

A REVISION OF *SEMIONOTUS* (PISCES: SEMIONOTIDAE) FROM THE TRIASSIC AND JURASSIC OF EUROPE

by AMY R. MCCUNE

ABSTRACT. The morphology and taxonomic identity of *Semionotus* Agassiz, 1832 is clarified, and the diversity of European species of *Semionotus* is assessed. Confusion about *Semionotus* dates back to Agassiz's original description in which he based the type species, *S. leptocephalus*, on a single specimen, and used it to argue that the Coburg Sandstone was Jurassic, a point necessary to support his concept of the threefold parallelism in nature. The specimen disappeared shortly thereafter, and subsequent authors, concluding that Agassiz's specimen of *S. leptocephalus* must have been a young *Lepidotes*, began to recognize *S. bergeri* as the type species. Following an extensive search for the missing holotype of *S. leptocephalus*, study of relevant *Semionotus* material in eleven European museums, and examination of Agassiz's research notes, I argue that the holotype of *S. leptocephalus* must be considered lost; that Agassiz did differentiate *Lepidotes* and *Semionotus*, as evidenced by his working sketches of those two genera; and that, based on newly described skull material and Agassiz's sketches, *S. bergeri* should be retained as the type species (a request to that effect is now pending with the International Commission on Zoological Nomenclature).

Semionotus can be distinguished from *Lepidotes* by the number of suborbitals; *Semionotus* has a single anamestic suborbital whereas *Lepidotes* has two or more suborbitals. Of the forty-one species of *Semionotus* named from European material, only four can be considered valid, suggesting that European semionotids are much less diverse than those of North America. The valid European species, *S. bergeri*, *S. kapffi*, *S. normanniae*, and *S. minor*, are redescribed.

SEMIONOTIDS are halecostome fishes which retain a suite of primitive actinopterygian features characteristic of the 'holostean' level of organization (see Woodward 1895; Schaeffer and Dunkle 1950; Patterson 1973). Members of this family were first described from the Triassic and Jurassic of Germany during the first third of the nineteenth century (Agassiz 1832; Berger 1832). Since then, numerous species ranging from Triassic to Cretaceous in age have been named (Woodward 1895). Semionotids have been found in both freshwater and marine sediments, and on all continents except Antarctica.

In lacustrine sedimentary cycles of the Newark Supergroup in eastern North America, semionotids are particularly abundant. They apparently dominated many of the lakes that, through time, repeatedly formed and evaporated in each of a series of rift valley basins. The fossil record left by their colonizations, extinctions, and speciation is unusually detailed. Most fishes are preserved whole and articulated in microlaminated sediments that provide us with a very fine-scale (perhaps yearly) chronology. Excavations of individual sedimentary cycles have yielded many thousands of specimens representing more than twenty new species of semionotids (McCune *et al.* 1984) and large numbers of better-preserved specimens of previously known species.

Before recent excavations it was generally thought that American semionotids were 'oversplit' (e.g. Woodward 1895; Schaeffer 1967). While many of the nineteenth-century descriptions are not diagnostic, recent studies have shown that the North American semionotid fauna is far more diverse than is apparent from the earlier literature (Olsen *et al.* 1982; McCune *et al.* 1984; McCune, in press *a*). All semionotids from the Newark have been referred to *Semionotus*, although Cornet *et al.* (1973) noted that at least some Newark semionotids strongly resemble *Lepidotes minor* from the Purbeckian of Dorset. Such difficulty in distinguishing *Semionotus* from *Lepidotes* dates back

to Agassiz's original description of the type species, *S. leptocephalus*, in which he pointed out its strong resemblance to a young *Lepidotes* (Agassiz 1836).

Those working with American semionotids have not been able to compare them with European type material because, shortly after Agassiz described the genus, the only existing specimen of the type species disappeared. Uncertainty about the morphology and taxonomy of *Semionotus* has been aggravated further by the incorporation of stratigraphic information into taxonomic judgements. Agassiz used *Semionotus* to argue a Jurassic age for the Coburg Sandstone which, had it been true, would have been consistent with Agassiz's ideas about the threefold parallelism in nature (see below). It has long been known, however, that the Coburg Sandstone is Triassic. Unfortunately the occurrences of *Semionotus* in the Triassic Coburg Sandstone and *Lepidotes* in the Jurassic Posidonienschiefer were generalized by some (e.g. Fraas 1861) to argue that *Semionotus* is found only in the Triassic and *Lepidotes* only in the Jurassic; this erroneous stratigraphic generalization has sometimes been used to distinguish the two genera.

In order to refer the numerous new semionotids from the Newark Supergroup to a genus it was necessary to re-examine the morphology and taxonomy of *Semionotus*. Study of the reference material in eleven European museums enabled me to examine most European specimens of *Semionotus*, including all type and figured specimens of currently valid species, and thus compare the morphological diversity of the European and North American faunas. I also searched extensively for the missing holotype of *S. leptocephalus*. From these studies and a literature review I have untangled the muddle of taxonomy, morphology, and stratigraphy that surrounds *Semionotus*, redefined the genus, reviewed the valid European species, and judged many other named species to be invalid.

HISTORY OF *SEMIONOTUS*

Louis Agassiz (1832), in a letter about his research on fossil fishes to his friend Professor Bronn of the University of Heidelberg, reported a new kind of ganoid fish from the Lias near Boll, Germany. He later described this fish, which he named *Semionotus* (Agassiz 1836, p. 222), and another closely related genus, *Lepidotes* (Agassiz 1837, p. 233), in his classic *Recherches sur les Poissons Fossiles*. The taxonomic and morphological distinctions between these two genera have always been blurred. Agassiz (1836, p. 226) himself noted that the type-species of *Semionotus*, *S. leptocephalus*, resembled a young *Lepidotes*. For most workers since Agassiz (cf. Fraas 1861) the distinction has been stratigraphic only, *Semionotus* being Triassic and *Lepidotes* Jurassic.

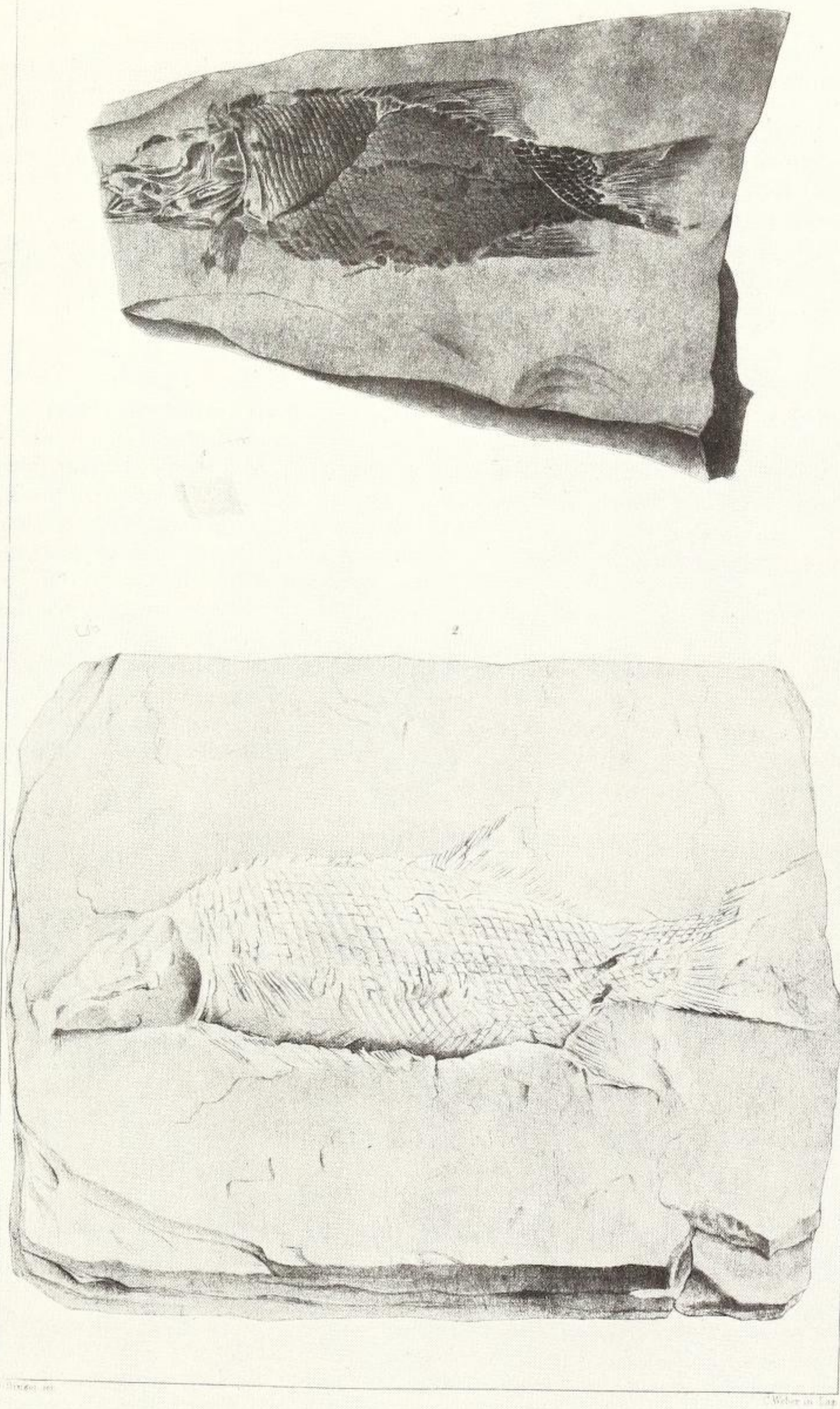
Agassiz (1832, 1836) based *Semionotus* on *S. leptocephalus*. He could not have been more explicit in his designation of *S. leptocephalus* as the type species: 'L'espèce type de ce genre est le *Semionotus leptocephalus* du Lias de Boll' (Agassiz 1836, p. 222). However, his description of *S. leptocephalus* was based on a single specimen (text-fig. 1) from the collections of the Agricultural Society of Wurtemberg at Stuttgart which he had seen in 1831 (Agassiz 1834, pl. 26, fig. 1; 1836, p. 224; 1837, pp. 225-227). By 1861, Fraas was unable to find the figured specimen in the Society's collections, and apparently none of the authors who had written on *Semionotus* in the meantime had seen this holotype and unique specimen of *S. leptocephalus*. It is clear that by 1843 the working standard for comparison was *S. bergeri* (Agassiz 1833, 1834, 1836), not *S. leptocephalus* (Berger 1843; Costa 1851; Schaueroth 1851; Borneman 1854), and *S. bergeri* has since been considered (erroneously) as the type species of *Semionotus* (cf. Woodward 1895).

Recognition of *S. bergeri* as the type-species dates back to a suggestion made by Fraas (1861). The substitution is improper by modern standards, but at the time it seemed common sense. Fraas never explicitly transferred the name *Semionotus* from *S. leptocephalus* to *S. bergeri*. Rather, he asked the rhetorical question, 'May the name *Semionotus* which Agassiz had proposed on the basis of another, Liassic fish [*S. leptocephalus*] be transferred to the Keuper fish [*S. bergeri*]?' (Fraas 1861, p. 89), and argued that the genus was apocryphal as it included only one poorly figured missing specimen (Agassiz 1834, pl. 26, fig. 1). Almost everyone since Fraas has adopted *S. bergeri* as the type species of *Semionotus* (Struver 1864; Deecke 1889; Woodward 1895; Schellwein 1901; Schaeffer and Dunkle 1950).

Fraas also suggested that Agassiz's interest in *Semionotus* was more than taxonomic, and chided Agassiz for trying to impose preconceived ideas about the organization of fishes on to the geological record (Fraas 1861, p. 85). Agassiz had described a Liassic fish, *S. leptocephalus*, which according to Agassiz resembled a

vol. 2

Tab. 20



TEXT-FIG. 1. *Semionotus leptocephalus* (top) and *S. bergeri* (bottom), from Agassiz (1834, pl. 26). Lithograph by Joseph Dinkel.

young *Lepidotes*. This single specimen came from a locality that had produced many *Lepidotes*. Although Agassiz himself could not distinguish his specimen from *Lepidotes* by description or by figure (Agassiz 1834, pl. 26, fig. 1; 1836, p. 22), he gave it a new name, *Semionotus*, and included in that genus the fish from the Coburg Sandstone, *S. bergeri*. Agassiz then used the similarity of the fish from Coburg (*S. bergeri*) to the Liassic fish (*S. leptocephalus*) to argue for a Liassic age for the Coburg Sandstone (Agassiz 1837, p. 226), which was thought to be Keuper then as well as now. As a Liassic fish, *Semionotus* was evidence for this threefold parallelism in nature, specifically the parallel between the succession of fossil fishes and the chief epochs of creation represented by geological periods (Agassiz 1832, p. 143). Fishes with homocercal tails first appeared in the Jurassic, and Triassic rocks were supposed to be dominated by fishes with heterocercal tails (Agassiz 1833, p. 3; 1834, pp. v-vi; Fraas 1861, p. 86). Therefore, to Agassiz, it was important to show that the beds at Coburg which produced fishes intermediate in morphology, with abbreviated heterocercal tails, were also intermediate in age, that is Liassic.

