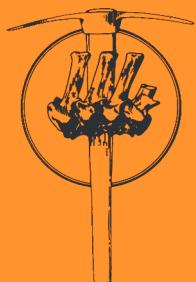
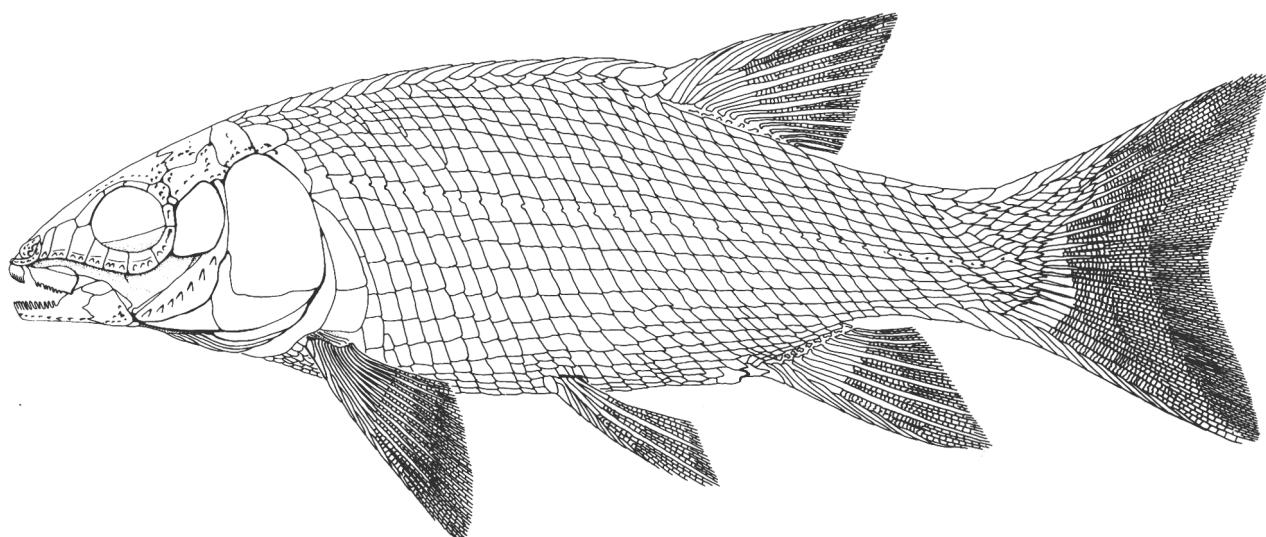


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MORPHOLOGY OF THE *SEMIONOTUS ELEGANS* SPECIES GROUP FROM THE EARLY JURASSIC PART OF THE NEWARK SUPERGROUP OF EASTERN NORTH AMERICA WITH COMMENTS ON THE FAMILY SEMIONOTIDAE (NEOPTERYGII)

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ABSTRACT—We describe the morphology of *Semionotus*, focusing on the *Semionotus elegans* group from the Newark Supergroup of eastern North America. Our description is based largely on specimens from the Boonton Formation (Early Jurassic) of New Jersey because they are particularly well-preserved and include good material of both the dermal skeleton and the endoskeleton. A single anamestic suborbital distinguishes *Semionotus* from its sister-genus *Lepidotes*. We restrict the Semionotidae, defined by the presence of dorsal ridge scales between the nape and dorsal fin as well as a large posteriorly directed process on the epiotic, to two genera, *Semionotus* and *Lepidotes*. We restrict the Semionotiformes, defined by four characters and five character losses, to the Lepisosteidae, Macrosemiidae, and Semionotidae. Our study of *Semionotus* and previous work on *Watsonulus* suggest new interpretations of characters and character polarities. These data support the hypothesis that the Semionotiformes as we define them are more closely related to teleosts than either is to *Amia*. Analysis of the same data using PAUP suggests an equally parsimonious hypothesis that the Semionotiformes and *Amia* form a monophyletic group that, in turn, forms the sister-group to teleosts.

INTRODUCTION

The neopterygian fish, *Semionotus*, is a frequently cited example of the “holostean” level of organization. Its prominence in the literature dates back to Louis Agassiz’s early description of *Semionotus* from Triassic and Jurassic sediments in Germany and his use of the genus to argue for the threefold parallelism in nature (Agassiz, 1833–1844; McCune, 1986). Subsequently, *Semionotus* has been used (erroneously) to indicate a Triassic age, and the genus has played an important role in the discussion of the relationships of actinopterygian fishes (Woodward, 1916–1919; Schaeffer and Dunkle, 1950; Patterson, 1977; Olsen, 1984).

The distribution of *Semionotus* is worldwide, but it is most abundant and diverse in lacustrine deposits of the Newark Supergroup in eastern North America (Olsen et al., 1982; McCune, 1986). Recent paleobiological, paleolimnological, and paleoclimatological studies of these Newark Supergroup deposits have generated new interest in the morphology, variation, systematics and biogeography of *Semionotus* (Olsen et al., 1978; Olsen et al., 1982; McCune et al., 1984; Olsen, 1980, 1984, 1986, 1988; McCune, 1987a, b, 1990). Despite the discovery of specimens of *Semionotus* in North America before the European members of the genus were described by Agassiz (Hitchcock, 1819), and despite the collection and description of hundreds of specimens through the 19th and 20th centuries (e.g., Redfield, 1837; Newberry, 1888; Eastman, 1905), even

the basic morphology of the genus remains poorly known. Using newly prepared material, it is our purpose to describe in detail the morphology of *Semionotus* from the Newark Supergroup and thus build a foundation for future systematic, evolutionary, and paleoecological studies.

We focus our description of *Semionotus* on the *S. elegans* species group (Olsen et al., 1982), primarily from the Boonton Fish Beds in the late Hettangian Boonton Formation, Newark Basin. The *S. elegans* group is a monophyletic clade within *Semionotus* and is defined by the presence of concave dorsal ridge scales (McCune, 1987a). Although there are as many as nine species in the *S. elegans* group (McCune, in prep.), we are primarily concerned here with characters that do not, as far as we know, vary between species. Occasionally we have supplemented the *S. elegans* group material with specimens from other species groups (Olsen et al., 1982) of Newark *Semionotus*, but these specimens are identified explicitly. Again, we believe the characters we discuss in these instances are not variable between species, and therefore serve to clarify the morphology of the genus.

MATERIAL AND METHODS

All but one of the specimens described consist of compressions in which bone histological structure is preserved and mineralized with calcite and pyrite. Most specimens from the Boonton Fish Bed and a number

of specimens from other localities were mechanically split through bony tissues during collection in the 19th century and had to be prepared negatively in dilute HCl to recover detail from the surfaces of bones. Latex rubber and Smooth-On brand polysulfide rubber casts were prepared from the natural mold according to the method described in Olsen (1984). All of the specimens from the Shuttle Meadow Formation at North Guilford and a number of specimens from other localities were prepared mechanically, with needles, a number 11 scalpel blade, and an air-abrasive unit. The acetic acid transfer technique of Toombs and Rixon (1950) was used on one specimen from the Feltville Formation. Most specimens were prepared by the authors. The North Guilford specimens were prepared by Bruce Cornet, and one Boonton specimen (AMNH 1328) was prepared by the staff of the American Museum of Natural History. We prepared drawings of all of the specimens using a Wild M-5 stereo microscope with a drawing-tube attachment.

Institutional abbreviations are as follows: AMNH, American Museum of Natural History, New York, New York; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MU, Bayerische Staatssammlung für Paläontologie und historische Geologie, München; NJSM, New Jersey State Museum of Natural History, Trenton, New Jersey; YPM-PU, Museum of Natural History, Princeton University (collection now at the YPM); UCMP, Museum of Paleontology, University of California at Berkeley, Berkeley, California; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History of Yale University, New Haven, Connecticut.

We used the following specimens in our study: AMNH 1328, partial skull, mechanically prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; AMNH 1540, whole fish, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; AMNH 2986 (counterpart to YPM 8601), disarticulated skull, negatively prepared, *S. elegans* group, Boonton Fm.; AMNH 2991, partial skull, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; AMNH 3980, disarticulated skull, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; MU AS.1.769; NJSM 2992, whole fish, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; USNM 1876, endoskeleton, mechanically prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; USNM 425666, endoskeleton, mechanically prepared, probably from the *S. elegans* group, Waterfall Fm, Haymarket, Virginia; YPM 5906, complete skeleton, osteological preparation, *Lepisosteus oculatus*; YPM 6567, whole fish, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; YPM 6571, whole fish, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; YPM 6572, partial fish, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; YPM 6573, partial fish, negatively prepared, *S. elegans* group,

Boonton, New Jersey, Boonton Fm.; YPM 7193, fragmentary skull, acetic acid preparation, *Semionotus* sp., Northhampden, Connecticut, Shuttle Meadow Fm.; YPM 7473, disarticulated skull, negative preparation, *Semionotus* sp., Oldwick, New Jersey, Feltville Fm.; YPM 7705, partial skull, acetic acid preparation, *S. tenuiceps* group, sp. indet., Martinsville, New Jersey, Feltville Fm.; YPM 8185 & 8187, partially dissociated fish, negatively prepared, *Semionotus* sp., Oldwick, New Jersey, Feltville Fm.; YPM 8226, disarticulated skull, negatively prepared, *Semionotus* sp., Oldwick, New Jersey, Feltville Fm.; YPM 8601 (counterpart to AMNH 2986), disarticulated skull, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; YPM 8602, disarticulated skull, negatively prepared, *S. elegans* group, Boonton, New Jersey, Boonton Fm.; YPM 8603, ventral squash, mechanically prepared, *S. micropterus* group (Olsen et al., 1982), North Guilford, Connecticut, Shuttle Meadow Fm.; YPM 8605, disarticulated skull, negatively prepared, *Semionotus* sp., North Guilford, Connecticut, Shuttle Meadow Fm.; YPM 9363, negatively prepared, *S. brauni* Newberry, 1888, cycle W6, Weehawken, New Jersey, Lockatong Fm.; YPM 9367, endoskeleton, negatively prepared, *Semionotus* sp., cycle P4, Wayne, New Jersey, Towaco Fm.

We also used much comparative material, not cited in the text, from the AMNH, MCZ, NJSM, YPM-PU, USNM and YPM.

SYSTEMATIC PALEONTOLOGY

Class Osteichthyes
Subclass Actinopterygii
Infraclass Neopterygii
Order Semionotiformes

Family Semionotidae

Lepidotidae Owen, 1860 (in part)
Semionotidae Berg, 1940 (in part)
Semionotidae Woodward, 1890 (in part)
Semionotidae Lehman, 1966 (in part)

Included Genera—*Semionotus* Agassiz, 1832 and *Lepidotes* Agassiz, 1832.

Revised Diagnosis—We restrict the family Semionotidae to *Semionotus* and *Lepidotes*, because only if the Semionotidae are severely restricted (see discussion below) can synapomorphies be identified. As such, the Semionotidae share the following synapomorphies: 1) dorsal ridge scales and 2) the presence of a large posteriorly directed process on the “epiotic” (probable pterotic of Patterson, 1975), as well as a suite of primitive actinopterygians have some sort of dorsal ridge scale (about one-third of the 27 genera pictured in Orlov, 1967), most genera which have them have only a partial series (e.g., *Paleoniscinotus*, *Elonichthyes*, *Bobastrania*), or the dorsal ridge scales lack well-developed spines (e.g., *Gyrolepidotes*, *Palaeobergia*). An exception is *Phanerorhynchus*, which is a very derived fish

in many respects. However, the well-developed dorsal ridge scales in the latter and in semionotids must be independently derived because no other neopterygians known from adequate material, including dapediids and *Acentrophorus*, have them except *Semionotus* and *Lepidotes* (*Woodthorbia* and *Hemicalypterus* have dorsal ridge scales but their position within actinopterygians is uncertain). The Semionotidae are further distinguished from their sister group, the Macrosemiidae + Lepisosteidae, by the retention of a suite of primitive character states including, 1) supramaxillae unreduced and 2) interoperculum unreduced (see discussion of semionotiform relationships below).

Although more than 20 genera have been referred to the Semionotidae at one time or another, most except *Semionotus*, *Lepidotes*, *Dapedium*, *Tetragonolepis*, *Heterostropheus* and *Acentrophorus* are poorly known (Patterson, 1973:290). The deep-bodied genera, *Dapedium* and *Tetragonolepis*, are so different from *Lepidotes* and *Semionotus* that Patterson (1973:290, 1975:449) suggested that they were not a natural group. Others have placed *Dapedium*, *Tetragonolepis*, and *Heterostropheus* in a separate family, the Dapediidae (Lehman, 1966; Wenz, 1967), and *Hemicalypterus* appears to be allied with this group as well (Schaeffer, 1967). We follow these authors in excluding *Dapedium* and *Tetragonolepis* from the semionotids. *Acentrophorus* Traquair has long been included in the Semionotidae (Woodward, 1895; Lehman, 1966) but some authors (e.g., Berg 1940; Wenz, 1967) have placed this genus in its own family. In contrast to *Semionotus* and *Lepidotes*, *Acentrophorus* retains several primitive characters such as: small nasal processes on the premaxillae, no supramaxillae, short upper caudal fin rays (according to Patterson, 1973), non-robust fin fulcra, and no dorsal ridge scales. Thus, because *Acentrophorus* lacks at least one of the synapomorphies of the Semionotidae as well as several characteristics of more general levels such as the Neopterygii, we agree with Berg (1940) and Wenz (1967) that *Acentrophorus* should be excluded from the Semionotidae.

SEMIOTONOTUS Agassiz, 1832

Semionotus Agassiz, 1832 is a neopterygian fish retaining a suite of primitive actinopterygian features characteristic of “holosteans” (Woodward, 1895; Schaeffer and Dunkle, 1950; Patterson, 1973). *Semionotus* can be distinguished from its sister group, *Lepidotes*, by the presence of a single anametic suborbital, whereas *Lepidotes* has two or more suborbitals (Schaeffer and Dunkle, 1950; McCune, 1986). As discussed by Patterson (1973:245) the number of suborbitals in primitive actinopterygians is variable. *Semionotus* and some teleosts (e.g. ichthyodectids and some leptolepids) are distinctive in having a single anametic suborbital, which surely arose in parallel. According to the tentative cladogram included in McCune (1982) and reproduced in McCune (1987a) without alteration, *Semionotus* appears not to be monophyletic, because

in that analysis, the single anametic suborbital was interpreted as primitive. However, as the weight of comparative evidence suggests that the single anametic suborbital is a derived feature, it becomes evidence for the monophyly of *Semionotus*. The taxonomic history of *Semionotus* has been reviewed in McCune (1986). We focus our description on the *Semionotus elegans* group. Although we believe this complex is monophyletic (see diagnosis below), we do not name it as a separate genus because to do so would render the remainder of *Semionotus* paraphyletic.

SEMIOTONOTUS ELEGANS SPECIES GROUP

Distribution—Towaco and Boonton formations (Hettangian and Sinemurian), Newark basin, New Jersey; Portland Formation (Sinemurian), Hartford basin, Connecticut; and Waterfall Formation (Hettangian), Culpeper basin, Virginia; Newark Supergroup.

Diagnosis of the *Semionotus elegans* Species Group—A member of the Semionotidae distinguished by the form of the dorsal ridge scales which run along the dorsal midline, from the nape to the dorsal fin (Fig. 1). Anterior dorsal ridge scales lack a spine and are dorsally concave. Successive spines rest in the trough of the adjacent posterior scale (Figs. 2, 3). Only members of the *S. elegans* group have concave dorsal ridge scales. All other *Semionotus* have convex dorsal ridge scales of varying forms (Olsen et al., 1982; McCune et al., 1984; McCune, 1987a, b).

Description

Dermal Skull—The skull of all *Semionotus* from the Newark Supergroup follows a single basic pattern (Figs. 4, 5, 6) directly comparable to that seen in *Semionotus kanabensis* (Schaeffer and Dunkle, 1950) and *Semionotus minor* (Woodward, 1916; McCune, 1986), and *Semionotus* sp. (Cornet et al., 1973; McDonald, 1975). The dermal bones of the snout are similar to *Semionotus minor* (Patterson, 1973) and *Lepidotes elvensis* (Wenz, 1967), and the quadrate region, palate, and braincase is like that described for *Lepidotes toombsi* (Patterson, 1973, 1975). The skull bones are smooth except for some areas of weak crenulation and patches of tubercles. Apart from the tubercles and occasional patches, ganoin cover is absent.

