SOME NEW OBSERVATIONS ON *LEPIDOTES MAXIMUS* (HOLOSTEI : SEMIONOTIFORMES) FROM THE GERMAN UPPER JURASSIC

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ABSTRACT

Lepidotes maximus Wagner, a holostean fish with strongly tritoral dentition, is known by complete fish and a number of fragmentary specimens. There are only two complete specimens; both are in Senckenberg Naturmuseum, Frankfurt. Of these only one is known with a description and illustration. The second fish is described here providing new information. A comparison of these two specimens has yielded knowledge about variation of certain characters and parameters in L. maximus. Validity of the three Upper Jurassic fishes, L. maximus. L. laevis and L. palliatus is upheld.

INTRODUCTION

Among the Mesozoic actinopterygians, Lepidotes has a long time range from Rhaetic to Cenomanian. It is known by a large number of species and numerous specimens (mostly fragmentary) exists in various European museums. Unfortunately the nomenclature and definition of many species is very confused. Woodward (1895) succeeded in his attempts to create order among holostean fishes. His detailed analyses of characteristics of Lepidotes, providing identification key, has withstood the test of several decades of research. Subsequently Saint-Seine (1949) made a definitive study of fossil fishes from French lithographic limestone at Cerin and Gardiner (1960) from the British Lower Lias. Both studies included a number of holosteans. Lehman (1966) revised the classification of fossil fishes in J. Piveteau's Triate de Paleontologie. In addition, our knowledge about Lepidotes has considerably increased in recent years due to studies by Gardiner (1963, 1967), Jain and Robinson (1963), Danil'chenko (1964), Wenz (1968), Patterson (1973, 1975) and Jain (1983), among others.

Upper Jurassic Solnhofen limestone (also known as Lithographic limestone) at Langaneltheim in West Germany has yielded some of the most celebrated vertebrate fossils. Included among these are Archaeopteryx lithographica, a small dinosaur Compsognathus, flying reptiles Pterodactylus and Rhamphorhynchus and a primitive lizard Homoeosaurus. It has also yielded finely preserved specimens of Lepidotes maximus, a shell crushing fish, which is the subject of present communication.

Lepidotes maximus Wagner, one of the largest semionotid fish, is known from only two uncrushed, well preserved specimens, in addition to a plaster cast of palate and lower jaw and a few fragmentary pieces.

Each complete fish is about 2 metre long. Both have been recovered from Solnhofen limestone at Langaneltheim and are on display at the Senckenberg Naturmuseum, Senckenberg Institute. Frankfurt-am-Main. While on a study tour of European museums, during March-April 1962, for examination of Lepidotes specimens, my attention was drawn to a large specimen of L. maximus (P. 2386) on display in the Museum. Except for occasional popular notes (e. g., Schmidt, 1946, referred as L. palliatus), this specimen has not been described. Though not specified, the photograph accompanying Schmidt's article is of SNM P. 325. During the World Fair in Montreal, Canada, in 1967 this fish (original) was loaned from the museum and displayed. Its photographs appeared in the newspapers e. g., Frankfurter Allgemein (Feb. 1967) and in The Bulletin (Bonn, March 1967). Viohl (1976) published a photograph of this fish in "Jura Museum Eichstatt" and Barthel (1978) in "Solnhofen". The latter erroneously referred the specimen as P. 2886 instead of the correct registration number P. 2386.

It may be mentioned that an earlier specimen L. maximus (P. 325) has been illustrated and described by Weitzel (1930) in detail. In an earlier publication (Jain, 1983) this specimen has been referred to as exhibiting diagnostic characters of the species, rather than associated squamation designated by Wagner 1863 as the type. The second specimen of L. maximus, in addition to being better preserved, provides new formation. With a view to better understanding Solnhofen vertebrate fossils a comparison of the two specimens was undertaken. It proved useful in determining the range in variations of certain characters of the skull. L. maximus is one the better known species among Lepidotes species-group having strongly tritorial

dentition and associated characters. A re-examination of all available, including fragmentary material, assignable to L. maximus in European museums has enabled me to provide a new definition and restoration of L. maximus.

MATERIAL

The following complete specimens have been used in this study:

- P. 325 Complete fish from Solnhofen limestone at Langanaltheium; described and illustrated by Weitzel (1930), Schmidt (1946).
- P. 2386 Complete fish from Solnhofen Limestone at Langanaltheim; photograph published, Vioh (1976) and Barthel (1978).

