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A SEMIONOTID FISH FROM THE CHINLE FORMATION, WITH CONSIDERATION OF ITS RELATIONSHIPS

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INTRODUCTION

In 1879 C. D. Walcott discovered isolated fish scales and teeth at several levels in an exposure of the Chinle formation near Kanab, Utah. Visiting this locality again in 1882, he found more complete fish remains at a horizon about 860 feet above the Shinarump conglomerate which were subsequently submitted to C. R. Eastman, then at Harvard University, for identification. Eastman recognized two forms in this collection, tentatively assigning one to *Pholidophorus* sp. (Eastman, 1905), and the other to a new species of *Lepidotes*, *L. walcotti* (Eastman, 1917). Further preparation of this material fails to confirm the identification of the specimens referred to *Pholidophorus*. The description and taxonomic evaluation of the latter constitute the basis for this paper. Through circumstances now unknown, the specimens of *L. walcotti* and the form herein described were divided between the United States National Museum and the American Museum of Natural History.

Fishes from the fresh-water Upper Triassic formations of western North America continue to be rare and mostly fragmentary in spite of rather intensive prospecting at a number of promising localities. In addition to the specimens mentioned above from the Upper Chinle of Kanab Canyon, Hesse (1935) has described *Semionotus* cf. *gigas* from about the same horizon in

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Zion Canyon and Camp (*in litt.*) reports unidentified fish scales, again at approximately the same level, from a locality south of Moab, Utah. Colbert (personal communication) and others have obtained *Ceratodus* teeth at various localities in the lower Chinle of the Petrified Forest area, Arizona. Branson and Mehl (1931) record the presence of isolated scales and teeth representing "at least three new genera and possibly four or five new species" from the top of the Chugwater formation in Wyoming, and Branson (1948) reports the discovery of a *Ceratodus* tooth from the Popo Agie member of the Chugwater. The Dockum formation in Texas has yielded two species of *Ceratodus*, *C. dorothea* (Case, 1921) and *C. crosbiensis* (Warthin, 1928), and also the quadrate of a coelacanth, very probably wrongly referred to *Macropoma* by Warthin. The coelacanth evidence is of particular interest, as Welles (1947) has figured some skull fragments from the Upper Moenkopi of Arizona that Westoll (letter to Welles) believes may also belong to the Coelacanthini.

In addition to the above occurrences, several specimens of an undetermined fish from the Dockum formation in Union County, New Mexico, are possessed by the Cleveland Museum of Natural History (catalog no. 7259). Unfortunately, the nature of their preservation does not permit conclusive identification. Nevertheless, these latter are indicated to be closely related to the presently described species from the Upper Chinle of Utah.

Brough (1931) is of the opinion that the fish fauna of the Newark series shows evidence of endemism. This conclusion is based on the large number of currently recognized species of *Semionotus* and on the presence of dictyopygids, which had apparently disappeared elsewhere (with the exception of *Dictyopyge* in Europe) by the end of the Middle Triassic. The coelacanths thus far described from this fauna may also support such a thesis (Schaeffer, 1948). In the western United States at least the lower portion of the Chinle was deposited contemporaneously with the Chugwater and the Dockum. In the absence of the physical barriers that may have limited the dispersal of the Newark fauna, it is reasonable to suppose that the fish fauna was well distributed. This is supported by the wide distribution of *Ceratodus*. The occurrence of *Lepidotes* and *Semionotus*, as well as *Ceratodus*, is not unexpected, as these genera are present in Upper Triassic faunas in other parts of the world. The absence of catopterids or other subholosteans as well as palaeoniscoids cannot be confirmed until

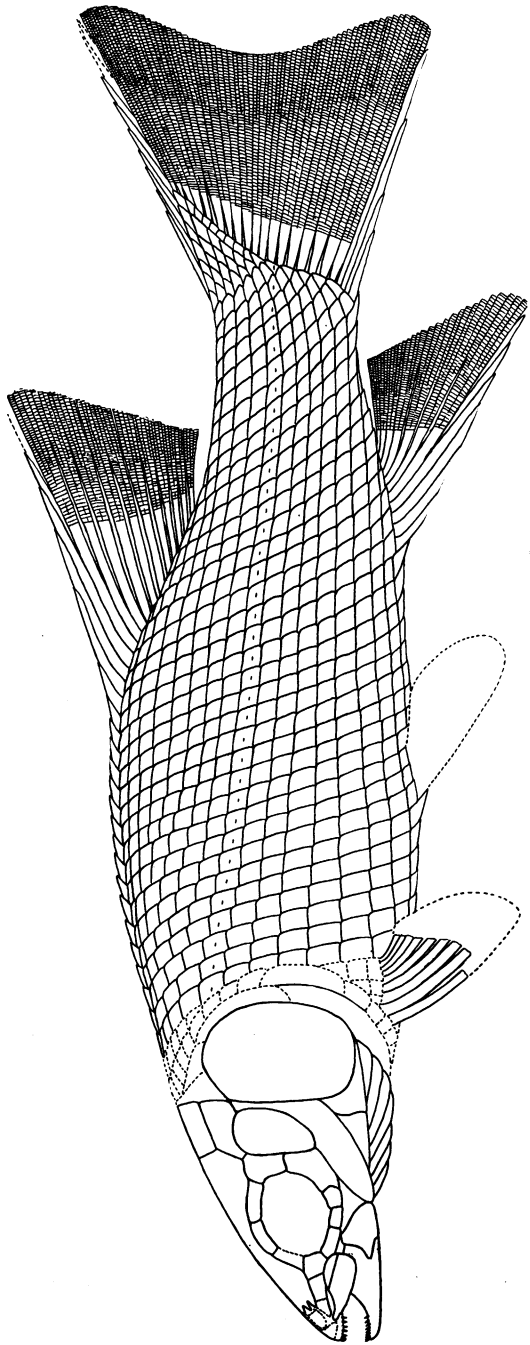

FIG. 1. *Semionotus kanabensis*. Reconstruction. Approx. × 2 1/3.

an attempt is made to identify the various collections of isolated scales. It is of interest that Welles has obtained scales possibly belonging to *Boreosomus* sp. in the Moenkopi.

There is thus fragmentary evidence of a more typical Upper Triassic fish fauna in the Chinle, Chugwater, and Dockum than in the Newark. Whether the paucity of collected material from the West is due entirely to a lack of proper conditions for fish preservation or at least in part to a failure to discover the proper facies is a matter that can be settled only by further exploration.

The drawings for this paper were prepared by Mr. John R. Le Grand and the photographs were taken by Mr. Elwood Logan.

TAXONOMY AND DIAGNOSIS

SEMIONOTIDAE

GENUS **SEMIONOTUS** AGASSIZ, 1832

GENOTYPE: *Semionotus bergeri* Agassiz.

Semionotus kanabensis, new species

TYPE: A.M.N.H. No. 8870. Complete fish with uncrushed skull.

HORIZON AND LOCALITY: Upper portion of Chinle formation, Upper Triassic, near Kanab, Kane County, Utah, approximately Sec. 27, T. 43 S., R. 6 W. According to Walcott's field notes (published in part by Cross, 1908) the fish occur in a fine-grained, light red sandstone layer about 860 feet above the top of the Shinarump conglomerate. Camp (1930) states that this horizon, which he probably identified in 1923, is about 1 mile east of, and 400 feet above, the Kanab schoolhouse.