From the preceding discussion it might seem clear that Agassiz was forcing an issue. *S. leptocephalus* was probably *Lepidotes*, and aside from *S. leptocephalus* it was reasonable for Fraas and others to associate *Semionotus* with the Triassic and *Lepidotes* with the Jurassic. Although Agassiz's published figures and descriptions do not distinguish these two genera convincingly, his working sketches of *S. leptocephalus* and *L. elvensis* (described by Agassiz as *L. gigas*), now in L'Archiv de L'État, Neuchâtel (text-fig. 2; Surdez 1973), show that he saw a significant difference between *Semionotus* and *Lepidotes*, though he neglected to mention the difference in his description. His sketch of *Lepidotes* illustrates several suborbitals below the circumorbital series (text-fig. 2B), but in *Semionotus* he figures only one suborbital (text-fig. 2A). *Semionotus* is also now known from throughout the Jurassic (Cornet *et al.* 1973; Olsen *et al.* 1982; *S.* (= *L.*) *minor*, this paper). Thus, while there are no other reports of *Semionotus* from the Jurassic Posidonienschiefer, it would not have been a stratigraphic anomaly to find *Semionotus* in the Lias near Boll. The rarity of *Semionotus* at Boll might even result from a taphonomic bias or a bias of collectors towards beds with more glamorous fossils like ichthyosaurs, plesiosaurs, or the large fishes. The probability of a collecting bias is increased by the fact that different taxa are segregated stratigraphically in the Holzmaden quarries (Dr Rupert Wild, pers. comm.).

The definitive answer to the question, 'What is *Semionotus*?' can only be supplied by Agassiz's specimen of *S. leptocephalus*, and I have made considerable efforts to relocate it. I have searched the Staatliches Museum für Naturkunde Stuttgart (which according to Dr R. Wild has held the collections of the Agricultural Society of Wurtemberg at Stuttgart since 1864), the Muséum National d'Histoire Naturelle in Paris (where Agassiz was studying when he described *S. leptocephalus*), the Institut de Géologie de l'Université de Neuchâtel (which now holds Agassiz's collection from the Académie de Neuchâtel, where he completed *Recherches sur les Poissons Fossiles*), and the collections in Tübingen, Munich, Göttingen, and Zurich; I have been informed by curators of the collections in Coburg, East Berlin, and Frankfurt that they do not have the specimen; I have examined Agassiz's research notes and manuscript for *Recherches sur les Poissons Fossiles* as well as selected correspondence at l'Archiv de l'État in Neuchâtel, and the Museum of Comparative Zoology and the Houghton libraries of Harvard University. All these efforts have been unsuccessful, so it would be unacceptable to restore *S. leptocephalus* as the type-species of *Semionotus*. Yet *Semionotus* has been so widely known for so many years that it is desirable to retain the name. Therefore, I have petitioned the International Commission on Zoological Nomenclature (McCune, in press *b*) to annul the original type designation of *S. leptocephalus* by Agassiz and to designate *S. bergeri* as the type species of *Semionotus* under Article 79. Under the provision of Article 80, common usage is to be continued until a ruling is made, so *S. bergeri* stands as the type species.

SYSTEMATIC PALAEONTOLOGY

Abbreviations for repositories. AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; BSM, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; BGS.GSM, British Geological Survey, Geological Survey Museum, London; IGUN, Institut de Géologie Université de Neuchâtel; LCUC, Larsonneur Collection, University of Caen; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MGAU, Geologisch-Paläontologisches Institut und Museum der Georg-August-Universität, Göttingen; MNHP, Muséum National d'Histoire Naturelle, Paris; RSM, Royal Scottish Museum, Edinburgh; SMNS, Staatliches Museum für Naturkunde Stuttgart; ULPS, Université Louis Pasteur Strasbourg, Institut de Géologie; UT, Institut und Museum für Geologie und Paläontologie Universität Tübingen; YPM, Peabody Museum of Natural History, Yale University, New Haven.

Class OSTEICHTHYES
Subclass ACTINOPTERYGII
Infraclass NEOPTERYGII
Order SEMIONOTIFORMES
Family SEMIONOTIDAE Woodward, 1890
Genus SEMIONOTUS Agassiz, 1832

Type species. *S. leptocephalus* Agassiz, 1836, by original designation; *S. bergeri* Agassiz, 1837 (cf. Woodward 1895), by common usage; subsequent designation of *S. bergeri* as the type-species by the International Commission on Zoological Nomenclature is pending (McCune, in press *b*).

Revised diagnosis. Halecostome fishes which share the following synapomorphies with *Macrosemius* and *Lepisosteus*: gular and intercalar lost; epiotic with large posteriorly directed process; premaxilla with long nasal processes; only arch of mesocoracoid ossified in shoulder girdle; first infraorbital subdivided; ethmoidal ossification reduced to splint (Olsen 1984). *Semionotus* lacks the synapomorphies which define the macrosemiids (Olsen 1984) and lepisosteids (Wiley 1976) and shares with most *Lepidotes* a series of simple, convex scales with moderate to well-developed, posteriorly directed spines along the dorsal midline between the extrascapulars and the origin of the dorsal fin (see text-fig. 6A). *Semionotus* has a single anamestic suborbital whereas *Lepidotes* has two or more suborbitals.

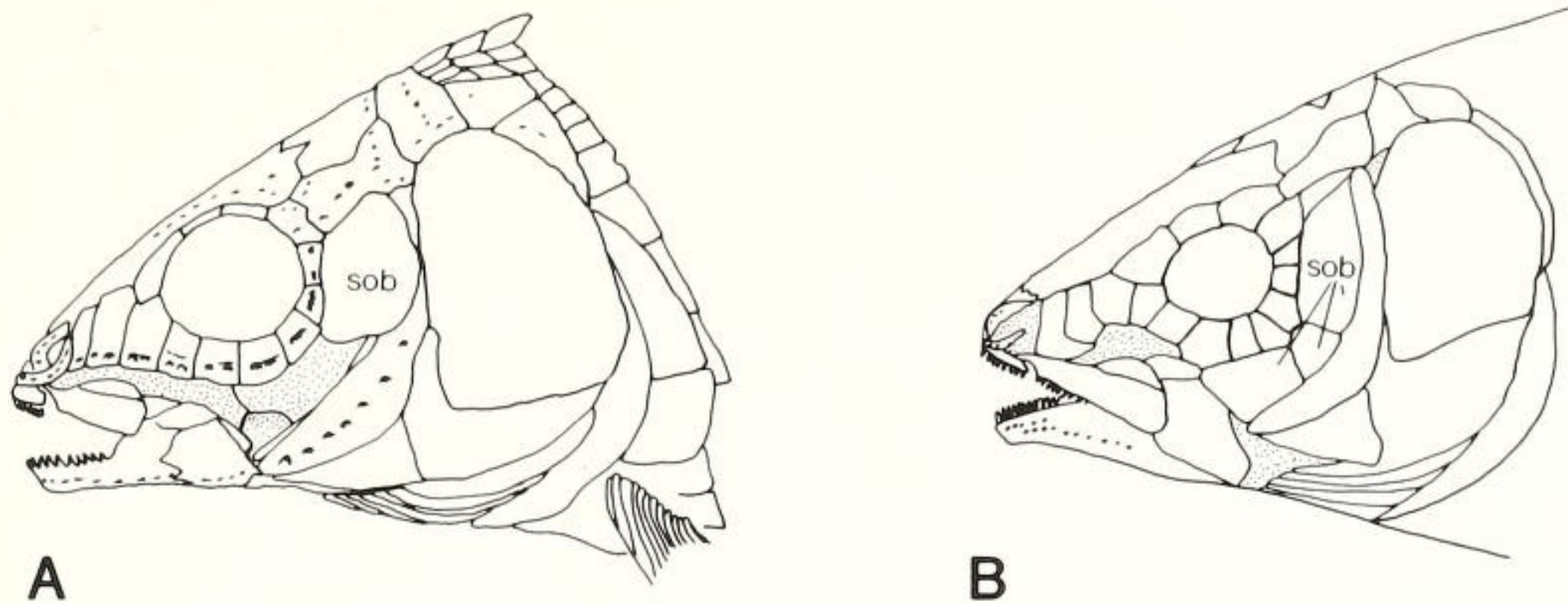
European species. *S. bergeri*, *S. kapffi*, *S. normanniae*, *S. minor*. European material formed the basis for *Semionotus* and is the focus of this paper. [*Semionotus* has also been described from many other parts of the world, although it is the author's opinion that, here too, there is confusion between *Lepidotes* and *Semionotus*, and that the validity of many of these other species is doubtful. Therefore, non-European species are not listed here. Readers interested in non-European semionotids are referred to Woodward (1895) and to the following selected literature: Africa (Brough 1931); North America (Newberry 1888; Eastman 1905, 1911, 1914; Schaeffer and Dunkle 1950; Schaeffer 1967; Olsen *et al.* 1982; McCune *et al.* 1984; McCune, in press *a*); South America (Rusconi 1950); Asia (Olsen *et al.* 1982; Dezao 1983).]

Distribution of European species. Stubenstein, Upper Triassic (Norian) of West Germany; Upper Triassic (Rhaetic) of France; Upper Jurassic (Purbeckian), Great Britain; Upper Triassic (Rhaetic) of Sweden.

Description. Good skull material of European *Semionotus* is rare, and I limit my discussion to individual skulls in the species descriptions that follow (see *S. bergeri*). Body shape is variable, from fusiform to rather deep-bodied. There is a single relatively small dorsal fin; its length at the base is approximately 20% of the standard length. Pectoral and pelvic fins are ventrally placed; the pelvics are about midway between the pectorals and the anal fin. The origin of the dorsal fin is slightly posterior to the middle of the back; the anal fin originates slightly posterior to that. The first lepidotrichium of all fins is preceded by paired basal and fringing fin fulcra. The body is sheathed by a fabric of interlocking ganoid scales. Scale margins are usually smooth but may be serrated as in *S. normanniae* (Larsonneur 1964) or *S. (= L.) minor* (Woodward 1916–1919). The outer layers of the scales are ganoine, the inner layers bone, and there is little or no dentine (Thomson and McCune 1984). The scale immediately anterior to the anal fin is enlarged, as are the scales along the dorsal and ventral margins of the caudal peduncle. Teeth are small, simple, and conical.

Discussion. *Semionotus* is defined here relative to the monophyletic group (*Macrosemius* + *Lepisosteus* + the '*S. elegans* group') discussed by Olsen (1984) and not the family Semionotidae Woodward, 1890 because the diagnostic (derived) features of the latter and taxa included in the family are uncertain. The Semionotidae may include as many as thirteen to twenty-two genera (Schaeffer and Dunkle 1950; Patterson 1973), and as such is most certainly a grade, there being no good synapomorphies to demonstrate monophyly of the family. Some have suggested that certain taxa, such as the dapediids (Wenz 1968), *Woodthorpia*, and *Archaeolepidotus* (Lehman 1966), should be excluded from the Semionotidae. For the Semionotidae to be monophyletic, it is likely that the family must be even further restricted, perhaps to *Lepidotes* and *Semionotus* only (Olsen and McCune, in prep.).

Semionotus is readily distinguished from *Lepidotes* by its single suborbital, whereas the latter



TEXT-FIG. 3. Comparison of the skulls of A, *Semionotus* after Olsen and McCune (in prep.) and B, *Lepidotes* after Wenz (1968). Stippled regions are deep relative to the dermal skull. Note that much of the palate is visible in *Semionotus* (stippled area) while the palate is almost completely covered by extra suborbitals in *Lepidotes*.

has two or more suborbitals in the cheek region (text-fig. 3). A single anamestic suborbital has been interpreted as a derived trait among primitive actinopterygians (Schaeffer and Dunkle 1950; Patterson 1973; Wiley 1976); if this is correct, then *Semionotus* and all Newark semionotids (Olsen *et al.* 1982) must be considered monophyletic.

