The Caudal Skeleton of the Catfishes, Order Siluriformes

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INTRODUCTION

The primitive condition for the adult teleost caudal skeleton is to have two separate centra (i.e. ural centra) posterior to the centrum that bears the last hemal arch (i.e. first preural centrum). In teleostean evolution there has been a trend to consolidate these caudal centra. In catfishes it is generally believed that both the first and second ural centra are co-ossified with the first preural centrum, a condition typical of many advanced groups of fishes.

The present study was initiated when the unexpected discovery was made of a separate second ural centrum in four unrelated catfish groups, a structure hitherto unreported in any ostariophysan. A survey of the caudal skeleton in the Siluriformes and related groups was undertaken in an attempt to determine the significance of this structure in the order.

In the course of the work several noteworthy trends and specializations were found in the caudal skeleton, which led to the present attempt to define the limits of diversity of the catfish caudal skeleton and to elucidate the trends in its evolution. We believe that focusing efforts on comparative studies of a single structural complex throughout the order will eventually lead to a better understanding of relationships

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within the Siluriformes. No innovations in siluriform classification will be made here, however.

Recently Gosline (1960, 1961), Nybelin (1963), Cavender (1966a, 1966b), and others have shown the systematic value of the teleostean caudal skeleton. Gosline (1960) pointed out the similarity between a basal siluriform (*Diplomystes*) and other basal Ostariophysi, and established some criteria for primitiveness of the caudal skeleton within this group. Published descriptions of the caudal skeleton of siluriform fishes, however, have left a false impression of structural constancy (McMurrich, 1884; Whitehouse, 1910; Gosline, 1960).

ABBREVIATIONS OF INSTITUTIONS

A.M.N.H., the American Museum of Natural History
I.U.M., Indiana University Museum (housed at the United States National Museum, Smithsonian Institution)
M.C.Z., Museum of Comparative Zoology, Harvard University
U.M.M.Z., University of Michigan, Museum of Zoology
U.S.N.M., United States National Museum, Smithsonian Institution
W.M.M., Witte Memorial Museum, San Antonio

ANATOMICAL ABBREVIATIONS

CA, point of emergence of caudal artery
EP, epural
FH, proximal foramen between hypurals 1 and 2
HS, hemal spine
HY_{1-6}, hypurals, 1–6
HYP, hypurapophysis
N, notochord
NS, neural spine
PH, parhypural
PU_{1-2}, preural centra, 1, 2
$PU_1 + U_1$ compound centrum formed from the first preural and the first ural centrum
R, outer principal ray
SHYP, secondary hypurapophysis
U_{1-2}, ural centra, 1, 2
UN, uroneural

MATERIALS AND METHODS

The material examined is listed below. The families and higher categories recognized and their arrangement follow Greenwood and others (1966). Within families the genera and species are arranged alphabetically.

Cleared and stained alizarin preparations were made using the

enzyme technique of Taylor (1967). On most specimens the cleared flesh was removed on one side to reveal more detail.

Radiographs were used as a supplementary tool, but in most cases information on the hypurapophyses was not provided by this technique.

Dissection of caudal musculature was made on specimens of *Pelteobagrus nudiceps, Ictalurus catus, Kryptopterus bleekeri, Trichomycterus rivulatus, Schilbe mystus,* and *Synodontis victoriae.* Developmental data were gathered primarily from growth series of *Ictalurus* and *Noturus.* Juvenile specimens of *Auchenoglanis ballayi, Mystus wolffi, Clarias batrachus, Plotosus anguillaris, Trichomycterus tiraquae,* an undetermined species of loricariid, *Gila atraria, Notropis cornutus, Carpiodes carpio,* and *Moxostoma erythrurum* were also examined.

MATERIAL EXAMINED
Clupeiformes

Clupeidae: *Brevoortia patronus* Goode: U.M.M.Z. No. 179139-S; *Dorosoma cepedianum* Lesueur: U.M.M.Z. No. 185340-S; *Opisthonema oglinum* (Lesueur): U.M.M.Z. No. 179137-S.

Engraulidae: *Anchoa hepsetus* (Linnaeus): U.M.M.Z. No. 179138-S.

Gonorynchiformes

Chanidae: *Chanos chanos* (Forskål): U.M.M.Z. uncatalogued (field no. L64-1289).

Cypriniformes

Characidae: *Brycon guatemalensis* Regan: U.M.M.Z. No. 183916; *Hoplias malabaricus* (Bloch): U.M.M.Z. No. 147344, uncatalogued (field No. B64-20); *Rhaphiodon vulpinus* (Agassiz): U.M.M.Z. uncatalogued (field No. B64-55); *Serrasalmus rhombeus* (Linnaeus): U.M.M.Z. uncatalogued (field No. B64-32).

Cyprinidae: *Cyprinus carpio* Linnaeus: U.M.M.Z. No. 182023-S; *Gila atraria* (Girard): U.M.M.Z. No. 141424; *Notropis cornutus* (Mitchill): A.M.N.H. No. 23780; *Opsariichthys uncirostris* (Schlegel): U.M.M.Z. No. 187604-S; *Ptychocheilus lucius* Girard: U.M.M.Z. No. 179579-S.

Catostomidae: *Carpiodes carpio* (Rafinesque): U.M.M.Z. uncatalogued; *Carpiodes cyprinus* (Lesueur): U.M.M.Z. No. 175896-S; *Cycleptus elongatus* (Lesueur): U.M.M.Z. No. 176973-S; *Moxostoma erythrurum* (Rafinesque): U.M.M.Z. No. 70849.

Siluriformes

Diplomystidae: *Diplomystes papillosus* (Valenciennes): M.C.Z. No. 8290, U.S.N.M. (I.U.M.) No. 15525.

Ictaluridae: *Ictalurus australis* (Meek): U.M.M.Z. No. 164711; *Ictalurus balsanus* (Jordan and Snyder): U.M.M.Z. No. 169854; *Ictalurus catus* (Linnaeus): A.M.N.H. No. 22031, U.M.M.Z. Nos. 186240, 186613, 186242; *Ictalurus dugesi* (Bean): U.M.M.Z. No. 179705; *Ictalurus furcatus* (Lesueur): U.M.M.Z. Nos. 155259, 186264, 186273, 169031, 186270; *Ictalurus lupus* (Girard): U.M.M.Z. No. 186503-S; *Ictalurus melas* (Rafinesque): A.M.N.H. No. 20991, U.M.M.Z. Nos. 116568, 116880, 98623, 165851; *Ictalurus natalis* (Lesueur): U.M.M.Z. Nos.

182060, 171788; *Ictalurus nebulosus* (Lesueur): U.M.M.Z. Nos. 182047, 163150, 165860; *Ictalurus platycephalus* (Girard): U.M.M.Z. Nos. 186257-S, 186241-S; *Ictalurus pricei* (Rutter): U.M.M.Z. No. 164539; *Ictalurus punctatus* (Rafinesque): A.M.N.H. No. 21013, U.M.M.Z. Nos. 169030-S, 186271-S, 186274-S, 186239-S, 186269-S, 186275-S, 186053-S; *Ictalurus serracanthus* Yerger and Relyea: U.M.M.Z. No. 186258; *Noturus eleutherus* Jordan: U.M.M.Z. No. 157575; *Noturus exilis* Nelson: U.M.M.Z. Nos. 128312, 162602; *Noturus flavus* Rafinesque: U.M.M.Z. Nos. 165842, 165833, 165842, 111742, 182039-S; *Noturus funebris* Gilbert and Swain: U.M.M.Z. No. 161058; *Noturus gilberti* Jordan and Evermann: U.M.M.Z. No. 165832; *Noturus gyrinus* (Mitchill): U.M.M.Z. Nos. 165861, 165862, 165863, 165867, 165868, 165869, 165856, 165858; *Noturus hildebrandi* (Bailey and Taylor): U.M.M.Z. No. 155338; *Noturus insignis* (Richardson): U.M.M.Z. Nos. 109631, 139453, 147590; *Noturus leptacanthus* Jordan: U.M.M.Z. Nos. 165880, 165878; *Noturus miurus* Jordan: U.M.M.Z. Nos. 165882, 165845, 165836; *Noturus nocturnus* Jordan and Gilbert: U.M.M.Z. Nos. 167214, 165883; *Noturus* sp.: U.M.M.Z. No. 167170; *Noturus* sp.: U.M.M.Z. No. 154650; *Noturus* sp.: U.M.M.Z. No. 142121; *Noturus* sp.: U.M.M.Z. No. 167654; *Noturus* sp.: U.M.M.Z. Nos. 165844, 165846, 107888, 110755; *Prietella phreatophila* Carranza: U.M.M.Z. No. 173788; *Pylodictis olivaris* (Rafinesque): U.M.M.Z. Nos. 152549, 169029, 186266; *Satan eurystomus* Hubbs and Bailey: W.M.M. 34, 20, 7, G; *Trogloglanis pattersoni* Eigenmann: W.M.M. 31, P, 61, 5.

Bagridae: *Auchenoglanis ballayi* (Sauvage): A.M.N.H. No. 6572; *Auchenoglanis occidentalis* Boulenger: A.M.N.H. No. 6632; *Bagroides malapterus* Bleeker: U.M.M.Z. No. 155695; *Bagrus docmac* Forskål: U.M.M.Z. No. 187332-S; *Bagrus ubangensis* Boulenger: A.M.N.H. No. 12375; *Chrysichthys cranchi* (Leach): A.M.N.H. No. 6598; *Chrysichthys ornatus* Boulenger: A.M.N.H. No. 6700; *Chrysichthys punctatus* Boulenger: A.M.N.H. No. 6541; *Clarotes laticeps* (Rüppell): A.M.N.H. No. 3181; *Coreobagrus ichikawai* Okada and Kubota: U.M.M.Z. No. 187544; *Gephyroglanis longipinnis* Boulenger: A.M.N.H. No. 6601; *Hemibagrus guttatus:* U.M.M.Z. No. 158517; *Heterobagrus bocourti* Bleeker: U.M.M.Z. No. 186738; *Liocassis dumerili* (Bleeker): A.M.N.H. No. 10361; *Liocassis siamensis* Regan: U.M.M.Z. No. 186730; *Liocassis ussuriensis* (Dybowski): A.M.N.H. No. 10359; *Mystus aor* (Hamilton): U.M.M.Z. No. 187866; *Mystus cavasius* (Hamilton): U.M.M.Z. No. 186731; *Mystus gulio* (Hamilton): A.M.N.H. No. 18300, U.M.M.Z. No. 186724; *Mystus micracanthus* (Bleeker): U.M.M.Z. No. 155714; *Mystus nemurus* (Valenciennes): U.M.M.Z. Nos. 186685, 186800; *Mystus rhegma* Fowler: U.M.M.Z. No. 186741; *Mystus vittatus* (Bloch): U.M.M.Z. Nos. 186780, 181190; *Mystus wijcki* (Bleeker): U.M.M.Z. No. 186785; *Mystus wolffi* (Bleeker): U.M.M.Z. Nos. 186686, 186753; *Pelteobagrus nudiceps* (Sauvage): U.M.M.Z. Nos. 183856-S, 187588-S, 187592-S; *Pseudobagrus aurantiacus* (Schlegel): U.M.M.Z. No. 183870; *Pseudobagrus fulvidraco* (Richardson): A.M.N.H. No. 10434; *Pseudobagrus vachelli* (Richardson): A.M.N.H. No. 10444; *Rita chrysea* Day: A.M.N.H. No. 20298; *Rita kuturnee:* U.S.N.M. No. 114950; *Rita rita* (Hamilton): U.M.M.Z. No. 187880.

Cranoglanididae: *Cranoglanis bouderius* (Richardson): U.S.N.M. No. 94590.

Siluridae: *Hemisilurus* sp. Bleeker: U.M.M.Z. No. 186853; *Hito taytayensis* Herre: U.M.M.Z. No. 100557; *Kryptopterus bleekeri* Günther: U.M.M.Z. No. 186726; *Kryptopterus cryptopterus* (Bleeker): U.M.M.Z. No. 186728; *Ompok bimaculatus* (Bloch): U.M.M.Z. No. 186684; *Parasilurus asotus* (Linnaeus):

A.M.N.H. No. 10404, U.M.M.Z. Nos. 180202, 187595, 187603; *Parasilurus lithophilus* Tomoda: U.M.M.Z. No. 187599-S; *Silurodes eugeneatus* (Vaillant): U.M.M.Z. No. 186479; *Silurodes hypophthalmus* (Bleeker): U.M.M.Z. No. 155679; *Silurus glanis* Linnaeus: A.M.N.H. No. 18758, U.M.M.Z. No. 174644; *Wallago dinema* Bleeker: U.M.M.Z. No. 186792; *Wallagonia attu* (Bloch): U.M.M.Z. No. 186736.