The frontals are similar to those seen in *Semionotus kanabensis* and *Semionotus minor*, with a constriction at the orbit and anteriorly and with posterior expansions of nearly equal width (Figs. 4–7). Externally, the course of the supraorbital canal is marked by a series of pores, and, medially, the canals are underlain by a strong ridge (Fig. 8A). A lateral branch of the supraorbital canal is possibly connected to the infraorbital canal on the dermosphenotic, but we have not been able to confirm a connection (see Arratia and Schultze, 1987). This lateral branch of the supraorbital canal is underlain by a ventral ridge on the frontal. Anteriorly, the frontal is notched where the supraorbital canal would have entered the connective tissue between the frontal and the

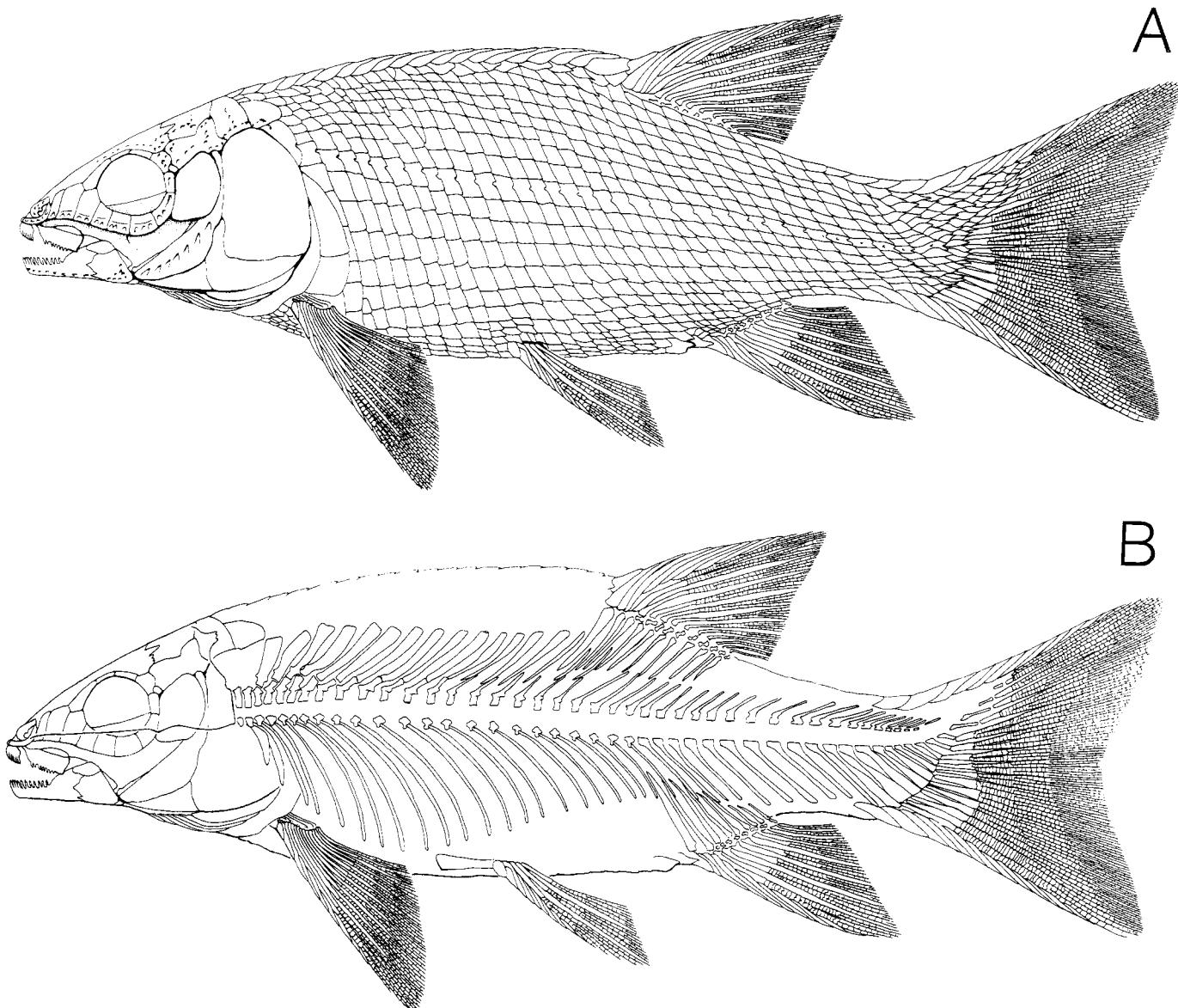


FIGURE 1. Reconstruction of complete individual of the *Semionotus elegans* group. A, external view based primarily on YPM 6567 (see Fig. 2 for actual scale). B, endoskeleton based on specimens of *Semionotus* indet., USNM 1876, YPM 9363, YPM 9367).

nasal (Fig. 8A). The anteroventral surface of each frontal is deeply grooved for the attachment of the premaxilla (Fig. 8A). The suture between the frontals is smoothly digitate posteriorly, but more or less straight anteriorly (Fig. 7).

The parietals (Figs. 4–7) are approximately square. The suture with the frontal is usually strongly digitate and that between the parietals is sinuous. There is a straight, narrow zone where the extrascapular laps onto the parietal. The supraorbital canal runs backward into the parietal where it passes out of the bone posteriorly. A branch of the main lateral line canal enters the parietal from the dermopterotic and terminates near the end of the supraorbital canal (Fig. 4).

The dermopterotic is hourglass-shaped and carries portions of the supraorbital, temporal, and possibly infraorbital canals, all of which appear to join (Figs. 4–6). Prominent descending laminae are present on the internal surface of the bone and there is a ridged, anteriorly directed lamina that fits below the dermosphenotic.

As in other Newark semionotids and all species of *Lepidotes* other than *L. lenneri* (Wenz, 1967), the circumorbital ring is complete and consists of the supraorbitals, dermosphenotic, infraorbitals, and lacrimal (Figs. 4–6). There are three anamestic (without canals) supraorbitals which are tuberculated to a variable extent. The dermosphenotic carries the infra-

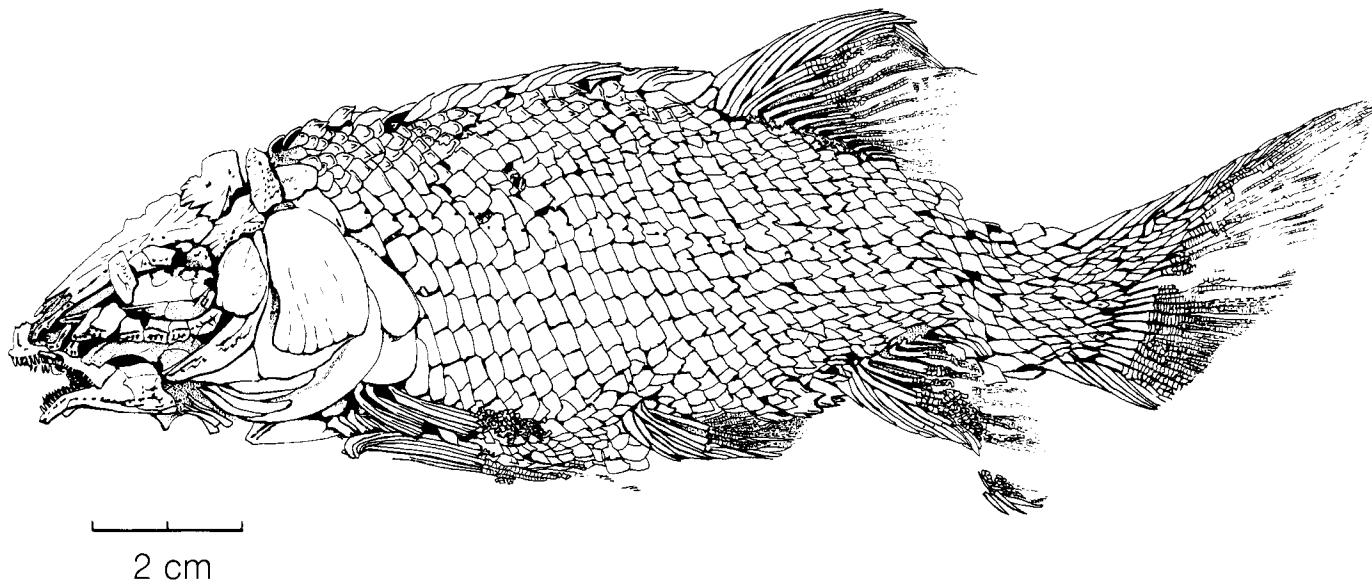


FIGURE 2. Camera lucida drawing of YPM 6567, *Semionotus elegans* group

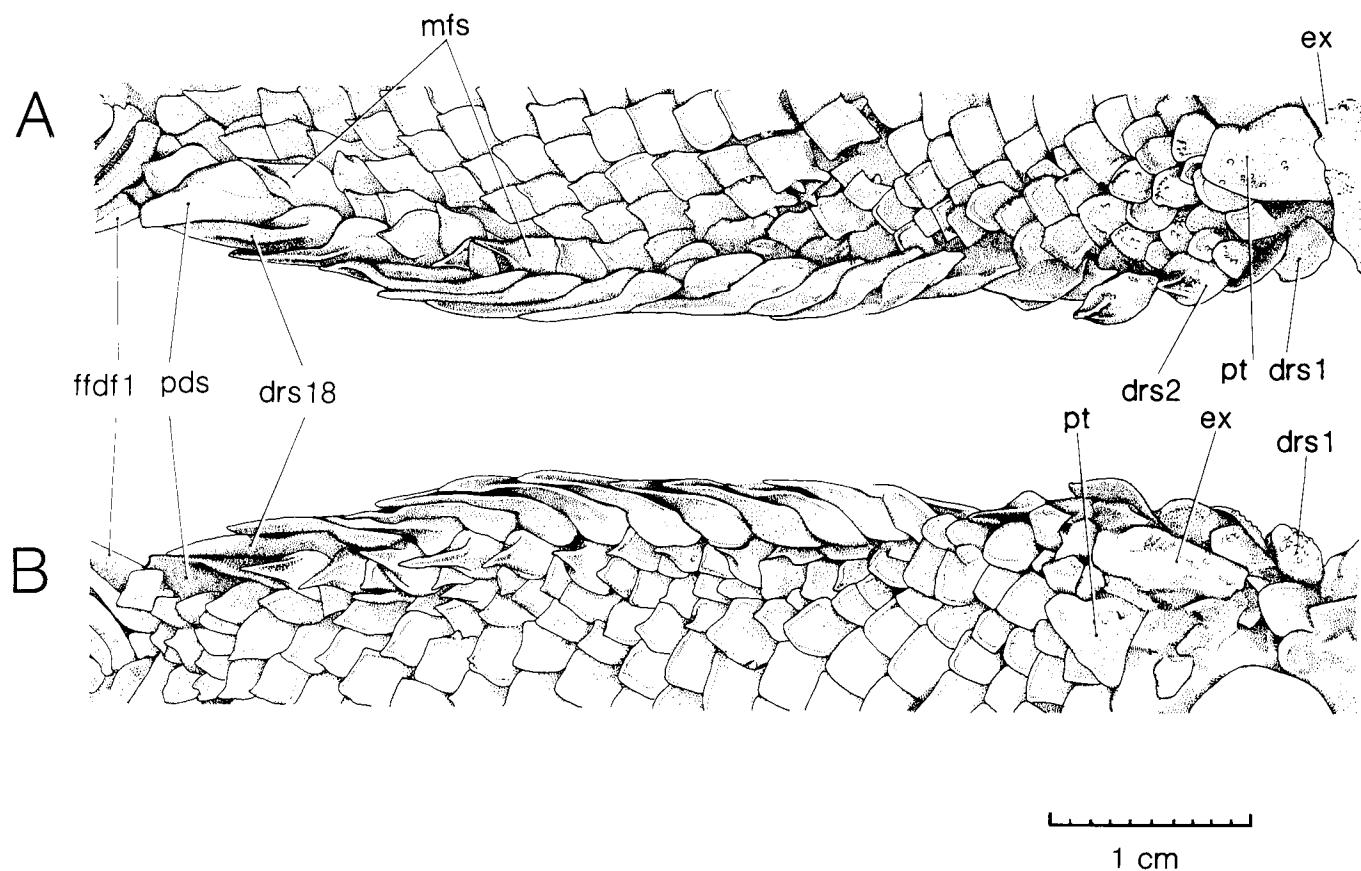


FIGURE 3. Dorsal ridge scale series viewed from left (A) and right (B) sides of the same specimen, YPM 6567, *Semionotus elegans* group. **drs**, dorsal ridge scale; **ex**, extrascapular; **ffdf**, fin fulcra of dorsal fin; **mfs**, modified flank scale; **pds**, pre-dorsal scale; **pt**, posttemporal.

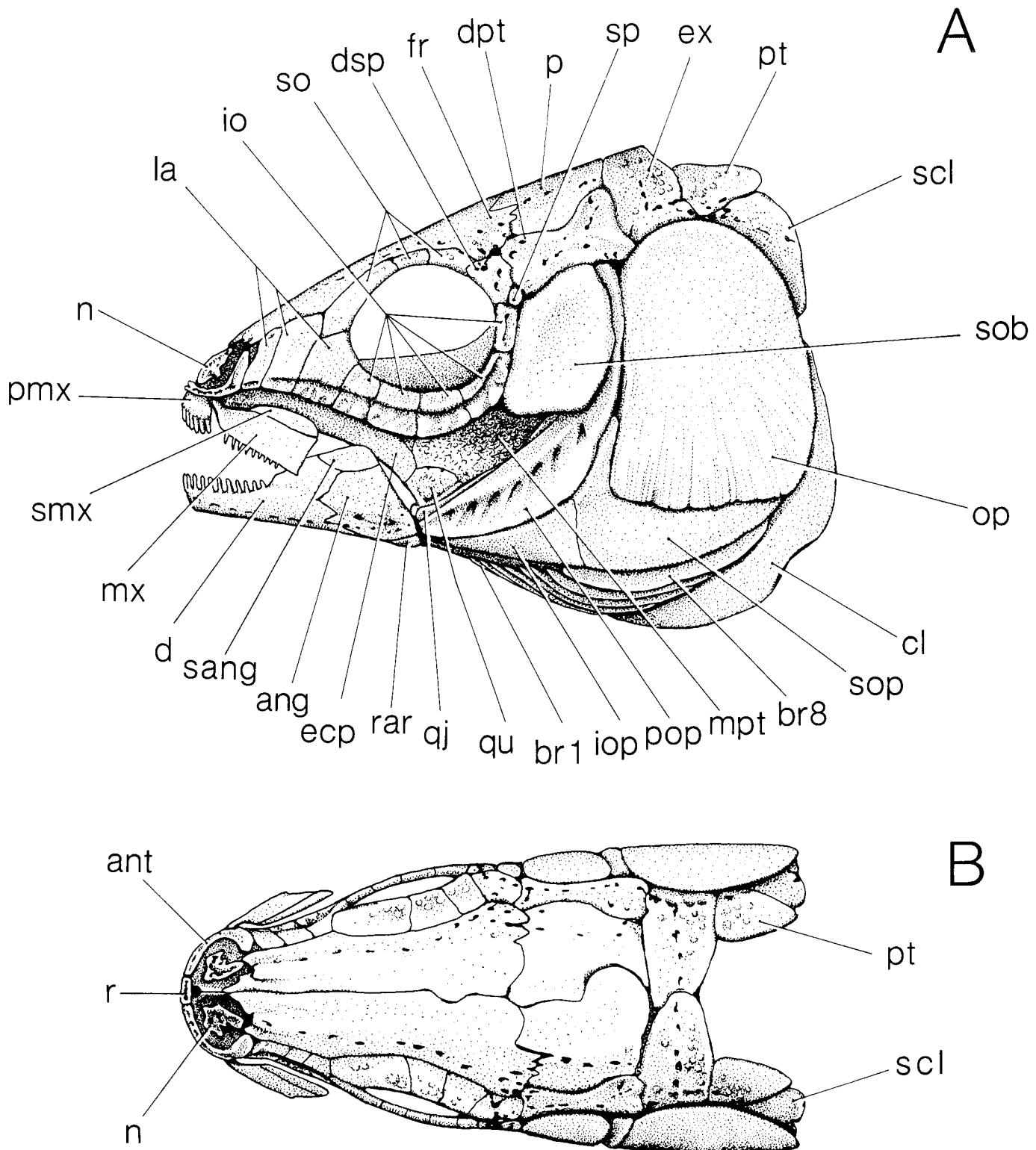


FIGURE 4. Reconstruction of *Semionotus* skull in lateral (top) and dorsal (bottom) aspect. Reconstruction was prepared by cutting out shapes of individual bones in sheet beeswax from paper templates based on camera lucida drawings. The models of individual elements were then deformed and shaped so that the skull fit together properly in 3-D. Reconstruction based on YPM 6567. Abbreviations: **ang**, angular; **ant**, antorbital; **br**, branchiostegal; **cl**, cleithrum; **d**, dentary; **dpt**, dermopterotic; **dsp**, dermosphenotic; **ecp**, ectopterygoid; **ex**, extrascapular; **fr**, frontal; **io**, infraorbital; **iop**, interopercular; **la**, "lacrimal"; **mpt**, metapterygoid; **mx**, maxilla; **n**, nasal; **op**, opercular; **p**, parietal; **pmx**, premaxilla; **po**, postorbital; **pop**, preopercular; **pt**, posttemporal; **qj**, quadratojugal; **qu**, quadrate; **r**, rostral; **rar**, retroarticular; **scl**, supracleithrum; **sang**, surangular; **smx**, supramaxilla; **so**, supraorbital; **sop**, subopercular; **sp**, "dermal" part of sphenotic.