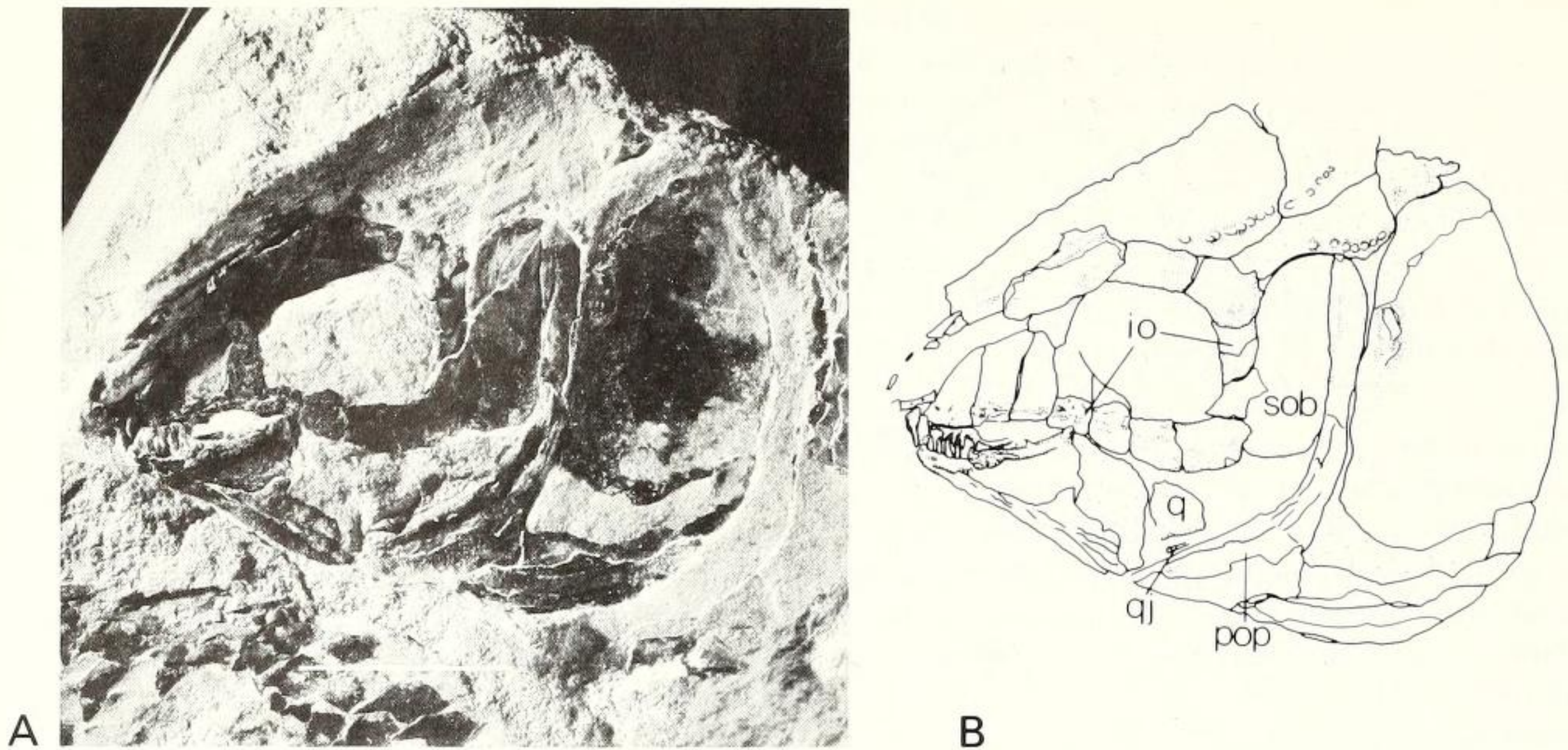
Other characters have been suggested to distinguish *Semionotus* from *Lepidotes*, but few of these hold up to further scrutiny. A median vomer has been described in *Lepidotes* (Woodward 1916–1919), whereas the vomer is paired in *Semionotus*. However, Jain (1983) discovered that fusion of the vomers in *Lepidotes* is correlated with size; the vomer is paired in smaller *Lepidotes*. Jain (1983) suggested several other characters that may distinguish the two genera, including: 1, preoperculum inclined forward in *Semionotus*, but almost vertical in *Lepidotes*; 2, *Lepidotes* has three antorbitals while *Semionotus* has one or two; 3, body form less deep in *Semionotus* than *Lepidotes*; 4, dorsal ridge scales conspicuous and acuminate in *Semionotus*, inconspicuous in *Lepidotes*; and 5, angles of overlap margin not produced forward as prongs in *Semionotus*, but produced forward as prongs in *Lepidotes*. As discussed below, study of new specimens of *Semionotus* from Europe and North America show that the two genera do not differ in these features.

The dorsal ramus of the preoperculum of both *S. bergeri* (text-figs. 3 and 4) and *Lepidotes* appears to be vertically oriented, curving ventrally and anteriorly at about 45° on the dorsal surface. Preoperculum shape and orientation does seem to vary in both genera but this variation is probably determined by preservation, especially the relative positions of the suborbitals and the opercular series.

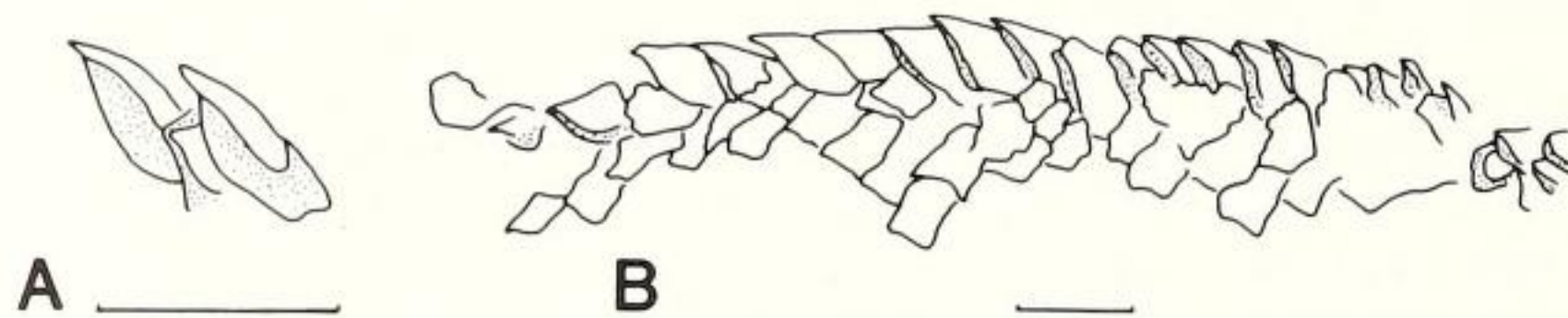
Jain (1983) suggested that *Lepidotes* has three antorbitals in contrast to one or two in *Semionotus*. While one antorbital and an adjacent infraorbital element lie anterior to the lachrymal (= two antorbitals in Jain's terminology), in *S. kanabensis* Schaeffer and Dunkle, 1950, and other American semionotids, the series of infraorbital elements anterior to the lachrymal (the bone joining the ventral and dorsal elements of the circumorbital series) may number three (Olsen *et al.* 1982, figs. 11, 12) or even four (*S. micropterus* (Newberry), YPM 8605) in others.

Not all *Semionotus* are more slender than *Lepidotes*; *S. kapffi* Fraas and a number of American *Semionotus* (McCune *et al.* 1984) are deeper-bodied than *Lepidotes*.

While the dorsal ridge scales of many *Semionotus* are conspicuous with well-developed spines, these scales in other species, such as *S. braunii* (Newberry), are relatively poorly developed (Olsen *et al.* 1982). Furthermore, some *Lepidotes*, such as *L. laevis* Agassiz (Saint-Seine 1949), have very well-developed spines. *L. minor* Agassiz, which I suggest below should be referred to *Semionotus*, may show dorsal ridge scales both with and without well-developed spines (text-fig. 5). The



TEXT-FIG. 4. Skull of *Semionotus bergeri* Agassiz, MGAU 1009-5, from the Keuper of Coburg. A, photograph, medial view. B, camera lucida drawing, medial view. Abbreviations: io, infraorbital; sob, suborbital; q, quadrate; qj, quadratojugal; pop, preoperculum. Scale bar = 1 cm.



TEXT-FIG. 5. Dorsal ridge scales of *Semionotus minor* (Agassiz). A, BMNH 41157. B, BMNH 36081. Spines point posteriorly; stippled area is bone; white is covered by ganoine. Scale bars = 1 cm.

probable primitive condition for dorsal ridge scale morphology in semionotids is convex with posteriorly directed spines.

Pegs or prongs on the flank scales are characteristic of *Semionotus* (Schaeffer and Dunkle 1950; Larsonneur 1964) as well as *Lepidotes* and therefore cannot be used to differentiate them.

One character that has not been discussed very seriously is size. Most recognize that *Lepidotes* is generally large relative to *Semionotus*, but obviously *Lepidotes* species are small sometimes, and the rarity of large *Semionotus* may be due to preservational or collecting biases. The usual difference in the size of individuals of these two genera is so great, however, that size may indeed be a useful character and one that can be tested by compiling length-frequency distributions and analysing growth rings in the scales (e.g. Thomson and McCune 1984).

Many but not all *Lepidotes* (e.g. some *L. elvensis*) have crushing dentition (Woodward 1916-1919; Jain and Robinson 1963; Jain 1983), although this character, like that of fused vomers, could be related to size. Large *Semionotus* (which are rare) may be nearly as large as some *Lepidotes*, but do not have crushing dentition (McCune, in press a). A possible exception is *L. toombsi* Jain and Robinson, which does have crushing dentition like other *Lepidotes* but, like *Semionotus*, has only a single suborbital (BMNH P25180). *L. toombsi* should perhaps be referred to *Semionotus*, but I leave it as *Lepidotes* until a comprehensive study of character distribution among the species of these two genera is undertaken.

Therefore, the characters distinguishing *Lepidotes* and *Semionotus* are limited to: 1, one suborbital in *Semionotus*, two or more in *Lepidotes*; 2, *Lepidotes* is generally larger than *Semionotus* and the vomers are generally fused in the former; and 3, semionotids with crushing dentition are *Lepidotes* (with the possible exception of *L. toombsi*). Each of the four European species of *Semionotus* can be recognized by one or more autapomorphies.

Semionotus bergeri Agassiz, 1833

Plate 22; text-figs. 4 and 6

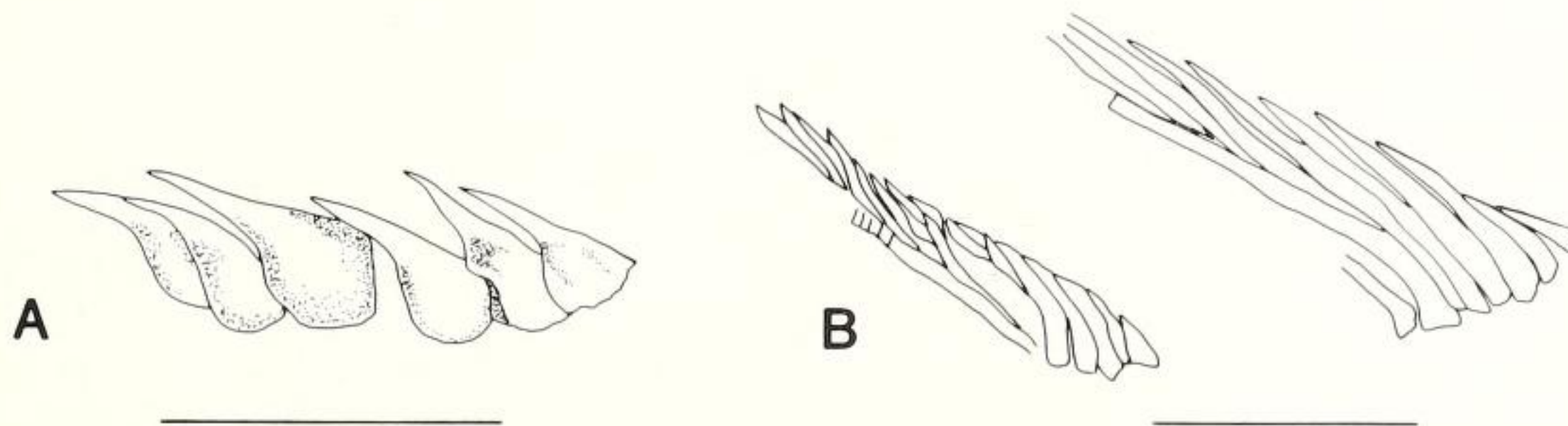
- 1832 *Palaeoniscum arenaceum* Berger, p. 18, pl. 1, fig. 1.
 1833 *Semionotus spixi* Agassiz, p. 8.
 1833–1836 *Semionotus bergeri* Agassiz, pp. 8 [name, 1833], 224 [descr. 1836], pl. 26, fig. 2 [1834a].
 1843 *Semionotus esox* Berger, p. 86.
 1861 *Semionotus elongatus* Fraas, p. 95, pl. 1, fig. 4.

Revised diagnosis. Semionotid with only one anamestic suborbital, shape moderately fusiform (see Table 1); vomers paired; four to six basal fulcra on dorsal fin; four to six fringing fulcra on dorsal fin; dorsal ridge scales simple, convex, with well-developed posteriorly directed spines; teeth small, simple, and conical.

