopercle, similar patch on posterior extension of opercle;

5) Preopercular bone lacking sensory canal;

6) Rictal barbel present in upper lip;

7) Supraoccipital crest lacking;

8) Epural lacking;

9) Adipose fin lacking;

10) Dorsal fin rays unmodified, origin of dorsal on posterior half of body, posterior to origin of pelvic;

11) The first pectoral ray articulates only with the scapulo-coracoid, and forms neither a spine nor a locking device;

12) Scapulo-coracoids very small, not meeting in the midline.

The significance of these characters and their distribution among trichomycterids and other siluriforms is discussed. It is found that *Nematogenys*, *Phreatobius* and cetopsids lack all or most of these advanced characters, and that the Trichomycteridae of Gosline (1945), Myers (1944) and earlier workers may therefore be modified to exclude these forms. The remaining trichomycterid genera of Myers (1944) form a monophyletic group.

A list of twenty advanced ostariophysan characters is given which define the Siluriformes as a monophyletic group. The following four of these have not been previously given in definition of the order:

1) Dermosphenotic and autosphenotic co-ossified;

2) Pelvic radials absent;

3) Basihyal absent;

4) Supraorbital bone absent.

A hypothesis of the condition of the common ancestor of the Siluriformes is proposed on the basis of the assumption that the Diplomystidae is the sister group of all other catfishes.

The closest relative (i.e. the sister group in the sense of Hennig, 1966) of the Trichomycteridae is found to be a group of South American catfishes consisting of four subgroups: 1.) the Loricariidae (the armored, sucker-mouthed catfishes), 2.) the Astroblepidae (the naked sucker-mouthed catfishes, sister group of the loricariids), 3.) Loricarioid sp. (an undescribed armored species, the sister group of the loricariids plus astroblepids), 4.) the Callichthyidae (armored catfish, the sister group of loricariids, callichthyids and Loricarioid sp.). These four groups plus the trichomycterids sharenine advanced features of the Weberian apparatus. These nine features are apart of the trend, found generally among ostariophysans, toward the consolidation and reduction of the Weberian apparatus and the associated swimbladder vesicles. This trend has been carried further in these catfishes than in any others. All of these catfishes also have integumentary teeth (conical structures, on the external surface of the body, consisting of dentine and enamel, with a pulp cavity, connected to bone by connective tissue at the base). The only other siluriform with such teeth is *Nematogenys inermis*. *Nematogenys* also shares a number of the advanced characters of the Weberian apparatus with the Trichomycteridae and its relatives, and it is therefore considered to be the sister group of the Trichomycteridae and its closest relatives (the Loricariidae, the Astroblepidae, Loricarioid sp. and the Callichthyidae). The suborder Loricarioidei of Peyer (1922) and Chardon (1968) is therefore modified to include all of these catfishes, but not cetopsids or bunocephalids.

Six of the subfamilies recognized by Myers (1944) and other workers are recognized here. These are the Trichomycterinae, Glanapteryginae, Sarcoglanidinae, Vandelliinae, Stegophilinae and Tridentinae. Members of the Nematogenyinae, Phreatobiinae and Cetopsinae are excluded from the family because they lack the advanced characters shared by the remaining trichomycterids.

Pareiodon microps (the only member of the *Pareiodon*tinae) is considered a member of the Stegophilinae because its closest relatives are some, but not all, of the Stegophilinae. The advanced trichomycterid characters listed below are considered evidence that the six recognized subfamilies each form a monophyletic group. Additional monophyletic groups within subfamilies are also defined on the basis of additional advanced characters.

Trichomycterinae:

Genera recognized - *Eremophilus*, *Rhizosomichthys*, *Scleronema*, *Trichomycterus*.

No advanced characters have been found in the Trichomycterinae which are not also found in other trichomycterids, but this subfamily is recognized for the sake of convenience, until the relationships of the included genera are investigated in more detail.

Vandelliinae:

Genera recognized - Branchioica, Paracanthopoma, Paravandellia, Plectrochilus, Vandellia.
Advanced characters:

1.) Vomer in middle of upper jaw:

2.) Vomer toothed:

3.) Claw-like teeth on distal end of premaxilla, enclosed in a pocket of skin:

4) Dentaries well separated in midline

5) Pterotic process:

6) Pharyngeal teeth and fifth Ceratobranchial lacking;

7) Hypobranchials two and three lacking;

8) Infrapharyngobranchial four unossified;

9) Upper pharyngeal tooth plate toothless;

10) Parasitic feeding on the blood from other vertebrates;

11) Mesocoracoid absent.

Stegophilinae:

Genera recognized - *Acanthopoma*, *Apomatoceros*, *Haemomaster*, *Homodiaetus*, *Ochmacanthus*, *Parastegophilus*, *Pareiodon*, Pleurophysus, *Pseudostegophilus*, *Schultzichthys*, *Stegophilus*.

Advanced characters:

1) Mouth opening a wide crescent-shaped disc;

2) Median premaxilla;

3) Fontanel closed;

4) Pterotic-supracleithral shelf;

5) Hyomandibular plate well developed;

6) Scapulo-coracoid ring.

Within the Stegophilinae, the *Haemomaster*-group, consisting of *Haemomaster*, *Pareiodon*, *Pseudostegophilus*, *Stegophilus*, *Homodiaetus*, and *Apomatoceros*, share advanced characters not found in *Ochmacanthus*. Within the *Haemomaster*-group, *Haemomaster* is the sister group of the remaining five genera, which together comprise the *Pareiodon*-group. Within the *Pareiodon*-group, *Pareiodon* is the sister group of the remaining four genera.