bital canal, and possibly its junction with the supraorbital and temporal canals and its lateral face rests on the anterior process of the dermopterotic. The anterior (orbital) lamina of the dermosphenotic rests on the orbital surface of the sphenotic. The dermosphenotic is definitely not sutured to any other elements and is often displaced like other circumorbital bones (Fig. 5). The infraorbital canal is housed in a groove traversing the six quadrangular infraorbitals, which increase smoothly in size from the dermosphenotic to the contact with the supraorbitals. Anterior to the infraorbital, which contacts the most anterior supraorbital, there are two additional canal-bearing infraorbitals. As noted by Gosline (1965) an extension of the infraorbitals anterior to a closed circumorbital ring is characteristic of *Semionotus*, *Lepidotes*, and gars. In gars, Wiley (1976) refers to the three infraorbitals anterior to the circumorbital ring as "lachrymals," a convention followed by us without implying specific homology with the lacrimal of primitive osteichthyans.

The canal-bearing bones of the snout consist of paired nasals and antorbitals and a single rostral (Figs. 4–6). The nasals are very delicate and little more than curved ribbons housing the supraorbital canal (Figs. 4–6) as in macrosemiids (Bartram, 1977a). There may also be a ventrally directed branch of the supraorbital canal on the nasal as in gars (internarial commissure of Wiley, 1976). The antorbitals are L-shaped with a long rostral process. The lateral ramus carries at least the junction of the infraorbital canal and the ethmoidal commissure in an open groove (Fig. 7). The dorsal ramus of the antorbital carries a dorsally widening trough that may have carried a branch of the infraorbital canal connected to the supraorbital canal as in *Amia*. As in *Semionotus minor* (Patterson, 1975), *Lepidotes elvensis* (Wenz, 1967), and parameionotids (Patterson, 1975; Olsen, 1984), there is a small, median rostral consisting of a narrow tube around the ethmoidal commissure (Figs. 4, 6, and 7). As in all Newark Supergroup semionotids, the snout is broadly fenestrated because of the narrowness of the canal-bearing bones, making determination of the position of the nares difficult.

The cheek region is completely open except for a single oval anamestic suborbital (Figs. 4–6). This suborbital almost completely hides the hyomandibular. A similar open cheek with a single suborbital is seen in all other species of *Semionotus* (Olsen et al., 1982; McCune, 1986, 1987a).

Semionotus has the usual neopterygian number and arrangement of opercular elements (Figs. 4–6). The operculum is by far the largest element, with its posterior margin at or below the line of infraorbitals. The suboperculum has a dorsally directed ramus passing along the anterior border of the operculum for nearly one half its height. The interoperculum is triangular with its acute tip running to the tip of the preoperculum and the jaw joint. The preoperculum is crescent-shaped with a narrow vertical ramus and a deeper anterior ramus. It carries the suborbital canal and contacts the dermopterotic dorsally and the quadrate antero-ven-

trally. Laterally, the preoperculum bears ventrally directed pores for the suborbital canal and medially there is a lamina that contacts the hyomandibular. The first two of the eight branchiostegals have relatively rounded anterior margins; they do not have the pointed margins as is usual with bones that are ligamentously attached to the hyoid arch (Figs. 4–6).

Upper Jaw—The dentigerous snout bones consist of paired premaxillae and maxillae, each of the latter bearing a single supramaxilla (Figs. 4–6). The premaxillae (Fig. 7) closely resemble those of gars and *Amia* (cf. Patterson, 1973). The elongate nasal process (Patterson, 1973) forms a cup for the nasal capsule and is sutured to the frontal. There is a large fenestra for the olfactory nerve in the deepest part of this cup and a small opening between the premaxillae anteriorly for the palatine branch of VII (Fig. 7). There are six to eight stout, pointed, and somewhat recurved teeth on each premaxilla. The maxillae, as in other Newark *Semionotus*, are relatively short and end posteriorly just anterior to the orbit (see Figs 4 and 6). Anteriorly, each maxilla bears a robust, medially-directed process, which extends between the premaxilla, the dermopalatine and vomer as in *Amia*, other holosteans, and teleosts. The ventral edge of the maxilla bears about 11 to 18 small, sharply pointed, and slightly recurved teeth, with the anterior two or three being slightly longer and more recurved than the rest. A single chord-shaped supramaxilla is present.

Neurocranium—All available neurocranial specimens of the *Semionotus elegans* species group are compressions of disarticulated elements. Additional details are available from other Newark *Semionotus* (Fig. 8). The disarticulated state of most neurocranial elements and irregular margins of elements that do not fit closely together suggests that there may have been a large amount of cartilage in the adult neurocranium as is seen in all but the largest *Amia*, gars and other semionotids (Patterson, 1973, 1975). Available material suggests the pattern seen in *Lepidotes toombsi* as described by Patterson (1975). Ethmoidal ossifications are very reduced or absent.

The parasphenoid (Figs. 8, 9) is a robust cross-shaped bone with laterally directed basipterygoid processes and long ascending wings. There are notches for the pseudobranchial arteries anterior to the basipterygoid processes and for the internal carotid arteries posterior to the ascending wings. Teeth are restricted to a tiny raised patch between the basipterygoid processes. The hypophysial canal punctures the parasphenoid just anterior to this patch. Unlike the described specimens of *Lepidotes* (Patterson, 1975; Woodward, 1916–1919), the parasphenoid bears thin, lateral flanges on the anterior ramus so that its total width is as great as that of the posterior ramus.

The dermal part of the sphenotic is partially exposed in most lateral views of articulated skulls (Figs. 4–6). It is cone shaped, with the apex of the cone apparently being exposed on the lateral surface of the the dermal skull roof between the dermopterotic, dermosphenotic,

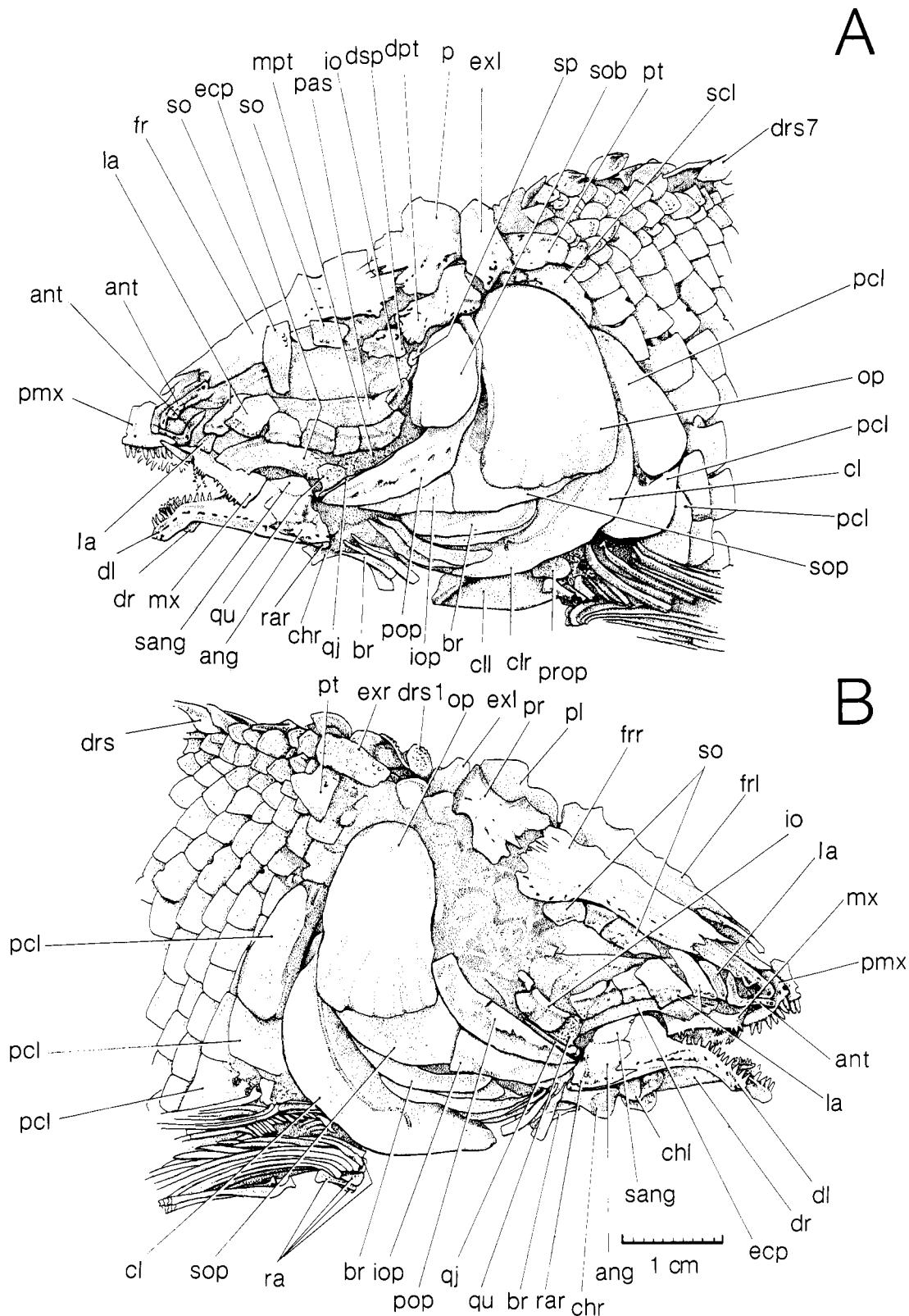


FIGURE 5. Camera lucida drawing of left (A) and right (B) sides of skull, *Semionotus elegans* group, YPM 6567, part and counterpart. Abbreviations: **ang**, angular; **ant**, antorbital; **br**, branchiostegal; **chl**, left ceratohyal; **chr**, right ceratohyal; **cl**, cleithrum; **cll**, left cleithrum; **clr**, right cleithrum; **dl**, left dentary; **dr**, right dentary; **dpt**, dermopterotic; **drs**, dorsal ridge scale; **dsp**, dermosphenotic; **ecp**, ectopterygoid; **exl**, left extrascapular; **exr**, right extrascapular; **fr**, frontal; **frl**, left frontal; **frr**, right frontal; **io**, infraorbital; **iop**, interopercular; **la**, "lacrimal"; **mpt**, metapterygoid; **mx**, maxilla; **op**, opercular; **p**, parietal; **pas**,

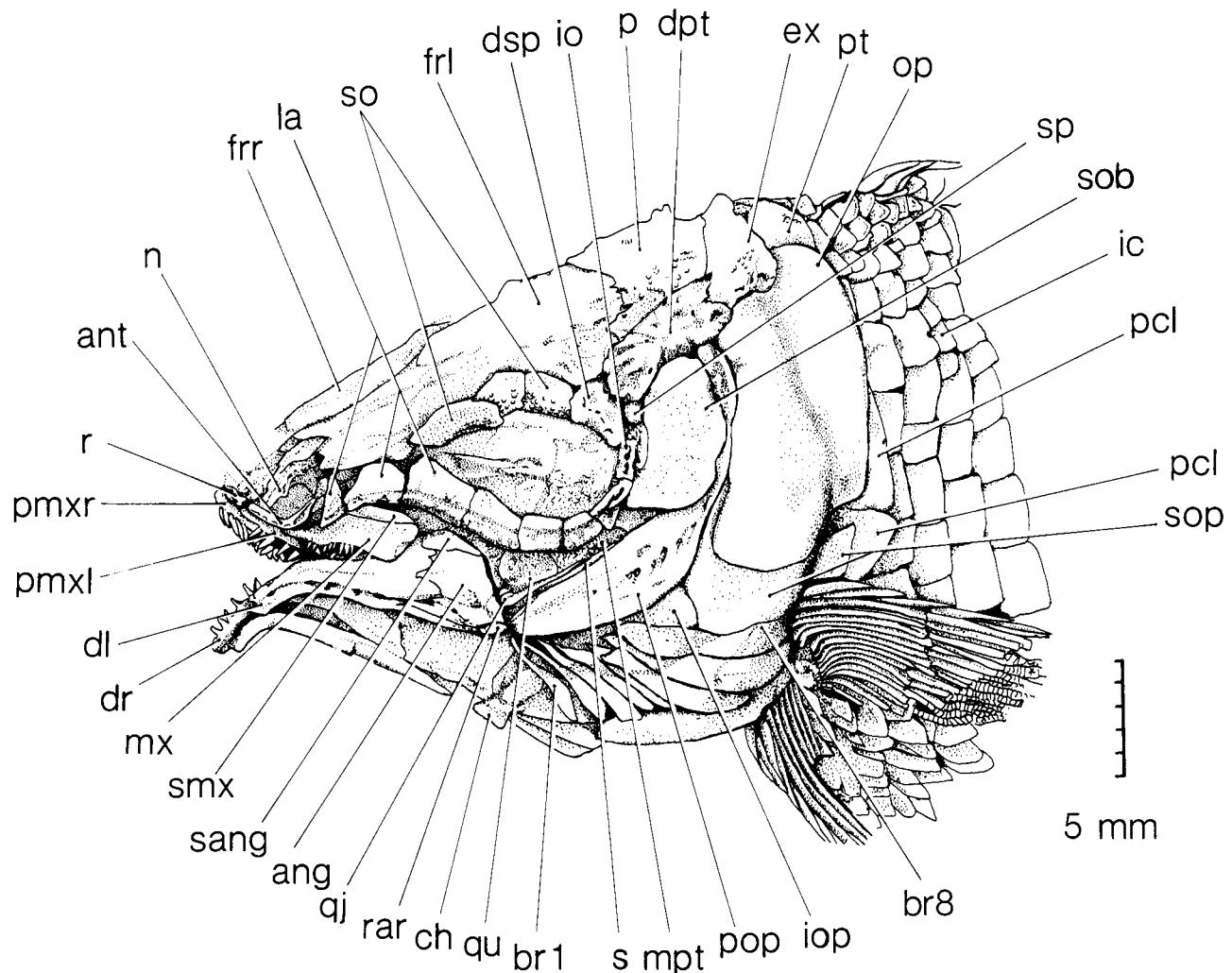


FIGURE 6. Camera lucida drawing of skull, *Semionotus elegans* group, AMNH 1540. Abbreviations: **ang**, angular; **ant**, antorbital; **br**, branchiostegal; **ch**, ceratohyal; **dl**, left dentary; **dr**, right dentary; **dpt**, dermopterotic; **dsp**, dermosphenotic; **ex**, extrascapular; **frl**, left frontal; **frr**, right frontal; **ic**, intercalary scales; **io**, infraorbital; **iop**, interopercular; **la**, lacrimal; **mpt**, metapterygoid; **mx**, maxilla; **n**, nasal; **op**, opercular; **p**, parietal; **pcl**, postcleithral scale; **pinf**, prelacrimal infraorbital **pmxl**, left premaxilla; **pmxr**, right premaxilla; **po**, postorbital; **pop**, preopercular; **pt**, posttemporal; **qj**, quadratojugal; **qu**, quadrate; **r**, rostral; **rar**, retroarticular; **s**, symplectic; **sang**, surangular; **smx**, supramaxilla; **so**, supraorbital; **sop**, subopercular; **sp**, "dermal" part of sphenotic.

and suborbital (Figs. 4, 6). The participation of the sphenotic in the skull roof also occurs in at least *Ophiopsis* (Bartram, 1975), gars, *Watsonulus* (Olsen, 1984), and *Amia* (Jarvik, 1980; Arratia and Schultze, 1987).