Type material. MGAU 489-1, from the late Triassic Coburg Sandstone, Coburg, West Germany, here designated lectotype, is complete but badly preserved (Pl. 22, fig. 4). Paralectotypes are BSM 572 (complete fish) and a slab of thirteen fish probably at Natur-Museum, Coburg; other Berger specimens mentioned by Agassiz are unrecognizable in the MGAU Berger collection.

Berger (1832) described '*Paleoniscum arenaceum*' in the same year that Agassiz (1832, p. 145) first named *Semionotus*. In this early publication, Agassiz neither described nor figured any species of *Semionotus*. Later, in *Poissons Fossiles*, he named and described *S. bergeri* (Agassiz 1833), and included Berger's specimen of *P. arenaceum* in that species (Agassiz 1836). Berger's specimen was clearly not *Paleoniscum* but, as the senior synonym, *arenaceum* should have been retained. Agassiz chose not to do so, probably because *arenaceum* (the root 'aren-' means sand) was meant to indicate the presence of this fish in Keuper sandstone (Fraas 1861), a possibility that Agassiz wanted to refute.

Although Agassiz clearly designated a type-species for *Semionotus*, he did not specify a holotype for *S. bergeri*. His artist, Joseph Dinkel, figured the Munich specimen for *Poissons Fossiles* (Agassiz 1834, pl. 26, fig. 2), but Agassiz noted in the accompanying text that Berger's material was superior. Woodward (1895) reported that the type of *S. bergeri* was in Göttingen, but he did not specify a particular specimen by number or description. Agassiz (1837) mentioned a number of specimens in Berger's Collection but only the specimen figured by Berger in 1832 (MGAU 489-1) is recognizable today. There are four other specimens from Berger's Collection in Göttingen but they cannot be matched with the brief descriptions given by Agassiz. I was not permitted to examine the material mentioned by Agassiz at the Natur Museum, Coburg. Thus, the best candidates for a lectotype are the specimen figured by Agassiz (1834, pl. 26, fig. 2: BSM 572) (Pl. 22, fig. 1) and the specimen figured by Berger (1832, pl. 1, fig. 1: MGAU 489-1) (Pl. 22, fig. 4). I designate MGAU 489-1 as the lectotype following Berger (1832) and Woodward (1895).



TEXT-FIG. 6. *Semionotus bergeri* Agassiz. Camera lucida drawings of A, dorsal ridge scales on Göttingen specimen (MGAU 489-1) figured by Berger (1832) and B, dorsal fins of MGAU 489-1 (right) and BSM 572 (left). Scale bar = 1 cm.

Other material. BMNH P1547; SMNS 4473, 50972, 51835, and 51841; MGAU 1009-5, 1009-1, 1009-4, 1009-2; UT, Stoll Collection, which does not include *S. kapffi* or *S. elongatus* as Stoll (1929) suggested (the 'deep-bodied' forms are two fish superimposed); BSM 307 (questionable, composite specimen).

Description. *S. bergeri* is easily recognized by the set of primitive characters given in the diagnosis. However, it has no characters which are derived within *Semionotus*. Most of the material is rather badly preserved, and a number of specimens in various museums have been misidentified. This description is based primarily on four specimens (BSM 572; MGAU 489-1 and 1009-5; SMNS 51835).

The lectotype (Pl. 22, fig. 4) is very poorly preserved, but its overall body shape is clearly fusiform; the dorsal ridge scales are convex with well-developed, posteriorly directed spines (see also text-fig. 6). The fins are fringed with fulcra and the body is covered with ganoid scales.

Dermal bones of the skull are easier to interpret in BSM 572 (Pl. 22, figs. 2 and 3) than in the lectotype. The former has only a single suborbital. The pattern of bones emphasized by retouching in Plate 22, fig. 3 is convincingly *Semionotus*-like (text-fig. 3A) rather than *Lepidotes*-like (text-fig. 3B). The ventral dentigerous portion of the premaxilla, part of its ascending process, the ventral border of the mandible, the preoperculum, part of the parasphenoid, the interoperculum, the supratemporal, the anterior, dorsal, and posterior borders of the operculum, part of the cleithrum, and the canal bearing dermopterotic are all visible. There is a condensation of bone, presumably the quadrate, wedged between the preoperculum and mandible. The cheek region is notably free of bone. There are other portions of the skull apparently free of bone, such as the anterior portion of the parietal, the operculum, suboperculum, and the dorsal circumorbitals, but these bones whose edges are defined by an outline of bone or an impression, were present. Although the suborbital is least well defined, assignment to *Semionotus* is confirmed by the facts that there are no *Lepidotes* known from Coburg, and that the only good semionotid skull examined from Coburg (MGAU 1009-5; a medial view of right side of skull; text-fig. 4A) is unquestionably *Semionotus*. Interpretation of MGAU 1009-5 (text-fig. 4B) depends on both preserved bone and negative impressions. The single suborbital and an impression of the quadrate and quadratojugal are obvious. There are clearly no extra suborbitals in the cheek region.

The dorsal fin comprises at least fifteen lepidotrichia, preceded by four to six basal fulcra and at least four to six fringing fulcra (text-fig. 6B). The first three are basal fulcra; seven more lie against the unsegmented portion of the first lepidotrichium. In the caudal fin there are about sixteen or seventeen lepidotrichia, about eight of which compose the lower lobe of the tail. Anal lepidotrichia number seven to ten. See table 1 for meristic and morphometric data.

Other details of semionotid morphology, especially relevant to relationships of the Semionotidae, are described by Larsonneur (1964) and below for *S. normanniae*, by Woodward (1916-1919) for *S.* (= *L.*) *minor*, and by Schaeffer and Dunkle (1950), Olsen *et al.* (1982), and Olsen and McCune (in prep.) for American semionotids.

Semionotus kapffi Fraas, 1861

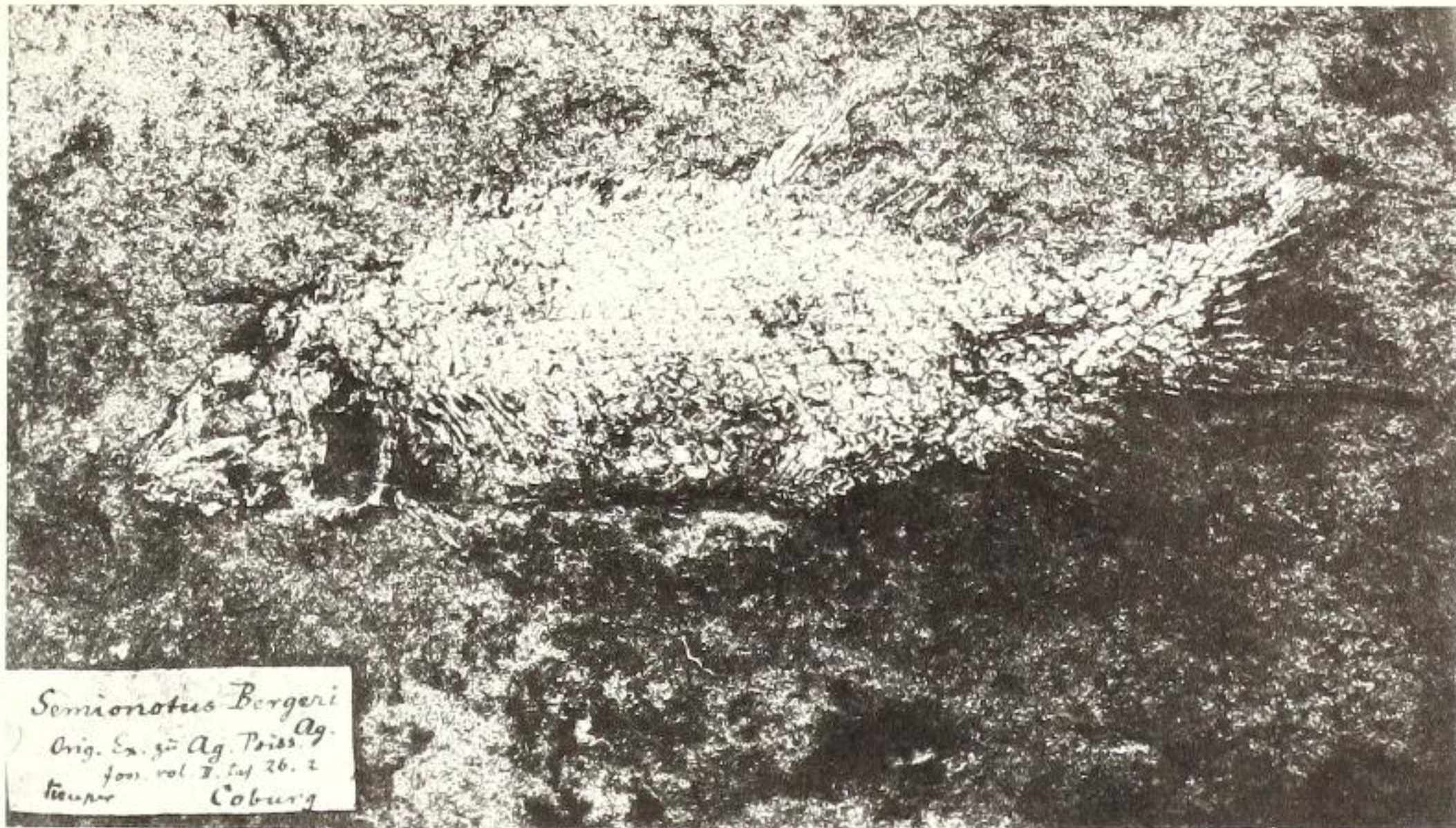
Text-fig. 8

1861 *Semionotus kapffi* Fraas, p. 95, pl. 1, figs. 1 and 2.

Revised diagnosis. A deep-bodied semionotid; simple convex dorsal ridge scales with well-developed spines; twenty-one to twenty-three scale rows between posterior edge of cleithrum and origin of

EXPLANATION OF PLATE 22

Figs. 1-4. *Semionotus bergeri* Agassiz. Late Triassic, Coburg Sandstone, Coburg, West Germany. 1-3, BSM 572, referred to and figured by Agassiz (1834, pl. 26, fig. 2), a paralectotype, showing 1, the complete specimen, $\times 0.53$; 2, the skull retouched; and 3, the skull unretouched, $\times 1.3$. 4, MGAU 489-1, specimen described and figured by Berger (1832, p. 18, pl. 1, fig. 1 as *Palaeoniscum arenaceum*), lectotype, $\times 0.54$.



Semionotus Bergeri
Orig. Ex. 50 Ag. Priss. Ag.
Journ. vol. 7, pag. 26. 2
Heunert Coburg