SPECIFIC DIAGNOSIS: A small, fusiform semionotid, differing from all other known species of the genus *Semionotus* by the following combination of characters: Body length not exceeding 7.40 cm. in available specimens, head about one-fourth that length, greatest body depth about one-fifth total length. Skull roof pattern essentially as in other species of genus, with a strongly interdigitating suture between nasal and frontal bones. Gape small, lower jaw articulation below middle of orbit. Premaxillaries in contact, with posterior process extending between the anterior borders of the frontals; dentigerous portion forming about one-third of jaw margin and bearing about 10 small pointed teeth. Maxillary very short, not reaching anterior border of

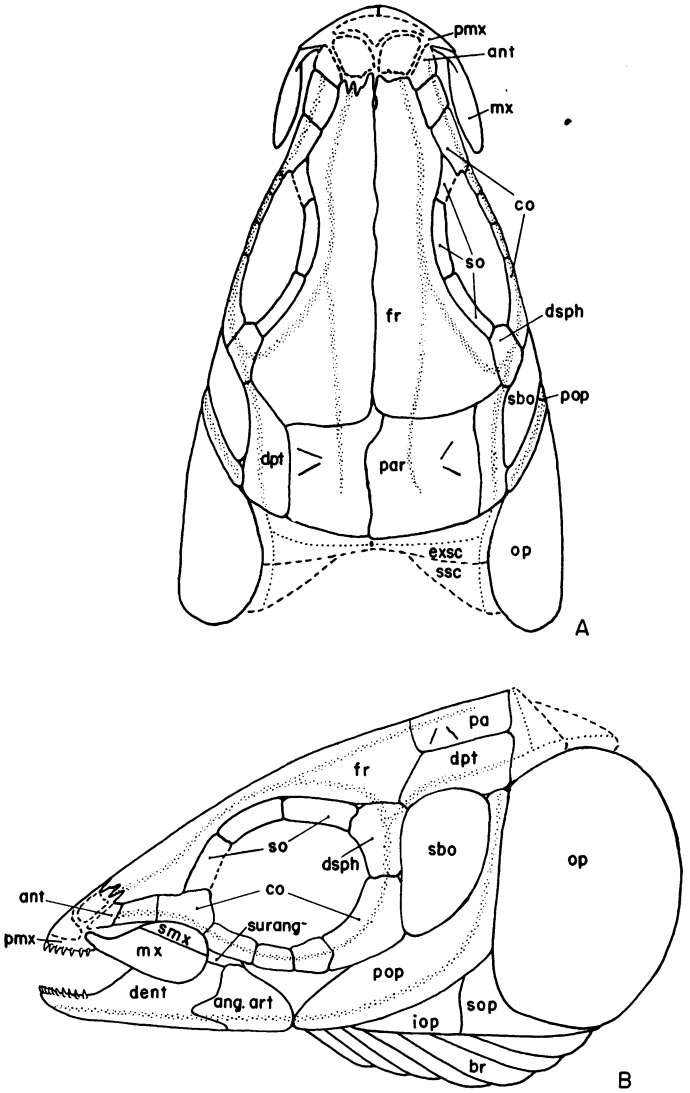

FIG. 2. *Semionotus kanabensis.* Reconstruction of the skull, × 5.25. A. Dorsal view. B. Lateral view. *Abbreviations:* ang art, angulo-articular; ant, antorbital; br, branchiostegal; co, circumorbital; dent, dentary; dpt, dermopterotic; dsph, dermosphenotic; exsc, extrascapular; fr, frontal; iop, interopercular; mx, maxillary; op, opercular; pa, parietal; pmx, premaxillary; pop, preopercular; sbo, suborbital; smx, supramaxillary; so, supraorbital; sop, subopercular; ssc, suprascapular; surang, surangular.

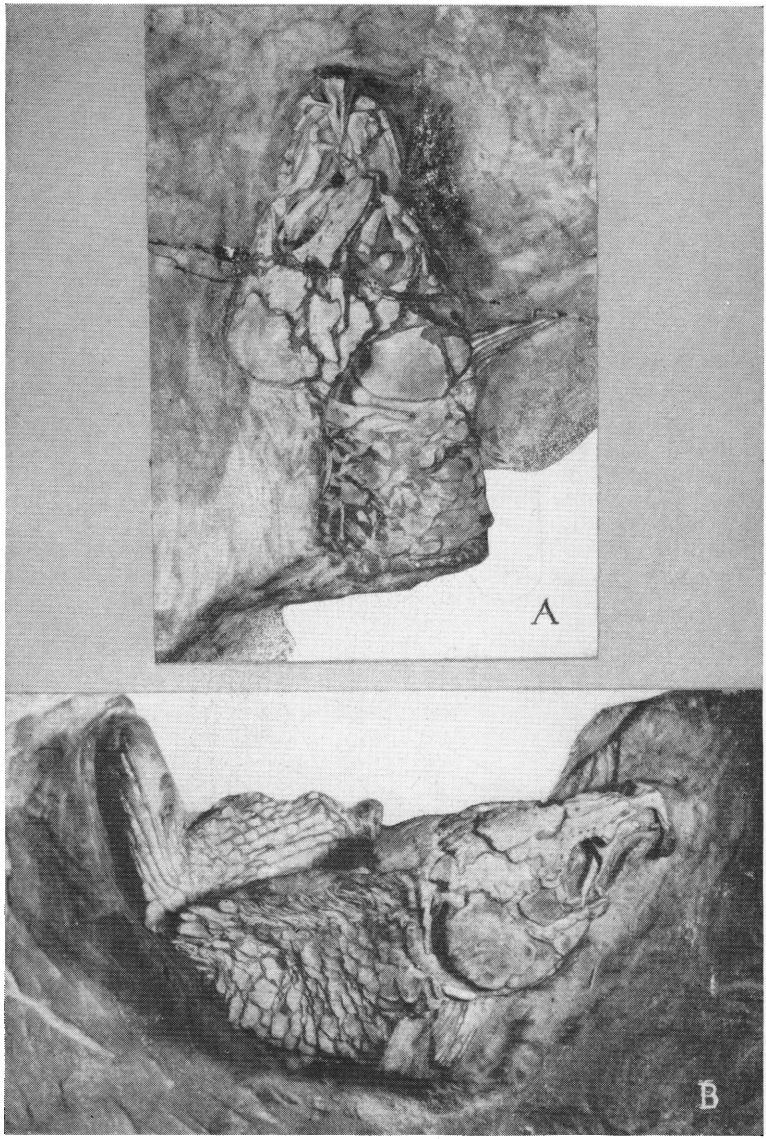

FIG. 3. *Semionotus kanabensis*. A. A.M.N.H. No. 8871, dorsoventrally crushed skull, × 2. B. A.M.N.H. No. 8870, anterior half of the type specimen, × 2.

orbit, expanded and rounded posteriorly, probably edentulous. At least one supramaxillary present. Mandible very narrow at symphysis, rising rapidly to high coronoid process, marginal teeth shaped as in premaxillary and procumbent at symphysis, inner teeth more robust. Circumorbital series complete and extending forward along lateral margin of frontal. Posterior circumorbital enlarged and in contact with anterior process of preopercular. Single large suborbital partially covering ascending process of preopercular. Suspensorium forwardly inclined. Anterior process of preopercular extending to middle of orbit. Opercular relatively large, with straight anterior border. Gular plate apparently absent.