Of the other bones of the neurocranium, only the prootic, epiotic, exoccipital and basioccipital are visible in the available material of the *S. elegans* species group (Fig. 8). In all respects these bones resemble what is seen in other *Semionotus* from the Newark Super-

group and those described in *Lepidotes toombsi* (Patterson, 1975).

Palate, Hyoid Arch, and Gill Arches—The palate consists of the parasphenoid (described above), paired vomers (Fig. 9), entopterygoids (Fig. 10b), ectopterygoids (Figs. 4, 5, and 10b), auto- and dermopalatines (Fig. 9) and metapterygoids (Figs. 4–6 and 10b). Anteriorly, each vomer bears from five to eight thin and pointed to short and blunt teeth. Posteriorly, the vomer is sutured to the toothless anterior portion of the para-

←
parasphenoid; **pcl**, postcleithral scale; **pl**, left parietal; **pmx**, premaxilla; **po**, postorbital; **pop**, preopercular; **pr**, right parietal; **prop**, propterygium; **pt**, posttemporal; **qj**, quadratojugal; **qu**, quadrate; **ra**, radials; **rar**, retroarticular; **sang**, surangular; **scl**, supracleithrum; **so**, supraorbital; **sop**, subopercular; **sp**, "dermal" part of sphenotic.

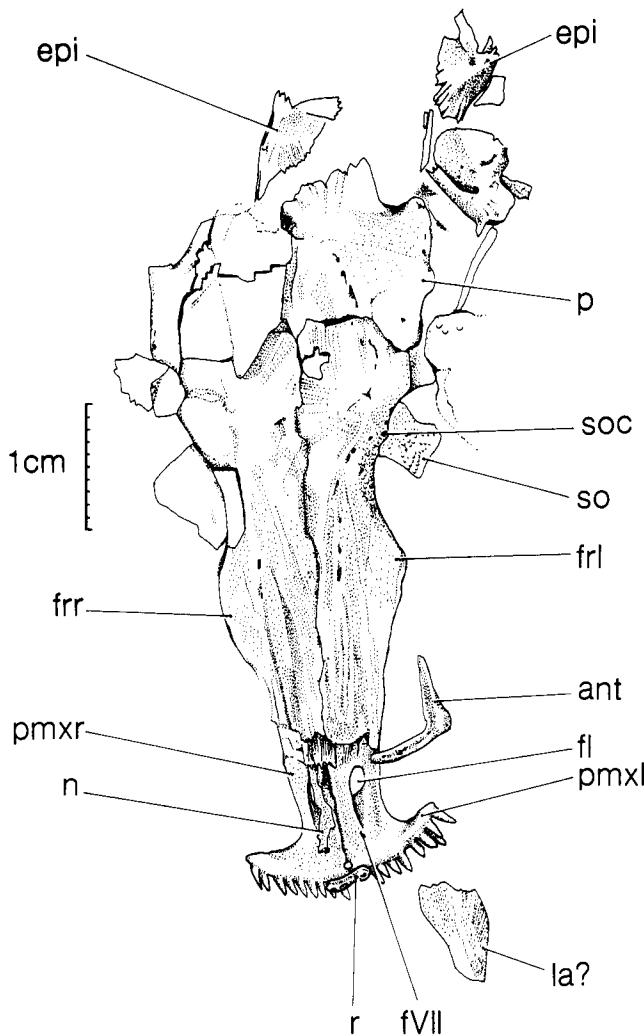


FIGURE 7. Frontals and premaxillae of AMNH 1328, *Semionotus elegans* group. Abbreviations: **ant**, antorbital; **epi**, epiotic; **fl**, foramen for olfactory nerve (I); **fVII**, foramen for palatine nerve (VII); **frl**, left frontal; **frr**, right frontal; **la**, lacrimal; **n**, nasal; **p**, parietal; **pmxl**, left premaxilla; **pmxr**, right premaxilla; **r**, rostral; **so**, supraorbital; **soc**, supraorbital canal.

sphenoid. Lateral to the vomer, there are two tooth-bearing dermopalatines, the more posterior and lateral of which is larger and underlies the autoplatine (Fig. 9). Posteriorly, the auto- and dermopalatines attach to the ectopterygoid which itself bears a few small teeth anteriorly. The ectopterygoid has a nearly vertically directed crescent-shaped lateral lamina, a medially directed lamina articulating with the entopterygoid, and an anterior bowl-shaped surface for the autoplatine (YPM 8605). The entopterygoid fills the gap between the metapterygoid, ectopterygoid, dermopalatine and dermopalatines, but because of its deep position it is poorly known. The metapterygoid is very thin and nearly circular in outline, shaped and oriented as in *Amia* (Fig. 8E1). Dorsally, the metapterygoid is split

into a medially directed flange forming the postero-medial portion of the palate, and a dorsally directed flange which laps onto the hyomandibular as in *Amia* and *Lepidotes* (Allis, 1897; Rayner, 1948; Jarvik, 1980; Olsen, 1984).

The quadrate region (Figs. 5, 6, 10A–B) is configured like that in *Lepidotes toombsi* (Patterson, 1973). The quadrate is triangular with a rounded dorsal edge. The posterior edge forms a strong lip as in *Amia*, but unlike the latter, the lip of *Semionotus* is closely appressed to the quadratojugal, not the symplectic. As preserved, the quadrate condyle is concave and cancellous and must have been covered by a convex cartilage cap during life. Medially, the quadrate has a blind pit into which the symplectic fits. The quadratojugal is spoon-shaped and rests for its entire length on the dorsal edge of the preoperculum. Its anterior end fits behind and supports the quadrate condyle but does not take part in the jaw articulation.

Elements of the hyoid arch are visible in almost every specimen. The hyomandibular is vertically oriented and has a posteriorly-directed opercular process for the operculum, a distinct lateral process for the preoperculum (Fig. 10G), and a foramen for a branch of cranial nerve VII. The symplectic is a nearly horizontally oriented rod fitting into the pit on the medial surface of the quadrate (Figs. 6 and 9). There is a small interhyal, a triangular epiphyal, an hourglass-shaped ceratohyal, and a small cubic hypohyal (Fig. 9), which appears to meet its opposite in midline. There is no gular.

Very little can be seen of the gill arches in the available specimens in the *S. elegans* species group. Small gill rakers and at least some small pointed infrapharyngeal teeth are present. At least some epibranchials bear small lateral projections comparable to the uncinate processes of Patterson (1973) and Wiley (1976). It is not yet possible to tell how these bones fit into the gill basket. The complete gill basket is exposed in an unidentified *Semionotus* (Fig. 9) from the Shuttle Meadow Formation. Unfortunately, the ventral elements obscure the dorsal ones and all that is certain is that Newark semionotids had four simple hypobranchials and five ceratobranchials as in gars and *Amia*, as well as some elongate epibranchials. There is a poorly ossified element which may be a basihyal.

Mandible—Externally, the mandible appears as in *Semionotus minor* (Patterson, 1975) and *Semionotus kanabensis* (Schaeffer and Dunkle, 1950). It has a prominent coronoid process arising just posterior to the tooth row on the dentary (Figs. 4–6, 10C–F). The mandible comprises a small retroarticular, a thin, triangular surangular, and a large angular and dentary. The dentary carries a single row of 8 to 11 pointed teeth, with its dentigerous portion being about twice the length of the rest of the bone. The retroarticular, angular, and dentary carry the mandibular canal forward from the preopercular, with the angular carrying radiating branches of the canal. Internally, there is an articular, a prearticular, and one or more coronoids.

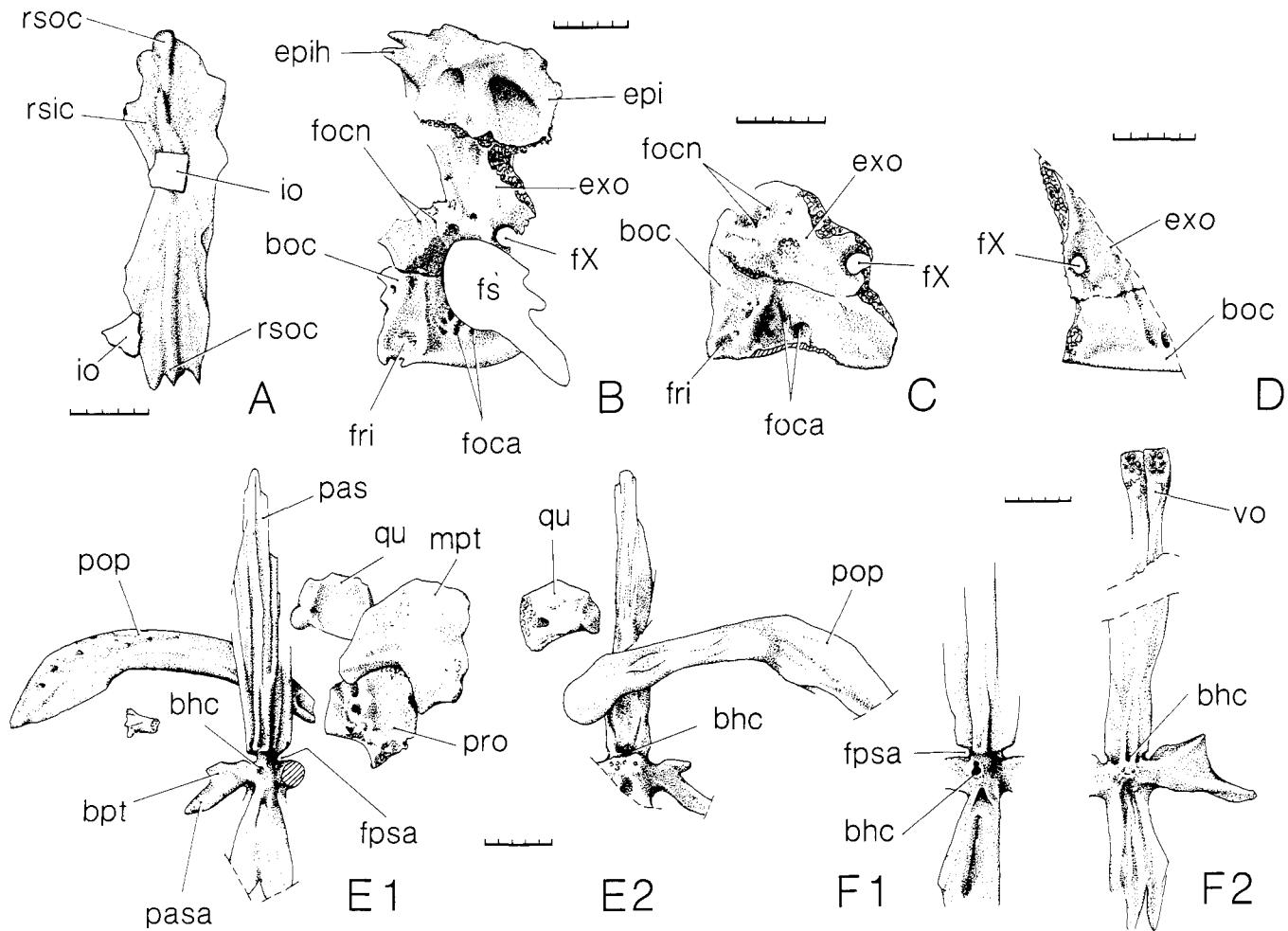


FIGURE 8. Neurocranial elements of *Semionotus*. A, frontal in ventral view, AMNH 3980. B, neurocranium, posterior portion in right lateral view, YPM 8226. C, basioccipital and exoccipital in lateral view, YPM 7193. D, basioccipital and exoccipital in left lateral view, YPM 7473. E, parasphenoid of YPM 8605 in dorsal (E1) and ventral (E2) view. F, parasphenoid of same individual in dorsal (F1, AMNH 2986) and ventral (F2, YPM 8601) view. Scales = 5 mm. Abbreviations: bhc, buccohypophyseal canal; bpt, basipterygoid process; boc, basioccipital; epi, epotic; epih, horn on epotic; exo, exoccipital; fx, foramen for vagus nerve (X); foca, foramen of occipital artery; focn, foramen or notch for occipital nerve; fspa, ascending branch of pseudobranchial artery; fri, facet for cranial rib on basioccipital; fs, flank scales; io, infraorbital; mpt, metapterygoid; pas, parasphenoid; pasa, ascending wing of parasphenoid; pop, preopercular; pro, protic; qu, quadrate; rsic, ridge underlying canal leading from supraorbital canal to infraorbital canal; rsoc, ridge underlying supraorbital canal; vo, vomer.

The articular is of the form seen in macrosemiids (Bartram, 1977a); it is large with a single concave surface for the quadrate condyle, above which is the posterior part of the Meckelian fossa. Anteriorly, an elongate process of the articular passes between the dentary and the particular. The retroarticular makes up the posteroventral portion of the mandible as is usual for holosteans (Patterson, 1973). There is no sign of a Meckelian ossification, but the area it would occupy is not clearly exposed in any Newark semionotid. The prearticular is V-shaped and bears one to three rows of small pointed teeth. One or more small tooth-bearing coronoids are present anterior to the prearticular.