Schilbeidae: *Clupisoma garua* (Hamilton): U.M.M.Z. No. 187881; *Eutropius grenfelli* Boulenger: A.M.N.H. No. 6636; *Eutropius niloticus* Rüppell: A.M.N.H. No. 8149; *Helicophagus waandersi* Bleeker: U.M.M.Z. No. 186797; *Laides hexanema* (Bleeker): U.M.M.Z. No. 186798; *Parailia longifilis* Boulenger: A.M.N.H. No. 8915; *Pseudeutropius atherinoides* (Hamilton): U.M.M.Z. No. 187870; *Schilbe mystus* Linnaeus: U.M.M.Z. No. 187334-S, A.M.N.H. No. 6617; *Silonia silondia* (Hamilton): U.M.M.Z. No. 187882.

Pangasiidae: *Pangasius micronemus* Bleeker: U.M.M.Z. No. 186691-S; *Pangasius nasutus* (?) (Bleeker): U.M.M.Z. No. 155721; *Pangasius pangasius* (Hamilton): U.M.M.Z. No. 187883; *Pangasius siamensis* Steindachner: U.M.M.Z. No. 186804; *Pteropangasius cultratus* Smith: U.M.M.Z. No. 186714.

Amblycipitidae: *Amblyceps mangois* (Hamilton): A.M.N.H. No. 15765, U.M.M.Z. No. 187411; *Liobagrus anguillicaudatus* Nichols: A.M.N.H. No. 11069; *Liobagrus marginatus* (Günther): U.M.M.Z. No. 158518; *Liobagrus reini* Hilgendorf: U.M.M.Z. Nos. 183862, 187543.

Amphiliidae: *Amphilius longirostris* (Boulenger): U.M.M.Z. No. 38872; *Amphilius pictus* Nichols and LaMonte: A.M.M.H. No. 12314; *Amphilius* sp.: A.M.N.H. No. 27688; *Doumea typica* Sauvage: A.M.N.H. No. 6695; *Phractura scaphirhynchura* Vaillant: A.M.N.H. No. 6622.

Sisoridae: *Bagarius bagarius* (Hamilton): U.M.M.Z. No. 186793; *Glyptothorax sinense* Regan: A.M.N.H. No. 10625; *Glyptothorax trilineatus* Blyth: U.M.M.Z. No. 186849.

Clariidae: *Allabenchelys longicauda* Boulenger: U.M.M.Z. No. 197671; *Channallabes apus* Günther: A.M.N.H. No. 6516; *Clarias angolensis* Steindachner: A.M.N.H. No. 6639; *Clarias batrachus* (Linnaeus): U.M.M.Z. Nos. 186690, 155711; *Clarias fuscus* (Lacépède): A.M.N.H. Nos. 11066, 12186; *Heterobranchus longifilis* Valenciennes: A.M.N.H. Nos. 3054, 3134, 21980; *Xenoclarias holobranchus* Greenwood: U.M.M.Z. No. 187331.

Heteropneustidae: *Heteropneustes fossilis* (Bloch): A.M.N.H. Nos. 1908, 7611, 17276, U.M.M.Z. No. 187862.

Chacidae: *Chaca chaca* (Hamilton): A.M.N.H. No. 9496.

Malapteruridae: *Malapterurus electricus* Lacépède: A.M.N.H. Nos. 6688, 17847, 17951, U.M.M.Z. No. 169005.

Mochokidae: *Chiloglanis batesi* Boulenger: A.M.N.H. No. 6592; *Chiloglanis deckeni* Peters: A.M.N.H. No. 14289; *Chiloglanis niloticus* Boulenger: U.M.M.Z. No. 182016; *Euchilichthys dybowskii* (Vaillant): A.M.N.H. No. 6690; *Euchilichthys royauxi* Boulenger: A.M.N.H. No. 6567; *Microsynodontis batesi* Boulenger: A.M.N.H. No. 11741; *Synodontis clarias* (Linnaeus): A.M.N.H. No. 19678; *Synodontis depauwi* Boulenger: A.M.N.H. No. 17133; *Synodontis notatus* Vaillant: A.M.N.H. No. 6524; *Synodontis schalli* (Bloch and Schneider): U.M.M.Z. No. 169014; *Synodontis victoriae* Boulenger: U.M.M.Z. No. 187335-S.

Ariidae: *Arius caerulescens* (Günther): A.M.N.H. No. 24272; *Arius felis* (Linnaeus): U.M.M.Z. Nos. 186481-S, 186995-S; *Arius gagora* (Hamilton): U.M.M.Z.

No. 187892; *Arius liropus* (Bristol): A.M.N.H. No. 24873; *Bagre scutatus* (Regan): U.M.M.Z. No. 177343-S; *Batrachocephalus mino* (Hamilton): U.M.M.Z. No. 155787; *Genidens genidens* (Valenciennes): A.M.N.H. No. 20725; *Hemipimelodus borneensis* (Bleeker): U.M.M.Z. No. 181175; *Netuma kessleri* (Steindachner): A.M.N.H. No. 7560; *Netuma* sp. Bleeker: U.M.M.Z. No. 70346; *Potamarius nelsoni* (Bleeker): U.M.M.Z. No. 143496-S; *Selenaspis hertzbergi* Bloch: U.M.M.Z. No. 14209.

Doradidae: *Doras hancocki* (Valenciennes): A.M.N.H. No. 12945; *Doraops zuloagai* Schultz: U.M.M.Z. No. 142485; *Hemidoras carinatus* (Linnaeus): A.M.N.H. No. 12946.

Auchenipteridae: *Auchenipterus demerarae* Eigenmann: A.M.N.H. No. 12949; *Centromochlas steindachneri* Gill: U.M.M.Z. No. 256134; *Centromochlas* sp. Kner: U.M.M.Z. uncatalogued (field No. B64-24); *Centromochlas* sp. Kner: U.M.M.Z. No. 173420; *Tatia aulopygia* (Kner): A.M.N.H. No. 12947; *Trachelyopterus coriaceus* (Valenciennes): U.M.M.Z. No. 66321; *Trachycorystes galeatus* (Linnaeus): U.M.M.Z. uncatalogued (field Nos. B64-24, J.R.B.- No. 1, 1941).

Aspredinidae: *Agmus lyriformis* Eigenmann: A.M.N.H. No. 13684; *Aspredinichthys tibicen* (Temminck): A.M.N.H. No. 4397; *Bunocephalus bifidis* Eigenmann: U.M.M.Z. No. 66329; *Bunocephalus* sp.: U.M.M.Z. uncatalogued (field No. B64-15).

Plotosidae: *Copidoglanis* sp. Günther: A.M.N.H. No. 15038; *Paraplotosus albilabris* (Valenciennes): U.M.M.Z. No. 100219; *Plotosus canius* Hamilton: U.M.M.Z. No. 155792; *Plotosus lineatus* (Thunberg): A.M.N.H. No. 27730, U.M.M.Z. No. 185455.

Pimelodontidae: *Acentronichthys leptos* Eigenmann and Eigenmann: A.M.N.H. No. 8670; *Brachyglanis frenatus* Eigenmann: A.M.N.H. No. 9620; *Brachyplatystoma vaillanti* (Valenciennes): A.M.N.H. Nos. 3861, 3902; *Callophysus macropterus* (Lichtenstein): U.M.M.Z. No. 56142; *Cetopsorhamdia nasus* Eigenmann and Fisher: U.M.M.Z. No. 66313; *Chasmocranus longior* Eigenmann: U.M.M.Z. No. 185337; *Cheirocerus eques* Eigenmann: U.M.M.Z. No. 187223; *Conorhynchus conirostris* Valenciennes: U.M.M.Z. No. 147403; *Duopalatinus goeldii* Steindachner: A.M.N.H. No. 12590; *Goeldiella eques* (Muller and Troschel): A.M.N.H. No. 13660; *Hemisorubim platyrhynchus* (Valenciennes): U.M.M.Z. uncatalogued (field No. B64-47-b); *Heptapterus mustelinus* (Valenciennes): A.M.N.H. No. 8668; *Microglanis cottoides* (Boulenger): U.M.M.Z. No. 143294; *Microglanis iheringi* Gomes: U.M.M.Z. No. 143294; *Microglanis* sp. Eigenmann: A.M.N.H. No. 20878; *Nannorhamdia guttata* Pearson: U.M.M.Z. No. 66483; *Perugia xanthus* (Eigenmann): A.M.N.H. No. 5340, U.M.M.Z. No. 48039; *Phractocephalus hemiliopterus* (Bloch and Schneider): U.M.M.Z. uncatalogued (field No. B64-55); *Pimelodella chagresi* (Steindachner): A.M.N.H. No. 11406, U.M.M.Z. No. 145376; *Pimelodella gracilis* Valenciennes: U.M.M.Z. No. 66342; *Pimelodella macturki* Eigenmann: A.M.N.H. No. 12943; *Pimelodella roccae* Eigenmann: U.M.M.Z. No. 66344; *Pimelodus clarias* (Bloch): A.M.N.H. No. 13456; *Pimelodus ornatus* Kner: U.M.M.Z. No. 187229; *Pimelodus pictus* Steindachner: U.M.M.Z. No. 72639; *Pinirampus pirinampu* (Spix): A.M.N.H. No. 3758; *Platynematichthys punctulatus* (Kner): U.M.M.Z. uncatalogued (field No. B64-23); *Platystomichthys sturio* (Kner): A.M.N.H. No. 9317; *Pseudopimelodus roosevelti* Borodin: A.M.N.H. No. 26942; *Pseudopimelodus villosus* Eigenmann: A.M.N.H. Nos. 4419, 13658, U.M.M.Z. No. 142493; *Pseudoplatystoma fasciatum* (Linnaeus):

U.M.M.Z. uncatalogued (field No. B64-55); *Rhamdella rusbyi* Pearson: U.M.M.Z. No. 66317; *Rhamdia guatemalensis* (Günther): A.M.N.H. No. 24871, U.M.M.Z. Nos. 108578, 172506, 184554, 184738; *Rhamdia hypselura* (Günther): A.M.N.H. No. 24871, U.M.M.Z. Nos. 184739, 184739-S; *Sorubim lima* (Bloch and Schneider): A.M.N.H. Nos. 12589, 19908, 20883, U.M.M.Z. No. 66345; *Sorubimichthys planiceps* (Agassiz): A.M.N.H. No. 12584; *Sovichthys abuelo* Schultz: U.M.M.Z. No. 142496; *Zungaro zungaro* (Humboldt): U.M.M.Z. Nos. 66332, 66312.

Ageneiosidae: *Ageneiosus caucanus* Steindachner: A.M.N.H. No. 11395.

Hypophthalmidae: *Hypophthalmus edentatus* Spix: A.M.N.H. No. 4089.

Helogeneidae: *Helogenes marmoratus* Günther: A.M.N.H. Nos. 7113, 7133, 13332, 27689, 27690, U.M.M.Z. No. 185336.

Cetopsidae: *Cetopsis coecutiens* (Lichtenstein): A.M.N.H. No. 3870; *Cetopsogiton occidentalis* (Steindachner): U.M.M.Z. No. 160164; *Hemicetopsis macilentus* Eigenmann: A.M.N.H. No. 27692; *Pseudocetopsis plumbea* (Steindachner): U.M.M.Z. No. 66316.

Trichomycteridae: *Apomatocerus alleni* (?) Eigenmann: U.M.M.Z. uncatalogued (field No. B64-64); *Eremophilus mutisii* Humboldt: A.M.N.H. No. 7072, U.M.M.Z. No. 179261; *Homodiaetus maculatus* (Steindachner): U.M.M.Z. No. 143054; *Nematogenys inermis* (Guichenot): I.U.M. No. 15060; *Ochmacanthus* sp. Eigenmann: A.M.N.H. No. 27693, U.M.M.Z. uncatalogued (field No. B64-63); *Trichomycterus oroyae* (Eigenmann and Eigenmann): U.M.M.Z. No. 185319; *Trichomycterus quechuorum* (Steindachner): A.M.N.H. No. 20351; *Trichomycterus rivulatus* (Valenciennes): U.M.M.Z. No. 185330; *Trichomycterus tiraquae* Fowler: U.M.M.Z. uncatalogued (field No. B64-24); *Trichomycterus vermiculatus* (Eigenmann): A.M.N.H. No. 9084; *Trichomycterus zonatus* (Eigenmann): A.M.N.H. No. 9082; *Tridensimilis venezuelae* Schultz: U.M.M.Z. No. 142492; *Vandellia cirrhosa* Valenciennes: A.M.N.H. and U.M.M.Z. uncatalogued (field No. B64-24), A.M.N.H. No. 20497.

Callichthyidae: *Aspidoras rochai* von Ihering: U.M.M.Z. No. 147336; *Corydoras aenus* Gill: A.M.N.H. No. 21772, U.M.M.Z. No. 169066-S; *Corydoras julii* Steindachner: A.M.N.H. No. 27691; *Hoplosternum* sp. Gill: U.M.M.Z. uncatalogued.