Pectoral fin with eight or more uniserial and biserial fulcra and rays, degree of segmentation unknown. Nature of pelvic fin not determinable, indicated origin midway between origins of pectoral and dorsal. Dorsal fin composed of one short uniserial fulcrum, three robust, biserial basal fulcra, at least one fringing fulcrum, and about 11 rays segmented for half of distal length, origin opposite that of anal. Anal fin with four basal fulcra, three being biserial, followed by two fringing fulcra and about seven segmented rays. Caudal fin moderately forked, hemiheterocercal, scaled caudal lobe extending about halfway along upper border, epichordal and hypochordal lobes of about equal size and bordered by fulcra.

Scales small, thin, rhombic, and smooth; some or all flank scales with serrations on posterior border. Lateral line scales notched on posterior border. Dorsal ridge scales slightly enlarged, attenuated posteriorly.

Referred Specimens

A.M.N.H. No. 8871, dorsoventrally crushed and partly dissociated skull and anterior portion of body

U.S.N.M. No. 18399, laterally compressed skull with well-preserved cheek area and mandible, also section of body including dorsal and anal fins

U.S.N.M. No. 18400, patches of scales and broken skull elements

DESCRIPTION

Skull: The three skulls available for this study lack the median rostral and paired nasals. The rostral, if present, would necessarily have been a small triangular and anteriorly placed element. The frontals are exceedingly narrow anteriorly and exhibit a strongly dentate anterior margin. This condition suggests that

the paired nasals approached each other closely in the median line, although they may not have been in contact, and covered the ascending processes of the premaxillaries. The frontal is about 2.5 times longer than its greatest width and is constricted

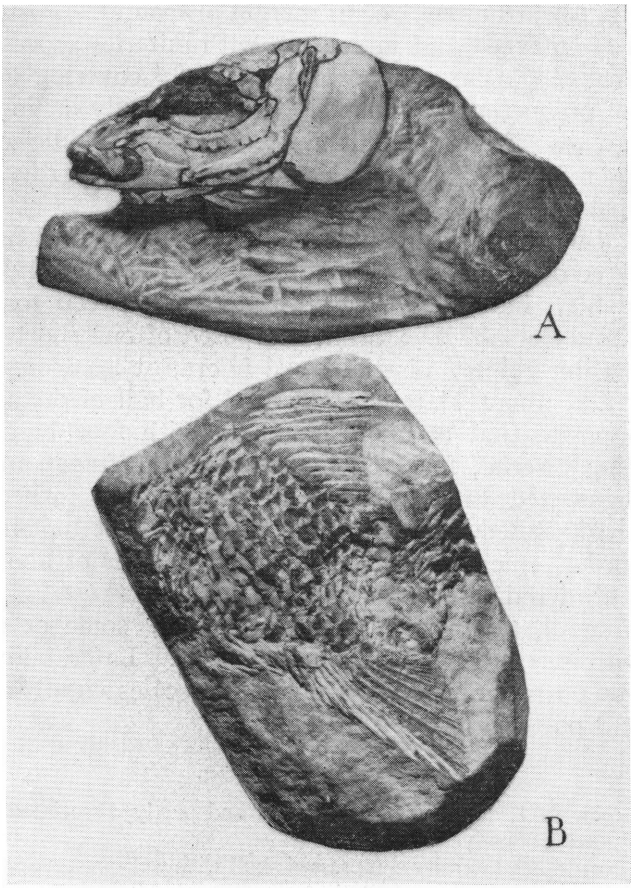

FIG. 4. *Semionotus kanabensis*. U.S.N.M. No. 18399, × 2. A. Skull in lateral aspect. B. Portion of body of same individual showing dorsal and anal fins.

in the orbital region. The supraorbital sensory canal is indicated by a row of relatively large pores close to the lateral borders of this element. Although the parietal area has been crushed and telescoped to some extent, it is evident that the parietals are

almost square and articulate with each other by an undulating suture. The median and posterior pit lines are indicated on the right parietal of the type specimen. The dermopterotic is longer than wide and has the usual contacts with the frontal, dermosphenotic, and parietal. The course of the postorbital sensory canal is represented by large pores. There is no clear indication that the supraorbital and infraorbital canals are united, although the orientation of the supraorbital canal along the lateral border of the frontal and towards the dermopterotic rather than the parietal suggests that such may be the case.[1] Extrascapulars are present but poorly preserved; the suprascapular series is obscured because of crushing.

The premaxillary is well preserved in all three skulls. The tooth-bearing or marginal portion is short and tapers to a point laterally along the articulation with the maxillary. It bears about seven robust, conical and bluntly pointed teeth which are attached along the outer border. The posterior process is wide anteriorly, gradually tapering to a point at the interdigitation with the anterior border of the frontal. The premaxillaries meet throughout their length along a rounded ridge, which may have been exposed dorsally, and lateral to which is a large foramen for the olfactory nerve. In front of this foramen there is a much smaller one, presumably for the terminal branch of palatine VII. As in *Amia* (Allis, 1898), the expanded posterior process must have formed part of the floor of the nasal pit.

The edentulous maxillary is exceedingly short, less than the length of the orbit. It has an extensive curved articulation with the marginal portion of the premaxillary and from this articulation widens rapidly posteriorly, with the greatest depth equaling about two-thirds of the length. The posterior border is gently rounded and shows no indication of notching. The most striking feature of the maxillary is the presence of a robust, medially directed process that extends between the marginal portion of the premaxillary and the autopalatine and terminates under the ascending process of the premaxillary. This is exactly comparable to the situation in other species of *Semionotus*, *Lepidotes*,

[1] The fusion of these canals, considered to be a character of the Semionotidae by Brough (1936), may not be a constant feature in this family, at either the generic or specific level. Fusion is evident in *Semionotus nilssoni* and *S. capensis* but not in *S. brauni*. It occurs in the specimen of *Lepidotes semiserratus* figured by Westoll (1937) but not in a specimen of the same species figured by Rayner (1948).

Sinamia, and *Amia*. The rod-like median process, in *Amia*, terminates in a shallow socket on the under side of the premaxillary, and it may do the same in the Kanab form, although this cannot be definitely determined. There is a single narrow supramaxillary.

The circumorbital series completely encircles the orbit and extends onto the snout in typical semionotoid fashion. In U.S.N.M. No. 18399 the posterior and ventral borders of the orbit are framed by five elements, including the dermosphenotic. At least two elements, indicated in the type specimen, frame the dorsal orbital rim between the dermosphenotic and the snout series. There are three elements in front of the orbit that articulate above with the frontal and presumably the nasal. In the absence of the rostral and nasal bones, and the lack of evidence for identifying the antorbital bones, it is not possible to determine the exact position of the anterior and posterior nares.