Both specimens are on display at Senckenberg Naturmuseum, Frankfurt-am-Main (SNM).

In addition, the following specimens, also examined, exhibit diagnostic characters of L. maximus:

- Lower jaw of L. maximus from the Upper Kimmeridgian of northern France described by Sauvage (1877, Plate 1, Fig. 2) and deposited in the Musée de Boulogne-sur-Mer, N. France; a plaster cast of this specimen is also in Museum National d'Histoire Naturelle, Paris.
- 2. Lower jaw described by Pictet (1860) as Sphaerodus gigas from the Upper Kimmeridgian of Neuchatelois Jurassic, Switzerland, original probably lost but a plaster cast is available in Museé de Soleure, Switzerland.
- 3. Lower jaw of *L. maximus* from the Kimmeridge clay of Shotover Hill, near Oxford, described by Etheridge and Willet (1889); original preserved in BM (NH) as P. 6723.
- Plaster cast of palate and lower jaw of whole tish from Solnhofen Limestone of Langenaltheim described by Weitzel (1930) as SNM 325 : BM(NH) P. 11166.

SYSTEMATIC DESCRIPTION

Class Actinopterygli Subclass Holostei . Order Semionotiformes Family Semionotidae

Lepidotes maximus WAGNER, 1863

Synonymy: All specimens assigned by Woodward (1895): Schmidt (1946) as L. palliatus, Viohl (1976) and Barthel (1978).

Holotype: Association squamation from Solnhofen limestone of Langaneltheim, West Germany, described

by Wagner (1963) and preserved in Bayerische Staatssammlung, Munich.

Revised diagnosis: large lanceolate semionotids with 8-11 postorbital cheekplates, in a single or double linear series; two or more pairs of extrascapulars; parietal asymmetry unknown; strongly tritoral dentition in upper and lower jaws; premaxillae with 2 teeth each; maxilla unknown; dentary with 4 teeth; palate without distinguishable pterygo-palatine and vomer, bearing 35-50 teeth; coronoid dentition in four rows; 15-18 teeth in each coronoid; body scales with deep furrows interrupting the ganoine.

Skull: P.2386 has well preserved skull (Plate 1, 2A) with the interfrontal suture nearly straight in the posterior region only; anteriorly the frontals are coossified. All the skull bones are tuberculated. The parietals can be partly seen but their asymmetry, if any, cannot be determined. The specimen is somewhat deficient in the region of the extrascapulars but at least two pairs are indicated. The dermopterotic is large and elongated. Eight completely preserved postorbital cheekplates are present on the left side (exposed side) of the fish. The first two posterodorsal cheekplates are nearly equal in size, although the second is more square than the first, then follow 5 alternating triangular bones and the most anterior is the largest (Fig. 2B). Among the fragments from P.2386 there are 6 postorbital cheekplates in the Museum's collection. It appears that the skilled preparator (Herr Strunz) having tried to prepare (around 1930-34) the right side of the fish, gave up later, but left 6 detached cheekplates which fit perfectly (Plate 2B). This row of cheekplates is obviously incomplete. My restoration of these right side cheekplates is shown in Fig. 2A. It will be seen that it is based on the left side pattern to make a set of 8, the most anterior being the largest. It may be noted that the left side has a linear series of 8 bones; the right side is also interpreted as having 8 bones but one bone is out of alignment as if suggesting a doubling of linear series.

A re-examination of P.325 (Weitzel's specimen) shows that it is considerably damaged in the region of the postorbital cheekplates. Weitzel determined 7 postorbital cheekplates in the linear row and a single in the second row, thus totalling 8 bones (Fig. 1A, B). I examined the ridges of matrix which indicate the sutures of cheekplates in this specimen and reconstructed the series (Fig. 1C). It has been found that infact this specimen has 10 cheekplates in the linear row instead of 7 determined by Weitzel. The second row, however, has a single bone. It therefore appears that in *L. maximus* the number of cheekplates may range from 8-11, in single or double series. No information is available on the left side of P.325 (Table 1).