Loricariidae: *Acestridium discus* Haseman: U.M.M.Z. No. 138203; *Ancistrus montanus* (Regan): U.M.M.Z. No. 66322; *Farlowella acus* (Kner): A.M.N.H. Nos. 8772, 14632; *Farlowella kneri* (Steindachner): U.M.M.Z. No. 187224; *Hypostomus latirostris* (Regan): U.M.M.Z. No. 177344-S; *Hypostomus plecostomus* (Linnaeus): U.M.M.Z. No. 187226; *Hypostomus* sp. Lacépède: U.M.M.Z. uncatalogued; *Loricaria filamentosa* (?) Steindachner: U.M.M.Z. No. 145366; *Otocinclus affinis* Steindachner: A.M.N.H. No. 22310; *Panaque dentex* (Günther): U.M.M.Z. No. 145396; Plecostominae, indeterminate: U.M.M.Z. No. 56127; *Pterygoplichthys multiradiatus* (Hancock): U.M.M.Z. No. 72632; *Rhinelepis levis* Pearson: U.M.M.Z. No. 66492; *Sturisoma panamense* (Eigenmann and Eigenmann): U.M.M.Z. No. 136268; *Xenocara gymnorhyncha* (Kner): U.M.M.Z. No. 143275.

Astroblepidae: *Astroblepus orientalis* (Boulenger): U.M.M.Z. No. 145378; *Astroblepus longifilis* (Steindachner): A.M.N.H. No. 11582.

TERMINOLOGY

Terminology for the caudal musculature follows Nursall (1963a). Terminology for the caudal skeleton is based on Nybelin (1963) except

for the modifications discussed below.

The last hemal spine is considered a hypural by Gosline (1960) and a typical hemal spine by Nybelin (1963). Following Monod (1967) this element is here termed the "parhypural." It is considered a distinctive structure for the following reasons: 1) It bears a process on its arch, the hypurapophysis, for the origin of the anterolateral portion of the hypochordal longitudinal muscle, which inserts on the upper principal caudal rays (Nursall 1963a, 1963b); 2) The posterior edge of its arch is notched, marking the point of emergence of the caudal artery from the hemal canal (Nybelin, 1963); 3) It supports the lowermost principal caudal fin ray. The remaining principal rays are supported by the hypurals, the lower two of which also serve as the origin for the remaining portion of the hypochordal longitudinal muscle (Nursall 1963a), which indicates that the parhypural is functionally related to the hypurals, rather than to the hemal spines.

Processes or shelves on the first and/or second hypurals, also for the attachment of the hypochordal longitudinal muscle, are termed "secondary hypurapophyses." The term "uroneural" replaces urodermal, following Patterson's (1968) recommendations.

The principal caudal fin rays were counted as all the branched rays plus one unbranched ray in each lobe, following Hubbs and Lagler (1947). Counts for each lobe, upper first, are separated by a plus sign.

RESULTS

Basic Pattern of the Siluriform Caudal Skeleton

The following description outlines the basic features of the caudal skeleton in the Siluriformes, which, taken together, distinguish fishes of this order from all other Recent fishes (see figs. 1, 2A).

1) The first preural (PU_1) and the first ural (U_1) centra are fused to form a compound centrum. Fusion takes place early in development before the onset of ossification in the caudal centra. Initially this compound centrum ($PU_1 + U_1$) is elongate and the zone of contact between PU_1 and U_1 is evident (fig. 2A). Marked shortening takes place with growth. This compound centrum has been interpreted as the terminal centrum by previous authors (Gosline, 1961; Greenwood and others, 1966). It is the functional terminal centrum in that it is the focal point of support for the remaining caudal elements. But, as will be shown below, there is a separate, although reduced, second ural centrum (U_2) which is structurally the terminal centrum.

2) A separate, usually reduced, second ural centrum (U_2) is present

and is fused with the bases of hypurals 3 and 4. Except in the few cases described below, U_2 does not develop as a normal centrum beyond the chordacentrum ("ring centrum") stage.[1] What are probably separate U_2 chordacentra are present in all ostariophysan young examined (fig. 2A, B) except the Loricariidae and Plotosidae. Early in the development of catfishes the bases of hypurals 3 and 4, and U_2 fuse. (In the Trichomycteridae only the base of hypural 3 fuses with U_2, as in the Cypri-
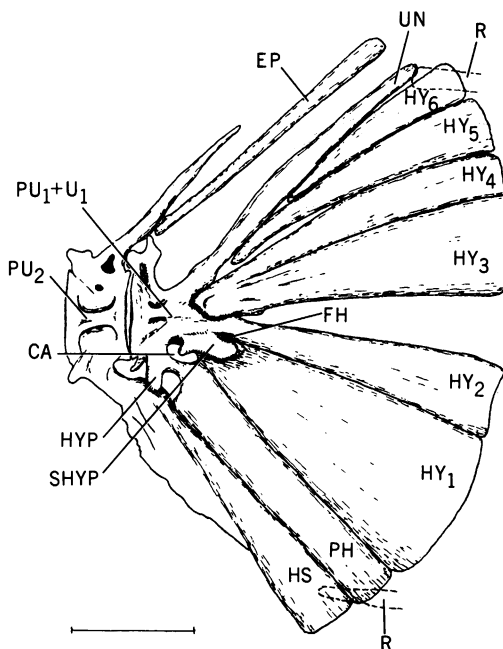

FIG. 1. Caudal skeleton of adult *Ictalurus punctatus* (U.M.M.Z. No. 186260-S), Type A (fig. 3), scale 5.0 mm.

niformes.) This fusion produces a knoblike mass at the base of hypurals 3 and 4 in which U_2 loses the appearance of a typical centrum. This structure, which is often further reduced, comes to lie in the cavity on the posterior face of the compound centrum (fig. 1). At this stage in development fusion of parts in this region most often ceases.

3) There is a maximum of four separate upper hypural elements.

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[1] Chordacentra, the ringlike calcifications in the fibrous sheath of the notochord, are present in the early development of teleosts. Autocentra, the definitive adult centra, appear later in development as ossifications in the perichordal sheath (François, 1966).
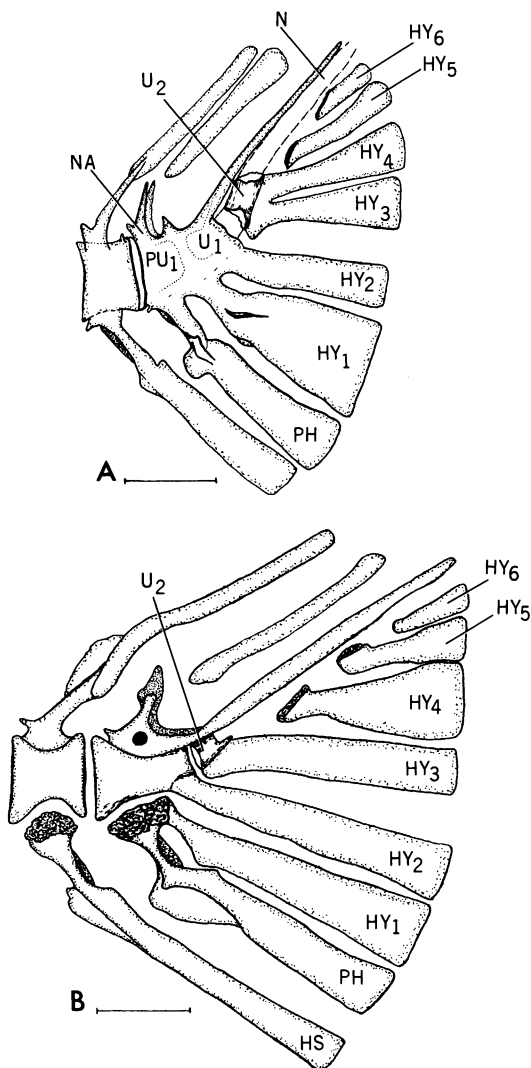
FIG. 2. Caudal skeletons: A. juvenile *Ictalurus punctatus* (U.M.M.Z. No. 178613); B. juvenile *Notropis cornutus* (Cyprinidae), (A.M.N.H. No. 23780).

4) Parhypural, hypural 1 and hypural 2 are fused with the compound centrum ($PU_1 + U_1$).

5) There is a secondary hypurapophysis. As in other teleosts the parhypural bears on its hemal arch the hypurapophysis, which serves as the site of origin for the anterolateral bundle of the hypochordal longi-

tudinal muscle (Nursall, 1963b). A similar structure, termed the secondary hypurapophysis, is present proximally on the first hypural and in some cases on the second hypural (fig. 3). The hypurapophysis and secondary hypurapophysis primitively take the form of separate processes, but in many catfishes they are continuous laterally, forming an extensive shelf in the horizontal septum. This shelf may extend from the parhypural to hypural 1 and hypural 2. Most of the hypochordal longitudinal muscle originates from the dorsal surface of this shelf. The ventral surface of the hypurapophyses is the site of origin for the posterior bundles of the deep ventral flexor muscles that insert on the lower caudal rays and the lowermost rays of the upper lobe. The over-all origin of the deep ventral flexor is more similar to that of salmonoids, Green and Green (1913), than to that of percoids (Nursall 1963a).

6) A nearly complete neural arch is fused to the anterior part of $PU_1 + U_1$.

7) A single, usually keeled, epural lies above the neural arch of $PU_1 + U_1$.

8) A single, paired uroneural element is fused completely with the posterior part of the compound centrum. It is probable that the uroneural element in catfishes is compound, being the result of fusion between anterior (first) and middle (second) uroneural elements, which are themselves compound (Patterson, 1968). An abnormal individual of *Parasilurus asotus* (U.M.M.Z. No. 187603-S) has the primitive ostariophysan uroneural condition with three separate elements, which is identical to the pattern described for *Brycon* by Gosline (1961) and Weitzman (1962).

9) All hemal arches are fused to their centra.

10) The caudal fin is distinctly lobed, with principal fin rays $9+9$ or $8+9$. The most primitive principal caudal ray count ($9+9$) occurs in *Diplomystes*. Most other fork-tailed catfishes possess the $8+9$ count. No catfish with a lobed caudal fin has more upper than lower principal rays. (See table 2 and discussion below.)

The following are advanced features, and may thus prove useful in determining the relationships of the order: 1) bases of hypurals 3 and 4 fused to a separate U_2; 2) parhypural and hypurals 1 and 2 fused to the compound centrum; 3) presence of a secondary hypurapophysis; 4) single epural; 5) single compound uroneural fused to the compound centrum; 6) all hemal arches fused to their centra; 7) principal caudal rays fewer than $10+9$, with lower principal rays equal to, or more numerous than, upper rays. Three of these advanced features, 1, 3, and 7, in addition to the patterns of hypural fusion, show phyletic trends

within the order and may thus be useful in determining relationships of subgroups within the Siluriformes.

PATTERNS OF HYPURAL FUSION

As in other teleosts, there has been an obvious trend within the Siluriformes to reduce the number of separate hypural elements through loss and fusion (table 1). Within the various siluriform groups similar or identical hypural patterns have evolved independently. For example, within the Mochokidae (African) the primitive pattern is PH + 1 + 2; 3 + 4;5 (see footnote to table 1 for an explanation of this notation) and the most primitive pattern of the Aspredinidae (South American) is PH; 1 + 2; 3 + 4 + 5. Most mochokids have fused the fifth hypural, and some aspredinids have fused the parhypural, thus both have arrived independently at the pattern PH + 1 + 2; 3 + 4 + 5.

As regards actual loss of elements, there is indirect evidence to suggest that the sixth hypural, i.e. the uppermost in the primitive siluriform tail, is lost. Some individuals with separate upper hypural elements (e.g. *Brachyglanis frenatus* and *Noturus leptacanthus*) are found to have in the position of the sixth hypural, median nodules of bone with staining properties similar to the fully formed hypurals. These may be the rudiments of the sixth hypural. Additional indirect evidence for the loss of hypural 6 is the absence of any fusion between hypurals 5 and 6. Various degrees of fusion have been observed between all other hypural elements. Gosline (1961) concluded that the sixth hypural element is lost also in some Catostomidae. There is no evidence that suggests the loss of any other hypural element in the Siluriformes.

As regards fusions between the remaining elements, there are problems with intraspecific and ontogenetic variation. For each species there is an absolute maximum number of separately ossified hypural elements, which occurs at least early in development. In many species this maximum number of separate hypural elements persists even in large adults. For example, six separate hypural elements are present in specimens of *Ictalurus furcatus* that reach 740 mm. in standard length. And, both small (83 mm. standard length) and large (310 mm. skull length) *Heterobranchus longifilis* have five separate hypural elements. Thus hypural fusion does not necessarily take place with increasing size.

The number of separate hypural elements, however, is often reduced by fusion during growth. In the most advanced forms (e.g. Loricariidae) the hypurals are fused very early in development. The composition of the resulting compound elements in the hypural complex is best determined by partial fusions between separate elements, and relative sizes

of single elements. This fusion has a constant pattern in many taxa, whereas in others fusion takes place seemingly at random. The most striking examples of high intraspecific variability are found in *Noturus gyrinus*. Sixteen juveniles from one population show the following distribution of fusion patterns:

> 1 specimen PH;1;2;3;4;5;6
> 4 specimens PH;1;2;3;4;5
> 2 specimens PH;1 + 2;3;4;5
> 2 specimens PH;1;2;3 + 4;5
> 2 specimens PH;1;2;3;4 + 5
> 3 specimens PH;1 + 2;3 + 4;5
> 2 specimens PH;1 + 2;3 + 4 + 5

Such data are not without systematic value, as this high variability is characteristic of this species and of several other species of the genus. In contrast, nine juvenile specimens of *N. exilis* from two populations all possess five separate hypural elements.