Pectoral Girdle—The dermal exoskeleton consists of paired extrascapulars, posttemporals, supracleithra, cleithra, serrated organ, and post-cleithral scales. The

extrascapulars meet in midline and are triangular (Figs. 4–6). A portion of the main lateral line canal and the supratemporal commissure are carried by this bone. The posttemporal is also triangular and bears the main lateral line canal (Figs. 4–6). Ventrally, it bears a long, robust, anteriorly-directed process which articulates with the epotic exactly as the same process articulates with the intercalar in *Amia* and in teleosts (Patterson, 1973); this is best seen in Fig. 9. The supracleithrum is D-shaped and carries the main sensory canal from the posttemporal to the flank scales (Figs. 4, 5). The cleithrum is a robust bone with a strong dorsal process fitting medial to the supracleithrum (Fig. 11). There is a narrow series of denticles running along the ridge between the branchial and lateral surfaces of the cleithrum as in *Protopterus* among the macrosemiids (Bar-

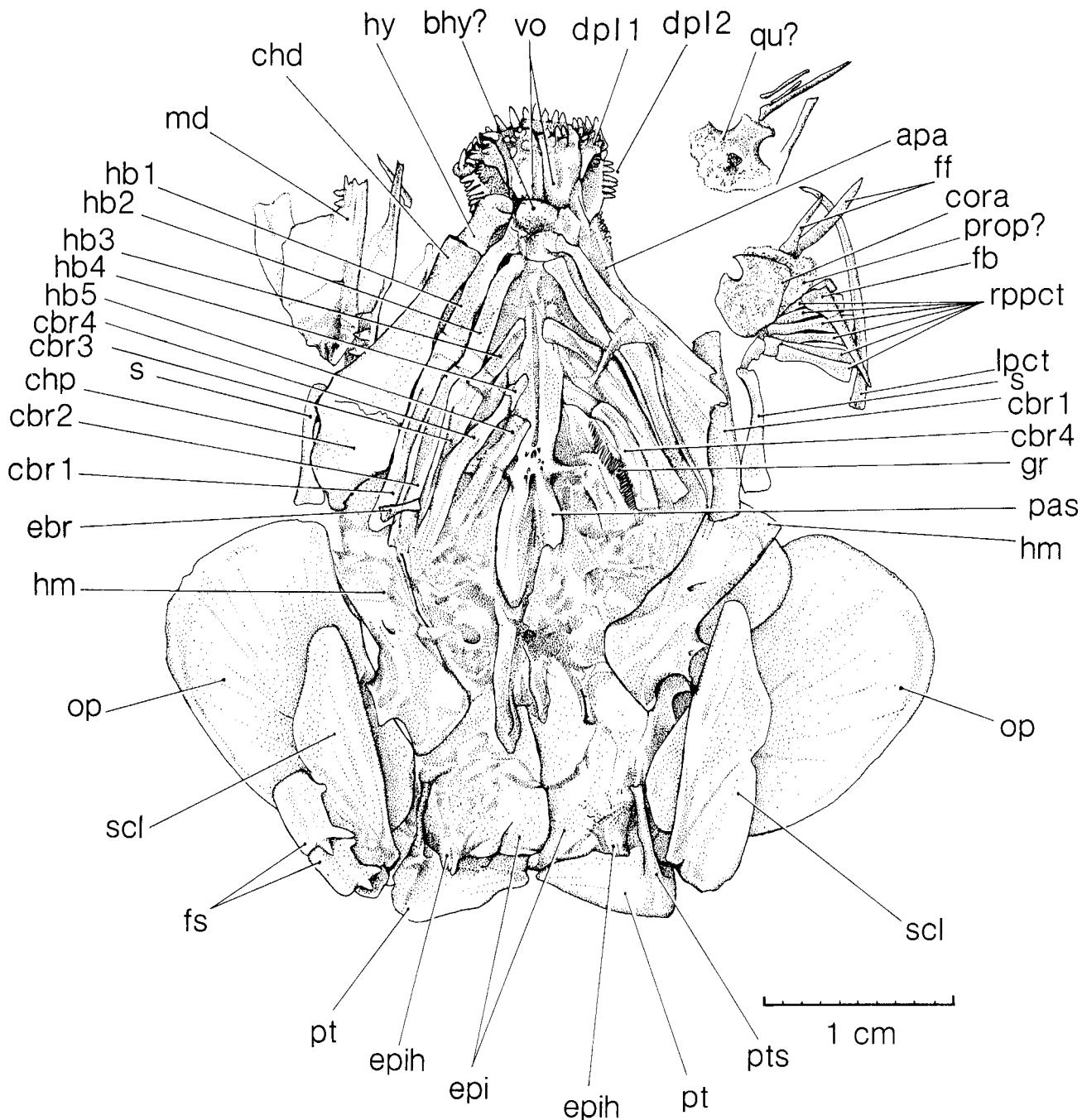
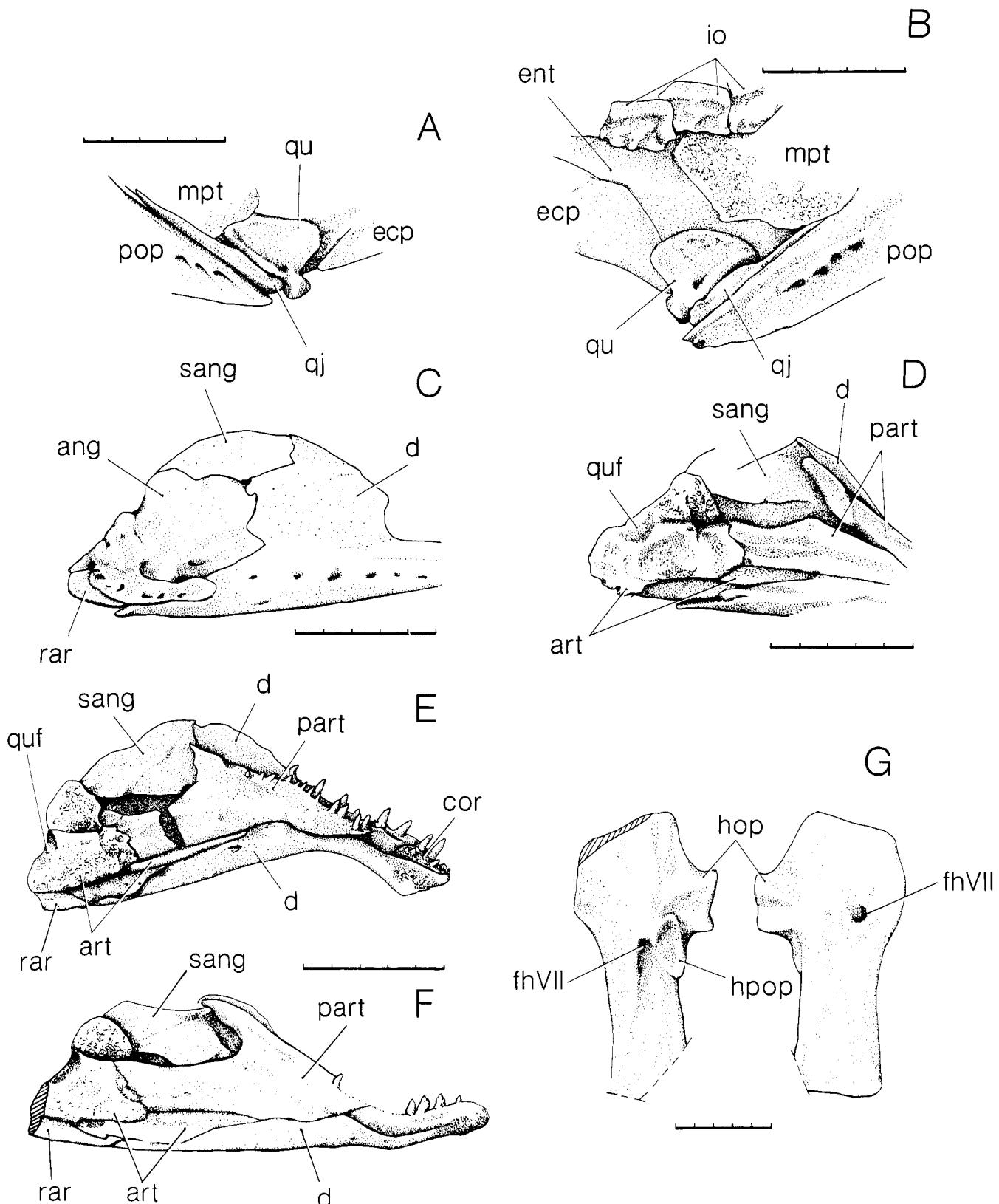


FIGURE 9. Ventral "squash" of skull of *Semionotus* showing parts of gill arches, palate, and neurocranium in ventral view, YPM 8603. Abbreviations: **apa**, autopalatine; **cbr**, ceratobranchial; **chd**, distal ceratohyal; **chp**, proximal ceratohyal; **cora**, coracoid; **dpl**, dermopalatines 1 and 2; **ebr**, epibranchial; **epi**, epiotic; **epih**, horn on epiotic; **fb**, basal fulcra; **ff**, fin fulcra; **fs**, flank scales; **gr**, gill rays; **hb**, hypobranchial; **hm**, hyomandibular; **hy**, hypohyal; **lpct**, pectoral fin lepidotrichia; **md**, mandible; **op**, opercular; **pas**, parasphenoid; **prop**, propterygium; **pt**, posttemporal; **pts**, posttemporal spine; **rppct**, proximal radial of pectoral fin; **qu**, quadrate; **s**, symplectic; **scl**, supracleithrum; **vo**, vomer.

FIGURE 10. Jaws and palate of *Semionotus*. **A**, jaw articulation in medial view, YPM 6573. **B**, jaw articulation and partial palate in lateral view, YPM 6572. **C**, mandible in lateral view, AMNH 2991. **D**, mandible in medial view, YPM 8601. **E**, mandible in medial view, YPM 8185. **F**, mandible in lateral view, YPM 8187. **G**, hyomandibular in lateral (left) and medial



(right) views, YPM 8187. Abbreviations: **ang**, angular; **art**, articular; **cor**, coronoid; **d**, dentary; **ecp**, ectopterygoid; **fhVII**, foramen for hyoid branch (VII); **ent**, entopterygoid; **hop**, process on hyomandibular for opercle; **hpop**, process on hyomandibular for preopercle; **io**, infraorbital; **mpt**, metapterygoid; **part**, prearticular; **pop**, preopercular; **qj**, quadratojugal; **qu**, quadrate; **quf**, quadrate fossa; **rar**, retroarticular; **sang**, surangular. Scale 5 mm.

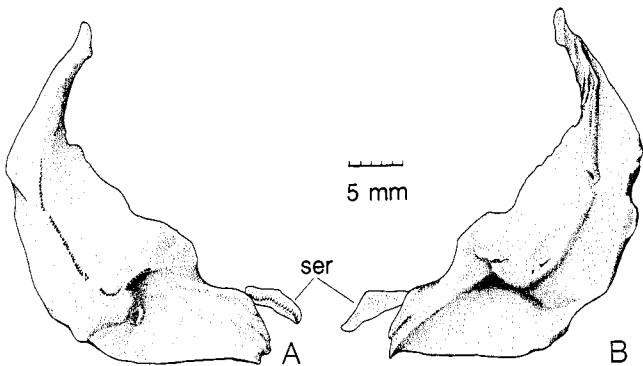


FIGURE 11. Cleithrum and serrated organ, *Semionotus elegans* group, YPM 8602. A, lateral and B, medial view. Abbreviation: ser, serrated organ.

tram, 1977a) and *Lepidotes*. In the middle of the widest part of the cleithrum, this row of denticles becomes more prominent, often turning sinuously before terminating (Figs. 5, 11). In other neopterygians, there is a patch, rather than a row, of denticles along the cleithrum (Arratia and Schultze, 1987). A small denticle-bearing strap-like bone lies in front of the anterior termination of the denticles on the cleithrum (Fig. 11) and probably represents the serrated organ, presumably homologous to the clavicle found in *Amia* (Wilder, 1877; Liem and Woods, 1973; Jarvik, 1980) and gars, among a growing list of neopterygians. There is a large dorsal postcleithral scale and at least one smaller oval postcleithral scale lying just above the origin of the pectoral fin (Figs. 5–6). As in gars (Jessen, 1972) and macrosemiids (Bartram, 1977a) the ossified endoskeleton of the shoulder girdle is reduced to a simple arch of bone (Fig. 9).

Axial Endoskeleton—As in a number of fossil holosteans, the vertebral column of Newark Supergroup semionotids consisted of an unrestricted notochord supporting neural arches dorsally, the basiventral ossifications or haemal arches ventrally (Figs. 1B, 12, and 13). There are no certain indications of hemicentra. There appear to be about 38 preural vertebral segments, all but the last three to five bearing paired neural spines on the neural arches. The last three to five bear median neural spines. There is some doubt about the exact number of segments because no single specimen is complete.

Anteriorly, there appear to be two neural arches which have no ossifications above them, but the succeeding 17 segments bear relatively robust unpaired supraneurals above, but not fused to, the neural spines (Figs. 1, 12, and 13). The first and second supraneurals are short and stout. Beginning with the third, these supraneurals become gradually shorter and slimmer as the neural spines become longer from front to back. The neural arches bear both anterior and posterior processes that touch the neighboring arches in the anterior segments. At least the first three supraneurals bear small anterior processes which articulate with the previous

supraneurals as in some teleosts (e.g., tarpon). The ventral portions of the first two proximal radials insert between the last three supraneurals.

The first basiventral seems to lack a rib, but the succeeding ones bear well-ossified ribs which articulate with a well-developed parapophysis. The first two ribs are short and broad. The last two ribs are separated by the first proximal radial of the anal fin. Posteriorly, there are 10 well-developed haemal arches with fused spines, in front of the caudal fin. From the few existing specimens showing the endoskeleton, we cannot assess individual or species-level variation in vertebral elements and associated structures.

Pectoral Fin—Six proximal radials plus a small, poorly ossified propterygium make up the preserved endoskeletal fin supports in the *S. elegans* species group and other Newark *Semionotus* (Fig. 9). There is no close correspondence between the number of radials and the number of fin rays, which number 11 to 12. The lepidotrichia are unsegmented for slightly less than half their length and bifurcate at least three times. There is one unpaired basal fulcral scale, at least two paired basal fulcral scales, and at least eight paired fringing fulcra. The precise number apparently varies at least among species.

Pelvic Fin—Endoskeletal supports for the pelvic fin are not visible in any of the specimens within the *S. elegans* group examined by us. Their reconstruction (Fig. 1) is based on impressions through the flank scales and those seen in *Semionotus brauni* (YPM 9363). In the dermal skeleton, there is always an unpaired basal fulcrum, at least two paired basal fulcra, about eight fringing fulcra, and a variable number of rays. These are unsegmented from 25–33% of their length and they

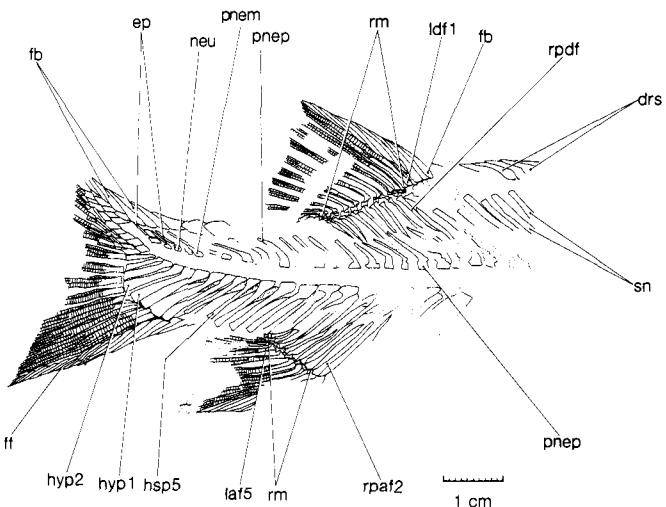


FIGURE 12. Endoskeleton of specimen from *Semionotus elegans* group, USNM 1876. Abbreviations: drs, dorsal ridge scales; ep, epurals; fb, basal fulcra; ff, fin fulcra; hsp, preural haemal spine; hyp, hypural; laf, anal fin lepidotrichia; ldf, dorsal fin lepidotrichia; neu, ural neural arch; pnem, preural neural arch, median; ptep, preural neural arch, paired; rm, middle radial; rpafl, proximal radial of anal fin; rpdf, proximal radial of dorsal fin; sn, supraneurals.

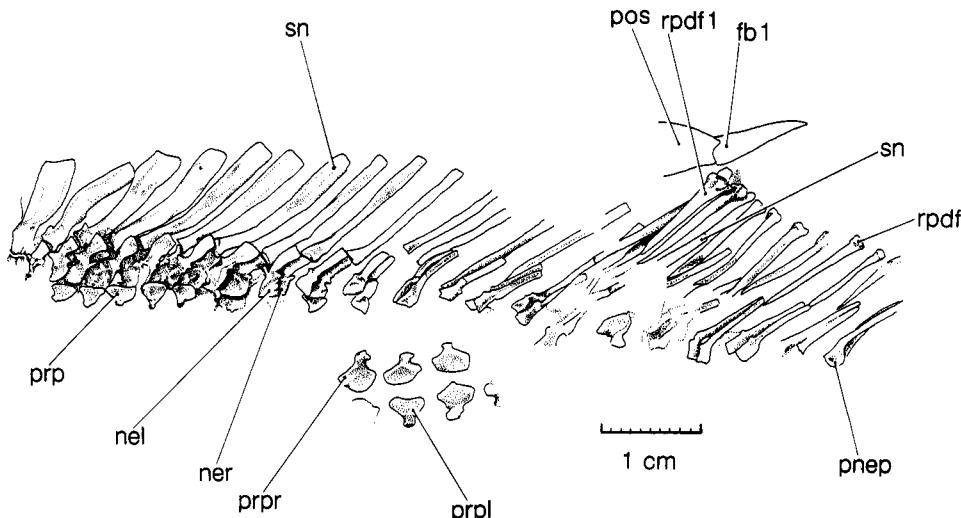


FIGURE 13. Endoskeleton of *Semionotus*. YPM 9367. Abbreviations: **fb**, basal fulcra; **nel**, left neural arch; **ner**, right neural arch; **ptep**, preural neural arch, paired; **pos**, predorsal scale; **prp**, parapophysis; **prpl**, left parapophysis; **prpr**, right parapophysis; **rpdf**, proximal radial of dorsal fin; **sn**, supraneurals.

bifurcate at least twice. The right and left pelvic fins of a single individual (YPM 6571 and NJSM 2992) bear three and four pelvic rays, respectively.