The single oval suborbital is of about the same relative size and shape as the single member of the suborbital series in *Semionotus nilssoni*. It appears to cover most or all of the ascending process of the preopercular. This feature, which is thus almost unique among semionotids, is associated with another one previously unknown in this family. The posterior circumorbital, lying immediately ventral to the dermosphenotic, is somewhat enlarged and in contact with the anterior ramus of the preopercular. These characters were perhaps responsible for Eastman's identification of these specimens as pholodophorid.

The preopercular is a crescent-shaped element with ascending and anterior processes of about equal length. The ascending process is narrow and rod-like, expanding ventrally into the anterior portion. The pores of the preopercular canal are prominent, and primary tubular extensions are evident on the anterior arm. The opercular is essentially oval, with a straight anterior border. As are the other dermal elements of the skull, it is smooth and unornamented. The subopercular has a rounded ventral margin, and its exposed area is about one-third or less of the opercular height. The interopercular is triangular and is covered in part by the preopercular.

The mandible is very low in the symphyseal region, with a straight inferior margin. Orally it rises rapidly to form a high coronoid process. There are about 10 slender, conical, pointed,

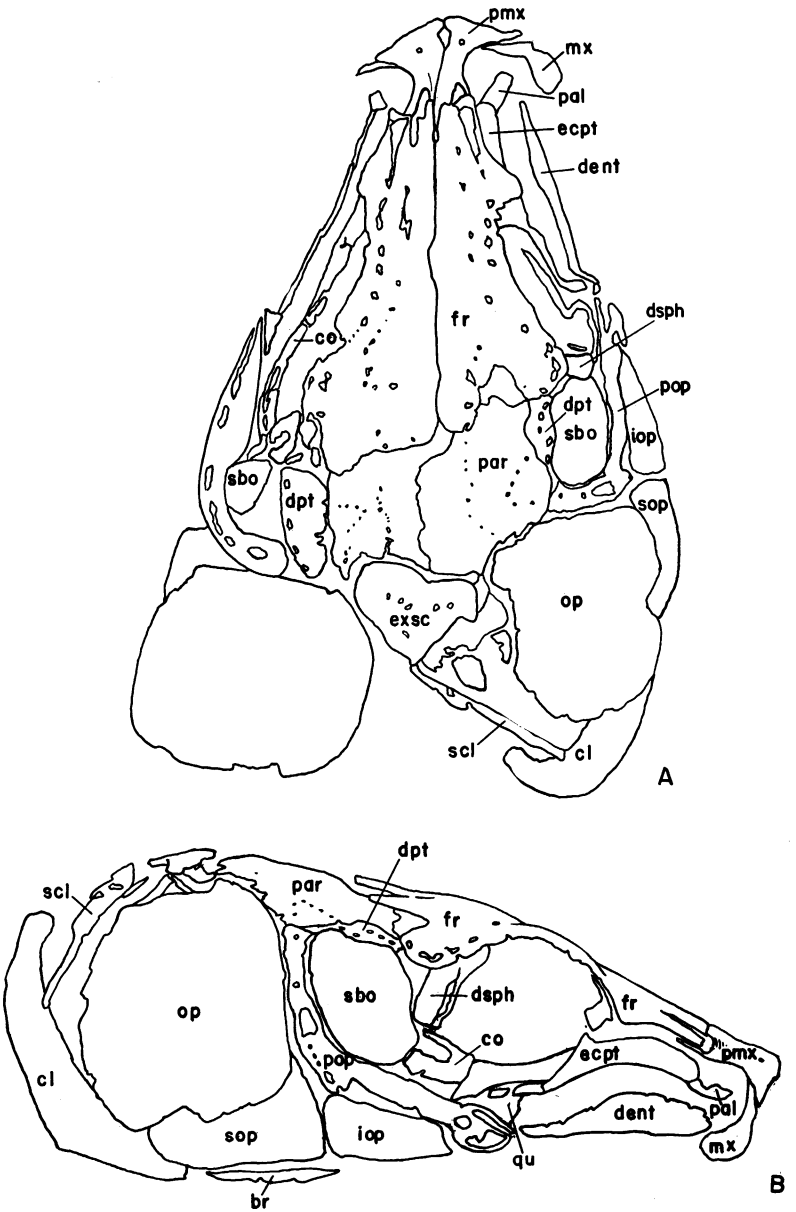

FIG. 5. *Semionotus kanabensis.* Skull of the type specimen, A.M.N.H. No. 8870, × 5 1/3. A. Dorsal view. B. Lateral view. *Additional abbreviations:* cl, cleithrum; scl, supracleithrum.

and somewhat procumbent marginal teeth on either side of the symphysis. An inner row of stouter teeth is also present, but their form cannot be determined. The angulo-articular is almost rectangular in shape, with a vertical posterior border, and is clearly separated from the dentary by an undulating suture. The surangular may also be distinguished, extending anteriorly beyond the suture between the dentary and the angulo-articular. The mandibular canal is very prominent, running close to the ventral border of the angulo-articular and the dentary. A gular plate is not indicated in any of the specimens, and it may have been absent as in *Lepidotes* (Woodward, 1895; Saint-Seine, 1949).

Elements of the hyoid arch and the palate are present in all three skulls but are obscured or poorly preserved. An impression of the hyomandibular in U.S.N.M. No. 18399 is in essentially a vertical position and is about three times longer than the width at the neurocranial articulation. The opercular process is small, although its exact shape cannot be determined. The symplectic is long and rod-like, with a proximal expansion where it connects with the hyomandibular. The epihyal cannot be observed. The ceratohyal consists of a single ossification, expanded proximally and distally, and lacking a fenestra. There is no indication of a groove for the hyoid artery. Two poorly defined ossifications in front of the ceratohyal represent the hypohyal and possibly the glossohyal. The branchiostegals number at least seven and are broad and plate-like, with no proximal constriction.

The quadrate is a relatively small triangular element, thickened and apparently rounded at the mandibular articulation and bearing posteriorly a splint-like process which abuts against the distal end of the symplectic. No evidence of the metapterygoid has been observed. The ectopterygoid is curved and narrow. It has a wide groove along the anterior half of the dorsal or mesial border, and the posterior wall of the groove expands into a medially directed process at its anterior end. This process supports in part the autopalatine and probably also the entopterygoid at their point of articulation. Seen in poorly defined impression in U.S.N.M. No. 18399, the entopterygoid is of the normal, broad triangular outline. The dermopalatine is a separate ossification and, as does the ectopterygoid, appears to lack teeth. The autopalatine has a broad articulation with the entopterygoid and