In all other cases where large samples are available, little or no intraspecific variation occurs. For example, a sample of 20 specimens of *Rhamdia guatemalensis* from four widely separate populations shows the following distribution of fusion patterns:

> 2 specimens PH;1 + 2;3;4;5
> 18 specimens PH;1 + 2;3 + 4;5

Similar situations occur in *Rhamdia hypselura, Liobagrus anguillicaudatus,* and various species of *Ictalurus, Mystus, Clarias,* and *Pimelodella.* For most species large samples from diverse populations are unavailable. Nevertheless, the relative constancy in patterns of hypural fusion in a variety of species and families justifies making a systematic evaluation of the hypural condition with the material available.

The most primitive hypural condition is one in which there are six separate hypurals and a separate parhypural. This is found in all or most species of the Diplomystidae, Ictaluridae, Bagridae, Cranoglanididae, Schilbeidae, Pangasiidae, and Cetopsidae. Occasional partial fusions may take place with growth in these species.

In the evolution of the catfishes the phyletic trend has been toward loss and fusion of hypurals. It is unlikely that this trend is ever reversed. Loss of the sixth hypural apparently takes place before species specific fusion patterns arise (*Malapterurus* may be an exception). In most cases the initial fusions are centrally placed, i.e. between hypurals 1 and 2 and/or 3 and 4. Subsequent fusions involve the addition of hypural 5, the parhypural, and finally fusion between hypurals 2 and 3. Examples of the most complete fusion patterns are found in the Plotosidae and Chacidae (PH + 1 + 2 + 3 + 4 + 5 + UN), and the Loricariidae

in which the uroneural and the epural ankylose to the hypural complex (figs. 6, 9).

HYPURAPOPHYSES

Within the catfishes, there is a repetitive trend toward the formation and elaboration of the complex processes and shelves referred to above as the hypurapophysis and secondary hypurapophysis. The hypurapophyses are found at various degrees of complexity (fig. 3). In its simplest form (fig. 3, Type A or E), the hypurapophysis is a projection on the parhypural arch and the secondary hypurapophysis takes the form of a lateral projection or ridge on the first or second hypural. The relatively primitive Type A condition of the hypurapophyses is found in *Diplomystes,* most ictalurids, schilbeids, pangasiids, and a few bagrids and silurids.

In some specimens of *Ictalurus* the hypurapophyses fuse distally, thus forming a horizontal shelf (fig. 3, Type B). This produces a dorsoventrally directed foramen between the bases of the hypurapophyses for a dorsal branch of the caudal artery. This shelf is consistently present in the Cetopsidae, Ageneiosidae, and Cranoglanididae and is found in some members of other families (table 1).

The Type B shelf may form a posterior projection lateral to the second hypural. Fusion of the base of this extension with hypural 2 produces the Type C condition that is the predominant pattern within the Siluriformes (fig. 3, Type C). In some groups the Type C shelf may shift dorsally to a position closer to the central axis of the vertebral column. This involves an equivalent shift of the hypurapophysis from the parhypural arch to the compound centrum. Most of the major shifts in this transition can be found within certain families (e.g. Bagridae) and sometimes within single genera (*Mystus*) but any one condition appears to be species specific. Some conditions are also specific for entire families (e.g. Pimelodontidae,[1] Type C).

In most Siluridae the secondary hypurapophysis forms a shelf on hypurals 1 and 2, whereas the hypurapophysis remains separate (fig. 3, Type D). This is probably an independent derivation from a Type A condition, rather than a reduction from a Type C condition. *Parasilurus* and *Silurus,* two silurid genera which retain other features primitive for the family (e.g. strong pectoral spines and a moderately large dorsal fin), possess the Type A pattern, but no silurid examined has the Type C condition. Type D hypurapophyses are also found in *Helogenes.*

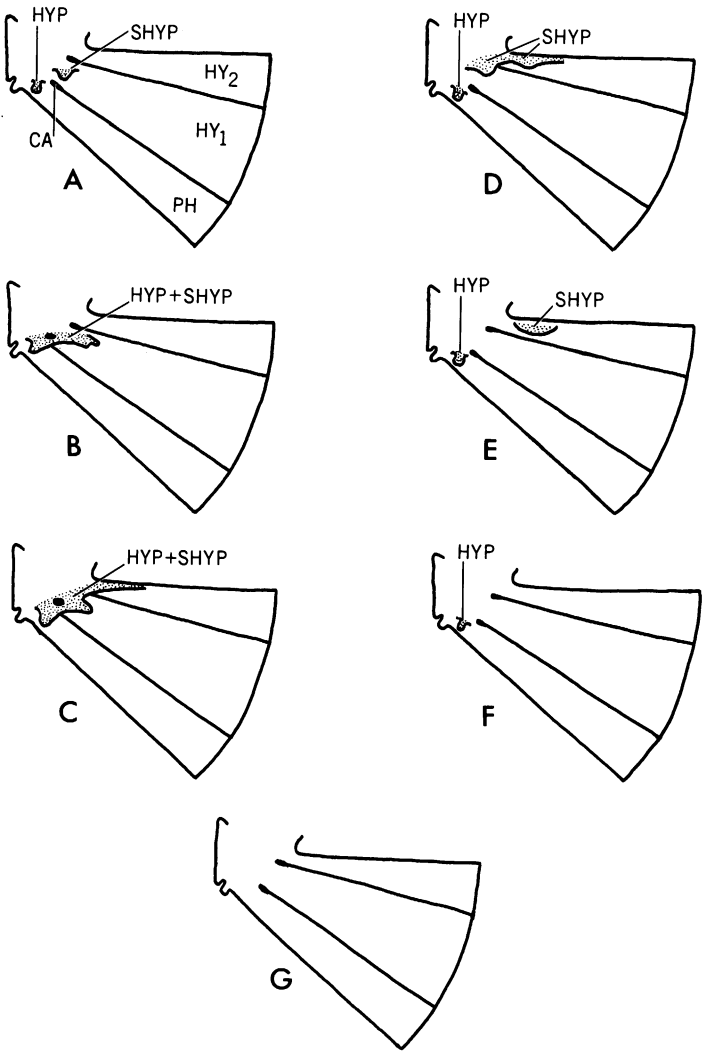[1] Romer (1965) corrected this name from Pimelodidae to Pimelodontidae.

FIG. 3. Types of hypurapophyses in the Siluriformes, semidiagrammatic. Hypurapophysis and secondary hypurapophysis stippled. Type A: Hypurapophysis on parhypural arch, secondary hypurapophysis on base of hypural 1. Type B: Hypurapophysis and secondary hypurapophysis continuous laterally, secondary hypurapophysis on hypural 1. Type C: Like Type B but secondary hypurapophysis on hypurals 1 and 2. Type D: Hypurapophysis on parhypural, secondary hypurapophysis on hypurals 1 and 2. Type E: Hypurapophysis on parhypural, secondary hypurapophysis on hypural 2. Type F: Hypurapophysis on parhypural, no secondary hypurapophysis. Type G: No hypurapophyses.

Weak or undeveloped sites for the origin of caudal musculature are found in a few unrelated forms. Within the Amblycipitidae, *Liobagrus anguillicaudatus* has Type C hypurapophyses. *Liobagrus reini* has the simpler condition of a hypurapophysis on the parhypural arch, and a separate secondary hypurapophysis present as a small ridge on the second hypural (fig. 3, Type E). *Amblyceps* lacks the small shelf on hypural 2 (fig. 3, Type F). Type F hypurapophyses are found also in *Heteropneustes* and many specimens of *Noturus*. The clariids, plotosids, and *Nematogenys inermis* lack hypurapophyses (fig. 3, Type G).

We are unable to reach a firm conclusion as to whether these weak or undeveloped patterns are primitive or the result of reduction. Their distribution among relatively advanced families perhaps argues for their being secondarily acquired (but see discussion of *Nematogenys* on page 42).

It is probable that at least most of these species with weak or undeveloped hypurapophyses tend toward the use of an eel-like type of locomotion in which the body forms one or more complete sine waves. In this type of locomotion the body provides a greater share of the thrust, and the caudal fin is rounded, with a low aspect ratio (Nursall, 1958). In these species, with less emphasis on the hypural and parhypural supported fin rays in locomotion, less well-developed caudal musculature might be expected (Nursall, 1963a), and hence less well-developed hypurapophyses. All of the species found to have Types F and G hypurapophysis conditions also have rounded caudal fins and a variable, often high number of principal caudal rays (see below and table 2). All of these features could be considered specializations for an eel-like type of locomotion.

FATE OF THE U_2 CENTRUM

A second ural centrum is represented in the young of most Ostariophysi as a chordacentrum. In catfishes, except the Trichomycteridae, the U_2 chordacentrum is fused with the bases of hypurals 3 and 4 from the earliest stages observed (fig. 2A). In the Trichomycteridae (and Cypriniformes and Gonorynchiformes) the U_2 chordacentrum is fused with the base of hypural 3 only.

In most adult catfishes (and all cypriniforms and gonorynchiforms examined) a well-developed U_2 autocentrum is absent. It is represented in adults only by a knoblike mass at the base of hypurals 3 and 4 (or hypural 3 only). This structure lies in the cavity on the posterior face of the compound centrum and is autogenous in most cases. Fusion of

the hypural bases and U_2 with $PU_1 + U_1$ is found in those groups with extensive hypural fusion. In the Loricariidae and Plotosidae (figs. 6A, 9) PU_1, U_1, and U_2 are fused together from very early stages of development. The Siluridae are exceptional in that they possess five separate hypurals with the upper three fused to the compound centrum. The occurrence of fusion between U_2 and $PU_1 + U_1$ is not correlated with size.

In the Siluriformes a U_2 autocentrum occasionally develops in the adult, making a full intervertebral joint with the compound centrum ($PU_1 + U_1$). It is developed in the only helogeneid examined (fig. 7A) and in all aspredinids (fig. 7B) except for one species of *Bunocephalus*. Within the Amblycipitidae it is absent from *Amblyceps* but present in the three species of *Liobagrus* examined (fig. 5A). Three of the 29 specimens of *Liobagrus anguillicaudatus* examined show fusion between U_2 and the compound centrum. Among the mochokids, a free U_2 autocentrum is found in two species of *Chiloglanis* (fig. 5B) but is absent from a third species. In the latter species the bases of the fused upper hypural elements lie in the posterior cavity on $PU_1 + U_1$. In all cases the closest relatives of the species with the U_2 autocentrum are species that lack it.[1]

The groups that have a separate U_2 autocentrum also have, in other features of their caudal skeletons, some or all of the traits here considered to be advanced within the Siluriformes, i.e. those involving hypural fusions, hypurapophysis development, and fin ray reduction (see tables 1, 2). In all except *Helogenes* the U_2 autocentrum is fused to a single compound upper hypural element. These families rank among the most advanced catfishes in other parts of their anatomy.

The fate of the ural centra in the Ostariophysi has an important bearing on the ancestry of the group. The discovery of a free second ural centrum in ostariophysan fishes means that the ancestors of the superorder must have possessed a U_2 in some stage of their development. The most common ontogenetic pattern in the Ostariophysi presumably involves the suppression of the U_2 autocentrum stage of development.

The almost universal presence of a U_2 chordacentrum and the absence of a corresponding autocentrum in the ostariophysans and gonorynchiforms may indicate that the autocentrum was also suppressed in a common ancestor of the two groups. The exceptional presence of a U_2 autocentrum in four unrelated catfish families indicates, however, that the potential for its independent redevelopment has not been lost, at least in the Siluriformes. Further investigation may reveal the presence

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[1] Dahl (1960) proposed a relationship between the Helogeneidae and the Cetopsidae.