Dorsal and Anal Fin—Endoskeletal supports for the dorsal fin (Figs. 1, 12, and 13) consist of one less knife-like proximal radial than there are rays, of which there are 10 to 13. The anterior proximal radial articulates with the basal fulcral scale and lepidotrichia of the first two rays. As in macrosemiids (Bartram, 1977a), the distal radials were not ossified or not present and each of the spool-shaped middle radials articulates with its own proximal radial, the succeeding middle radial, and the lepidotrichia (Figs. 1 and 13). The lepidotrichia are unsegmented for about one-third of their length and branch at least three times. There is one unpaired basal fulcral scale, three or more basal paired fulcra, and at least 10 fringing fulcra. Endoskeletal supports for the anal fin resemble those of the dorsal (Fig. 1, 12, and 13). There is, however, one more proximal radial than there are rays. The first radial articulates with the basal fulcra, as in the dorsal fin. The pattern of middle radials follows the pattern seen in the dorsal fin. There are from 9 or 10 rays, which are unsegmented for 25–50% of their length, and they bifurcate at least twice. The anal fin has one basal fulcral scale, two paired basal fulcra, and at least eight or nine fringing fulcra. We did not assess intra- or interspecific variation in the above counts.

Caudal Fin: Endoskeleton—The caudal skeleton is visible in only one specimen definitely belonging to the *S. elegans* group (Fig. 12) and one specimen from the Waterfall Formation of the Culpeper basin (Fig. 14A) which probably belongs to the same species group. There are no notable differences between these two specimens. The hypochordal lobe of the caudal fin is supported by 18 haemal spines, five of which are probably hypurals and the rest pre-ural. The bifurcation of

hypurals is difficult to observe because these specimens are compression fossils. Our distinction between the pre-ural and hypural haemal spines relies on the association dorsally of unattached epurals above what

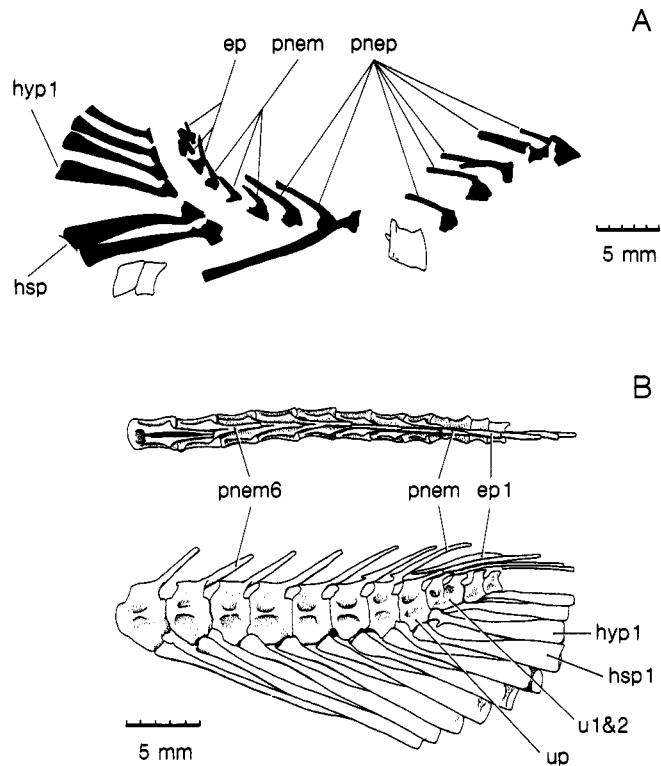


FIGURE 14. Comparison of caudal skeleton of *S. elegans* group and *Lepisosteus*. **A**, *S. elegans* group, USNM 42566. **B**, *L. oculatus*, dorsal and lateral views, YPM 5906. Abbreviations: **ep**, epurals; **hsp**, preural haemal spine; **hyp**, hypural; **pnem**, preural neural arch, median; **ptep**, preural neural arch, paired; **u**, ural centrum; **up**, preural centrum.

could be the first ural neural arch as well as a subtle change in shape and slight indications of a transverse groove for the caudal blood vessels of the hypurals which are usually associated with their bifurcation. The last three pre-ural neural arches definitely have median neural spines and the spines anterior to those are definitely not fused in the one specimen which shows three dimensional structure (Fig. 14A). There are at least three epurals and no indications of urodermals. The median neural spines of *Semionotus* are particularly interesting because this character has been used as evidence to support a relationship between *Amia* and teleosts; the Lepisosteidae are supposed to have paired pre-ural neural spines (Wiley, 1976; Patterson, 1973, 1975). However, in *Lepisosteus*, there is actually considerable variation. One small specimen of *L. oculatus* (Fig. 14B) definitely has six median pre-ural neural spines. A specimen of *Atractosteus spatula* (UCMP 131052) has two median pre-ural neural spines while other *Atractosteus* specimens lack them entirely. Median pre-ural neural spines are found in semionotids, *Amia*, teleosts and sometimes in gars. Thus, in most aspects the caudal skeleton of *Semionotus* resembles that of lepisosteids (Nybelin, 1977; Schultz and Arratia, 1986), except in the absence of centra, and perhaps a reduced number of epurals.

In most specimens, there are eight rays above the lateral line and eight rays below, and one ray acting as the continuation of the axial lobe of the tail (Figs. 1 and 12). The rays bear a one-to-one relationship to the haemal spines except for the most ventral four rays which are born on two pre-ural haemal spines. In this feature, the members of the *Semionotus elegans* species group resemble both *Amia* and *Lepisosteus* and differ strongly from the teleosts. Both the dorsal and ventral margins of the caudal fin bear three or more unpaired basal fulcra and six or more paired fringing fulcra. In all members of this species group, the lepidotrichia are unsegmented for 10-20% of their length and the caudal fin is slightly forked. Most lepidotrichia branch three times except the most dorsal and ventral rays which branch only once or twice.

Squamation—There are about 35 vertical scale rows along the lateral line. Dorsal intercalary scale rows may occur anterior to the dorsal fin (Figs. 1 and 2). There are about seven horizontal scale rows between the lateral line and the pelvic fin, eight or nine horizontal scale rows between the lateral line and the dorsal fin, and 14 horizontal scale rows on the caudal peduncle. Anterior to the anal fin, there are 17 vertical scale rows, nine vertical scale rows anterior to the pelvic fin, and 23 vertical scale rows anterior to the dorsal fin (including intercalary rows). The axial caudal lobe bears seven or eight vertical scale rows of typically "reversed squamation." Presumably, these scale counts vary both within and between species (cf. McCune, 1987).

Flank scales anterior to the dorsal fin and above the lateral line tend to be smaller and less angular than those on the rest of the flank (Fig. 1). The most dorsal

flank scales sometimes approach the dorsal ridge scales in sculpture and shape (Fig. 3). The distribution of intercalary scale rows and the pattern of sculpture is rarely exactly symmetrical on left and right flanks (Fig. 3).

Scale and Tooth Histology—Among Newark semionotids, we have sectioned only vomerine teeth of a specimen of the *S. tenuiceps* species group from the Feltville Formation (Fig. 15). It closely resembles the vomerine teeth of *Lepidotes* in having a well-developed cap of acrodin (often termed modified dentine in older literature) and a distinct organic matrix-poor enamel-like collar. Scale histology of the *Semionotus elegans* group has been described by Thomson and McCune (1984).

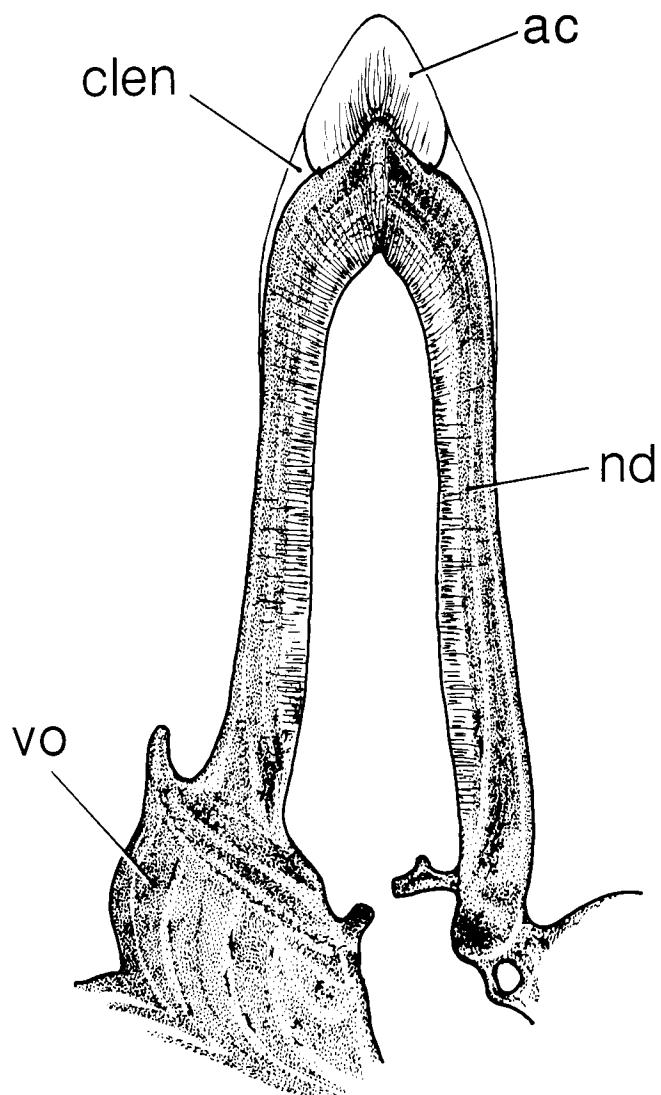


FIGURE 15. Section of vomerine tooth of *Semionotus*, *S. tenuiceps* group, YPM 7705. Feltville Formation, Martinsville, New Jersey. Abbreviations: *ac*, acrodin cap; *clen*, collar "enamel"; *nd*, normal dentine; *vo*, vomer. Tooth is about 1 mm long.

RELATIONSHIPS

In this section, we discuss the relationships of *Semionotus* within the Semionotidae and the Semionotiformes. We also elaborate on evidence for the hypothesis of neopterygian relationships first presented by Olsen (1984), although complete treatment of neopterygian relationships is beyond the scope of this paper.

Some characters discussed below were first identified by Olsen (1984). For other characters, we have reinterpreted the polarities or the morphology itself. Characters that can be assessed only in living taxa are not discussed. In a group with only three living taxa (i.e., gars, bowfin, and teleosts), "soft" characters may be misleading. For example, without knowing the condition of a character in the numerous relevant fossil taxa, soft characters that are really symplesiomorphies of *Amia* and teleosts may be mistaken for synapomorphies. Together, the data presented below provide strong evidence that the Semionotiformes (semionotids, macrosemiids, and lepisosteids) are a monophyletic group (Fig. 16). Because the semionotiforms constitute a highly corroborated clade, parsimony forces the polarity of certain characters to be reversed contrary to conventional wisdom (e.g., the lack of supramaxillae in gars is a secondary reduction, not a primitive feature).

In the discussion below, we explain the basis for our determination of character polarities. Given these polarity decisions, phylogenetic analysis yields the unconventional result that semionotiforms are the sister-group to teleosts (Fig. 16). However, we note that this hypothesis is dependent on our interpretation of character polarities and the semionotiform-teleost node itself is supported by only a single character, the jaw joint. If one makes no assumptions about polarities, and the data (summarized in Appendix 1) are analyzed using Phylogenetic Analysis Using Parsimony (PAUP, version 2.4.1; Swofford, 1985), there is another equally parsimonious tree in which *Amia* and gars form a monophyletic group, which is, in turn, the sister-group to teleosts. We present both hypotheses to stimulate further work on the relationships of neopterygians.

The Semionotidae: *Semionotus* and *Lepidotes*

In recent classifications, the Semionotidae have included as many as 20 genera, and, as such, the family is clearly not monophyletic (Patterson, 1973). Following the lead of Lehman (1966) and Wenz (1967), who excluded *Dapedium* and its relatives from the Semionotidae, we further restrict the family Semionotidae to *Lepidotes* and *Semionotus*, because this is the largest subgroup of the Semionotidae sensu Woodward (1890) that we can show to be monophyletic. We thus exclude *Acentrophorus*, *Dapedium*, and a number of lesser known genera from the family. The Semionotidae in this restricted sense is defined by the presence of dorsal ridge scales (see earlier discussion of the distribution

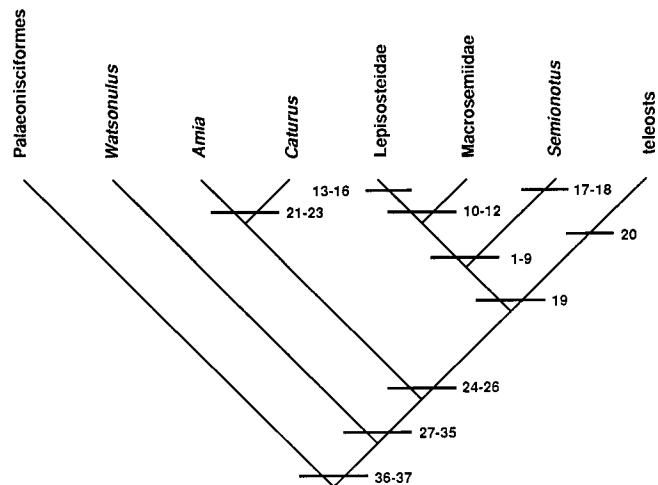


FIGURE 16. Relationships of the Neopterygii. Characters are represented by numbers, as indicated below. References for characters are given in text except as noted: 1, series of "lacrimals" anterior to the orbit; 2, epiotic is modified pterotic; 3, forward extension of exoccipital around vagus nerve; 4, premaxillae with greatly elongated nasal processes; 5, loss of opisthotic; 6, reduction of ethmoidal ossifications to splints; 7, only mesocoracoid arch of endochondral pectoral girdle ossified in the same way; 8, gular lost; 9, intercalar lost; 10, supratemporals subdivided; 11, interopercular removed from jaw joint and reduced; 12, supramaxillae lost; 13, loss of articular heads of premaxillae (Patterson, 1973); 14, "infraorbitals" bearing teeth (Wiley, 1976); 15, symplectic removed from quadrate (Patterson, 1973; Veran, 1988); 16, lepisosteid-type dentine (Wiley, 1976); 17, dorsal ridge scales; 18, single anamestic suborbital; 19, symplectic removed from jaw joint, ending blindly on quadrate; 20, characters listed by Patterson (1973) including quadratojugal fused to quadrate; 21, membranous growths of intercalar of amiid type; 22, quadratogual lost; 23, dermosphenotic integral part of skull roof; 24, clavicles reduced; 25, preoperculum with narrow dorsal limb; 26, vomers molded to underside of ethmoidal region and sutured to parasphenoid; 27, paired vomers differentiated; 28, compound coronoid process on mandible; 29, suspensorium vertical; 30, mobile maxillae with internally-directed articular head; 31, supramaxillae present; 32, interoperculum present; 33, upper caudal fin rays elongate; 34, dorsal and anal fin rays about equal in number to their supports; 35, large posttemporal fossa present; 36, anterior and posterior myodomes present (Patterson, 1975); 37, preoperculum with broad dorsal margin (Olsen, 1984).

of this character) and a large posteriorly directed process on the epiotic. If additional characters are discovered, and as other genera become better known, it may become appropriate to include other genera in the family.

The Semionotidae, even so restricted, is a very diverse group, perhaps more than 50 species. This overwhelming diversity has hampered elucidation of relationships within the family. *Semionotus* is defined by a single anamestic suborbital (McCune 1986), a derived condition within the Actinopterygii (Schaeffer and Dunkle, 1950; Patterson, 1973; Wiley, 1976). *Lepi-*

idotes, defined by a median vomer and tritoral dentition, is easily distinguishable from *Semionotus* by the series of anametic suborbitals that fills the cheek region.