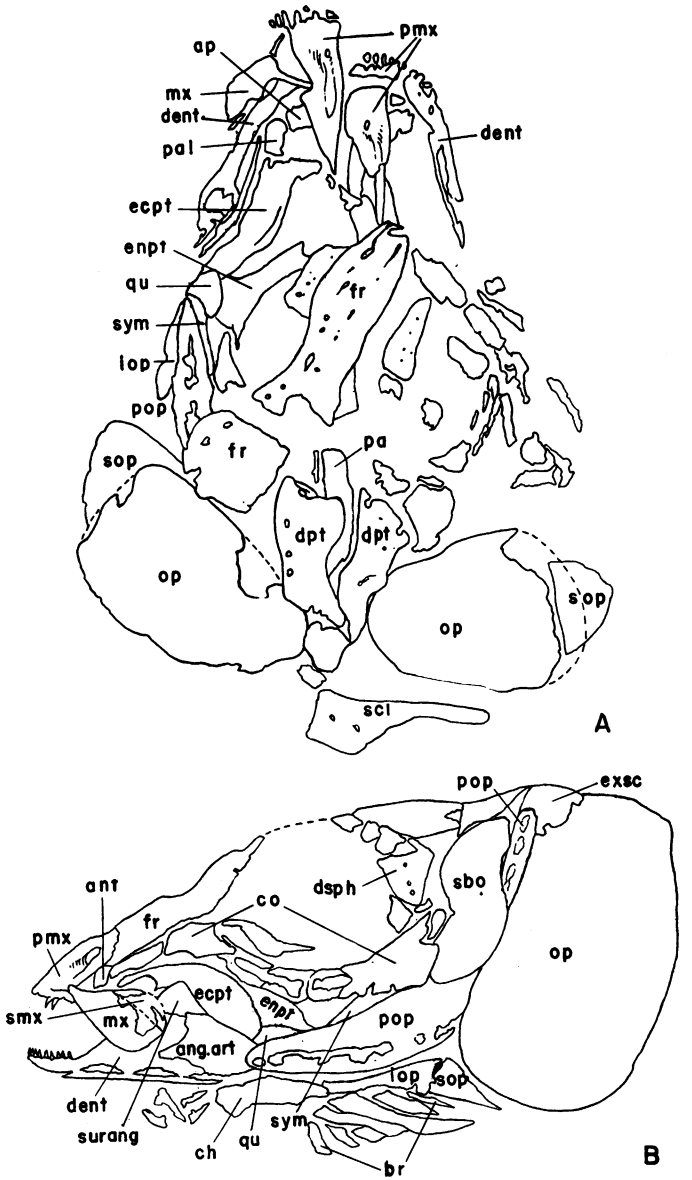

FIG. 6. *Semionotus kanabensis.* A. Details of dissociated skull, A.M.N.H. No. 8871, × 4.5. B. Details of U.S.N.M. No. 18399, × 4.5. *Additional abbreviations:* ap, autopalatine; ch, ceratohyal; ecpt, ectopterygoid; enpt, entopterygoid; pal, dermopalatine; qu, quadrate; sym, symplectic.

occupies the area between that bone and the median process of the maxillary as in *Amia*.

A few neurocranial structures can be observed, but unfortunately adequate comparison with Rayner's work (1948) is not possible. As partially exposed in U.S.N.M. No. 18399, the parasphenoid is a narrow but relatively robust element, with distinct lateral grooves accommodating the palatine branches of the facial nerve. It overlaps dorsally, opposite the anterior border of the orbit, the posterior extremity of the vomer which is undoubtedly paired.

POSTCRANIAL SKELETON: The shoulder girdle as exposed on the right side of the type specimen exhibits only the cleithrum in the normal position. An element that may be the supracleithrum is turned on edge in front of the upper part of the cleithrum, but its position prevents preparation. Fragments representing one or more postcleithral ossifications are present, one attached to the cleithrum at the base of the pectoral fin. The exposed portion of the cleithrum is narrow and curved only in its dorsal portion. The expanded ventral part is completely covered by the operculum. The pectoral fin is composed of an unknown number of uniserial and biserial fulcra plus rays that are not clearly segmented and are therefore difficult to distinguish from the fulcra. At least eight fulcra and rays are evident in the type specimen.

The pelvic fins are not preserved in any of the specimens. Their position is indicated in the type by several incomplete rays that appear to be undisturbed and place the origin about midway between the origins of the pectoral and dorsal.

The triangular dorsal fin arises somewhat anteriorly to the origin of the anal. It is made up of one short, uniserial, fulcral scale followed by three basal, biserial fulcra of increasing length, and at least one fringing fulcrum and about 11 rays, segmented and dichotomized for half their length. The anal fin is of similar shape, consisting of about four basal fulcra, at least three of which are biserial, two fringing fulcra, and seven rays, divided and segmented in the distal half.

The caudal fin is completely preserved in the type, but is twisted in such a fashion that several important details are obscured. The scale pattern on the caudal axis cannot be exactly determined, but it is evident that the axis extends about half the distance to the tip of the epichordal lobe. The tail is moderately forked. The fulcra bordering both lobes of the tail are thin and

attenuated. Those along the hypochordal lobe are biserial, the ones bordering the epichordal probably so.

SQUAMATION: The scales are smooth and rhombic. They are somewhat enlarged in the flank area but otherwise show no appreciable variation in size except in the caudal extension, where they are smaller. An occasional isolated scale will show an anterodorsal extension, demonstrating the presence of a peg-and-socket articulation. A number of flank scales show about four fine serrations on the posterior edge. Some lateral line scales have a very low, median, superficial ridge, but usually the scale surface is quite smooth, and the only evidence of the sensory canal is a slight notching of the posterior border of the scale. The dorsal and ventral ridge scales are essentially ovate and acuminate. Histologically, the scales are composed internally of a relatively thick, bony, foot plate containing sparse, simple canals and externally of a thinner, entire enamel cap.

DISCUSSION

HOLOSTEAN ORIGINS

Within the last two decades information on the origin and structural relationships of the various holostean orders has been greatly amplified. This has led to the important conclusion that the Holostei do not constitute a natural group, but rather that the included orders were independently derived from different subholostean or palaeoniscoid stocks. The diverse evolutionary trends involved in attaining the holostean level, and within the level itself, have been considered by a number of authors. The general phylogenetic picture, however, is still incomplete, owing partly to a lack of transitional stages and partly to the difficulties involved in the interpretation and evaluation of the existing evidence. The apparently unusual combination of characters occurring in *S. kanabensis* presents such an interpretative problem, and a brief review of opinions on the origin of, and observed evolutionary trends in, certain of the holostean orders appears desirable in order to determine its taxonomic position.

For obvious reasons, in the present state of knowledge, Romer (1945) has retained the category Holostei as a superorder. It is composed of the following five orders, apparently natural monophyletic units: the Semionotoidea, Aspidorhynchoidea, Amioidea, Pholidophoroidea, and, with reservations, the Pycnodontoidea.

The second and the last may be eliminated from consideration here, as they represent highly specialized trends clearly not related.

The origins of the remaining three orders have been the subject of much discussion. Prior to the description of the Lower Triassic Parasemionotidae (Ospiidae) by Stensiö (1932) and Piveteau (1934) and the recognition of the Subholostei by Brough (1936), these orders were considered to have a single monophyletic origin from some unknown palaeoniscoid stock (see Brough, 1939, p. 3).

Stensiö (1932, p. 296) was the first to suggest that the Holostei are really a polyphyletic group. He notes the approach of the pholidopleurids to the pholidophoroids in the structure of the vertebral column and scales, the perleidids to the amioids in scale structure, and of the entire ospiid skeleton to the semionotids and amioids. The resemblance of *Ospia* and *Broughia* to the semionotids includes the absence of a postrostral, form of the nasals, freeing of the maxillary, structure of the mandible, nature of the median fins, and finally the scales. He concludes that the "ospiids" may be transitional between the perleidids and the semionotids. Stensiö (*ibid.*, pp. 275–276) makes the interesting suggestion that there is a functional correlation between the freeing of the maxillary and the modification of the dermal bones in the snout area.