TABLE 1

SUMMARY OF CAUDAL SKELETON MORPHOLOGY IN THE SILURIFORMES

(Range of standard length measured in millimeters [in parentheses].)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Diplomystidae				
Diplomystes				
papillosus (110–165)	PH;1;2;3;4;5;6	None	A	—
Ictaluridae				
Ictalurus				
13 species (13–740)	PH;1;2;3;4;5;6	None	A or B	—
Noturus				
funebris (54)	PH;1;2;3;4;5;6	None	—	—
insignis (27–91)	PH;1;2;3;4;5;6	None	—	—
14 others (12–186)	PH;1;2;3;4;5	None	A or F	See discussion of variable hypural fusion patterns
Prietella				
phreatophila (35–45)	PH+1+2; 3+4+5	None	—	—
Pylodictis				
olivaris (86–765)	PH;1;2;3;4;5;6	None	A	—
Satan				
eurystomus (68)	PH;1+2; 3+4+5	None	—	—
Trogloglanis				
pattersoni (66)	PH+1+2; 3+4+5	None	—	—
Unnamed Eocene fossil	PH;1;2;3;4;5;6	None	A	—
Bagridae				
Auchenoglanis				
ballayi (36)	PH;1;2;3;4;5;6	3,4	A	Hypurals 2 and 3 fused proximally

TABLE 1—*(Continued)*

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
occidentalis (28–146)	PH;1;2;3;4;5;6	3,4	A	Hypurals 2 and 3 fused proximally
Bagroides				
malapterus (86)	PH;1;2;3;4;5;6	None	B	—
Bagrus				
docmac (234)	PH;1;2;3;4;5;6	None	B	—
ubangensis (75)	PH;1;2;3;4;5;6	None	B	—
Chrysichthys				
cranchi (51)	PH;1;2;3;4;5	None	C	—
ornatus (48)	PH;1+2; 3+4;5	None	C	—
punctatus (66)	PH;1;2;3;4;5	None	B	—
Clarotes				
laticeps (208)	PH;1;2;3+4;5	None	—	—
Coreobagrus				
ichikawai (62)	PH;1;2;3;4;5;6	None	B	—
Gephyroglanis				
longipinnis (53)	PH;1;2;3+4;5	None	B	—
Hemibagrus				
guttatus (167)	PH;1;2;3+4;5	None	B	—
Heterobagrus				
bocourti (73–97)	PH;1;2;3;4;5	None	B	—
Liocassis				
dumerili (38–45)	PH;1;2;3;4;5;6	None	B	—
siamensis (42–55)	PH;1;2;3;4;5;6	None	B	—
ussuriensis (44–61)	PH;1;2;3;4;5;6	None	B	—
Mystus				
aor (252)	PH;1;2;3;4;5;6	None	B	—

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
cavasius (58)	PH;1;2;3+4;5	3,4	B	—
gulio (44–54)	PH;1;2;3;4;5;6	None	B	—
micracanthus (41–89)	PH;1;2;3;4;5;6	None	—	—
nemurus (46–104)	PH;1;2;3;4;5;6	None	C	—
rhegma (46–61)	PH;1;2;3+4;5	None	—	—
vittatus (58–110)	PH;1;2;3;4;5;6	None	C	—
wijki (202)	PH;1;2;3;4;5;6	None	B	—
wolffi (29–84)	PH;1;2;3;4;5;6	None	C	—
Pelteobagrus				
nudiceps (166–188)	PH;1;2;3;4;5;6	None	B	—
Pseudobagrus				
aurantiacus (64)	PH;1;2;3;4;5;6	None	B	—
fulvidraco (63)	PH;1;2;3;4;5;6	None	B	—
vachelli (49–130)	PH;1;2;3;4;5;6	None	B	—
Rita				
chrysea (93–106)	PH;1;2;3;4;5	None	B	—
kuturnee (66)	PH;1;2;3+4;5	None	B	—
rita (128–143)	PH;1;2;3;4;5	None	B	—
Cranoglanididae				
Cranoglanis				
bouderius (256)	PH;1;2;3;4;5;6	None	B	—
Siluridae				
Hemisilurus				
sp. (413)	PH;1;2;3;4;5	3,4,5	D	—
Hito				
taytayensis (150)	PH;1;2;3+4+5	3,4,5	D	—

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Kryptopterus *bleekeri* (80–118)	PH;1;2;3;4;5	3,4,5	D	One specimen with third uroneural on left side
cryptopterus (71–87)	PH;1;2;3+4+5	3,4,5	D	—
Ompok *bimaculatus* (53)	PH;1;2;3;4;5	3,4,5	D	—
Parasilurus *asotus* (71–405)	PH;1;2;3;4;5	None	A	One specimen with distinct first, second, and third uroneurals
lithophilus (187–265)	PH;1;2;3;4;5	None	A	—
Silurodes *eugeneiatus* (67)	PH;1;2;3;4+5	3,4,5	D	—
hypophthalmus (101)	PH;1;2;3;4;5	3,4,5	D	—
Silurus *glanis* (85)	PH;1;2;3;4;5	None	A	—
Wallago *dinema* (142)	PH;1;2;3+4+5	3,4,5	D	—
Wallagonia *attu* (242)	PH;1;2;3;4;5	3,4,5	D	—
Schilbeidae *Clupisoma* *garua* (119)	PH;1;2;3;4;5;6	None	—	Lateral line forked over caudal rays
Eutropius *grenfelli* (38–65)	PH;1;2;3;4;5;6	None	B	Lateral line forked over caudal rays
niloticus (54)	PH;1;2;3;4;5;6	None	A	Lateral line forked over caudal rays
Helicophagus *waandersi* (77)	PH;1;2;3;4;5;6	None	A	Lateral line forked over caudal rays

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Laides				
hexanema (63)	PH;1;2;3;4;5;6	None	B	Lateral line not forked over caudal rays
Parailia				
longiflis (77)	PH+1+2;3;4;5	None	A	—
Pseudeutropius				
atherinoides (50–58)	PH;1;2;3;4;5;6	None	—	Lateral line not forked over caudal rays
Schilbe				
mystus (48–200)	PH;1;2;3;4;5	None	A	Lateral line forked over caudal rays
Silonia				
silondia (139)	PH;1;2;3;4;5	None	A	Lateral line forked over caudal rays
Pangasiidae				
Pangasius				
micronemus (315)	PH;1;2;3;4;5;6	None	A	Lateral line forked over caudal rays
nasutus (?) (261)	PH;1;2;3;4;5;6	None	—	Lateral line forked over caudal rays
pangasius (146)	PH;1;2;3;4;5;6	None	B	Lateral line forked over caudal rays
siamensis (48–60)	PH;1;2;3;4;5;6	None	A	Lateral line forked over caudal rays
Pteropangasius				
cultratus (63)	PH;1;2;3;4;5;6	None	A	Lateral line forked over caudal rays
Amblycipitidae				
Amblyceps				
mangois (50–75)	PH;1+2;3+4+5	None	F	No U_2 autocentrum
Liobagrus				
anguillicaudatus (49–79)	PH;1+2;3+4+5	None	C	U_2 autocentrum
marginatus (104)	PH;1+2;3+4+5	None	—	U_2 autocentrum

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
reini (52–60)	PH;1+2;3+4+5	None	E	U_2 autocentrum
Amphiliidae				
Amphilius				
longirostris (78)	PH+1+2;3+4+5	3,4	C	—
pictus (33)	PH+1+2;3+4+5	3,4	C	—
Doumea				
typica (51)	PH+1+2;3+4+5+UN	3,4,5	C	Procurrent rays platelike; neural and hemal spines in caudal peduncle appressed
Phractura				
scaphirhynchura (57–84)	PH+1+2;3+4+5+UN	3,4,5	C	Procurrent rays platelike; neural and hemal spines in caudal peduncle appressed
Sisoridae				
Bagarius				
bagarius (91)	PH;1+2;3+4;5	None	C	Lateral line forked over caudal rays. Procurrent rays platelike; neural and hemal spines in caudal peduncle appressed
Glyptothorax				
sinense (47)	PH;1+2;3+4;5	None	B	Procurrent rays platelike
trilineatus (72)	PH;1;2;3+4;5	None	B	Procurrent rays platelike
Clariidae				
Allabenchelys				
longicauda (107)	PH;1;2;3;4;5	None	—	—

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Channalabes				
apus (82)	PH;1;2;3;4;5	None	G	—
Clarias				
angolensis (43–83)	PH;1;2;3;4;5	None	G	—
batrachus (13–213)	PH;1;2;3;4;5	None	G	—
fuscus (150–260)	PH;1;2;3;4;5	None	—	—
Heterobranchus				
longifilis (68–310)	PH;1;2;3;4;5	3,4,5	G	—
Xenoclarias				
holobranchus (148)	PH;1;2;3;4;5	None	—	—
Heteropneustidae				
Heteropneustes				
fossilis (129–224)	PH;1+2;3+4+5	3,4,5	F	—
Chacidae				
Chaca				
chaca (144)	PH+1+2+3+4+5+UN	3,4,5	—	Epural reduced or absent
Malapteruridae				
Malapterurus				
electricus (60–295)	PH;1;2;3+4;5;6	None	C	—
Mochokidae				
Chiloglanis				
batesi (21–22)	PH+1+2;3+4+5	None	C	U_2 autocentrum
deckeni (41–47)	PH+1+2;3+4;5	None	C	No U_2 autocentrum
niloticus (24)	PH+1+2;3+4+5	None	C	U_2 autocentrum
Euchilichthys				
dybowski (54)	PH+1+2;3+4;5	3,4,5	C	—

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to PU$_1$ + U$_1$	Hypurapophyses[b]	Comments
royauxi (34)	PH+1+2;3+4+5	3,4,5	C	—
Microsymodontis				
batesi (58)	PH+1+2;3+4+5+UN	3,4,5	C	—
Synodontis				
clarias (46)	PH+1+2;3+4+5	3,4,5	C	—
depauvi (31)	PH+1+2;3+4+5	3,4,5	C	—
notatus (42)	PH+1+2;3+4+5	3,4,5	C	—
schalli (256)	PH+1+2;3+4+5	3,4,5	C	—
victoriae (110)	PH+1+2;3+4+5	3,4,5	C	—
Ariidae				
Arius				
caerulescens (46–62)	PH;1;2;3+4;5	None	C	—
felis (250–332)	PH;1+2;3;4;5	None	C	—
gagora (119–132)	PH;1+2;3+4,5	None	C	—
liropus (48–62)	PH;1+2;3;4;5	None	C	—
Bagre				
scutatus (250)	PH;1+2;3;4;5	None	C	—
Batrachocephalus				
mino (45)	PH;1;2;3;4;5	None	C	—
Genidens				
genidens (54–59)	PH;1;2;3;4;5	None	C	—
Hemipimelodus				
bornensis (145)	PH;1+2;3+4;5	None	C	—
Netuma				
kessleri (270)	PH;1+2;3+4;5	None	C	—
sp. (51–54)	PH;1+2;3;4;5	None	C	—

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Potamarius				
nelsoni (400)	$PH;1;2;3;4;5$	None	C	—
Selenaspis				
herzbergi (205)	$PH;1+2;3;4;5$	None	C	—
Doradidae				
Doraops				
zuloagi (380)	$PH;1+2;3+4;5$	None	C	—
Doras				
hancocki (30)	$PH+1+2;3+4;5$	None	C	—
Hemidoras				
carinatus (58)	$PH;1+2;3+4;5$	None	C	—
Auchenipteridae				
Auchenipterus				
demerarae (87)	$PH+1+2;3+4;5$	None	C	Lateral line forked over caudal rays
Centromochlas				
steindachneri (73)	$PH+1+2;3+4;5$	None	C	Lateral line not forked over caudal rays
sp. (27)	$PH+1+2;3+4;5$	None	—	Lateral line not forked over caudal rays
sp. (31)	$PH+1+2;3+4;5$	None	—	Lateral line not forked over caudal rays
Tatia				
aulopygia (72)	$PH+1+2;3+4;5$	None	C	Lateral line not forked over caudal rays
Trachelyopterus				
coriaceous (113–20)	$PH+1+2;3+4;5$	None	C	Lateral line forked over caudal rays

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Trachycorystes				
fisheri (47–59)	PH+1+2;$\underline{3+4}$;5	None	C	Lateral line forked over caudal rays
galeatus (55–103)	$\underline{PH+1+2;3+4;5}$	None	C	Lateral line forked over caudal rays
Aspredinidae				
Agmus				
lyriformes (36)	PH;1+2;$\underline{3+4+5}$	None	C	U_2 autocentrum. Epural fused to uroneural
Aspredinichthys				
tibicen (81–112)	PH+1+2;$\underline{3+4+5}$	None	C	U_2 autocentrum
Bunocephalus				
bifidus (33)	PH+1+2;$\underline{3+4+5}$	None	—	U_2 autocentrum
sp. (12)	$\underline{PH+1+2+3+4+5+UN}$	3,4,5	B	No U_2 autocentrum
Plotosidae				
Copidoglanis				
sp. (44–54)	$\underline{PH+1+2+3+4+5+UN}$	3,4,5	G	Epural lacking in two of three specimens
Paraplotosus				
albilabris (225)	$\underline{PH+1+2+3+4+5+UN}$	3,4,5	—	No epural
Plotosus				
canius (47)	PH;1+2+3+4+5+UN	3,4,5	G	Epural small
lineatus (17–172)	$\underline{PH+1+2+3+4+5+UN}$	3,4,5	—	No epural
Pimelodontidae				
Acentronichthys				
leptos (74)	PH+1+2;$\underline{3+4}$;5	None	C	—
Brachyglanis				
frenatus (91)	$\underline{PH+1+2;3+4;5}$	None	C	Ossicles between hypural 5 and uroneural may represent hypural 6