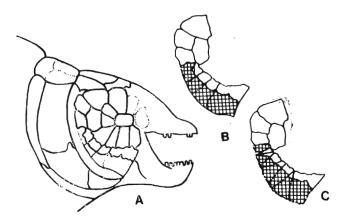


Fig. 1 A, reconstruction of skull and jaw of Lepidotes maximus based on P. 325 in Senckenberg Naturmuseum, Frankfurt (after Weitzel, 1930). B, postorbital cheekplates restoration (after Weitzel, 1930). C, new restoration. Shaded area indicates matrix with ridges, indicating position of bones.

Weitzel's specimen is poorly preserved in the anterior region of the orbit; it does not permit an estimation of the number of infrabitals (or "subdivided lachrymals" of Olson, 1984). P.2386 however, has 3 well preserved infraorbitals. The number of circumorbitals is variable: P.325 probably has 9 and P.2386 has 11. The five circumorbitals adjacent to the postorbitals also show the course of sensory canals (Fig. 2).

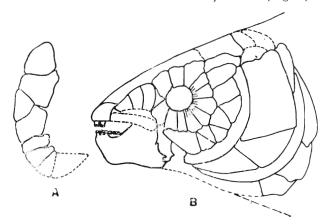


Fig. 2 A, restoration of right side postorbital cheekplates and B, restoration of skull and jaw of Lepidotes maximus based on P. 2386 at Senckenberg Naturmuseum, Frankfurt.

The opercular apparatus consists of the usual elements, preopercular, opercular, subopercular and interopercular. Weitzel (1930) determined opercular as 250×110 mm for P.325. This could not be re-checked as when I re-examined the specimen it was damaged in this region. However, the opercular is 195×120 mm in P. 2386. The cleithrum and supra-cleithrum

Table 1. Comparison of Lebidotes maximus specimens at Senckenberg Naturmuseum, Frankfurt.

		aturmuseum, Frankfurt.	
		P. 325	P. 2386
1. Maximum length of	fish	180 cms.	202 cms.
2. Maximum depth		68 cms.	81 cms.
3. Operculum : width/le	ength ratio	2:5 appx. (Weitzel's figures)	3:5 appx.
4. Interfrontal suture		Probably straigh	Straight
5. Parietal asymmetry		Unknown	Unknown
6. Number of extrascapulars		? 2 pairs	? 2 or more pairs
7. Postorbital cheekplat			
	Left	Unknown ·	Single series-8
	Right	double series (10+1)	Single series-8 (indication of doubling)
8. Infraorbitals (or "Subdivided lachrymals")		Unknown	3
9. Circumorbitals		? 9	11
10. Vomer and Pterygo-palatine		Coossified	Coossified
11. Premaxilla-number o	of teeth		
	Left	2	2
	Right	2	2
12. Number of teeth in palate		35	50
13. Length of lower jaw		186 mm	205 mm
14. Depth of symphysis		76 mm	86 mm
15. % Jaw length/symph		40.1%	40.2%
16. Dentary—number of	teeth Left	damaged	4
	Right	4	4
17. Length of dentary tooth row		76 mm	77 mm
18. Coronoid—number of	of teeth		
	Left	damaged	18
	Right	15	18
19. Coronoid—tooth rov	vs Left	damaged	4
	Right	4	4
20. Coronoid— max. dia	Ü	-	-
	Left	damaged	93 mm
	Right	90 mm	90 mm

are robust in proportions, followed by 3 large postcleithral scales, nearly devoid of ganoine in P.2386.

Jaws and dentition: The maxilla is unknown in any material of L. maximus. The right and left premaxillae are preserved in P.2386 and each bears two stout and strongly tritoral teeth. The same condition is observed in P. 325. In L. maximus, as in other strongly tritoral Lepidotes species, the palate is indistinguishable into vomer and pterygo-palatine. Only two specimens are known which show the palate in association: P.325 described by Weitzel and occuring in association with postcranial skeleton (a cast of this dentition is in BM (NH) as P.11166) and P.2386. In addition, Peyer (1954) has described a specimen of dentition as L. maximus from Upper Jurassic of Thayngen, Switzerland. Peyer has considered the dentition to be coronoid but judged from his figures (Peyer 1954: Fig. 2 and Plates I & II) it seems likely to be a palatal dentition.