Tridentinae:

Genera recognized - *Miuroglanis*, *Tridens*, *Tridensimilis*, *Tridentopsis*.

Advanced characters:

1.) Fontanel expanded;

2.) Maxillary bone very small;

3.) Eyes exposed ventrally;

4.) Opercular and interopercular tooth patches juxtaposed;

5.) Opercular bone with a short ventral process;

6.) Origin of dorsal fin just above or posterior to anal origin;

7.) Hyomandibular with distal process;

8.) Anal rays 15 or more.

Within the Tridentinae the members of the *Tridens* group, consisting of *Tridens*, *Tridensimilis* and *Tridentopsis* share advanced characters not found in *Miuroglanis*. Within the *Tridens*-group, *Tridentopsis* is the sister group of the remaining two genera.

Sarcoglanidinae:

Genera recognized - *Malacoglanis*, *Sarcoglanis*.

Advanced characters:

1) Compact, little elongate body form;

2) Very large, relatively deep head;

3) Long adipose fin:

4) Extremely large, broad pectoral fins, their length far greater than that of large head: tips of pectoral rays not filamentous hut all tips project far beyond membrane.

5) upper jaw toothless; dentary teeth uniserial, long, cylindrical, conical and hooked inward at tip:

6) A conspicuous, sac-like, fat-filled, adipose organ on each side immediately above pectoral fins.

Glanapteryginae:

Genera recognized - *Glanapteryx*, *Pygidianops*, *Typhlobelus*.

Advanced characters:

1) Dorsal fin absent:

2) Pectoral rays one or none:

3) Opercular and interopercular teeth absent:

4) Fewer than seven anal rays, none segmented or branched:

5) Principle caudal rays 5/6 or fewer:

6) Pelvic fins minute or absent.

The trichomycterid subfamilies recognized here are divided into two monophyletic groups, the Trichomycterinae-group (the Trichomycterinae, Glanapteryginae and Sarcoglanidinae) and the Vandelliinae-group (the Vandelliinae, Stegophilinae and Tridentinae).

The advanced characters of the Vandelliinae-group are:

1) Absence of the lacrimal bone;

2) Large eyes (the maximum eye length more than half of the snout length):

3) Parasitic feeding habits of the Stegophilinae and Vandelliinae:

4) Lateral opening of the Weberian capsule at the end of a neck-like constriction.

The relationships among the three subfamilies of the Vandelliinae-group are problematic. The Stegophilinae share several advanced characters with the Vandelliinae, and several with the Tridentinae. Present evidence favors the relationship of the Stegophilinae with the Vandelliinae rather than with the Tridentinae.

The only clearly advanced character uniting the Trichomycterinae-group is the presence of a frontolacrimal tendon bone. The members of this group also have a nasal barbel and three pairs of ossified hypo- ' .. branchial bones. Both of these last two characters could either be advanced or primitive characters for the Trichomycteridae.

The Glanapteryginae and Sarcoglanidinae share the following advanced characters not found in the Trichomycterinae:

1) Opercular and interopercular teeth reduced or absent;

2) Opercular bone with a long posterior process;

3) A dorsal membrane present:

4) Anal rays fewer than s:

5) Reduced number of premaxillary teeth.

A classification is presented which expresses the relationships proposed within the Loricarioidei and within the Trichomycteridae.

Some features of an undescribed species of loricarioid are discussed, and these features indicate that this species is the sister group of the Loricariidae and Astroblepidae together. The presence of tooth bearing bony plates in the skin of this undescribed species indicates that the Astroblepidae have secondarily lost this character.

The proposed sister group relationships among loricarioid catfishes leads to hypotheses of the evolutionary trends that have occurred among these fishes. One such trend is the development and subsequent loss of integumentary teeth. It is hypothesized that integumentary teeth developed first on the pectoral fin in the common ancestor of all loricarioids. Opercular teeth, and perhaps also a fully armored condition, later developed in the common ancestor of trichomycterids and loricariids. Teeth were lost from the pectoral fin in the common ancestor of the Trichomycteridae. Armor and teeth were also lost from the head, body and opercular bones in astroblepids, and perhaps also in trichomycterids.

The common ancestor of all loricarioids bad a full set of Weberian ossicles and partially encapsulated swimbladder vesicles. Loricarioids other than *Nematogenys* lost the claustrum and intercalarium, and developed the fully encapsulated condition of the Weberian apparatus. The Weberian capsule has been independently reduced in size and modified into a vase shape in the Astroblepidae and Trichomycteridae.

The common ancestor of all trichomycterids is hypothesized to have developed all twelve of the advanced characters of the family. Many of these characters which involve a loss of a particular condition (*e.g.* pectoral and dorsal fin spines) can be considered advantageous to a parasitic fish. The common ancestor of the Trichomycteridae is, however, hypothesized to have been a non-parasitic species. Parasitism evolved only in the common ancestor of the Vandelliinae and Stegophilinae. The Vandelliinae and Stegophilinae have also developed enlarged eyes and distinctive feeding mechanisms, which may be adaptations for their parasite habits·. *Pareiodon* microps, the only species of the Stegophilinae not reported to be parasitic, lacks most of these features (i.e., lacks enlarged eyes, crescent shaped mouth, anterior tooth rows, median premaxillary bone).

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