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Brachyplatystoma vaillanti (120–222)	PH;1;2;3;4;5	None	C	—
Callophysus macropterus (128)	PH;1;2;3;4,5	None	C	—
Cetopsorhamdia nasus (76)	PH;1+2;3+4;5	None	C	—
Chasmocranus longior (67)	PH;1+2;3+4;5	None	C	—
Cheirocerus eques (99)	PH;1;2;3+4;5	None	C	—
Conorhynchus conirostris (402)	PH;1;2;3;4;5	None	C	Lateral line forked over caudal rays
Duopalatinus goeldi (166)	PH;1;2;3;4;5	None	C	—
Goeldiella eques (76)	PH;1+2;3+4+5	3,4,5	C	—
Hemisorubim platyrhynchus (303)	PH;1;2;3+4;5	None	C	—
Heptapterus mustelinus	PH+1+2;3+4;5	None	C	—
Microglanis cottoides (35)	PH+1+2;3+4;5	None	—	—
iheringi (27)	PH+1+2;3+4;5	None	—	—
sp. (35–75)	PH+1+2;3+4;5	None	C	—
Nannorhamdia guttata (42)	PH+1+2;3+4;5	None	C	—

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Perugia				
xanthus (72–77)	PH;1+2;3+4;5	3,4	C	—
Phractocephalus				
hemiliopterus (420)	PH;1;2;3;4;5	None	C	—
Pimelodella				
chagresi (60–80)	PH;1+2;3+4;5	None	C	—
gracilis (52)	PH;1+2;3+4;5	None	C	—
macturki (40)	PH;1+2;3+4;5	None	C	—
roccae (58)	PH;1+2;3+4;5	None	C	—
Pimelodus				
clarias (63)	PH;1;2;3+4;5	None	C	—
ornatus (113)	PH;1;2;3;4;5	None	C	—
pictus (77)	PH;1+2;3+4;5	None	C	—
Pinirampus				
pinirampu (252)	PH;1;2;3+4;5	None	C	—
Platynematichthys				
punctulatus (430)	PH;1+2;3+4;5	None	C	—
Platystomichthys				
sturio (205–278)	PH;1;2;3;4;5	None	C	—
Pseudopimelodus				
roosevelti (143)	PH;1+2;3+4;5	None	C	—
villosus (47–105)	PH+1+2;3+4;5	None	C	—
Pseudoplatystoma				
fasciatum (613)	PH;1;2;3;4;5	None	C	—
Rhamdella				
rustyi (167)	PH;1+2;3+4;5	None	C	—

TABLE 1—*(Continued)*

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Rhamdia				
guatemalensis (62–185)	PH;1+2;3;4;5[c]	None	C	—
hypselura (68–72)	PH;1+2;3;4;5[c]	None	C	—
Sorubim				
lima (117–328)	PH;1;2;3;4;5	None	C	—
Sorubimichthys				
planiceps (261)	PH;1;2;3;4;5	None	—	—
Sovichthys				
abuelo (163)	PH;1;2;3;4;5	None	C	—
Zungaro				
zungaro (112–130)	PH+1+2;3+4;5	None	C	—
Ageneiosidae				
Ageneiosus				
caucanus (66)	PH+1+2;3+4;5	None	B	—
Hypophthalmidae				
Hypophthalmus				
edentatus (90–130)	PH;1;2;3;4;5	None	C	Lateral line turns upward over caudal rays. A superior commissure on caudal peduncle
Helogeneidae				
Helogenes				
marmoratus (38–59)	PH;1+2;3;4;5	None	D	U_2 autocentrum
Cetopsidae				
Cetopsis				
coecutiens (224)	PH;1;2;3;4;5;6	None	B	—
Cetopsogiton				
occidentalis (181)	PH;1;2;3;4;5;6	None	B	—

TABLE 1—*(Continued)*

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Hemicetopsis macilentus (70)	PH;1;2;3;4;5;6	None	B	—
Pseudocetopsis plumbea (99)	PH;1;2;3;4;5;6	None	B	—
Trichomycteridae				
Apomatocerus alleni (?) (47)	PH+1+2;3;4+5	None	—	No epural
Eremophilus mutisii (108–153)	PH;1+2;3;4;5	None	C	No epural
Homodiaetus maculatus (49)	PH+1+2;3;4+5	None	—	No epural
Nematogenys inermis (32–42)	PH;1+2;3;4;5	None	G	Full epural
Ochmacanthus sp. (33–38)	PH+1+2;3;4+5	None	—	No epural
Trichomycterus oroyae (22–86)	PH+1+2;3;4+5	None	—	No epural
quechuorum (50–65)	PH;1+2;3;4+5	None	C	No epural
rivulatus (22–89)	PH+1+2;3;4+5	None	C	No epural
tiraquae (35–39)	PH+1+2;3;4+5	None	C	No epural and U_2 only slightly reduced
vermiculatus (50)	PH;1+2;3;4+5	None	C	No epural
zonatus (73)	PH+1+2;3;4+5	None	C	No epural
Tridensimilis venezuelae (18)	PH+1+2;3;4+5	None	—	No epural

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Vandellia cirrhosa (42–60)	PH;$\underline{1+2};\underline{3};\underline{4+5}$	3	C	No epural, but one with a full PU_1 neural spine (=epural)
Callichthyidae				
Aspidoras rochai (31)	PH$+1+\underline{2};\underline{3+4+5}$	3,4,5	C	Small denticulations on outer caudal fin rays
Corydoras aenus (33–54)	PH$+1+\underline{2};\underline{3+4+5}$	3,4,5	C	Small denticulations on outer caudal fin rays
julii (23)	PH$+1+\underline{2};\underline{3+4+5}$	3,4,5	C	Small denticulations on outer caudal fin rays
Hoplosternum sp. (64)	PH$+1+\underline{2};\underline{3+4+5}$	3,4,5	C	Small denticulations on outer caudal fin rays
Loricariidae				
Hypostomus latirostris (227)	PH$+1+\underline{2};\underline{3+4+5}$+UN+EP	3,4,5	C	Small denticulations on outer caudal fin rays. Expanded epural, neural, and hemal spines. Bony bridge between hypurals 2 and 3
sp.	PH$+1+\underline{2};\underline{3+4+5}$+UN+EP	3,4,5	C	Small denticulations on outer caudal fin rays. Expanded epural, neural, and hemal spines. Bony bridge between hypurals 2 and 3

TABLE 1—(Continued)

Species	Hypural Fusion Pattern[a]	Upper Hypurals fused to $PU_1 + U_1$	Hypurapophyses[b]	Comments
Otocinclus affinis (26)	PH+1+2;3+4+5+UN+EP	3,4,5	C	Small denticulations on outer caudal fin rays. Expanded epural, neural, and hemal spines. Bony bridge between hypurals 2 and 3
Plecostominae indeterminate (9)	PH+1+2;3+4+5	3,4,5	C	Small denticulations on outer caudal fin rays. Expanded epural, neural, and hemal spines. Bony bridge between hypurals 2 and 3
Astroblepidae Astroblepus orientalis (65)	PH+1+2;3+4+5+UN	3,4,5	C	Small denticulations on outer caudal fin rays. Expanded epural, neural, and hemal spines. Bony bridge between hypurals 2 and 3
longifilis (40)	PH+1+2;3+4+5+UN	3,4,5	C	Small denticulation on outer caudal fin rays. Expanded epural, neural, and hemal spines. Bony bridge between hypurals 2 and 3

[a] Maximum number of separate hypurals found in each species. PH, parhypural; UN, uroneural; EP, epural; 1–6, hypurals. A semicolon means that two adjacent elements are separate or at least distinguishable. Indistinguishably fused elements are shown by a plus sign and underscoring, but no underscoring is used in the text. Where the sixth hypural is not distinguishable, it is considered lost rather than fused (see text) and is deleted from the hypural fusion formula.

[b] See figure 3.

[c] Predominant pattern: PH;1+2;3+4;5.

of a separate U_2 autocentrum in additional catfish groups and other Ostariophysi.

CAUDAL FIN RAYS

Few workers have published caudal fin ray data on catfishes, and it is not certain that these data are, in all respects, comparable. For this reason only data from specimens examined in this study are presented in table 2.

The principal fin ray number is constant within catfish species with forked tails. (A distinctly lobed or forked caudal fin is the primitive condition for catfishes.) The constancy of principal fin ray number generally extends to forms with emarginate or even truncate tails. In the groups with uniform principal fin ray counts all principal rays articulate with the parhypural and hypurals only.

Within the Siluriformes there is a trend toward a reduction in the number of principal caudal rays, as is commonly found throughout the teleosts (e.g. Patterson, 1968). No siluriform examined has the primitive ostariophysan principal ray formula of $10+9$. *Diplomystes* with $9+9$, most closely approaches this condition. Most catfish groups, however, have lost an additional upper ray, resulting in $8+9$. Further reduction has taken place in various groups. Some, such as the Ariidae and Callichthyidae, have developed a fixed reduced number. Within other groups, such as the Loricariidae, various levels of reduction are found. The fewest principal rays, $5+5$, are found in most of the Aspredinidae.

Throughout this reduction and variation the Siluriformes retain at least an equal, and usually a greater number of principal rays in the lower lobe. The difference between the upper and lower lobe is rarely more than one ray. The over-all pattern of reduction within the Siluriformes is probably one of deletion of a principal ray from the upper lobe before the deletion of one from the lower lobe. The only exception is *Helogenes* $(6+8)$ among the groups with a constant formula.

As in catfishes, some exocoetoids have more principal rays in the lower caudal lobe than in the upper (Rosen, 1964), and in both of these groups the lower lobe is often larger. Exocoetoids are neutrally buoyant, surface feeding fishes, some of which use the lower lobe in a skittering type of locomotion over the surface of the water. In contrast, catfishes are denser than water (Alexander, 1965). Most siluriforms live on the bottom, but many feed in mid-water at least some of the time. A larger lower caudal lobe may provide the necessary lift component by inclining the body upward in locomotion.

TABLE 2

PRINCIPAL CAUDAL FIN RAY COUNTS IN THE SILURIFORMES

Count	Distribution
9+9	Diplomystidae
8+9	Ictaluridae (except *Noturus* and *Prietella*), Bagridae (except *Clarotes*), Cranoglanididae, Siluridae, Schilbeidae, Pangasiidae, Amphiliidae (*Phractura*), Amblycipitidae (*Amblyceps*), Sisoridae, Malapteruridae, Mochokidae, Doradidae, Auchenipteridae (*Auchenipterus* and *Centromochlas*), Pimelodontidae (except *Sorubim, Microglanis* and *Pseudopimelodus*), Ageneiosidae, Hypophthalmidae, Cetopsidae
7+9	Helogeneidae
8+8	Bagridae (*Clarotes*), Loricariidae (*Ancistrus, Hypostomus, Otocinclus, Panaque, Pterygoplichthys, Rhinelepis, Xenocara*)
7+8	Ictaluridae (*Prietella*), Amphiliidae (*Amphilius longirostris*), Ariidae, Trichomycteridae (*Nematogenys*)
7+7	Callichthyidae, Loricariidae (*Acestridium, Farlowella, Sturisoma*)
6+7	Amphiliidae (*Amphilius pictus*), Trichomycteridae (except *Nematogenys*), Astroblepidae
6+6	Loricariidae (*Loricaria, Farlowella*)
5+6	Aspredinidae (*Bunocephalus* sp.)
5+5	Aspredinidae (except *Bunocephalus* sp.)
Variable lower lobe (8+10–13)	Auchenipteridae (*Trachycorystes, Trachelyopterus*), Pimelodontidae (*Sorubim*)
Variable both lobes	Ictaluridae (*Noturus*), Amblycipitidae (*Liobagrus*), Clariidae, Heteropneustidae, Chacidae, Plotosidae, Pimelodontidae (*Microglanis* and *Pseudopimelodus*)

A few groups of catfishes do not conform to the pattern described above. In these groups (listed as "variable" in table 2), the shape of the caudal fin is aberrant, usually rounded. They have a variable increase in the number of branched rays. *Sorubim, Trachelyopterus,* and *Trachycorystes* have increased the number of branched rays in the lower lobe only. Also, in contrast to the fork-tailed forms, the branching extends (in all except the clariids and heteropneustids) to those rays not supported by the parhypural and hypurals. Thus, the application of a concept of principal rays based on branched versus simple rays loses much of its systematic value here. In *Noturus,* according to Taylor (MS.), "The variation in the number of branched rays is probably due to a continuation of the branching process, in the long rays, throughout life." Even in such variable species, however, there tends to be species

specific ranges of variation in at least the total number of branched rays (Taylor, MS.).

Thus, if meaningful comparisons are to be made, it will be necessary to determine which set of caudal rays, if any, in round-tailed forms is homologous to the principal rays in fork-tailed forms. Perhaps a definition of principal rays as only those rays which are supported on the parhypural and hypurals would produce comparable data for all catfish groups. Initial attempts to obtain such comparable data by this means have thus far proved unrewarding. Another approach might be to use a definition based on muscle insertions.