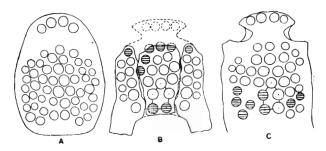


Fig. 3 Palatal dentition in Lepidotes maximus. A, arrangement of teeth as in P. 2386; B, reconstruction from left pterygopalatine (Cornuel, 1877) and vomer (Sauvage, 1877) from N. France; C, arrangement as in P. 325 (Weitzel, 1930); all x x apprx. Teeth not fully erupted are shaded.

P. 325 has a symmetrical palate, maximum diameter 108 mm, bearing 27 completely erupted and 8 half erupted teeth (Fig. 3 C). No sutural boundaries between pterygo-palatines and vomer can be made out. However a set of five teeth (3 completely erupted and 2 half erupted) forming a pentagon in the midposterior region of the dentition, mark the hind margin of the vomer. These "characteristically arranged five posterior teeth" in vomer have been noticed earlier by Woodward (1895, p. 115) in BM(NH) specimens of L. mantelli. It seems that the condition is similar in L. maximus. BM(NH) P.325 has 35 teeth in the palate. SNM P. 2386 has a partly exposed palate and it has been possible to make a plasticine mould and photograph the palate (Fig. 3A). It has 50 teeth. Even though the size of palate in P. 325 and P. 2386 is almost the same the wide range in the number of palatal teeth (35-50) is remarkable. However the posterior part of the vomer as indicated by a pentagon of teeth, is not well marked in P.2386.

Cornuel (1877) described but did not figure a pterygo-palatine of Lepidotes as L. giganteus from the Kimmeridgian of France. This specimen is available in Paris at Muséum National D'Histoire Naturelle. It is 94 mm long and bears 10 teeth in two rows. It is evidently a right side pterygo-palatine of L. maximus. A vomer from Cornuel's locality has been described as L. maximus (Sauvage, 1877). Woodward (1895: 106) considered both the materials as belonging to L. maximus. A restoration of the palate based on these specimens, with additional information on the premaxilla from P. 325, is given in Fig. 3B. Thus there are three specimens of the palate of L. maximus, two from Upper the Jurassic of Solnhofen and one from the Kimmeridgian (Upper Jurassic) of France. These show close resemblance in the morphology and arrangement of the palatal teeth (Fig. 3, A, B, C). Cornuel's specimen is the smallest of the three and evidently belongs to a smaller fish. It also indicates that the pterygo-palatines and voner had not been completely co-ossified since the pterygo-palatine and vomer were detached.

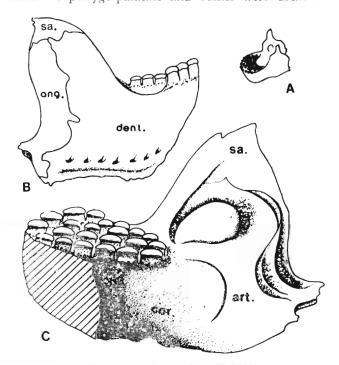


Fig. 4 Left lower jaw of Lepidotes maximus (P. 2386) at Senckenberg naturmuseum, Frankfurt. A, Schematic representation; B, labial view, x 1/2; C, mesial view (a bit posteriorly) x 2/3. Ang.—angular; art.—articular; cor.—cornoid; dent.—dentary; sa.—surangular.

The lower jaws of P.2386 are detachable due to the excellent preparation work of Herr Strunz (Fig.4; Plate 2C). Because of this detailed observations can be made. The left lower jaw (exposed side) was slightly damaged in the surangular region (Plate 2A) when 22 SOHAN L. JAIN

I photographed the fish in 1962 but has been subsequently restored (Plate 1, photograph supplied in 1985). However the right side is excellently preserved and can be examined in outer and inner aspects. A comparison of P. 2386 and P. 325 reveals that the former is slightly stouter in proportion. The externally rugged dentary occupies a large area with surangular and angular sutured to it by sinuous sutures (Fig. 4B). Mesially (Fig. 4C) the surangular occupies a larger area because it overlaps the angular. The articular is short and stout and the articulating surface is prominent. The prearticular is fore-shortened but robust in general proportions with an ovoid outstanding tuberosity dorsally. The dentary bears four stout teeth with strongly tritoral surface. There are 18 similar teeth on each side in the coronoid, arranged in four or five rows. The lower jaws of right and left side are firmly sutured providing a stable tritoral surface. P.325 is deficient in the left side of lower jaw. A restoration of upper and lower jaw dentition of L. maximus based on P.2386 is given in Fig. 5. A number of observations and parameters on P.2386 and P. 325 are given in Table 1. The depth of the symphysis (as percentage of jaw length) in both specimens is almost similar, even though these are different in dimensions of overall size.