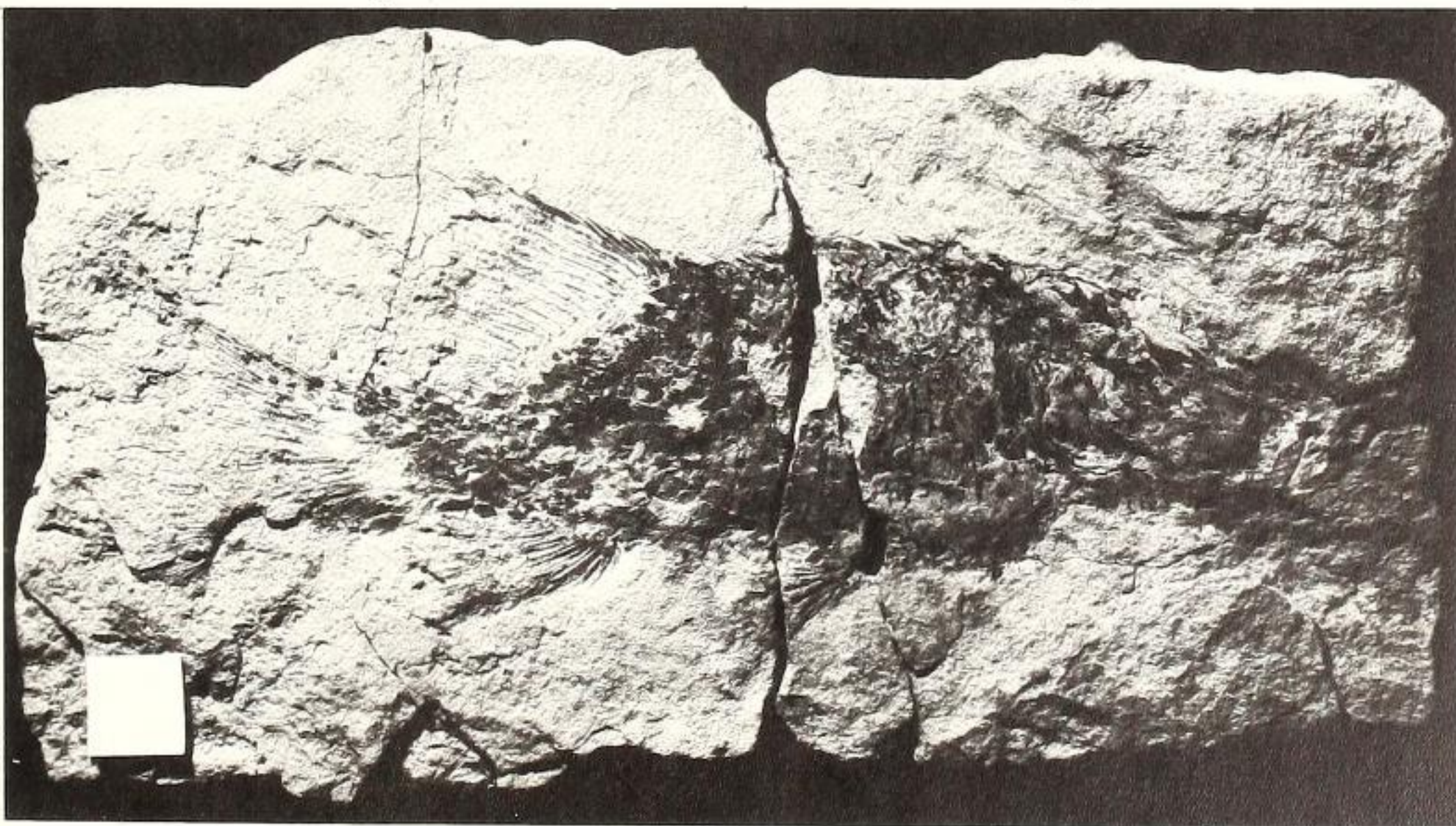
1



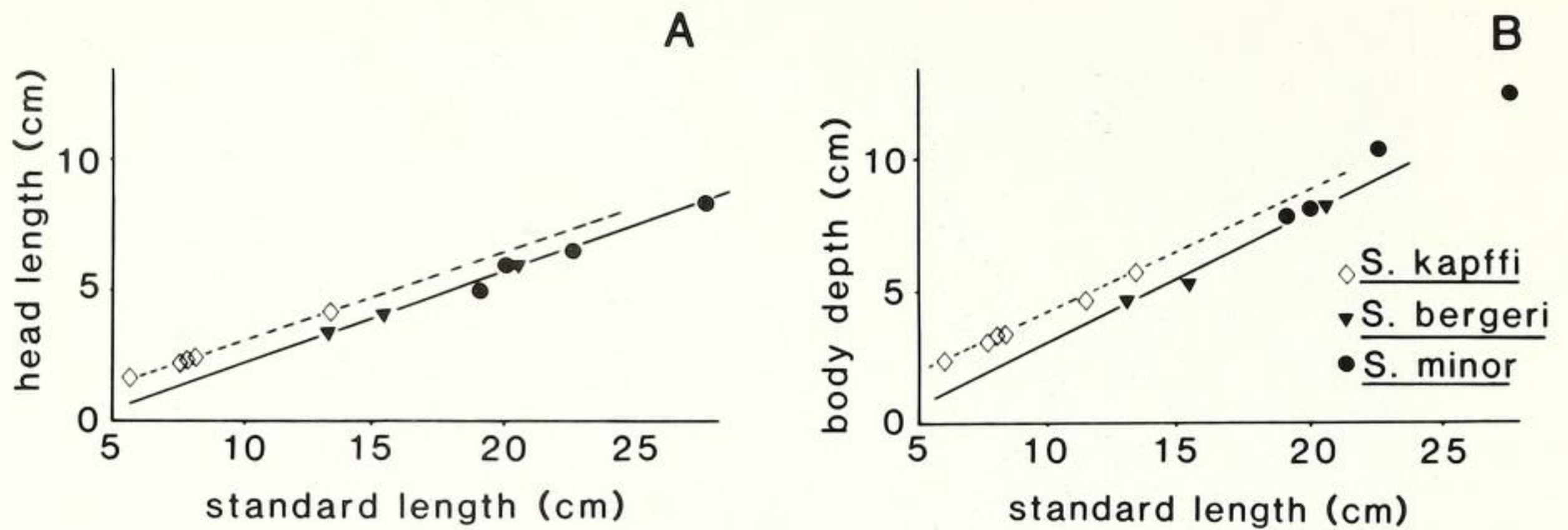
2



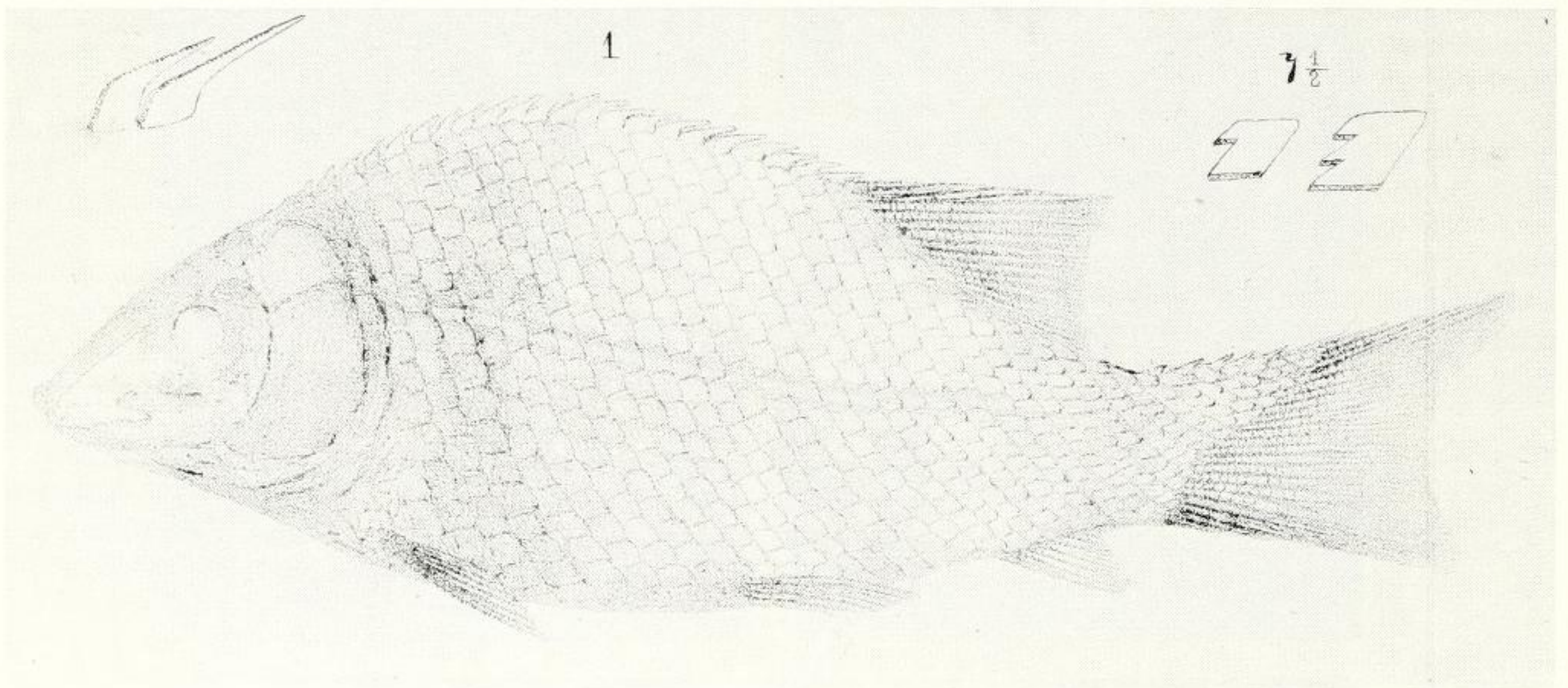
3



4



TEXT-FIG. 7. Bivariate plots for *Semionotus bergeri* Agassiz, *S. kapffi* Fraas, and *S. minor* (Agassiz). A, head length against standard length. B, body depth against standard length.



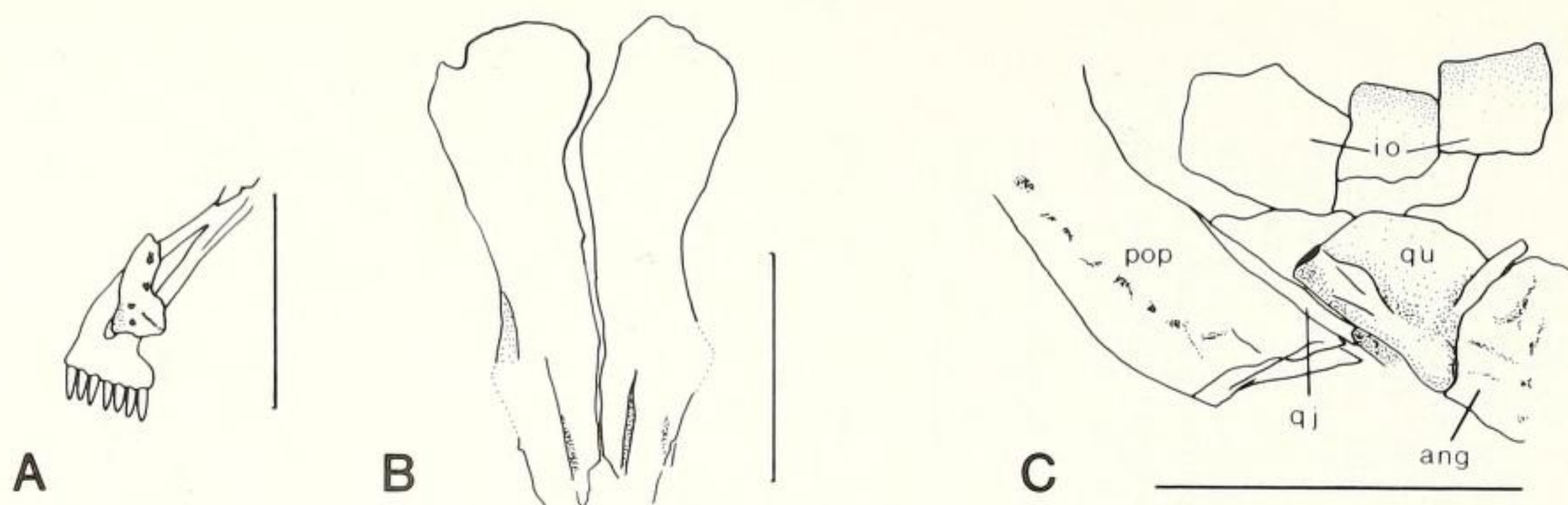
TEXT-FIG. 8. *Semionotus kapffi* Fraas, lectotype, SMNS 3998, from Fraas (1861, pl. 1, fig. 1).

dorsal fin; thirty-two scale rows to base of heterocercal lobe; body length about $2.5 \times$ body depth; head length (relative to standard length) longer than in *S. bergeri* (see table 1; text-fig. 7).

Type material. SMNS 3998 (Fraas 1861, pl. 1, fig. 1), lectotype here designated, collected by Dr Kapff in 1859 from the Stubenstein (Norian, late Triassic) of Heslack, near Stuttgart, West Germany. SMNS 51836 (Fraas 1861, pl. 1, fig. 2) is a paralectotype.

Other material. BMNH 38654 (three specimens), 38655 (two specimens), 38656, plus numerous specimens from Stuttgart, Wurtemberg; SMNS 3998, 50972, 51835.

Description. *S. kapffi* is the most easily recognized species of *Semionotus* because of its distinctive body shape (text-fig. 8). It has a relatively longer head (text-fig. 7A) and greater body depth (text-fig. 7B) than *S. bergeri*. There are about six long, delicate fin fulcra which lie next to the first principal rays of the dorsal and anal fins. No specimens are sufficiently well preserved for fin rays or caudal rays to be counted. The best skull material is not good enough to figure a complete skull but there is nothing inconsistent with other non-*Lepidotes* semionotids. See table 1 for meristic and morphometric data.



TEXT-FIG. 9. *Semionotus normanniae* Larsonneur. A, left premaxilla and nasal. B, frontals. C, jaw joint. Scale bars = 1 cm; ang = angular; io = infraorbital; pop = preoperculum; qj = quadratojugal; qu = quadrate.

Semionotus normanniae Larsonneur, 1964

Text-fig. 9

1964 *Semionotus normanniae* Larsonneur, p. 115, pls. 1 and 2.

Revised diagnosis. Dorsal ridge scales simple, convex with well-developed spines; nasals robust; twenty-one lateral line scales anterior to dorsal fin; body fusiform; posterior scale margins serrated with six to eight teeth on anterior scales and fewer on posterior scales.

Type material. Larsonneur did not designate a single holotype but referred to all of his syntypes as holotypes. The specimen collected and illustrated by Larsonneur (1964, pl. 1, fig. 8), LCUC unreg., from the Rhaetic (late Triassic) of Airel de Basse-Normandy, France, is here designated lectotype. None of the type-series is catalogued, but the most important paralectotypes are figured by Larsonneur (1964).