The procurrent rays are present in about equal number in each lobe of most groups, being about 12–25. A few groups have a greatly reduced number, e.g. Aspredinidae 1–2 per lobe or absent, and the Plotosidae have a greatly increased number of upper lobe procurrents.

DISCUSSION

Diplomystes, in agreement with other features of its anatomy, possesses over-all the most primitive caudal skeleton in the Siluriformes, i.e. six separate hypurals, upper hypurals unfused to $PU_1 + U_1$, Type A hypurapophyses, and a $9 + 9$ principal fin ray count.[1]

The Ictaluridae (figs. 1, 2A), Bagridae, Cranoglanididae, Schilbeidae, Pangasiidae, and Cetopsidae have, however, some members that share these primitive features of the caudal skeleton with *Diplomystes* except that they all have $8 + 9$ principal fin rays and some have Type B hypurapophyses.

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[1] McAllister (1968, p. 72) has recently concluded that the Diplomystidae are a "moderately advanced family . . . derivable from the Pimelodidae or its relatives." This conclusion is based on the assumptions that few branchiostegals (8), pelvic rays (6), and barbels (2) are advanced conditions for catfishes, and that maxillary teeth and separate fifth vertebra are "secondary rather than primitive." Not only is it probable that two maxillary barbels and six pelvic rays are primitive for catfishes, but it is certain that the maxillary bone (not necessarily maxillary teeth only) of *Diplomystes* is strikingly similar to the basal characoid condition in its shape and relationships to surrounding bony and soft tissues. It is equally certain that *Diplomystes* possesses the most primitive Weberian apparatus within the Siluriformes not only in lack of consolidation of centra but also in features of the Weberian ossicles (Myers and Weitzman, 1966). The present data extends the list of primitive features retained in *Diplomystes* to the caudal fin and skeleton and a case could also be made for its having retained a primitive shoulder girdle. In marked contrast, however, *Diplomystes* possesses a highly specialized pattern of jaw muscle invasion of the skull roof. The presence of a few advanced traits in *Diplomystes* cannot negate the fact that it has retained more primitive features than any other known catfish, fossil or living.

Within the Ictaluridae the troglodytic forms (*Prietella, Satan, Troglo-glanis*) have advanced hypural fusion patterns, and *Prietella* has 7 + 8 principal rays. *Noturus* presents a special problem in that all species have a variable number of branched caudal rays, reduced hypurapophyses, and most have highly variable hypural fusion patterns.

Within the Bagridae, *Auchenoglanis* has two advanced features which occur in no other bagrid, i.e. fusion of hypurals 3 and 4 and U_2 with the compound centrum and a proximal bony bridge between hypurals 2 and 3. They are also unusual among the bagrids in the retention of Type A hypurapophyses. This may support Jayaram's (1966) subfamilial separation of the Auchenoglaninae. Jayaram also erected the subfamily Ritinae for *Rita* and *Rama,* which he considered to be the most primitive of the bagrids. The species of *Rita* examined here, however, do not have the most primitive caudal skeleton in the family.

The caudal skeleton yields no information on the systematic position of the monotypic Cranoglanididae. (See Jayaram, 1956, for a discussion of this problem.) In most features of its tail *Cranoglanis* is similar to generalized bagrids, schilbeids, and pangasiids. *Cranoglanis* does not, however, possess a bifurcation of the lateral line over the caudal rays which is present in all pangasiids and most schilbeids. This peculiar condition of the lateral line is also found in some of the sisorids (*Bagarius*), pimelodontids (*Conorhynchus*), auchenipterids, and *Hypophthalmus*.

The advanced features of the ariid caudal skeleton (i.e. fin ray reduction, hypural fusion, and hypurapophyses) are in agreement with recent ideas on the relatively advanced position of this family (Greenwood and others, 1966).

The silurid catfishes possess some primitive osteological features, but their caudal skeleton is peculiar. Silurids never have a sixth hypural and although the hypurals are rarely fused to each other the bases of the third through fifth are usually fused to the compound centrum. Type D hypurapophyses are found in this group. Exceptions to these conditions occur in *Silurus* and *Parasilurus,* which appear to be less specialized in their possession of Type A hypurapophyses, and the lack of fusion between the upper hypurals and the compound centrum. The peculiarities of the silurid tail may be correlated with their unusual hovering habits in mid-water but the schilbeid *Parailia,* which is similar to the silurid "glass catfishes" in locomotor behavior and external morphology, has a very different caudal skeleton.

Tilak (1963, p. 437) concluded that the Siluridae and the Plotosidae are "closely related." These two families share no specializations in the caudal skeleton. Unlike the silurids, losses and fusions are carried to ex-

tremes in the plotosids (fig. 6A). Not only have they ankylosed the uro-neural to the fused hypural complex but the epural has generally been lost. Also, where the Siluridae have reduced the number of upper procurrent rays (never more than 13 rays and usually fewer), all plotosids have greatly increased the number of upper rays (more than 100 in most). The Plotosidae, however, may be closely related to the Chacidae. They share several advanced features, i.e. epural reduced or absent, hypurals 3, 4, and 5 fused to the compound centrum, complete fusion of hypurals $(PH + 1 + 2 + 3 + 4 + 5 + UN)$, and a rounded caudal fin with a variable number of principal caudal rays (figs. 6A, 6B).

Within the Amphiliidae the Doumeinae are generally considered to be more advanced than the Amphiliinae (Regan, 1911; Harry, 1953). The caudal skeletons of the Doumeinae are certainly more advanced. In *Amphilius* there is less fusion between hypurals, and the hypurapophyses are Type C. *Doumea* and *Phractura* (fig. 4) have distinctively advanced hypurapophyses in which the hypurapophysis and secondary hypurapophysis, which form a strong shelf, lie on a horizontal line passing through the center of the compound centrum and along the dorsal border of hypural 2 (fig. 4). Harry (1953) has briefly described the tails of *Amphilius* and *Doumea*. The latter, however, is figured upside down and labelled incorrectly.

The often stated resemblance between the Amphiliidae and Sisoridae (Regan, 1911; Harry, 1953; Chardon, 1967) does not extend to the caudal skeleton. These groups share no advanced features and the sisorids appear to be more primitive in hypural fusion patterns, hypurapophyses, and number of principal fin rays.

In clariids and heteropneustids the structure of the caudal skeleton is similar in many respects. In these elongate fishes the angle between the uroneural and the parhypural is more acute than in other catfishes. This results in a crowding of hypural elements. The bases of hypurals 1 and 2 are united or closely approximated where they join the compound centrum. The foramen between hypurals 1 and 2 ("foramen hypurale" of Monod, 1967, see our fig. 1), normally present in catfishes, is lost. Unlike clariids, *Heteropneustes* possesses a distinct hypurapophysis and the hypurals are highly consolidated.

The two Old World families containing members with a well-developed U_2 autocentrum, the Amblycipitidae (fig. 5A) and the Mochokidae (fig. 5B), are relatively advanced catfishes with regard to both the caudal skeleton and other parts of the anatomy. All the Amblycipitidae examined have the same advanced hypural fusion pattern. *Liobagrus* has a rounded tail and a highly variable branched ray count. *Amblyceps*,
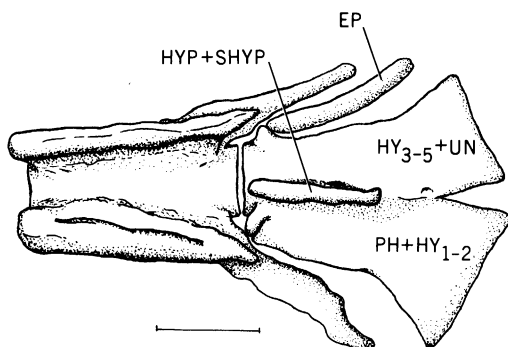
FIG. 4. Caudal skeleton of *Phractura scaphirhynchura* (A.M.N.H. No. 6622), Type C (fig. 3), scale 0.5 mm.

which lacks the U_2 autocentrum, has a primitive caudal ray count, $8 + 9$. *Liobagrus* has an advanced condition of the hypurapophyses, Type C or E. *Amblyceps* has no secondary hypurapophyses, Type F.

The mochokids have advanced hypurapophyses and hypural fusion patterns. *Chiloglanis* (fig. 5B) is the only genus with a free U_2 autocentrum. All other genera of this family lack the separate U_2 autocentrum and have the upper hypurals fused to $PU_1 + U_1$. A single species of *Chiloglanis* which lacks the U_2 autocentrum has the bases of the upper hypurals reduced and appressed, not fused, to the compound centrum.
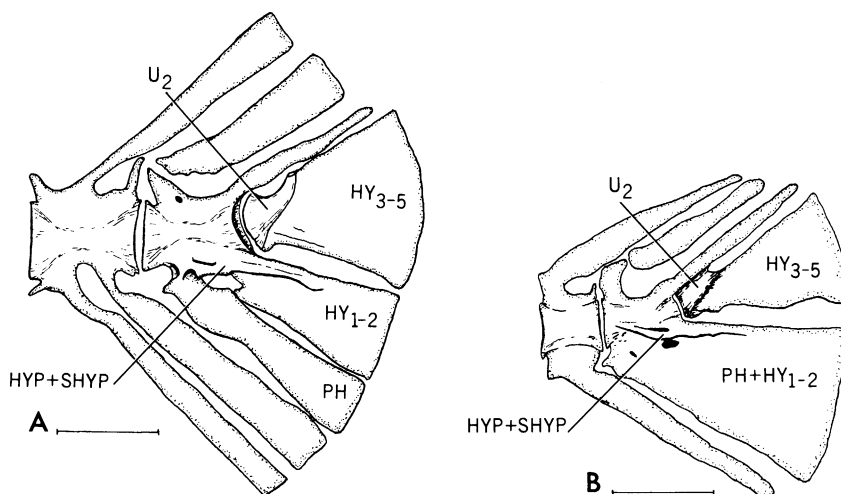
FIG. 5. Caudal skeletons: A. *Liobagrus anguillicaudatus* (A.M.N.H. No. 11069), Type C (fig. 3); B. *Chiloglanis batesi* (A.M.N.H. No. 6592) Type C (fig. 3), scale 0.5 mm.

This condition may be intermediate between the fused condition and a separate U_2 autocentrum. Most of the mochokid species which have the fused condition rather than the separate condition have further increased rigidity by developing a bony bridge between hypurals 2 and 3.

The Pimelodontidae are, as a group, more advanced in most features of the caudal skeleton than their Old World bagrid counterparts. No pimelodontid has more than five separate hypurals and all have Type C hypurapophyses. Many have a greater degree of hypural fusion than any bagrid. Of the subfamilies within the Pimelodontidae as outlined by Schultz (1944) and Gosline (1945), the Callophysinae and Sorubiminae have the least consolidated caudal skeletons in the family. The hypural pattern typical of these groups is PH;1;2;3;4;5, in which the bases of
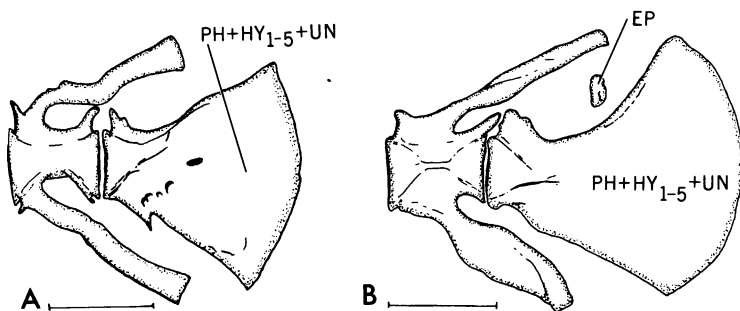
FIG. 6. Caudal skeletons: A. *Copidoglanis* sp. (A.M.N.H. No. 15038), Type G (fig. 3), scale 0.5 mm.; B. *Chaca chaca* (A.M.N.H. No. 9496), Type G (fig. 3), scale 1.0 mm.

hypurals 3 and 4 never fuse with the compound centrum. The predominant pattern in the Pimelodontinae and Luciopimelodontinae is PH;1 + 2;3 + 4;5, in which the upper hypurals fuse with the compound centrum in some cases. Few members of the latter groups show less fusion but more often, such as in *Microglanis, Pseudopimelodus,* and *Zungaro* (closely related genera, Gomes, 1946), the parhypural is fused with the lower hypural complex.

The two closely related New World families, Doradidae and Auchenipteridae, share advanced features in various parts of their anatomy. In the caudal skeleton they share the same advanced hypural fusion patterns and hypurapophysis condition. The principal ray counts are generalized (8 + 9), except for *Trachycorystes* and *Trachelyopterus* which have increased the number of branched rays in the lower lobe. Most auchenipterids have the distinctive feature of a forked lateral line over

the caudal rays.