A preliminary hypothesis of the relationships of European and North America *Semionotus* has been formulated (McCune 1987a, b), but this very tentative phylogeny did not include undescribed and poorly known species of *Semionotus*, let alone *Lepidotes*. Furthermore, as discussed earlier, when this tentative phylogeny was constructed, we regarded the single suborbital as primitive. We now concur with other authors that this feature is a synapomorphy for *Semionotus*. *Lepidotes* is badly in need of revision to determine the relationships within the family, especially the position of problematical taxa such as *L. toombsi* which has both a single suborbital and tritoral dentition, and to determine whether the poorly developed spines on the dorsal ridge scales of *L. laevis* are secondarily reduced or indicative of this species being the primitive sister group to all other semionotids. Thus, the relationships within the Semionotidae require further study.

The Semionotiformes: Semionotidae, Macrosemiidae and Lepisosteidae

Synapomorphies Defining the Semionotiformes—The Semionotiformes, restricted to the Semionotidae, Macrosemiidae, and Lepisosteidae, is defined by the following synapomorphies. Numbers in parentheses refer to the characters in Figure 16.

(1) Series of lacrimals anterior to the circumorbital ring. This condition is, as far as we know, unique to the Semionotiformes as defined above (Gosline, 1965; Bartram, 1977a). While the homologies of these elements with infraorbitals, antorbital or lacrimals (Wiley, 1976) are unclear, the condition is unique to this group and provides evidence of relationship.

(2) Epiotic as modified pterotic. Rayner (1948) first pointed out the uniquely shared features of the "epi-otic" in *Lepisosteus* and semionotids. The possible homology of the these "epi-otics" with the pterotic is discussed extensively by Patterson (1975:452–454) although he does not comment explicitly on whether this similarity should be interpreted as primitive, convergent, or uniquely derived. The epiotic in the *Macrosemius* figured by Bartram (1977a:fig. 3) appears to be like that in lepisosteids and semionotids.

(3) Forward extension of exoccipital around vagus nerve. Olsen (1984) regards this as a synapomorphy, while Patterson (1973) argues that the enclosure of the vagus nerve by the exoccipital may be the result of "precocious closure of the cranial fissure."

(4) Premaxillae with elongate nasal process. *Semionotus*, macrosemiids, lepisosteids and *Amia* have elongate nasal processes. Except in macrosemiids, the nasal processes are perforated by an opening through which the olfactory nerve travels to the nasal capsule. Olsen (1984) interprets the elongate nasal processes in lepisosteids, semionotids, and macrosemiids as a synapomorphy. However, developmental evidence sug-

gests that the elongate nasal processes of the premaxillae of *Amia* and gars are derived independently (Wiley, 1976).

(5) Loss of opisthotic. The opisthotic has been lost in gars, macrosemiids, semionotids, and *Amia*. The loss of the opisthotic in macrosemiids was not observed by Bartram (1977a), however, who apparently misinterpreted a lateral view of the braincase he figured as a medial view. Study of an AMNH cast of this specimen (MU AS.1.769) suggests the view figured by Bartram (1977a: fig. 3) is a lateral view. Interpreted in this way, the right ascending process of the parasphe- noid is shown clearly attached to the prootic; the braincase lacks the opisthotic and is directly comparable to semionotids and gars. Olsen (1984) assumes that the opisthotic was lost independently in *Amia*.

(6) Ethmoidal ossifications reduced. Reduction of the ethmoidal ossification occurs in gars, semionotids, macrosemiids and *Amia*. Reduction of these ossifications in *Amia* occurs differently than in the other three taxa (Patterson, 1973; Bartram, 1977a). The absence of the anterior myodome in these taxa can be explained as a result of the reduction of ethmoidal ossification, in that a hole through a structure cannot occur if there is no structure.

(7) Reduction of ossification in the endochondral component of the shoulder girdle to the mesocoracoid arch. In gars, macrosemiids, and semionotids, ossification in the shoulder girdle occurs only in the mesocoracoid arch. We regard this condition as derived because the shoulder girdle of paleoniscoids, *Acipenser*, *Watsonulus*, *Mimia* and teleosts is massively ossified and remarkably similar in most details (compare Jessen, 1973; Olsen 1984; Gardiner, 1984). The endochondral component of should girdle of *Amia* is completely unossified; however, the shape of the meoscoracoid region is different than in semionotiformes suggesting reduction in these two taxa has occurred in parallel.

(8) Loss of gulars. The presence of one or more gulars is typical of most palaeonisciformes so that its loss must be derived. Loss of gulars has also occurred in most modern teleosts, *Acentrophorus*, and *Hulettia* (Patterson, 1973; Bartram, 1977a; Schaeffer and Patterson, 1984), however, and is only weak evidence of relationship.

(9) Intercalar lost. The intercalar is present primitively in actinopterygians (Patterson, 1973) and its absence must be derived.

Macrosemiids and Lepisosteids

According to Patterson (1973), gars are the sister-group to all other neopterygians because they lack a supramaxilla, the maxilla lacks an internally-directed head, and an interoperculum is absent. The presence of these structures defines the Halecostomi (Patterson, 1973). However, given the evidence for monophyly of the Semionotiformes given above, the absence of these characters in lepisosteids must be secondary losses, which together with reductions or losses in the same

features in macrosemiids, suggest a relationship between these two taxa (Olsen, 1984) as discussed below.

(10) Supratemporals subdivided. The single pair of supratemporals in halecostomes has been interpreted as a synapomorphy of that group relative to the two pair of supratemporals in lepisosteids (Wiley, 1976). However, both conditions, having one and two pairs of supratemporals, are known in palaeoniscoids (Gardiner, 1984; Pearson, 1982). Furthermore, in some macrosemiids, there appear to be two pairs of supratemporals, with the more dorsal pair partially fused to the parietals (e.g., Bartram, 1977a:fig. 24). The condition in macrosemiids suggests that two pairs of supratemporals is a synapomorphy for macrosemiids and gars, with partial or complete fusion of the dorsal pair to the parietals being unique to macrosemiids. This is supported by the condition seen in *Aphanepygus*, which very closely resembles gars in the temporal region and is closely related to macrosemiids (Bartram, 1977b).

(11) Interoperculum reduced or absent. In macrosemiids, the interoperculum is very small and well-isolated from the jaw joint (Bartram, 1977a). This is exceptional among neopterygians where the extension of the interopercular to the jaw joint is a very consistent and functionally important feature (Patterson, 1973; Lauder, 1979). Associated with this reduction in macrosemiids is an expansion of the posterior margin of the preoperculum into the space that is occupied by the interoperculum in other fishes (Bartram, 1977a:fig. 13). Notably, macrosemiids are the only fishes known to us where the anterior edge of the interoperculum is not adjacent to the jaw joint. The expansion of the preoperculum is even more pronounced in gars, which lack the interoperculum altogether. The preoperculum in gars occupies the entire "interopercular space." Given the evidence of relationships of gars, macrosemiids, and semiontids described above, and the increasing invasion of the "interopercular space" by the preoperculum in macrosemiids and gars, we suggest that it is most economical to hypothesize that the expansion of the preoperculum and lack of an interoperculum in gars is a secondary reduction, not the primitive condition. No palaeonisciform approaches the gar configuration of the preoperculum and suboperculum.

(12) Supramaxilla lost. Gars and macrosemiids share the loss of the supramaxilla. The snout of gars is elongate and the maxilla is reduced to a tiny sliver of bone isolated from the premaxilla. Without a less modified taxon to establish polarity, it is difficult to say whether the absence of the supramaxilla in gars is primitive, or a consequence of the extremely reduced maxilla. Bartram (1977a) apparently believed that a supramaxilla was lost in macrosemiids because he refers to the family as basal halecostome, implying that, primitively, they would have had a supramaxilla. It is possible that macrosemiids never had a supramaxilla, but if macrosemiids, semiontids (which have a supramaxilla), and gars are a monophyletic group as argued above, then the presence of a supramaxilla would be primitive for the Semionotiformes. The loss of the supramaxilla within the Semionotiformes would therefore be a syn-

apomorphy uniting macrosemiids and gars. Apparently the supramaxilla has been lost independently in some teleosts and some amiids (Bryant, 1987) as well.

Semionotiformes and Teleosts

Monophyly of the Semionotiformes plus teleosts is based on the nearly identical form of the jaw joint (Fig. 16; character 19). In the "semionotid-lepisosteid condition," also seen in teleosts, the symplectic is removed from the jaw joint and the quadratojugal is a splint-like bone that braces the quadrate against the preoperculum (Patterson, 1973). The teleost jaw joint differs from the "semionotid-lepisosteid condition" only in the fusion of the quadratojugal with the quadrate in teleosts (Patterson, 1973). In contrast, in *Amia* and other halecomorphs, the symplectic is massive and has a separate articulation with the jaw joint, a condition interpreted by Patterson (1973) as derived among neopterygians. However, in palaeoniscoids (Nielsen, 1942; Veran, 1988) and *Watsonulus* (Olsen, 1984), there is a bone in the same position as the neopterygian symplectic, which participates in the jaw joint. This condition in paleoniscoids and *Watsonulus* has led Olsen (1984) and Veran (1988) to hypothesize that the double articulation in halecomorphs is primitive.

We should also note that the elements identified tentatively as the symplectics by Bartram (1977a:fig. 25 A, ?S.r, ?S.l) in *Propterus* are probably gill arch elements. A cast of *Macrosemius* (AMNH cast of MU AS.1.769) shows that the macrosemiid symplectic is a splint-like bone without a surface for articulation with the mandible as in semionotids. In our view, gars possess a modified semionotid-macrosemiid style symplectic which has moved away from the quadrate entirely and is in contact with the quadratojugal only. Our inclusion of gars within the Semionotiformes requires the loss of contact between the symplectic and mandible to occur only once within the neopterygians rather than twice as suggested by Veran (1988).

In *Amia*, *Watsonulus*, *Caturus*, and other fishes grouped by Patterson (1973) in the Halecomorphi, the symplectic has a separate articulation with the mandible. However, Nielsen (1942) and Veran (1988) show that the symplectic has a similar contact with the mandible in a variety of forms usually grouped in the Palaeonisciformes, suggesting that the contact of the symplectic with the mandible may be primitive at the osteichthyan level (Veran, 1988; Olsen, 1984). If the amiid type of double jaw joint is, in fact, primitive, the Halecomorphi should be defined by other characters as discussed by Veran (1988). This leaves the status of several taxa (e.g., *Macrepistius*, *Ophiopsis*, pycnodonts, parasemionotids) included in the Halecomorphi by Patterson (1973) and Bartram (1975) within the neopterygians uncertain.

Amia and *Caturus*

Three characters support the monophyly of *Amia* and *Caturus* (Patterson, 1973). These are membranous growths of the intercalar (21) of the amiid type;

loss of the quadratojugal (22); and dermosphenotic incorporated as an integral part of the skull roof (23).

(*Amia* and *Caturus*) + (Semionotiformes and Teleostei)

This group is also supported by three characters: clavicle reduced to a small denticulated splint of bone (24; Patterson, 1973); preoperculum with narrow ascending limb (25; Olsen, 1984); vomers molded to underside of ethmoidal region and sutured to parasphenoid (26; Olsen 1984).

Neopterygians

Monophyly of the neopterygians [*Watsonulus* + (*Amia* + *Caturus*) + (Semionotiformes + Teleostei)] is supported by the following eight characters, all from Patterson (1973): differentiated paired vomers (27); compound coronoid process on mandible (28); suspensorium vertical (29); mobile maxillae with internally-directed articular head (30); supramaxillae present (31); interoperculum present (32); upper caudal fin rays elongate (33); dorsal and anal fin rays about equal in number to their supports (34) (Patterson, 1973:296). A large posttemporal fossa (35) is present in all neopterygians except gars, and we follow Patterson (1973) in suggesting that it is a synapomorphy of neopterygians. If the Semionotiformes are the sister-group to teleosts as we suggest here, then the large posttemporal fossa must be secondarily reduced in gars, perhaps as a consequence of the greatly reduced posttemporal region.

Analysis of the Data Without a priori Determinations of Polarities

We also analyzed the above data (see Appendix) with PAUP version 2.4.1 (Swofford, 1985). We used the "branch and bound" option, which guarantees finding the most parsimonious trees (i.e., is not heuristic) and "outgroup rooting," which does not require one to make polarity decisions for characters. With outgroup rooting, character polarities are not determined relative to a specified outgroup; instead, the program includes the outgroup in the analysis, and character polarities are determined so that the resulting tree is most parsimonious (Swofford, 1985). PAUP found two equally parsimonious trees (length: 45; consistency index: 0.844), shown in Figure 17. The trees are identical except for the sister-group to teleosts. In one tree (Fig. 17b), the Semionotiformes emerge as the sister-group to teleosts. This tree is identical to the phylogeny already presented (Fig. 16). In the other tree (Fig. 17a), halecomorphs and Semionotiformes emerge as a monophyletic group which, in turn, is the sister group to teleosts. While it is not possible at present to choose between these two trees, it is worth noting the parallelisms and reversals that occur in each.

The semionotiform-teleost hypothesis (Fig. 17b) is the hypothesis first proposed by Olsen (1984) based on character polarities determined by outgroup com-

parison, development, and parsimony, as discussed for each character in the above text. However, the single jaw joint is the only character supporting the semionotiform-teleost node. This hypothesis requires: parallel evolution of the long ascending arm of the premaxillae (4) in *Amia* and Semionotiformes, for which there is supporting developmental evidence (Wiley, 1976); independent losses of the opisthotic (5) in the same two groups; and loss of an equal number of supports to rays in the dorsal and anal fins (34) of teleosts.

An alternative hypothesis is that Semionotiformes and halecomorphs are monophyletic and together these holosteans are the sister-group to teleosts. The holostean-teleost node is supported by four characters (4, 5, 7 and 34), not all of which are entirely convincing. According to developmental evidence cited by Wiley (1976), the long ascending arm of the premaxilla (4) is thought to be non-homologous in *Amia* and gars. Character losses, such as loss of the opisthotic (5), are never as convincing as character acquisitions. As discussed earlier, reduction of the shoulder girdle (7) occurs differently in Semionotiformes and halecomorphs. Presence of equal numbers of fin rays and supports in the dorsal and anal fins (34) is the most convincing character supporting the holostean-teleost node. This "holostean monophyly hypothesis" also requires that *Caturus* regained the opisthotic (5) and lost the long ascending processes of the premaxillae (4). Further, the hypothesis requires the double jaw joint (19) to have been lost at the holostean-teleost node, and then reacquired in halecomorphs. Based on the morphological characters discussed here, the holostean monophyly hypothesis is less convincing than the semionotiform-teleost hypothesis; however, sequence data from mitochondrial DNA (Normark, McCune, and Harrison, 1991), support the monophyly of *Amia* and gars.