Description. Although this species was rather thoroughly described by Larsonneur (1964), I can add a few details. The quantity of *S. normanniae* specimens is small, but their quality is superb. The bone is preserved in three dimensions and the matrix can be removed by acetic acid or mechanically. Unfortunately, there are no complete specimens.

Dermal bones of the skull. The premaxillae have long ascending processes (text-fig. 9A) like *Amia*, *Lepidotes* (Deschaseaux 1943; Patterson 1973), and North American semionotids (Olsen and McCune, in prep.). The nasals are robust (text-fig. 9A) rather than delicate as in North American forms. They are similarly robust in *Amia*, *Lepidotes*, and to a lesser degree *S. (= L.) minor*, so I interpret this as the primitive condition for semionotids. The maxilla is free from the cheek and has a peg-like internal maxillary process (see Larsonneur 1964, pl. 1, fig. 1). There appear to be two infraorbitals anterior to the circumorbital ring. Larsonneur figured two suborbitals between the preoperculum and circumorbital series, but the more ventral one is clearly the metapterygoid of the palate (Larsonneur 1964, pl. 1); thus, like other semionotids except *Lepidotes*, *S. normanniae* has a single anamestic suborbital. The frontals are constricted over the orbit and, like most Newark semionotids (Olsen and McCune, in prep.), are narrow rather than broad (text-fig. 9B).

Palate and lower jaw. Further preparation of a specimen pictured by Larsonneur (1964, pl. 1, fig. 6) shows that the jaw joint (text-fig. 9C) is identical to that of North American semionotids (Olsen and McCune, in prep.) and to that of *L. toombsi* (Patterson 1973). The quadratojugal is a splint-like bone which lies along the dorsal edge of the preoperculum.

Post-cranial morphology. Although there appear to be twenty-four scale rows between the cleithrum and dorsal fin (Larsonneur 1964, pl. 2, fig. 1), there are remnants of a dorsal fin at the twenty-first scale row. There is an obvious joint between that point and the dorsal fin labelled by Larsonneur. The specimen is probably a composite of two or more specimens, the more obvious dorsal fin being from a different fish. The number of vertical scale rows anterior to the dorsal fin is therefore twenty-one, and total lateral line scale count is unreliable. The most posterior fragment does not fit the specimen and, as it has been assembled, the caudal rays point ventrally not posteriorly. No other specimens are complete enough to count scales or take body measurements.

Fins. There are at least eighteen caudal fin rays; seven or eight comprise the ventral lobe of the tail. There are no reasonably complete anal or pelvic fins, although an isolated pectoral fin shows fifteen rays fringed by about nineteen fulcra (Larsonneur 1964, pl. 2, fig. 2).

Semionotus minor (Agassiz, 1837)

Text-figs. 5 and 10

1833–1837 *Lepidotes minor* Agassiz, pp. 9 [name, 1833], 260 [descr. 1837], pl. 34 [1834b].
1895 *Lepidotes minor* Agassiz; Woodward, p. 94.

Revised diagnosis. Deep-bodied semionotid with sloping forehead; twenty-one to twenty-four scale rows anterior to dorsal fin and thirty-eight or thirty-nine scale rows to base of heterocercal lobe; fin fulcra very robust; dermal bones of skull heavily tuberculated; some anterior flank scales serrated. Dorsal ridge scales dorsally convex, with prominent spines. Unlike *S. bergeri*, only central axis of scale covered by ganoine (text-fig. 5).

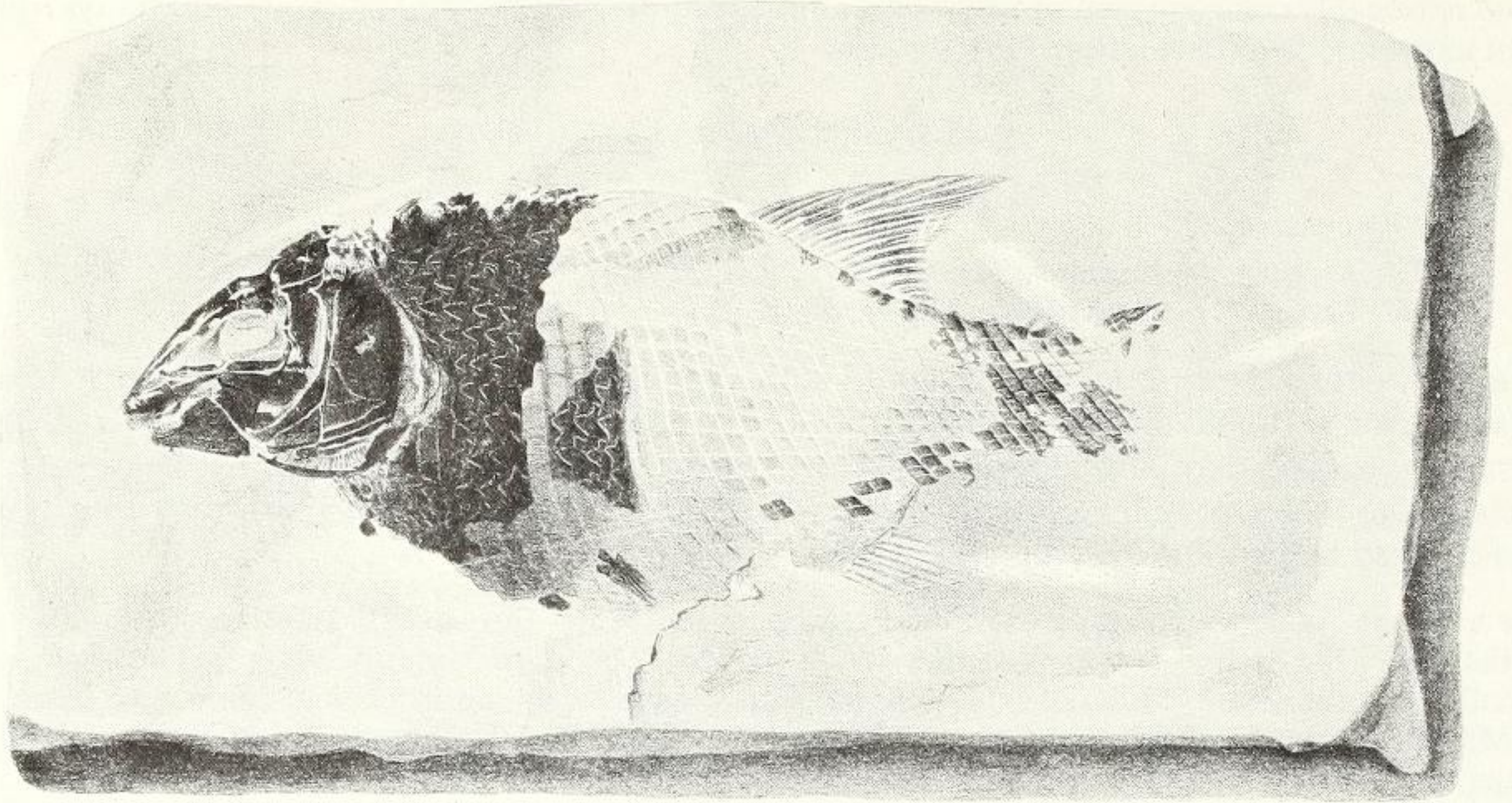
Type material. Agassiz's holotype from the Paris School of Mines (text-fig. 10A) has been lost or destroyed. (At the end of the Second World War, one side of the Paris School of Mines building was bombed. Some of the collection was destroyed in the explosion and many of the better specimens remaining were stolen. When the MNHP assumed the School of Mines Collection in the 1960s, this holotype was not included (Daniel Goujet and Sylvie Wenz, MNHP, pers. comm.). Although Agassiz (1837, p. 260) stated that he had seen several particularly good examples in the Geological Society of London (now BGS.GSM), no individual specimens were discussed.

Among the *S.* (= *L.*) *minor* at the British Museum (Natural History) there is some variation in body shape, counts of vertical scale rows, counts and size of dorsal fin fulcra, and degree of serrations on the flank scales (Woodward 1916–1919, p. 28). However, examination of the specimens shows that this variation in body shape appears to result from distortion. There are relatively deep-bodied forms and more slender forms, but in the latter the belly is pushed up so that the pelvic fins originate at the 'ventral' margin. It is unclear whether the variation in scale counts, fin fulcra, and degree of serration on the flank scales is continuous. I designate here a neotype to avoid confusion over the characteristics of this species, choosing a beautifully preserved 'deep-bodied' form which is clearly not distorted: BGS.GSM 27975 (text-fig. 10B) from the Purbeck (Upper Jurassic) of Swanage, Dorset. No features of this specimen are inconsistent with Agassiz's original figure (1834, pl. 34; see text-fig. 10A). Based on analysis of the matrix the neotype is probably from the Herston Fields Quarry (Hancock) at the Middle Purbeck outcrop (R. W. Sanderson, Petrology Unit, BGS.GSM, pers. comm.). The specimen is included in a catalogue of 1904, but there is no record of when and how it was acquired. It is possible, but by no means certain, that it was one of the exemplary specimens in the Geological Society of London Collection on which Agassiz (1837, p. 260) commented so favourably.

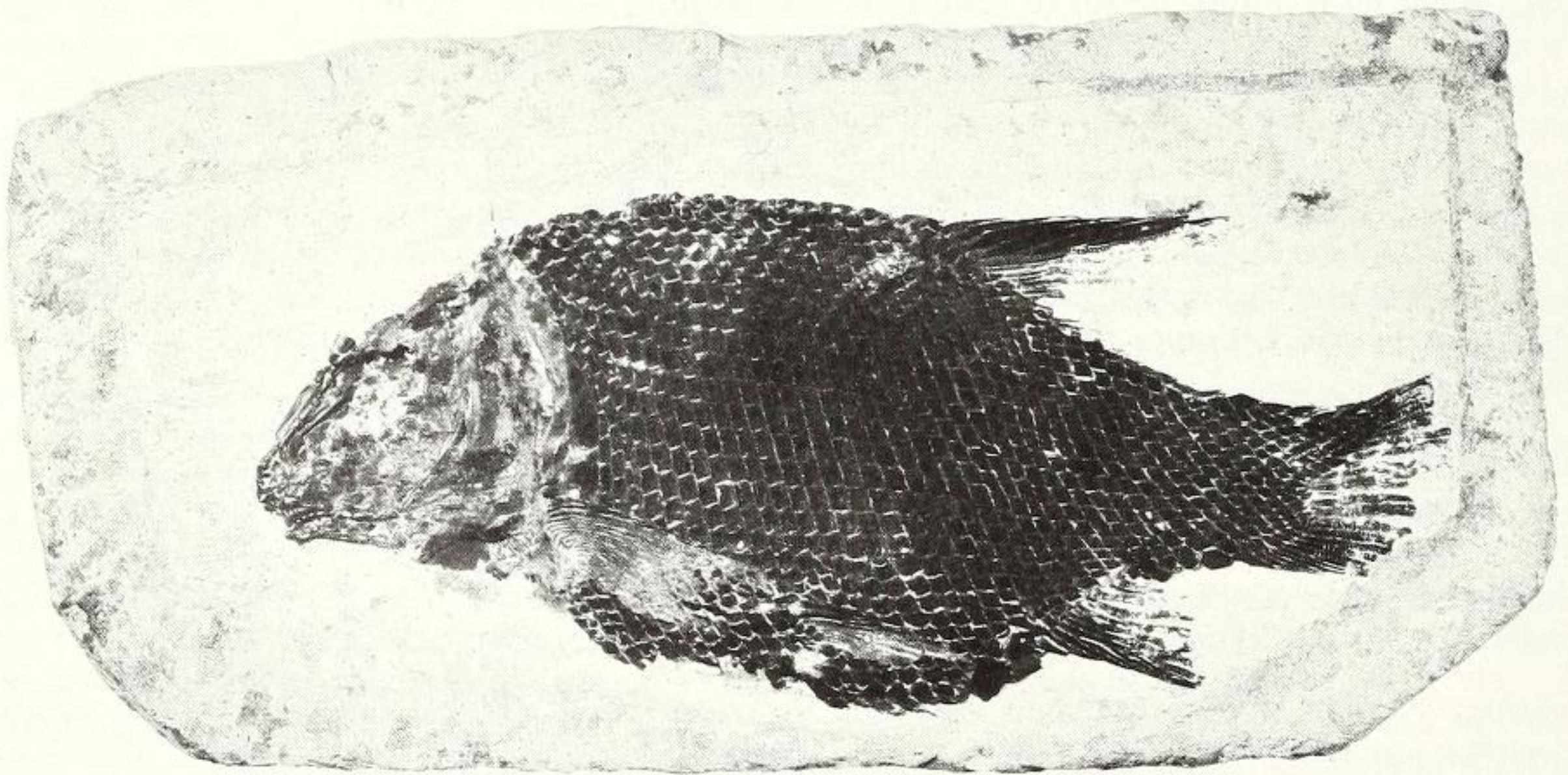
Other material. BMNH P2006, 36081, and many more; BGS.GSM 117512, 27974, 41157; MGAU 369-1 (slab with seven fish from Volksen-Wealden).