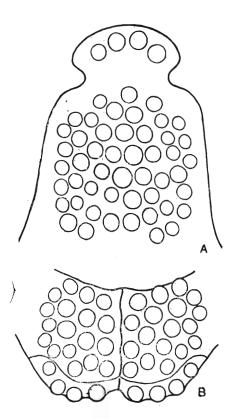


Fig. 5 Restoration of jaws and dentition of Lepidotes maximus based on P. 2386 at Senckenberg Naturmuseum, Frankfurt, x x. A, palatal dentition; B, mandibular dentition.

Squamation and fins: In P. 2386 the body scales have deep furrows in the ganoine. In most scales the furrows converge towards the centre of the scale i.e., they are radiating furrows. There are a few scales in the flank region where the furrows do not radiate but run almost parallel to each other. Flank and abdominal scales in the lower half of the body of the fish have more or less complete ganoine covering except for sparse interruption by furrows. In the more dorsal scales, the ganoine is patchy and disappears nearly completely in some scales (Fig. 6 and Plates 1, 2). A number of scales in the dorsal flank region are devoid of ganoine. All scales have tuberculations but this feature is less pronounced or absent in the caudal region. In P. 325 there are radiating furrows on the scales and patchy ganoine in fewer scales than in P. 2386. P. 2386 has upto 17 furrows in the anterior flank scales but these are reduced to 3-4 in the posterior region. There are 25 flank scales vertically and 29 near anal region from dorsal to ventral side in P. 2386. There are 40 scales transversely from anterior to posterior region along the lateral line canal in P. 2386.



Fig. 6 Squamation in Lepidotes maximus, in P. 2386 at Senckenberg Naturmuseum; cleithral and post-cleithral scales of the body from 10th row vertically. Loss of ganoine (white areas) as deep grooves in the scales may be noted.

All fins, except the polyic, are preserved in P. 2386. The dorsal fin has 5 basal fulcra embedded in the body; 5th is about 3 times as long as the first. These are followed by about 24 fringing fulcra. There are 15 fin rays in the dorsal fin. The fulcral scales of pectoral fin cannot be studied due to damage but 12 fin rays are preserved. The anal fin is opposite the dorsal fin, having 13 basal fulcra embedded in the body and 20 fringing fulcra. There are 8 fin rays in the anal fin. The caudal fin has numerous fulcral scales and 24 fin rays. In general the fins are better preserved in P. 2386 than in P. 325.

COMMENTS

During 19th century a number of species of Lepidotes were erected which were based upon fragmentary material. It has been found not only that fragmentary material has very few characters, but often fragments which may be parts of a single individual have been given different names. Woodward (1895: 82-83) made a remarkable attempt at devising a useful key, based upon important diagnostic characters, to delineate 16 species of Lepidotes from a very large number, based on fragmentary material, known at that time. Subsequently many attempts have been made to define some species or suggest synonymies (e. g., Saint Seine, 1949; Peyer, 1954; Jain and Robinson, 1963; Lehman, 1966; Jain, 1983).

Among the species of Lepidotes from the Upper Jurassic horizons, L. maximus, L. palliatus and L. laevis are relevant to the present discussion. The holotypeof L. maximus is an associated squamation from Solnhofe-Limestone of Langaneltheim (W. Germany) and preserved at Bayerische Staatssammlung, Munich. The types of both L. palliatus Agassiz and L. laevis Agassiz are detached scales preserved in Muséum National d'Histoire Naturelle, Paris and Museé de Soleue Southern, Switzerland. Woodward (1895: 107) had remarked "this species (L. maximus) as yet is only clearly distinguished from L. palliatus by the characters of mandibular dentition, and some of the fragments entered above under the last named species may belong to L. maximus". Saint-Seine (1949) considered L. palliatus a synonym of L. maximus as distinct and used the character of the mandibular dentition (number of rows of coronoid teeth) to distinguish the species as suggested by Woodward (1895). Schmidt (1946) however, referred to a specimen at Senckenberg Naturmuseum (P. 325) as L. palliatus even though it was described in detail by Weitzel (1930) and assigned to L. maximus. Weitzel's description included illustrations of palatal and mandibular dentition.