Piveteau (1934) considers the parasemionotids to be intermediate between the Chondrostei and the Holostei, with definite advances towards the latter. He states, however, that this family cannot be considered as being directly ancestral to the Holostei because the definitive semionotid *Acentrophorus* was already present in the Upper Permian.

Brough, in 1936, developed the subholostean concept, pointing out that certain families formerly relegated to the Palaeoniscoidea had independently developed various advances towards the holostean level. He believes that while the Dictyopygidae (Catopteridae), Perleididae, and particularly the Parasemionotidae show such changes, there is no evidence that any of them gave rise directly to the Semionotidae, the age of *Acentrophorus* again being a stumbling block.

In 1939 Brough again considered the origin of certain of the holostean orders. He describes the many points of resemblance between certain of the parasemionotids and the caturids (eugna-

thids), such as the presence of large paired nasals, the similar shape of the frontals bordered by a row of supraorbitals, the small parietals with a similar relationship to the large dermopterotics, the resemblances of the extrascapulars, suprascapulars, and the dermosphenotic and the presence of an interoperculum almost anterior to the suboperculum (*Watsonulus*), the close duplication of jaw structure, and the disposition of the first branchiostegal ray. The absence of a suborbital series in the described specimens of the Parasemionotidae is considered at variance with the condition in an eugnathid ancestor. Brough states, however, that this region is figured only in type "A" of *Watsonulus*. It should be pointed out that Piveteau (1934) also indicates the absence of suborbitals in *Parasemionotus* and that the specimens of *Watsonulus* and *Parasemionotus* in the American Museum show no evidence of these elements. They are unknown in *Ospia* and *Broughia*.

As a result of this comparison Brough is of the opinion that the Parasemionotidae may be considered as ancestral to the Eugnathidae, hence the entire Amioidea. He states that such semionotid specializations as the forwardly directed suspensorium, narrow preopercular with anterior arm, reduced and forwardly situated jaws, unique styliform teeth, and narrow parasphenoid, all present in *Acetrophorus*, indicate that the eugnathids cannot be descended from the semionotids. Thus he believes that the eugnathids and semionotids may have had a common palaeoniscoid ancestor, and, by inference, that the parasemionotids are excluded from the ancestry of the semionotids.

Rayner (1941) considers the origin of the holostean orders an open question, but does admit the significance of the resemblance between the dermal skulls of the Parasemionotidae and the Eugnathidae. She points out that no known subholostean or palaeoniscoid family clearly foreshadows the structure of the semionotids or the pholodophoroids.

Westoll (1944) states that the Parasemionotidae and Semionotidae are different in the known structure of the snout area (this is here presumed to mean the dermal bones), the cheek region, and the nature of the transition from the ancestral heterocercal tail to the more hemiheterocercal type. In contrast to other opinions, he believes that good evidence (unpublished) is available for deriving the semionotids from the palaeoniscoid Elonichthyidae.

Rayner (1948), on the basis of her study of Jurassic holosteans,

concludes that information on the holostean neurocranium is yet too meager to permit any basic conclusions regarding phylogenetic relationships in this group. On the basis of all available evidence, she considers the parasemionotid-eugnathid transition as the only well-defined link between the Subholostei and the Holostei, and further recognizes some similarities between the semionotids and the less-specialized eugnathids.

The evidence now available indicates that the parasemionotids are the only fishes at the subholostean level advanced enough to give rise to the eugnathids. The semionotoids, when they first appear in the Upper Permian, already possess their definitive ordinal characters and could hardly have arisen from the Lower Triassic parasemionotids. The characteristic semionotid jaw structure and related changes in the cheek are not clearly foreshadowed in any chondrostean group. From the standpoint of morphological change alone, however, it would appear less radical to derive a semionotid from the parasemionotid type than from any other known palaeoniscoid or subholostean.

In regard to Westoll's statement (1944) concerning the difference between the parasemionotid and semionotid snouts, the present writers are of the opinion that Gill's description (1923) of the snout area of *Acentrophorus* presents the only recorded deviation from the parasemionotid snout pattern among the semionotids. Gill figures four elements across the snout between the "adnasals," two on each side of the midline, but this arrangement is not clearly discussed in the text. In his paper Gill labels the median elements as nasals and states that they are usually crushed against the posterior processes of the premaxillaries. Gregory (1933), however, considers the lateral ones nasals and the median bones to be possibly postrostrals. As *Acentrophorus* is strikingly similar to *Semionotus* and *Lepidotes*, particularly in jaw and cheek structure, it is difficult to believe that either of these descriptions represents the true situation in this genus. As far as can be determined from available material, the nasals of *Semionotus* approach each other in the midline, preceded by a single rostral element. This is also the case in *Lepidotes* (Piveteau, 1934; Rayner, 1948) and *Dapedius* (Woodward, 1895, and specimen). So far as known, therefore, the semionotid snout has a dermal bone pattern like that of the parasemionotids.

The circumorbital series in the parasemionotids is complete and consists (in *Watsonulus*) of eight elements of varying size.

It could, with minor modification, give rise to either the semionotid or the eugnathid type. In similar vein, while it is possible that the palaeoniscoid-subholostean first branchiostegal ray was modified into a true interopercular bone more than once, it is just as plausible to assume that parasemionotids possessing an interopercular existed early enough in the Permian to give rise to the semionotids.

The absence of a clearly distinguishable suborbital series in the parasemionotids might well be regarded as a factor removing them from holostean ancestry. This particular problem and the origin of the holostean suborbitals in general have been considered by several authors. Watson (1925, p. 868) suggests that the bone lying along the anterior border of the preopercular in the palaeoniscoid *Coccocephalus* may represent the possible source of the "postorbital plates" in the lepidosteoids. In 1928, (p. 58) he points out that the three bones between the posterior circumorbitals and the anterior border of the preopercular in *Elonichthys caudalis* represent the single bone in *Coccocephalus*. These bones, Watson states, are the source for the holostean postorbitals (suborbitals).

Aldinger (1937, pp. 364–365) is of the opinion that the holostean suborbitals arose through disintegration of the anterior expanded portion of the palaeoniscoid-subholostean preopercular and that this process may have occurred independently in different groups below the holostean level. This concept is suggested by the apparent transfer of horizontal and vertical pit lines on the preopercular of *Watsonia* and *Parasemionotus* to the suborbitals of certain holosteans, and also by the presence of three small bones arranged in an anteroposterior series in an excavation on the dorsal border of the *Parasemionotus* preopercular, as well as by the occurrence of a small ossification at the lower end of the *Ospia* preopercular. Aldinger believes that this disintegration was associated with the development of a preopercular-palatoquadrate attachment and with the inclusion of the anterior rim of the preopercular in the origin of the adductor mandibulae muscle. With these changes in the architecture of the cheek, he believes that the expanded anterior portion of the preopercular present in many palaeoniscoids and subholosteans would interfere with the action of the adductor mandibulae, and reduction of this portion would occur. The principal objection to this theory is the presence of suborbitals in forms with the anterior expansion (*Palaeonis-*

cus) as well as in those with a vertical suspensorium (*Canobius*).