Description. Woodward (1916–1919) thoroughly described and figured *S.* (= *L.*) *minor* from the Purbeck beds at Swanage, Dorset. Most of these individuals are rather large (about 20–40 cm). Some smaller individuals (about 10 cm SL) from the Deistersandstein of northern Germany (Volksen-Purbeck) have also been referred to *S.* (= *L.*) *minor* (Branco 1887). See table 1 for meristic and morphometric data.

Discussion. Earlier, I distinguished *Semionotus* from *Lepidotes* by the number of suborbitals: *Semionotus* has only one and *Lepidotes* has more than one. Although Agassiz did not point specifically to this distinction, I have shown that it is reflected in his sketch of *S. leptocephalus* and *L. elvensis* (= *gigas*) which are the type species of these two genera. *L. minor* Agassiz is figured by Woodward (1916–1919, fig. 14) as having only one suborbital, although earlier Woodward (1895) figured *L. minor* as having several suborbitals. Thus, *L. minor* should be referred to *Semionotus*, as I have redefined it. I refer *L. minor* to *Semionotus* here because its similarity to *Semionotus* has been noted in particular with reference to Newark semionotids (Cornet *et al.* 1973; McDonald 1975). Other species of *Lepidotes*, such as *L. toombsi* (BMNH P25180) in which the metapterygoid or other elements of the palate have been mistaken for dermal cheek plates (Jain and Robinson 1963), should probably also be referred to *Semionotus*, although this species is somewhat



A



B

TEXT-FIG. 10. A, '*Lepidotes minor*' Agassiz, original figure from Agassiz (1834, pl. 34). B, *Semionotus* (= *L.*) *minor* (Agassiz), BGS.GSM 27975, neotype, from the Purbeckian (late Jurassic) of Swanage, Dorset.

problematical as discussed earlier. In contrast, *L. mantelli* (Woodward 1916–1919), *L. elvensis* (Deschaseaux 1943; Wenz 1968), and *L. laevi* (MHNP 1907–17), to name a few well-known species, clearly have more than one suborbital covering the cheek region. A re-examination of *Lepidotes* is evidently needed, but this is beyond the scope of the present work.

COMMENTS ON OTHER NAMED SPECIES OF *SEMIONOTUS*, INVALID OR DUBIOUS

S. altolepis Deecke, 1889, *nomen dubium*. Single specimen, whole, but badly preserved. Université de Strasbourg, Institut de Géologie. Gres bigarre (Zwischensch). Wasselanne. It is definitely not *Semionotus*, and probably a perleidiid. The skull bones are heavily sculptured; the maxilla is long and cleaver-shaped. Fin fulcra are very delicate. The tail is barely heterocercal, with a notch in the dorsal portion.

S. brodei Newton, 1887, *nomen dubium*. Upper Keuper, Shrewley, near Nottingham. BMNH P7615 includes five syntypes. Syntype material includes neither skull material nor a view of dorsal ridge scales, so there is no evidence that these specimens are even semionotid. Furthermore, the one fin that is preserved (Newton 1887, fig. 4) does not have the usual semionotid arrangement: rather than a series of paired lepidotrichia, unsegmented at the base, segmented distally, and fringed with fulcra, the rays are divided into several segments proximally, like some palaeoniscids.

S. dubius Bellotti, 1857, *nomen dubium*. Upper Triassic, Perledo, Como. This material, along with that of several other species of *Semionotus* described by Bellotti, was supposed to be in the 'Museo Civico proviente da Perledo [Milan]'. There is no museum in Perledo today; other material collected by Bellotti was deposited in the Milan Museum but all specimens collected before the Second World War were destroyed in the bombing of Milan (Dr. R. Wild, SMNS and Herr Professor Dr Rieber, Institut de Pal., Univ. Zurich, pers. comm.).

S. elongatus Fraas, 1861, *nomen dubium*. Stubensandstein (Norian), Stuttgart, Heslach. Fraas figured two specimens (1861, pl. 1, figs. 4, 5). It is definitely a semionotid, and not *Lepidotes*, as shown by the dorsal ridge scales and single suborbital. Unfortunately, the better specimen (fig. 4) has been lost or destroyed. The remaining one (fig. 5) is not good enough to distinguish it from *S. bergeri*. There is another specimen (SMNS 51835) which is a slab of thirteen fish. Many of these are *S. kapffi*, though some are small, slender-bodied forms and more slender than *S. bergeri*. In addition, while the skull of *S. bergeri* is rather short and stout, the slender Stuttgart specimens appear to have longer, more pointed skulls, and the dorsal fin placed more posteriorly. It might seem that the two should be considered separate species, but the only slender forms known are small (SL = 7.2 cm) whereas the smallest individual of *S. bergeri* is much larger (estimated SL = 13.4 cm). It is possible that *S. bergeri* becomes deeper bodied with increased length and that slight differences in shape are due to differences in size. Study of a larger number of complete *S. bergeri*, especially in the smaller sizes, would resolve this question, but none is currently available.

S. gibbus Seebach, 1866, *nomen nudum*. This species was named without description or figure. The specimen label is in the Institute of Geology, University of Göttingen, but the specimen itself is missing.

S. gibbus [*gibber* error] Bassani, 1896, *nomen dubium*. The type was supposed to have been in the Milan Museum before the collection's destruction during the Second World War.

S. inermis Bellotti, 1857, *nomen dubium*. Destroyed in the Milan Museum during the Second World War.

S. inornatus Henry, 1876, *nomen dubium*. As an isolated scale, from Boisset, France, it shows no diagnostic characters of the family Semionotidae, let alone *Semionotus*. The denticulations described and figured by Henry (1876) are probably the result of a broken edge.

Heterolepidotes (*S.*) *joassi* Woodward, 1887. Jurassic, Strath Brora, Sutherland, Scotland. RSM 1966.41.3. These specimens are definitely not *Semionotus*. There are no visible dorsal ridge scales. The skull, though perhaps too poorly preserved, does not show the large single suborbital. The internal view of the scales is like that of *Heterolepidotes*. Both of these features were figured by Woodward (1887), and he later suggested that *S. joassi* might be related to *Heterolepidotes* (Woodward 1895, p. 314).

S. leptcephalus Agassiz, 1836, *nomen dubium*. Liassic, near Boll, West Germany. This missing specimen has been discussed thoroughly in the introductory remarks above.

S. letticus Fraas, 1861. Upper Letten Keuper, Lettenkohle, Hoheneck. Seven specimens in SMNS, all very poorly preserved. On SMNS 4189 the general form of the body is fusiform and the flank scales have smooth, not serrated, margins. The skull material is too poorly preserved to see any structure. There are neither fins

nor dorsal ridge scales on any specimens. Oertle (1927) referred the holotype of this species to *Engycolobodus*, but claimed that the assorted syntypes should remain as *S. letticus*. Clearly, Oertle's action effectively refers *S. letticus* to *E. letticus*.

S. metcalfi Swinnerton, 1928, *nomen dubium*. Keuper, near Nottingham, England. The whereabouts of this specimen is unknown. From Swinnerton's figure, the skull of the holotype could be a parasemionotid. However, he mentioned spiny dorsal scales along the dorsal midline, and if that is correct, it is not a parasemionotid. If the skull is figured incorrectly, and the specimen is *Semionotus*, there is nothing else in Swinnerton's description to distinguish it from *S. kapffi*.

S. nilsonni Agassiz, 1837, *nomen dubium*. MCZ 5067, Rhaetic, Schonen, Sweden. It is clearly *Semionotus*, but is too distorted and incomplete to be identified to species (other than to say it is not *S. normanniae*).

S. serratus Fraas, 1861, *nomen dubium*. Stubensandstein (Norian), Mainhardt Woods near Hutton, Germany. The holotype is the only known specimen. It is a badly preserved and incomplete fish which includes shoulder girdle, part of the frontals, and the flank just to and not including the dorsal fin. It is a semionotid, as shown by a few dorsal ridge scales. There are twenty-one scale rows anterior to the dorsal fin, and the scale margins are serrated. If the specimen is *Semionotus*, there would be nothing to distinguish it from *S. normanniae*. However, the skull is so poorly preserved that it cannot be identified as either *Semionotus* or *Lepidotes*.

S. trotti Bellotti, 1857. Upper Triassic, Perledo, Como. This specimen was destroyed in the Milan Museum during the Second World War.

NAMED SPECIES OF *SEMIONOTUS* (OUTSIDE NORTH AMERICA) PREVIOUSLY REFERRED TO OTHER TAXA

| | |
|-------------------------------------------------------|-----------------------------------------------------|
| <i>alsaticus</i> Deecke, 1889 | <i>Perledius</i> by Stensiö (1921) |
| <i>australis</i> Woodward, 1890 | <i>Zeuchthiscus</i> by Wade (1940) |
| <i>basalmi</i> Bellotti, 1857 | <i>Archaeosemionotus</i> by Alessandri (1910) |
| <i>bellotti</i> Ruppell, 1857 | <i>Allolepidotes</i> by Alessandri (1910) |
| <i>brevis</i> Bellotti, 1857 | <i>Heterolepidotes</i> by Alessandri (1910) |
| <i>carinulatus</i> Costa, 1856 | <i>Eugnathus brachilepis</i> Bassani (1896) |
| <i>curtulus</i> Costa, 1851 | <i>Colobodus ornatus</i> by Woodward (1895) |
| | <i>Pholidophorus latiusculus</i> by Woodward (1895) |
| | <i>Peltopleurus humilio</i> by Woodward (1895) |
| <i>hermesi</i> Bellotti MS, 1873 | <i>Eugnathus hermesi</i> by Alessandri (1910) |
| <i>labordei</i> Priem, 1924 | <i>Parasemionotus</i> by Piveteau (1929) |
| <i>latus</i> Agassiz, 1837 | <i>Colobodus latus</i> by Alessandri (1910) |
| <i>macropterus</i> Schafhautl, 1851 | <i>Caturus</i> by Woodward (1895) |
| <i>manseli</i> Egerton, 1872 | <i>Lepidotes</i> by Woodward (1895) |
| <i>minutus</i> Egerton, 1843 | <i>Pholidophorus</i> by Woodward (1895) |
| <i>pentlandi</i> Egerton, 1843 | <i>Colobodus latus</i> by Woodward (1895) |
| <i>pustulifer</i> Egerton, 1843 | <i>Colobodus latus</i> by Woodward (1895) |
| <i>rhombofer</i> Agassiz, 1837 | <i>Heterolepidotus latus</i> by Woodward (1895) |
| <i>socialis</i> Berger, 1843 | <i>Dictyopyge</i> by Struver (1864) |
| <i>spinifer</i> Deecke, 1889 | <i>Colobodus ornatus</i> by Woodward (1895) |
| <i>striatus</i> Agassiz, 1837 | <i>Heterolepidotes</i> by Woodward (1895) |
| <i>tenuis</i> Woodward, 1890 | <i>Zeuchthiscus</i> by Wade (1940) |
| <i>tenuiserratus</i> Egerton, MS; from Woodward, 1895 | <i>Colobodus latus</i> by Woodward (1895) |

CONCLUSION

An understanding of the morphology of *Semionotus*, and therefore its taxonomic identity, has been hampered by poor preservation of specimens, few in number. In the fourteen European museums visited or contacted during this study there are almost fewer specimens identifiable as *Semionotus* than there are named species of the genus. The better preserved *S. normanniae* and *S. (= L.) minor* were described too late in the history of the genus to have affected earlier revisions. By comparing

these two species and previously undescribed material of *S. bergeri* and *S. kapffi* with *Lepidotes*, I have shown that *Semionotus* can be distinguished from *Lepidotes* by its single anamestic suborbital.

Of the forty-one species of *Semionotus* included in Woodward's (1895) *Catalogue*, only two are justifiable. Since then, Larssonneur (1964) has added one and I suggest that at least one '*Lepidotes*' should be considered a fourth—*Semionotus* (= *L.*) *minor*. From this taxonomic revision the question about the diversity of *Semionotus* in the European Mesozoic can be answered. In marked contrast to the American semionotid fauna the European fauna is quite impoverished. This reassessment of species diversity provides a beginning for future consideration of the geographic and temporal distributions of a group that is, under some circumstances, remarkably diverse.