In an earlier communication (Jain, 1983), L. maximus distinct from L. laevis I had considered on the basis of specimen assigned by Weitzel (1930) to L. maximus and specimen described and figured by Priem (1908) and Seine-Saint (1949) for L. laevis. L. palliatus was not discussed because of the lack of a suitable figured specimen assigned to it. Upon intensive search it has been found that BM(NH) P. 338 (labelled as L. gigas) on display and purchased in 1881 is indeed an excellent specimen. It is a plaster cast of the original (natural mould) preserved at Bayerische Staatssammlung, Munich (Woodward, 1895: 105). The original has probably been destroyed in World War II as informed during a visit in 1962. This specimen has been assigned to L. palliatus by Woodward. Some observations made on BM (NH) P. 338 (L. palliatus) and SNM P. 2386 (L. maximus) reveal close resemblance of scale counts: number of flank scales in vertical row-P. 338 (22), P. 2386 (25); vertical row of scales near anal region-P. 338 (25), P. 2386 (29) and transverse row of scales along lateral line-P. 338 (39), P. 2386 (40). Number of fin rays in the caudal fin are identical (24). BM(NH) P. 338 has 52 visible teeth in the palate

which are strongly tritoral; the premaxilla is not preserved. The mandibular dentition is well preserved; there are 6 teeth on the dentary and coronoid teeth are arranged in 7 concentric rows.

During nine decades since the publication of Woodward's (1895) catalogue, our knowledge of holostean morphology has made a great advance. However, it seems that the distinction based on mandibular dentition proposed by Woodward (p. 83) to distinguish the three species, *L. laevis*, *L. palliatus* and *L. maximus* is so far most reliable. This is as follows: "Scales in part marked with radiating furrows:

(1) Majority of inner teeth oval, with apical tubercle, those of splenial in more than *three* irregular concentric series

L. laevis

(2) Maximum width of operculum two-thirds as great as its depth, and equalling about one-third the length of the head; majority of inner teeth round, without apical tubercle, arranged on splenial in six or seven irregular concentric series

L. palliatus

(3) Majority of inner teeth round, without apical tubercle, arranged on splenial in four or five irregular concentric series

L. maximus"

In view of above, I consider all the three species of Lepidotes, namely L. laevis, L. palliatus and L. maximus valid. Reference to specimens assigned to L. maximus and L. laevis has been made. BM(NH) P. 338, as originally assigned by Woodward (1895: 105) to L. palliatus, is confirmed. The fish exhibits diagnostic mandibular dentition.

Among the Lepidotes species-groups distinguished on evolutionary characters (Jain, 1983), L. maximus obviously belongs to that having a strongly tritoral dentition with deep jaw symphysis, thick coronoid with large tooth-bearing areas, and co-ossified vomers with a long tooth-bearing area. The nature and configuration of dentition is suited for a shell-crushing habit. Even though L. maximus is conspicuous by its enormous size among Lepidotes species or even among holosteans in general, precise knowledge about its features has been very limited. Scattered among the collections in various museums in Europe are isolated teeth, associated dentitions and squamations attributed to L. maximus. It may be useful to ascertain whether the new information made available here contradicts or supports or the Lepidotes species-group suggested earlier.

The characters which show changes in time (Jain, 1983) are: (1) loss of ganoine from the scales, (2) increase in the number of extrascapulars, (3) inc-

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rease in the number of cheekplates and (4) decrease in the size of orbit. The development of radiating, ganoine free furrows and complete absence of ganoine in some scales has been noticed in L. maximus. Although the region of the extrascapulars is somewhat deficient in both articulated specimens of L. maximus, there are at least 2 pairs of extrascapulars. Jain and Robinson (1963) made two groups of Lepidotes as far as the number of postorbital cheekplates are concerned: cheekplates varying within 6-2, and those with 7 or more. Among the latter group, to which obviously L. maximus belongs, are variants having cheekplates in a single linear row, double row or even an irregular masaic. One specimen of L. maximus (P. 2386) has 8 cheekplates in a single linear series on both right and left sides but the second (P. 325) has 10 in the first and 1 in the second row. Hence the number is somewhat variable within the species A similar situation has been noted in L. mantelli (Jain, 1983), where out of 9 specimens, 3 have 7, 2 have 8, 3 have 9 and 1 has 10 cheekplates. The orbit in both P. 325 and P. 2386 is small. The new information on L. maximus thus confirms the species-group division of Lepidotes.