Stensiö (1947, p. 148) is of the opinion that the suborbitals of the palaeoniscoids and subholosteans have arisen either from anamestic components of the postorbital infraorbitals or from the anamestic anterior portion of the preopercular or from both sources. They are accordingly not considered to be equivalent in the various forms possessing them. Furthermore, he believes the suborbitals may fuse with the suprapreoperculum, as in *Helichthys elegans*, or include bone rudiments formed along the anterior division of the supramaxillary line (defined below) as in *Canobius ramsayi*.

In regard to the origin of the holostean suborbital series, Stensiö (*ibid.*, pp. 153 ff.) proposes two different hypotheses which are briefly and perhaps inadequately summarized as follows: The first is similar to Aldinger's thesis and is also based on the interpretation of the ossifications on the dorsal border of the *Parasemionotus* opercular. These elements, called supraspiraculars by Piveteau (1934), are considered by Stensiö to be suborbitals derived from "the anamestic component of the preopercular." The incorporation of additional preopercular rudiments more ventrally or, as he states it, further subdivision of the anterior border of the preopercular would result in a typical holostean suborbital series. The ventral suborbitals would thus include the vertical and horizontal pit lines formerly situated on the preopercular. (In the *Amia* embryos figured by Allis, 1889, Stensiö interprets the horizontal pit line of the cheek as the middle and anterior divisions of the supramaxillary line in larval urodeles, anurans, and dipnoans and the vertical pit line of the cheek as a postmaxillary line.)

The second hypothesis involves a direct inheritance of the suborbital elements present in many palaeoniscoids and subholosteans, as postulated previously by Watson. The form of the suborbitals in *Ptycholepis curta*, as interpreted by Stensiö, suggests that the holostean pattern was obtained by a moderate posterior expansion of these elements, accompanied by a reduction of the preoperculum to the holostean type. As that portion of the preoperculum carrying the horizontal and vertical pit lines was eliminated, these pit lines became secondarily associated with the ventral suborbitals.

The primary origin of the suborbital series, according to Stensiö's interpretation, requires a subdivision (or possibly a regroup-

ing of rudiments) of the posterior circumorbitals or the anterior border of the preopercular. Certain fusions are also considered likely, for instance, a union of anamestic and sensory line components to form the semionotid ventral suborbitals and a combination of a posterior circumorbital and suborbital to form the enlarged posterior circumorbital of pholidophoroids. In the present writers' opinion the available evidence, experimental, embryological, and morphological, is not conclusive enough to permit such a detailed analysis of evolutionary change in the cheek pattern. The paleontological data alone, however, would appear to favor his second hypothesis for the origin of the holostean suborbitals.

Since the suborbitals are anamestic elements, their number, size, and shape could presumably be readily affected by alterations in the inclination of the suspensorium, the length of the jaws, enlargement of the posterior circumorbitals, and other changes concerned with cheek design. Westoll (1937) has discussed the secondary association of the vertical and horizontal pit lines with the enlarged posterior circumorbitals in *Amia*, and this is probably also the situation in the suborbital mosaic of *Lepisosteus*.

In the last analysis, a really airtight case for the important phylogenetic position assigned to the parasemionotids requires further elucidation of the suborbital problem, particularly since these elements are present in most palaeoniscoids and other subholosteans. Perhaps the situation in *Perleidus* is of some significance in this connection. *P. madagascariensis* (Piveteau, 1934) and *P. stochiensis* (Stensiö, 1932) apparently lack suborbitals, while Stensiö (1921) is of the opinion that several are present in *P. woodwardi*. The cheek area of *Pholidophorus* is also of interest. *P. bechei* (Rayner, 1948) has three posterior circumorbitals, with one meeting the preopercular below a single suborbital; *P. similis* (Saint-Seine, 1949) has two enlarged posterior circumorbitals, the lower one meeting the preopercular but not extending along the ventral border of the suborbital; *P. segusianus* (Saint-Seine, 1949) has a single greatly expanded posterior circumorbital but no suborbital. If such variation can occur at the interspecific level, the presence of these elements in some unknown parasemionotid or in a parasemionotid descendant appears more reasonable. Conversely, the loss of all but one suborbital in *Semionotus kanabensis* and *S. nilssoni* also seems plausible.

Holostean Relationships

The character complexes of the dermal skull separating the Semionotoidea, Amioidea, and Pholidophoroidea have been analyzed at some length by Brough, Rayner, Saint-Seine, Stensiö, and Westoll. In the brief review below of certain of the differences and resemblances in skull pattern, some additional points may be mentioned that possibly have a bearing on the interrelationship of these orders.

The arrangement of the semionotoid skull roof, with the exceptions noted below, is almost identical with that of the other two orders, including the usual presence of a median rostral that may or may not separate the paired nasals. The semionotoid premaxillary has a strong ascending process that usually extends to or under the frontal. The maxillary is expanded and rounded or blunt posteriorly and does not extend beyond the middle of the orbit. It has an anterior median process that fits between the marginal portion of the premaxillary and the palatine elements. A single supramaxillary is present in *Semionotus* and *Lepidotes*. The circumorbital series is complete and is usually composed of 10 to 12 almost square elements, although neither the number nor the shape is constant. The infraorbitals extend forward to the snout, in series with the antorbital and the nasal. The number of elements in the suborbital series is probably subject to considerable intraspecific and interspecific variation, evident in both *Semionotus* and *Lepidotes*, with most genera having one to six bones, except *Lepisosteus* where the number is greatly increased. The preopercular is narrow and crescent shaped; the anterior arm may meet the vertical one at a distinct but wide angle and almost equal it in length. The size of the opercular in relation to the subopercular is also variable, small in *Acentrophorus* and *Lepidotes*, large in at least some species of *Semionotus*. The dentigerous portion of the mandible is short (except in *Lepisosteus*), with the dorsal border rising rapidly but not abruptly to a high coronoid process.

The semionotoids are known from the Upper Permian to the Recent. During this period, according to available evidence, there have been several evolutionary trends away from the basic design of the order as typified by *Acentrophorus* and *Semionotus*. One culminated in the deepened skull and hypsisomatic body form of *Dapedius* and *Tetragonolepis*, the other in the long-skulled,

long-bodied *Lepisosteus*. The hypsisomatic trend also occurred in the palaeoniscoids and the subholosteans, and the lepidosteoid trend in the subholostean and another holostean group; both developed a number of times in the teleosts.

The amioid skull roof exhibits significant modification only in the more specialized macrosemiids which have apparently lost the median rostral and have the elongated ethmoid exposed between the frontals and the reduced nasals. The amioid premaxillary has a robust posterior process, definitely known in *Heterolepidotus*, *Caturus*, *Oeonoscopus*, *Sinamia*, *Amia*, and *Ophiopsis*. The maxillary is long, except in the advanced macrosemiids, usually extending to the posterior border of the orbit. The posterior border is often notched, although in *Macrosemius*, *Distichole pis*, and *Notagogus* it is rounded as in the semionotids. An anterior median process has been described in several genera which bears the same relationship to the premaxillary and palatines as in the semionotids. The infraorbitals are relatively larger and not so numerous as in the semionotoids, again excepting the advanced macrosemiids where they are greatly reduced. The supraorbitals are variable; they resemble, for instance, the semionotid type in *Eoeugnathus*, are irregular, small, and greatly multiplied in *Caturus;* they are present in *Sinamia* but are absent in *Amia*. As in the semionotids, the suborbitals show great variation in size, shape, and number, and may be absent entirely as in *Amia*. The preopercular is crescent shaped and narrow. The anterior extension of the preopercular characteristic of the semionotoids is missing, except where the gape has been secondarily reduced as in *Notagogus*.