Acknowledgements. For access to specimens and for their kind hospitality I thank Drs C. Patterson, P. H. Greenwood, P. Forey, Ms S. Young, and Ms A. Longbottom (BMNH); Drs S. Wenz, P. Janvier, D. Goujet, and E. Buffetaut (MNHP and CNRS, Paris); Dr J.-C. Gall and Ms M. Wolf (University of Louis Pasteur, Strassbourg); Dr C. Larssonneur and Mr M. Rioult (University of Caen); Dr R. Wild (SMNS); Professor Chère (University of Neuchâtel); Dr O. Rieppel (University of Zurich); Dr P. Wellenhofer (BSM); Dr W.-E. Reif, Mr J. Troster, and Ms C. Vogt (University of Tübingen); Dr H. Janke (MGAU); Professor P. Dullemeijer, Drs C. Barel, B. Otten, and M. Stiasney (University of Leiden); Dr S. M. Andrews (RSM); and Dr I. Cook (BGS.GSM).

Travel funds for this research were granted by the National Geographic Society Committee for Research and Exploration, the Theodore Roosevelt Memorial Fund, and Sigma Xi. Additional support for preparation of the manuscript was provided by Hatch Project 183-421. Mr A. Pivorunus made my work much easier by translating hundreds of pages of nineteenth-century German. The photographs were taken by W. K. Sacco and the author. I thank Drs P. Olsen, B. Schaeffer, D. Schindel, K. Thomson, and D. Winkler for valuable discussion and comments on the manuscript.

REFERENCES

- AGASSIZ, L. 1832. Untersuchungen ueber die fossilen Fische der Lias-Formation. *Neues Jb. Miner. Geol. Paläont.* **1832**, 139-149.
- 1833-1837. *Recherches sur les Poissons Fossiles*, Livraison I, 1833; II, 1834a; III, 1834b; VI, 1836; VIII & IX, 1837. Imprimerie de Petitpierre, Neuchâtel.
- ALESSANDRI, G. DE. 1910. Studii sui pesci triasici della Lombardia. *Memorie Soc. ital. Sci. nat.* **7** (1), 1-147, pls. 1-9.
- BASSANI, F. 1896. La ittiofauna della Dolomia principale di Giffoni (Salerno). *Palaeontogr. ital.* **1**, 169-210, pls. 9-15.
- BELLOTTI, C. 1857. Descrizione di alcune nuove specie de pesci fossili di Perledo e di altre localita lombarde. In STOPPANI, A. (ed.). *Studii geologici sulla Lombardia*, 419-438. Biblioteca Polytecnica, Milano.
- MS 1873. Catalogo (manoscritto) dei Pesci fossili del Museo Civico di Milano, fol. 83. [Not seen; cited in Alessandri (1910) and also in the annotated copy of Woodward (1859) in the E. I. White Library, British Museum (Natural History).]
- BERGER, H. A. C. 1832. *Die Versteinerungen der Fische und Pflanzen im Sandsteine der Coburger Gegend*, 29 pp., 4 pls. Coburg.
- 1843. No title [letter on *Semionotus* and *Thalassides*, dated Coburg, 24 October 1842]. *Neues Jb. Miner. Geogn. Geol. Petrefakt.* **1843**, 86.
- BORNEMAN, J. G. 1854. Ueber *Semionotus* im oberen Keupersandstein. *Z. dt. geol. Ges.* **1854**, 615, pl. 25.
- BRANCO, W. 1887. *Lepidotes minor*. *Abh. geol. Speckarte preuss. thür. St.* **7**, 363, pl. 6, fig. 2.
- BROUGH, J. 1931. On fossil fishes from the Karroo system, and some general considerations on the bony fishes of the Triassic period. *Proc. zool. Soc. Lond.* **1931** (1), 235-296, pls. 1-4.
- CORNET, B., TRAVERSE, A. and McDONALD, N. G. 1973. Fossil spores, pollen and fishes from Connecticut indicate Early Jurassic age for part of the Newark Group. *Science, N.Y.* **182**, 1243-1247.
- COSTA, O. G. 1851. Mittheilungen an Professor Bronn gerichtet [letter to E. Ruppell on the fossil fishes of the kingdom of Naples]. *Neues Jb. Miner. Geogn. Geol. Petrefakt.* **1851**, 182-184.
- 1856. *Ittiologia fossile italiana opera da servire de supplemento alle ricerche sui pesci fossili de l'Agassiz*, viii + 48 pp., 4 pls. Naples, Italy.
- DEECKE, W. 1889. Ueber Fische aus verschiedenen Horizonten der Trias. *Palaeontographica*, **35**, 97-138.

- DESCHASEAUX, C. 1943. Contribution à l'étude du genre *Lepidotes*. *Annls Paléont.* **1943**, 3-13.
- DEZAO, S. 1983. Note on a new *Lepidotes* from the Cretaceous of Sichuan. *Vertebr. palasiat.* **21**, 177-187.
- EASTMAN, C. R. 1905. The Triassic fishes of New Jersey. *Rep. New Jers. geol. Surv.* **1904**, 67-102.
- 1911. *Triassic Fishes of Connecticut*, 75 pp. State Geological and Natural History Survey, Hartford, Connecticut.
- 1914. Notes on Triassic fishes belonging to the families Catopteridae and Semionotidae. *Ann. Carneg. Mus.* **9**, 139-148.
- EGERTON, SIR P. DE M. G. 1843. On some new ganoid fishes. *Proc. Geol. Soc. Lond.* **4**, 183-184; *Ann. Mag. nat. Hist.* **13**, 51-55.
- 1872. Figures and descriptions of British organic remains, Kimmeridge Clay, Dorsetshire. *Mem. geol. Surv. U.K.*, Dec. **13**, Articles 2-9, pls. 2-9.
- FRAAS, O. 1861. Ueber *Semionotus* und einige Keuper-Conchylien. *Jh. Ver. vaterl. Naturk. Württ.* **17**, 81-101.
- HENRY, J. 1876. *Memoires de la Société d'Émulation du Doubs*, ser. 4, vol. 10. Dodivers, Besançon Imprimerie.
- JAIN, S. L. 1983. A review of the genus *Lepidotes* (Actinopterygii: Semionotiformes) with special reference to the species from Kota Formation (Lower Jurassic), India. *J. palaeont. Soc. India*, **28**, 7-42.
- and ROBINSON, P. L. 1963. Some new specimens of the fossil fish *Lepidotes* from the English Upper Jurassic. *Proc. zool. Soc. Lond.* **141**, 119-135.
- LARSONNEUR, C. 1964. *Semionotus normanniae* du Trias supérieur de Basse-Normandie (France). *Annls. Paléont.* **50**, 101-117.
- LEHMAN, J. P. 1966. Actinopterygii. In PIVETEAU, J. (ed.). *Traité de Paléontologie*, **4** (3), 1-242. Masson, Paris.
- MCCUNE, A. R. In press a. Toward the phylogeny of a fossil species flock: semionotid fishes from a lake deposit in the Early Jurassic Towaco Formation, Newark Basin. *Bull. Peabody Mus. nat. Hist.*
- In press b. *Semionotus* Agassiz, 1832 (Osteichthyes): proposed designation of *Semionotus bergeri* Agassiz, 1833 as type species. Z.N.(S.)2434. *bull. zool. Nom.*
- THOMSON, K. S. and OLSEN, P. E. 1984. Semionotid fishes from the Mesozoic lakes of North America. In ECHELLE, A. A. and KORNFIELD, I. (eds.). *Evolution of fish species flocks*. University of Maine Press, Orono, Maine.
- MCDONALD, N. G. 1975. Fossil fishes from the Newark Group of the Connecticut Valley, 230 pp. Masters thesis (unpublished), Wesleyan University, Middletown, Connecticut.
- NEWBERRY, J. S. 1888. Fossil fishes and fossil plants of the Triassic rocks of New Jersey and the Connecticut Valley. *Monogr. U.S. geol. Surv.* **14**, 1-152.
- NEWTON, E. 1887. On the remains of fishes from the Keuper of Warwick and Nottingham. *Q. Jl geol. Soc. Lond.* **43**, 537-540.
- OERTLE, G. F. 1927. '*Semionotus letticus* O. Fraas' und andere Ganoiden aus dem Höhenecher Kalk von innen geschen. *Neues Jb. Miner. Geol. Paläont. Beil Bd*, Abt. B, **58**, 309-334.
- OLSEN, P. E. 1984. The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the Early Triassic Sakamena Group of Madagascar with comments on the relationships of the holostean fishes. *J. Vert. Paleont.* **4**, 481-499.
- MCCUNE, A. R. and THOMSON, K. S. 1982. Correlation of the Early Mesozoic Newark Supergroup by vertebrates, principally fishes. *Amer. J. Sci.* **282**, 1-44.
- PATTERSON, C. 1973. Interrelationships of holosteans. In GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds.). *Interrelationships of fishes*, 233-305. Academic Press, London.
- PIVETEAU, J. 1929. Sur un type de poisson fossile provenant du nord de Madagascar. *C. r. hebd. Séanc. Acad. Sci., Paris*, **189**, 1017-1019.
- PRIEM, F. 1924. Paleontologie de Madagascar XII—Les poissons fossiles. *Annls Paléont.* **13**, 1-28, pls. 1-7.
- RUPPELL, E. 1857. In STOPPANI, A. (ed.). *Studii Geol. e Paleont.* 425. Lombardia, Milano.
- RUSCONI, C. 1950. Notas Sobre Faunas Paleozoicas de Mendoza por Carlos Rusconi. *Annls Soc. Cient. Argentina*, **149**, 157-177.
- SAINT-SEINE, P. DE. 1949. Les poissons des calcaires lithographiques de Cerin. *Nouv. Archs Mus. Hist. nat. Lyon*, **2**, 1-357.
- SCHAEFFER, B. 1967. Late Triassic fishes from the western United States. *Bull. Am. Mus. nat. Hist.* **153**, 287-342.
- and DUNKLE, D. 1950. A semionotid fish from the Chinle formation, with consideration of its relationships. *Am. Mus. Novit.* **1457**, 1-29.
- SCHAFHAUTL, K. F. E. 1851. *Geognostische Untersuchungen des Sudbayerischen Alpengebirges*, xxxvi + 208 pp., 44 pls., map. Munich.

- SCHAUROTH, K. VON. 1851. Ueber das vorkommen des *Semionotus bergeri* im Keuper bei Coburg. *Z. dt. geol. Ges.* **3**, 405–410.
- SHELLWEIN, E. 1901. Ueber *Semionotus* Ag. *Schr. phys.-ökon. Ges. Königsberg*, **42**, 1–33.
- SEEBACH, K. VON. 1866. [*Semionotus gibber*, etc., from the Triassic of Germany.] *Z. dt. geol. Ges.* **18**, 7.
- STENSIÖ, A. E. 1921. *Triassic fishes from Spitzbergen*, Part I, xxviii + 307 pp., 34 pls. Adolf Holzhausen, Vienna.
- STOLL, H. VON. 1929. Versuch einer stratigraphischen Gliederung des Stubensandsteins im westlichen Württemberg. *Jber. Mitt. oberrhein. geol. Ver.* (n. 8), **18**, 1–63.
- STRUVER, J. 1864. Die fossilen Fische aus dem Keupersandstein von Coburg. *Z. dt. geol. Ges.* **16**, 303–331, pl. 13.
- SURDEZ, M. 1973. *Catalogue des Archives de Louis Agassiz*. Université de Neuchâtel, Institut de Géologie et Séminaire d'Histoire.
- SWINNERTON, H. H. 1928. On a new species of *Semionotus* from the Keuper of Nottingham. *Geol. Mag.* **65**, 406–409.
- THOMSON, K. S. and A. R. MCCUNE. 1984. Scale structure as evidence of growth patterns in fossil semionotid fishes. *J. Vert. Paleont.* **4**, 422–429.
- WADE, R. T. 1940. Triassic fishes of Gosford, New South Wales. *J. Proc. R. Soc. N.S.W.* **73**, 206–217.
- WENZ, S. 1968. *Complements à l'Étude des Poissons Actinopterygiens du Jurassique Française*, 276 pp., 48 pls. Centre National de Recherche Scientifique, Paris.
- WILEY, E. O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). *Misc. Publs Univ. Kans. Mus. nat. Hist.* **64**, 1–111.
- WOODWARD, A. S. 1887. On a new species of *Semionotus*, from the lower Oolite of Brora, Sutherlandshire. *Ann. Mag. nat. Hist.* **10** (5), 175–179.
- 1890. The fossil fishes of the Hawkesbury Series at Gosford. *Mem. geol. Surv. N.S.W. (Paleontol. Ser.)*, **4**, i–xiii, 1–56.
- 1895. *Catalogue of the fossil fishes in the British Museum*, 4 vols. British Museum (Natural History), London.
- 1916–1919. The fossil fishes of the English Wealden and Purbeck formations. *Palaeontogr. Soc. (Monogr.)*, 1–148, pls. 1–26.

AMY R. MCCUNE

Section of Ecology and Systematics
Division of Biological Sciences
Cornell University, Ithaca
New York 14853, USA

Typescript received 31 August 1984

Revised typescript 26 June 1985