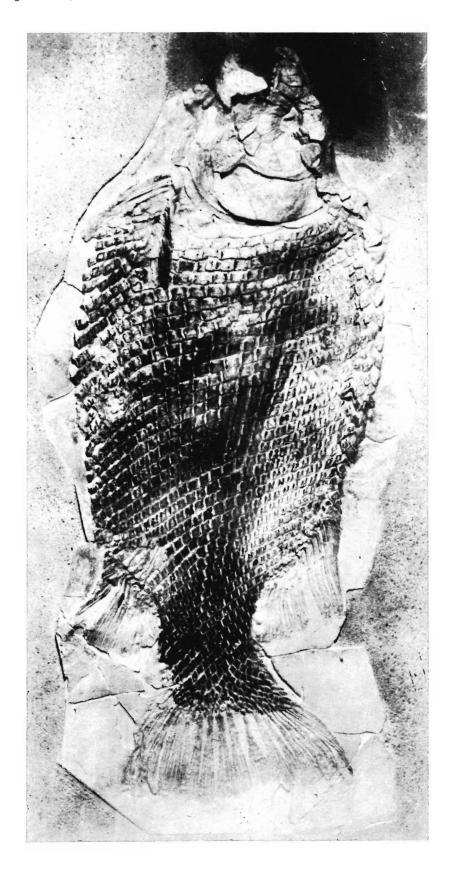
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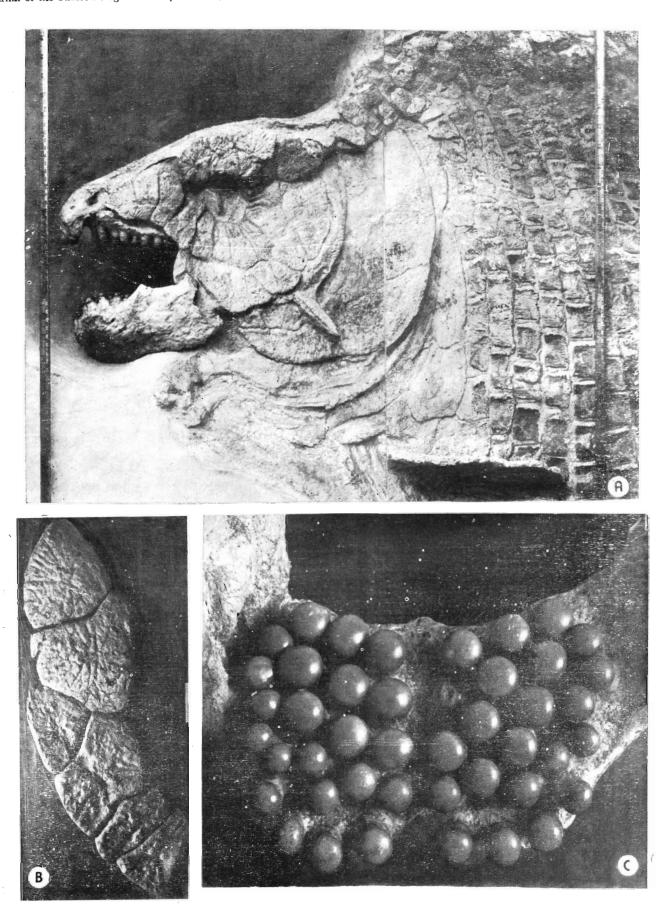
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EXPLANATION OF PLATES

PLATE I

Lepidotes maximus, whole fish (P. 2385) at Senckenberg Naturmuseum, Frankfurt, x appx. 1/10 (Courtesy Dr. G. Plowdowski).

PLATE II

Lepidoles maximus (P. 2386) at Senckenberg Naturmuseum, furt.

A. Frankskull x and 1/4.5; to flank region, avoid distortion two photographs were taken and pasted together vertically (marked ++) with an error of $\pm 1\%$.

B. right side postorbital cheekplates, x 1/2.

C. occlusal view of mandibular dentition, x 2/3.