CONCLUDING REMARKS

While it does not seem to be possible at this time to resolve neopterygian relationships, our studies of *Watsonulus* (Olsen, 1984), *Semionotus*, and their relationships to other actinopterygians lead us to two conclusions. First, there is convincing evidence that the Semionotiformes, including lepisosteids, macrosemiids, and semionotids, constitute a monophyletic group. Second, morphological evidence suggests either that the Semionotiformes are the sister-group to teleosts or that a monophyletic subset of the Holostei (at least gars, *Amia*, macrosemiids and semionotids) is the sister-group to teleosts. Ultimately, understanding neopterygian relationships will require both molecular data from living neopterygians and study of more fossil taxa. As Gauthier et al. (1988) have demonstrated, fossil taxa can play a crucial role in polarity decisions and determination of relationships. Consideration of fossil taxa is especially critical in groups like the Neopterygii where much of the morphological diversity can only be seen in fossils. It would be especially in-

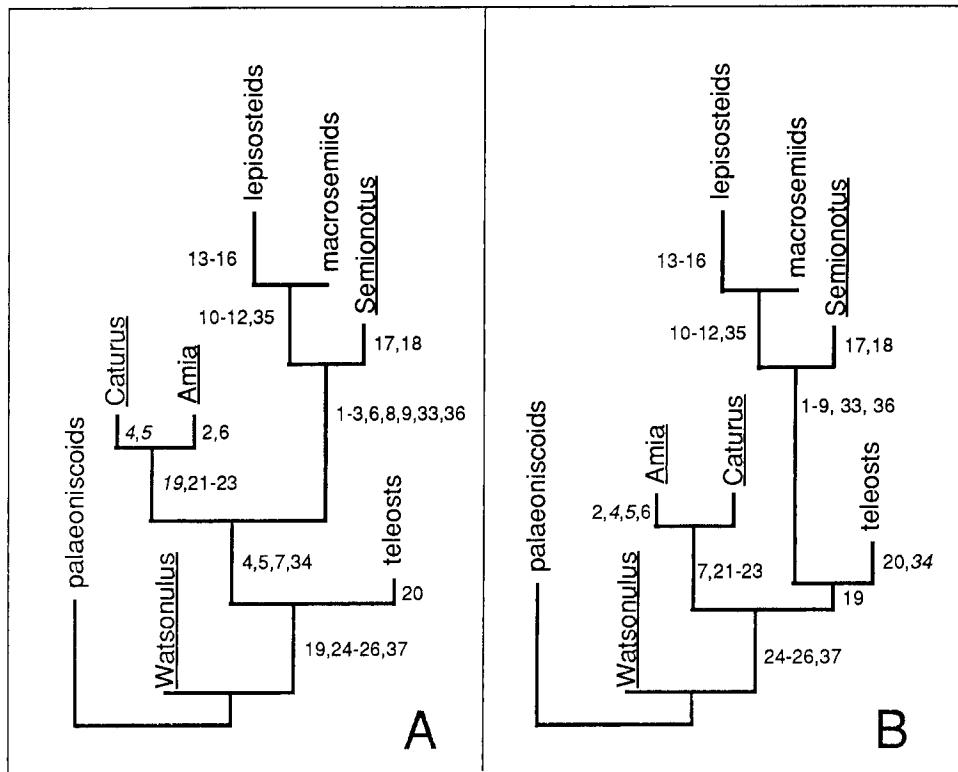


FIGURE 17. Results of PAUP without *a priori* determinations of character polarities. There are two most parsimonious trees, which are identical except for the sister group to teleosts. A, Halecomorphs plus Semionotiformes are the sister-group to teleosts. B, Semionotiformes are the sister-group to teleosts. Numbers in the figures correspond to those given in the text and in Appendix 1. See text for a discussion of parallelisms and reversals required for each hypothesis.

formative to study close relatives of gars and macrosemiids that might illuminate, through intermediate conditions, the polarity of crucial characters that are otherwise too difficult to assess in a taxon as specialized as gars.

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LITERATURE CITED

- Agassiz, L. 1832. Untersuchungen über die fossilen Fische der Lias-Formation. Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1832, part 3:139–149.
- . 1833–44. Recherches sur les Poissons Fossiles. Nauchâtel, Imprimerie de Petitpierre.
- Allis, E. P. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. Journal of Morphology 2: 463–540.
- Arratia, G., and H.-P. Schultzze. 1987. A new halecostome fish (Actinopterygii, Osteichthyes) from the Late Jurassic of Chile and its relationships; pp.1–13 in J. E. Martin and G. E. Ostrander (eds.), Papers in Vertebrate Paleontology in Honor of Morton Green. Dakoterra 3.
- Bartram, A. W. H. 1975. The holostean fish genus *Ophiopsis* Agassiz. Zoological Journal of the Linnean Society 56:183–205.
- . 1977a. The Macrosemiidae, a Mesozoic family of holostean fishes. Bulletin of the British Museum (Geology) 29(2):137–234.
- . 1977b. A problematical Upper Cretaceous holostean fish genus *Aphanepygus*. Journal of Natural History 11:361–370.
- Berg, L. S. 1940. [Classification of fishes, both Recent and

- fossil.] Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR (Leningrad) 5:85–517. [In Russian.]
- Bryant, L. 1987. A new genus and species of Amiidae (Holostei; Osteichthyes) from the Late Cretaceous of North America, with comments on the phylogeny of the Amiidae. *Journal of Vertebrate Paleontology* 7(4):349–361.
- Cornet, B., N. McDonald, and A. Traverse. 1973. Fossil spores, pollen and fishes from Connecticut indicate Early Jurassic age for part of the Newark Group. *Science* 182: 1243–1247.
- Eastman, C. 1905. The Triassic fishes of New Jersey. Report of the Geological Survey of New Jersey 1904:67–102.
- Gardiner, B. 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum of Natural History (Geology)* 4:239–384.
- Gauthier, J., A. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209.
- Gosline, W. A. 1965. Teleostean phylogeny. *Copeia* 1965(2): 186–193.
- Hitchcock, E. 1819. Remarks on the geology and mineralogy of a section in Massachusetts on the Connecticut River, with a part of New Hampshire and Vermont. *American Journal of Science* 1:105–116.
- Jarvik, E. 1980. Basic Structure and Evolution of Vertebrates. Academic Press, New York, 2 vols.
- Jessen, H. 1972. Schultergürtel und Pectoralflosse bei Actinopterygiern. *Fossils and Strata* 1:1–101.
- . 1973. Interrelationships of actinopterygians and brachiopterygians: evidence from pectoral anatomy; pp. 227–232 in P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. Academic Press, London.
- Lauder, G. V., Jr. 1979. Feeding mechanics in primitive teleosts and in the halecomorph fish *Amia calva*. *Journal of Zoology*, London 187:543–578.
- Lehman, J.-P. 1966. Actinopterygii; pp. 1–242 in J. Piveteau (ed.), *Traité de Paléontologie*. Masson et Cie., Paris.
- Liem, K. F. and L. P. Woods. 1973. A probable homologue of the clavicle in the holostean fish *Amia calva*. *Proceedings of the Zoological Society of London* 170:521–531.
- McCune, A. R. 1982. Early Jurassic Semionotidae (Pisces) from the Newark Supergroup: Systematics and Evolution of a Fossil Species Flock. Ph.D. thesis, Yale University, New Haven, Connecticut., 371 pp.
- . 1986. A revision of *Semionotus* (Pisces: Semionotidae) from the Triassic and Jurassic of Europe. *Palaeontology* 29:213–233.
- . 1987a. Toward the phylogeny of a fossil species flock: semionotid fishes from a lake deposit in the Early Jurassic Towaco Formation, Newark Basin. *Bulletin of the Peabody Museum of Natural History*, Yale University 43:1–108.
- . 1987b. Lakes as laboratories of evolution: endemic fishes and environmental cyclicity. *Palaios* 2:446–454.
- . 1990. Evolutionary novelty and atavism in the *Semionotus* complex: relaxed selection during colonization of an expanding lake. *Evolution* 44(1):71–85.
- , K. S. Thomson, and P. E. Olsen. 1984. Semionotid fishes from the Mesozoic great lakes of North America; pp. 27–44 in A. A. Echelle and I. Kornfield (eds.), *Species Flocks of Fishes*. University of Maine Press, Orono.
- McDonald, N. G. 1975. Fossil fishes from the Newark Group of the Connecticut Valley. Unpublished M.S. thesis, Wesleyan University, Middletown, Connecticut, 230 pp.
- Newberry, J. S. 1888. Fossil fishes and fossil plants of the Triassic rocks of New Jersey and the Connecticut Valley. U.S. Geological Survey, Monograph XIV, 152 pp.
- Nielsen, E. 1942. Studies on Triassic fishes from East Greenland. I *Glaucolepis* and *Boreosomus*. *Meddelelser om Grønland* 138:1–403.
- Normark, B., A. R. McCune, and R. G. Harrison. 1991. Phylogenetic relationships of neopterygian fishes inferred from mitochondrial DNA sequences. *Molecular Biology and Evolution*, in press.
- Nybelin, O. 1977. The polyural skeleton of *Lepisosteus* and certain other actinopterygians. *Zoologica Scripta* 6:233–244.
- Olsen, P. E. 1980. Fossil great lakes of the Newark Supergroup in New Jersey; pp. 352–398 in W. Manspeizer (ed.), *Field Studies in New Jersey Geology and Guide to Field Trips*. 52nd Annual Meeting of the New York State Geological Association, Newark College of Arts and Sciences, Rutgers University, Newark.
- . 1984. The skull and pectoral girdle of the parasemi-onotid fish *Watsonulus eugnathoides* from the Early Triassic Sakemena Group of Madagascar with comments on the relationships of the holostean fishes. *Journal of Vertebrate Paleontology* 4:481–499.
- . 1986. A 40-million year lake record of early Mesozoic climatic forcing. *Science* 234:842–848.
- . 1988. Paleontology and Paleoecology of the Newark Supergroup: Early Mesozoic eastern North America; pp. 185–230 in W. Manspeizer (ed.), *Triassic–Jurassic Rifting: Continental Breakup and the Origin of the Atlantic Ocean and Passive Margins*. Elsevier, New York.
- , C. L. Remington, B. Cornet, and K. S. Thomson. 1978. Cyclic change in Late Triassic Lacustrine Communities. *Science* 201:729–733.
- , A. R. McCune, and K. S. Thomson. 1982. Correlation of the Early Mesozoic Newark Supergroup by vertebrates, principally fishes. *American Journal of Science* 282:1–44.
- Orlov, Y. A. (ed.). 1967. Fundamentals of Paleontology. Vol. 11, Agnatha, Pisces. Translated from Russian by the Israeli Program for Scientific Translation, 825 pp.
- Owen, R. 1860. Palaeontology; or, a systematic summary of extinct animals and their geological remains. Edinburgh, 420 pp.
- Patterson, C. 1973. Interrelationships of holosteans; pp. 233–305 in P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), *Interrelationships of Fishes*. Academic Press, London.
- . 1975. The braincase of pholidophorid and lepto-lepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London, B*, 269:275–579.
- . 1977. The contribution of paleontology to teleostean phylogeny; pp. 579–643 in M. K. Hecht, P. C. Goody and B. M. Hecht (eds.), *Major Patterns in Vertebrate Evolution*. Plenum Press, New York.
- Pearson, D. M. 1982. Primitive bony fishes, with especial reference to *Cheirolepis* and palaconisciform actinopterygians. *Zoological Journal of the Linnean Society of London* 74:35–67.
- Rayner, D. 1948. The structure of certain Jurassic holostean fishes with special reference to their neurocrania.

- Philosophical Transactions of the Royal Society of London, B, 233:287–345.
- Redfield, J. H. 1837. Fossil fishes of Connecticut and Massachusetts, with a notice of an undescribed genus. Annals of the Lyceum of Natural History, New York 4:35–40.
- Schaeffer, B. 1967. Late Triassic Fishes from the Western United States. Bulletin of the American Museum of Natural History 135:287–342.
- and D. Dunkle. 1950. A semionotid fish from the Chinle Formation, with considerations of its relationships. American Museum Novitates 1457:1–29.
- and C. Patterson. 1984. Jurassic fishes from the Western United States, with comments on Jurassic fish distribution. American Museum Novitates 2796:1–86.
- Schultze, H.-P., and G. Arratia. 1986. Reevaluation of the caudal skeleton of Actinoptergian fishes: I. *Lepisosteus* and *Amia*. J. Morphology 190:215–241.
- Swofford, D. L. 1985. Phylogenetic Analysis using Parsimony, version 2.4.1. Urbana, Illinois.
- Thomson, K. S., and A. R. McCune. 1984. Scale structure as evidence of growth patterns in fossil semionotid fishes. Journal of Vertebrate Paleontology 4:422–429.
- Toombs, H. A., and A. E. Rixon. 1950. The use of plastics in the transfer method of preparing fossils. Museum Journal 50:501–507.
- Veran, M. 1988. Les éléments accessoires de l'arc hyoidien des poissons téléostomes (Acanthodiens et Osteichthyes) fossiles et actuels. Mémoires du Muséum National d'Histoire Naturelle, Paris séries C, tome 54.
- Wenz, S. 1967. Compléments à l'étude des poissons actinoptérygiens du Jurassique française. Centre national de la recherche scientifique, 272 pp.
- Wilder, B. G. 1877. On the serrated appendages of the throat of *Amia*. Proceedings of the American Association for the Advancement of Science 25:259–267.
- Wiley, E. O. 1976. The phylogeny and biogeography of fossil and Recentgars (Actinopterygii: Lepisosteidae). Miscellaneous Publications of the University of Kansas 64:1–111.
- Woodward, A. S. 1890. The fossil fishes of the Hawkesbury series at Gosford. Memoirs of the Geological Survey of New South Wales (Palaeontology) 4:1–56.
- 1895. Catalogue of Fossil Fishes in the British Museum (Natural History), Trustees of the British Museum, London, 4 vols.
- 1916–1919. The fossil fishes of the English Wealden and Purbeck Formations. Palaeontographical Society Monograph, 148 pp.

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APPENDIX 1. Data used for phylogenetic analysis of the Neopterygii. Derived character states are listed in the left-hand column and numbers correspond to those in the text and Figure 16. Presence of a derived character state in a taxon is indicated by a '1' in the appropriate column. '2' indicates a derived state different from state one. '0' denotes the primitive condition. For PAUP, multistate characters 2, 6, and 7 were run as unordered. Characters 31 and 32 were used to label character transitions in Figure 16 but were omitted from the PAUP analysis as being redundant on information already included in characters 12 and 11. Abbreviations for taxa are as follows: A, *Amia*; C, *Caturus*; L, lepisosteids; M, macrosemiids; P, paleoniscoids; S, *Semionotus*; W, *Watsonulus*.

	P	W	A	C	L	M	S	T
1. lacrimals anterior to circumorbital ring	0	0	0	0	1	1	1	0
2. epiotic is modified pterotic	0	0	2	0	1	1	1	0
3. extension of exoccipital around vagus	0	0	0	0	1	1	1	0
4. premaxillae with long ascending process	0	0	1	0	1	1	1	0
5. opisthotic lost	0	0	1	0	1	1	1	0
6. ethmoidal ossification reduced	0	0	2	0	1	1	1	0
7. ossification of shoulder girdle reduced	0	0	2	?	1	1	1	0
8. gulars lost	0	0	0	0	1	1	1	0
9. intercalar lost	0	0	0	0	1	1	1	0
10. supratemporals subdivided	0	0	0	0	1	1	0	0
11. interoperculum reduced or absent	1	0	0	0	1	1	0	0
12. supramaxillae lost or absent	1	0	0	0	1	1	0	0
13. articular head of premaxillae lost or absent	1	0	0	0	1	0	0	0
14. "infraorbitals" bearing teeth	0	0	0	0	1	0	0	0
15. symplectic removed from quadrats	0	0	0	0	1	0	0	0
16. lepisosteid-type dentine	0	0	0	0	1	0	0	0
17. dorsal ridge scales present	0	0	0	0	0	0	1	0
18. single anamestic suborbital	0	0	0	0	0	0	1	0
19. single (1) vs. double (0) jaw joint	0	0	0	0	1	1	1	1
20. quadratojugal fused to quadrate	0	0	0	0	0	0	0	1
21. membranous growths of intercalar, amiid type	0	0	1	1	0	0	0	0
22. quadratojugal lost	0	0	1	1	0	0	0	0
23. dermosphenotic incorporated into skull roof	0	0	1	1	0	0	0	0
24. clavicles reduced	0	0	1	1	1	1	1	1
25. preoperculum with narrow ascending limb	0	0	1	1	1	1	1	1
26. vomers sutured to parasphenoid (see text)	0	0	1	1	1	1	1	1
27. vomers paired	0	1	1	1	1	1	1	1
28. coronoid process on mandible compound	0	1	1	1	1	1	1	1
29. suspensorium vertical	0	1	1	1	1	1	1	1
30. maxillae mobile	0	1	1	1	1	1	1	1
[31. supramaxillae present	0	1	1	1	0	0	1	1]
[32. interoperculum present	0	1	1	0	0	2	1	1]
33. upper caudal fin rays not elongate	0	?	0	0	1	1	1	0
34. dorsal and anal fins; rays equal supports	0	?	1	1	1	1	1	0
35. large posttemporal fossa (not reduced/absent)	0	1	1	1	0	?	1	1
36. anterior myodome present	1	1	1	1	0	0	0	1
37. preoperculum with broad dorsal margin	0	0	1	1	1	1	1	1