In spite of statements to the effect that the eugnathids and amiids have a characteristic opercular pattern (Brough, 1939, p. 84), it is possible to observe considerable variation in the relative size and shape of the opercular, subopercular, and to a lesser extent the interopercular. It appears practically impossible to define the amioid opercular complex in such a way as to exclude the semionotids and, for that matter, either the pholidophoroids or the archaeomenids. The mandible, as Rayner points out, has a characteristic form in most eugnathids and amiids that is not entirely shared by the macrosemiids.

The eugnathid-amiid group has had a remarkably conservative history. The few discernible trends, all more or less minor, have been discussed by Brough (1939), Rayner (1941), and Saint-Seine

(1949). From the eugnathid stock a trend towards a long-snouted, istiophorid-like habitus developed in the pachychormids, culminating in *Protosphyraena*. The skull of *Pachycormus* (Lehman, 1949) shows unmistakable eugnathid resemblances in spite of certain obvious specializations. Among the macrosemiids, Saint-Seine (1949, p. 287) has described the apparently progressive change in the series *Ophiopsis-Macrosemius-Notagogus-Propterus*, consisting of elongation and exposure of the ethmoid region, relative reduction of the frontals, forward migration of the suspensorium with accompanying modifications in jaw structure, reduction of the ventral circumorbitals, and loss of the suborbitals. The jaw structure of the more specialized macrosemiids, particularly *Distichole pis*, is very suggestive of that found in the semionotids. The great difference in the structure of the cheek area in these two groups indicates, therefore, the range of modification that may be expected in this area in holosteans with a forwardly directed suspensorium.

Saint-Seine (1949) has revived the category Halecostomi to include the pholidophorids, leptolepids, oligopleurids, pleuropholids (*Pleuropholis* only), and also the aspidorhynchids and protelopids (*Eoprotelops* only). These families are considered to be "progressive" among the holosteans in that they share certain teleost characters such as a habitual absence of the basipterygoid process, a mandible composed only of dentary and angulo-articular, the usual absence of a gular, a mobile premaxillary, an ossified but covered supraoccipital, and a consistent disappearance of the suborbital series. With the exception of the inclusion of the aspidorhynchids and the new genus *Eoprotelops* (placed in the new family Protelopidae and the new Order Elopoidea), the Halecostomi agree in their range with the Pholidophoroidea of Romer's classification. The pholodophorid-leptolepid-*Eoprotelops* group clearly foreshadows the teleosts and more specifically the Elopidae and, as Saint-Seine points out, the leptolepids may be ancestral to the chirocentrids. The oligopleurids and *Pleuropholis* represent specialized and isolated types with obscure antecedents; they may have evolved from some amioid stocks. Although the aspidorhynchids share a number of characters in common with the other halecostomids, they are, as Saint-Seine states, highly specialized at their first known appearance.

The skull roof of the conservative pholidophoroids conforms to the semionotid-amioid pattern, more strikingly so in the archaeo-

maenids than in the phelidophorids. The premaxillary is generally small, lacks a posterior process, and may have been partly mobile. The maxillary has a median process, evident in *Pholidophorus* and *Aphnelepis*, which probably has the customary relationship with the premaxillary and palatines. The archaeomaenids, closely related to the pholidophorids, show a tendency towards a small gape, shortened maxillary, and reduced suborbital series. The convergence towards the semionotid skull is remarkably close.

The impossibility of postulating, at the present time, a common ancestral stock for the variety of distinct evolutionary trends included in the Halecostomi suggests that the characters shared in common may actually have evolved independently and that the Halecostomi represent a structural grade rather than a natural taxonomic unit. As various subholostean groups separately approached the holostean level, so it seems entirely reasonable, in fact probable, that different holostean lines separately evolved teleostean characters. It still has not been demonstrated, however, that the Teleostei had a polyphyletic origin; their ancestry is as yet restricted to the pholidophorids. The inclusion of the leptolepids and *Eoprotelops* in either the Pholidophoroidea or the Teleostei represents a taxonomic problem similar to that regarding the position of *Seymouria;* the more complete the evidence the more arbitrary are the systematic boundaries.

In summary, the semionotoids, amioids, and pholidophoroids (as used in Romer's classification) have essentially the same skull roof pattern. The first two have a similarly constructed premaxillary, while all three have a median process on the maxillary. Whether these resemblances are simply parallelisms or are indicative of common ancestry cannot be determined at the present time. This evidence does suggest, however, that semionotoids and amioids had a common ancestral stock in the Permian, with the former developing its short-jawed specialization by the Upper Permian. The pholidophoroids may well have evolved from the same stock, possibly the parasemionotids, at a later time. The modifications in *S. kanabensis* further indicate the intimate relationship that must exist between the form of the jaws, the direction of the suspensorium, and the pattern of the cheek area and suggest that the suborbital series is particularly sensitive to any changes in this relationship.

The taxonomic position of *S. kanabensis* may now be considered in the light of this discussion. On the basis of the skull roof pat-

tern, it could be assigned to each of the three orders just considered, while the structure of the premaxillary would permit allocation to either the semionotids or the amioids. The maxillary and the mandible are, however, typically semionotid and are quite distinct from the paralleling archaeomaenid type. The slender, conical, marginal dentition, the more robust inner teeth, and their arrangement further indicate semionotid affinity. The arrangement of the circumorbital series is likewise semionotid, with the exception of the enlarged posterior member which meets the anterior border of the preopercular. The suborbital series, being reduced to one element, agrees in this respect with *S. nilssoni*, a condition formerly reported only for the pholidophoroid-leptolepid line. The opercular complex of *S. kanabensis*, particularly in the relative size and shape of the opercular bone and the form of the preopercular, resembles rather closely that of other species of *Semionotus*. The squamation, fins, and general body form further support allocation to the Semionotidae.

Rayner (1941) has pointed out that the stability of the skull roof, the palate, and even fin structure at the holostean level reduces the importance of these character complexes in classification. Jaw structure appears to be one of the most reliable diagnostic criteria at the ordinal and, in some cases, at the familial level. Since adaptive modification in jaw form is reflected in the cheek area, this region is also of value. The cheek area of *S. kanabensis* and *S. nilssoni* indicates, however, that the design of this region may vary considerably within a family having a more or less uniform jaw structure. While such variation appears to be exceptional, it can and does occur.

The assignment of *S. kanabensis* to the Semionotidae requires a greater adaptive variation in the cheek area than has been suspected for this family. The desirability of placing *S. kanabensis* in a new family has been considered. Of the 13 genera currently placed in the Semionotidae, however, the cheek pattern is sufficiently known only in *Acentrophorus*, *Semionotus*, *Lepidotes*, and *Dapedius*. There is thus but little evidence for determining the possible range of cheek modification or for believing that all genera assigned to this family must have a cheek pattern essentially like that of *Acentrophorus*. At the present time, therefore, a more conservative designation is considered desirable.

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