Advanced features of the caudal skeleton and fin indicate a relationship among three Neotropical families, the armored Callichthyidae and Loricariidae (fig. 9) and the Astroblepidae. These features are: 1) a high degree of hypural fusion, 2) Type C hypurapophyses, 3) a low number of principal fin rays, 4) a low number of platelike procurrent rays, 5) numerous small teeth on the leading edges of the caudal fin (see Bhatti, 1938, for a discussion of these teeth). The Loricariidae and Astroblepidae share a hypural fusion pattern which is more advanced than that of the Callichthyidae. This indicates that these two nominal families may be more closely related to each other than either is to the callichthyids. Of these groups at least the loricariids have U_2 fused with the compound centrum in the very early stages of development.

Two advanced and unrelated Neotropical groups have members with a well-developed U_2 autocentrum in the adults, namely, the Helogeneidae (fig. 7A) and Aspredinidae (fig. 7B). The Helogeneidae are advanced in the condition of the hypurapophyses and distinctive principal fin ray formula. The bizarre Aspredinidae (banjo catfishes) have even more advanced patterns of hypural fusion and hypurapophyses, and a markedly reduced principal fin ray count, $5+6$ or $5+5$. Some have expanded neural and hemal spines with serrated distal borders. The procurrent rays, if present, are platelike and greatly reduced in number (1–2 in each lobe).

The anatomy of the hypurals in the Trichomycteridae (figs. 8A, 8B) sets this family apart from all other siluriforms. The trichomycterids have a maximum of three separate upper hypurals, 3, 4, and 5. In all other catfishes the bases of hypurals 3 and 4 are fused with each other and with whatever U_2 material is present. In the trichomycterids, as in the Cypriniformes (see below), the lowermost upper hypural, hypural 3, is the only hypural fused with U_2 at all stages of development, a primitive condition relative to that of other catfishes. Hypural 4 is separate in the smallest specimens examined and only fuses indistinguishably with hypural 3 in the largest specimen of one species. Hypural 4 never fuses with the compound centrum, although it is often fused with hypural 5. Hypurals 1 and 2 are always co-ossified and are often fused to the parhypural.

In one specimen of *Trichomycterus tiraquae* (fig. 8B) the U_2 material at the base of hypural 3 develops a limited articulating surface with the posterior face of $PU_1 + U_1$. This is approximately intermediate between the reduced condition of U_2 and a full intervertebral joint.

Another distinctive, but not exclusive, feature of the trichomycterids

is the lack of an epural. It is consistently present only in *Nematogenys* (fig. 8A). *Nematogenys* further reflects its primitive position in the family in the dearth of hypural fusion, its higher principal fin ray count, and the absence of any hypurapophyses. It is also considered primitive (Myers and Weitzman, 1966) on the basis of other anatomical features, e.g., lack of opercular spines, presence of a pectoral spine, and form of the Weberian ossicles.

The Cetopsidae have been thought to be related to the trichomyc-terids (Regan, 1911). The cetopsids share none of the advanced traits described for the trichomycterids. The cetopsid caudal skeleton is primi-
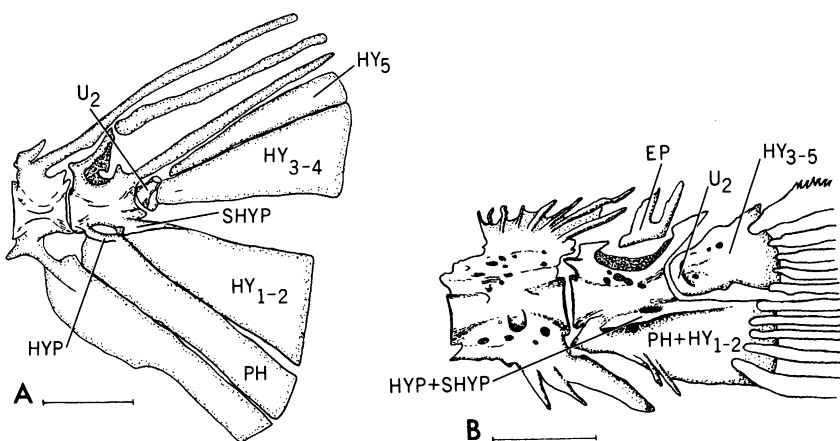
FIG. 7. Caudal skeletons: A. *Helogenes marmoratus* (A.M.N.H. No. 3332), Type D (fig. 3); scale 1.0 mm., B. *Aspredinichthys tibicen* (A.M.N.H. No. 4397), Type C (fig. 3), scale 0.5 mm.

tive in most respects, i.e. principal caudal rays 8 + 9 and hypural con-dition. It is the only family in the Neotropics, except for the Diplomys-tidae, that has the primitive condition of six separate hypurals.

When compared with the Cypriniformes, the basic caudal anatomy of the Siluriformes is more advanced. Among the cypriniforms at least some have the parhypural, hypural 1 and hypural 2 autogenous; three epurals; three separate pairs of uroneurals; an autogenous hemal arch on PU_2, and 10 + 9 principal caudal rays. As described above (pp. 8–12) all siluriforms are more advanced in each of these features. Also, no cypriniform is known to have a secondary hypurapophysis whereas al-most all catfishes have one. In cypriniforms only the third hypural is associated with the second ural centrum, a condition which is found
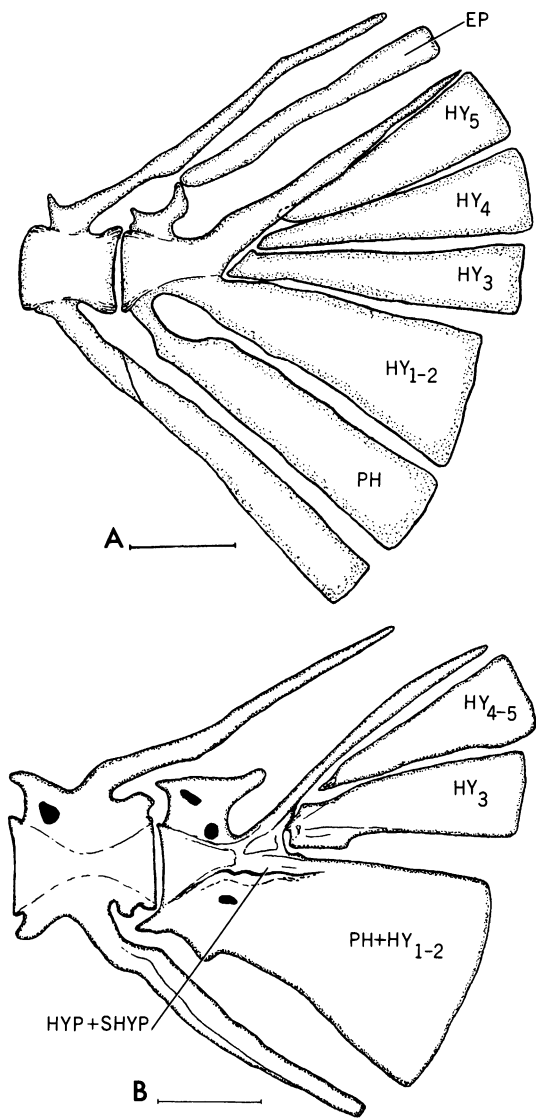
FIG. 8. Caudal skeletons: A. *Nematogenys inermis* (U.S.N.M., I.U.M. No. 15060), Type G (fig. 3); scale 2.0 mm., B. *Trichomycterus tiraquae* (U.M.M.Z. uncatalogued, field number B64-8), Type C (fig. 3), scale 0.5 mm.

among siluriforms only in the Trichomycteridae.

The cyprinoids are more primitive than the characoids in having the

parhypural, and usually the PU_2 hemal arch autogenous. The chara-
coids are more primitive than cyprinoids in having as many as three
separate epurals and three separate pairs of uroneurals.

In some larval ostariophysans (see especially fig. 2A) the zone of con-
tact is visible between PU_1 and U_1 within the compound centrum. The
second hypural is fused with the U_1 portion of the compound centrum,
and a neural arch is ankylosed with the PU_1 portion. Clupeoids are more
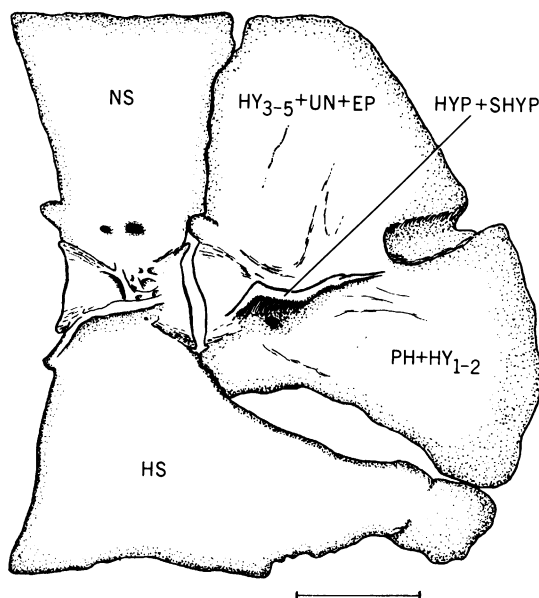
FIG. 9. Caudal skeleton of *Hypostomus latirostris* (U.M.M.Z. No. 177344-S),
Type C (fig. 3), scale 5.0 mm.

primitive than ostariophysans usually in having well developed, separate
first and second ural centra but, as pointed out by Gosline (1961), they
also have hypural 2 fused with U_1 and a fused PU_1 neural arch. In
addition, most clupeoids have the anteriormost uroneural fused to the
U_1 centrum. As in the characoids the first hypural has no basal contact
with the compound centrum, and a distinct process is present on hypural
1 which resembles the secondary hypurapophysis of siluriforms.

Strong evidence has recently been presented for a relationship be-
tween the Gonorynchiformes and the Ostariophysi (Greenwood and
others, 1966). Based on the caudal skeleton these two groups appear to
be more closely related to one another than either is to any other group.

Based on observations of adult structure, the fate of the caudal centra in the Gonorynchiformes appears to be identical to that in the Cypriniformes, as the base of hypural 3 is associated with a much reduced U_2 and lies in the cavity on the posterior face of the compound centrum (Gosline, 1960; our observations on *Chanos*). These features, in which the Gonorynchiformes resemble the Ostariophysi, are the same features that characterize the Ostariophysi as a whole. In fact, the caudal skeleton of the Gonorynchiformes is as similar to that of the Cypriniformes as that of the latter is to the Siluriformes.

SUMMARY

To achieve a better understanding of the evolution of catfishes, comparative studies of single character complexes throughout the entire order is believed to be a rewarding approach. A survey of the caudal skeleton of the Siluriformes reveals 10 basic features which, taken together, distinguish catfishes from other fishes. Of these the most diagnostic are: 1) bases of hypurals 3 and 4 fused with a distinct U_2 chordacentrum in the young and with a usually reduced second ural centrum in the adults; 2) a secondary hypurapophysis; 3) principal rays of the caudal fin fewer than $10+9$, with upper principal rays equal to, or fewer than, the lower rays.

Within the Siluriformes four features of the caudal skeleton are found to exhibit group specific patterns of variation and trends from primitive to advanced conditions, and may thus be useful in determining relationships:

1. In the trend from the primitive condition of six separate hypurals to the most advanced condition of complete fusion of caudal elements, various groups have reached different structural levels. In this process the sixth hypural is lost.

2. The trend toward elaboration of the sites of caudal muscle origin (hypurapophysis and secondary hypurapophysis) has involved the formation and elaboration of shelves from originally distinct projections, and a subsequent dorsal shift of these sites.

3. While the most primitive principal caudal fin ray number in siluriforms is $9+9$, most groups have $8+9$. The trend toward a reduction of principal rays always involves loss of an upper ray before loss of a lower so that upper principal rays are never more numerous than lower ones.

4. A separate U_2 chordacentrum is present in the young of all Ostariophysi except the Loricariidae, Plotosidae, and probably the Chacidae. In the adults of the majority of catfishes a reduced second

ural centrum fused with one or more hypurals lies in the cavity on the posterior face of the compound centrum, $PU_1 + U_1$. In some groups the second ural centrum fuses to the compound centrum. In the Loricariidae and Plotosidae the second ural centrum is fused with $PU_1 + U_1$ in early development. A separate, well-developed second ural autocentrum occurs in some members of four specialized and unrelated families. This is interpreted as independent redevelopment of a presumedly primitive pre-ostariophysan condition.

The advanced conditions of each of these four features of the caudal skeleton tend to occur together in forms which are also regarded as advanced in most other parts of their anatomy. The primitive character states of these features tend to be retained together in a number of families, i.e. Diplomystidae, Ictaluridae, Bagridae, Cranoglanididae, Schilbeidae, Pangasiidae, and Cetopsidae.

Advanced features in the caudal skeleton indicate a relationship between the Clariidae and Heteropneustidae, the Doradidae and Auchenipteridae, the Loricariidae, Astroblepidae, and Callichthyidae, and the Plotosidae and Chacidae.

The siluriform caudal skeleton shares many features with that of the cypriniforms but it is consistently more advanced. The ostariophysan caudal skeleton is similar to that of the clupeoids, but it resembles the caudal skeleton of the Gonorynchiformes more closely than that of any other group.

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