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## A New Species of *Lepidotes* (Actinopterygii: Semiontiformes) from the Cenomanian (Upper Cretaceous) of Morocco

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### ABSTRACT

A species of semionotiform fish, *Lepidotes pankowskii* sp. nov. is described from the Cenomanian Kem Kem Beds of south-eastern Morocco, based on two three-dimensionally well-preserved partial heads. The new species is distinguished by the presence of suborbitals lying anterior to the orbit. It is most closely similar to other late Mesozoic tritoral species of *Lepidotes*.

KEY WORDS: new species; anatomy; actinopterygians; neopterygian

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### INTRODUCTION

In this paper we describe a new species of *Lepidotes* based on two specimens of heads from the Cenomanian Kem Kem beds of Morocco. These deposits were presumably laid down in fluvial conditions and are dated as Cenomanian (Serenio et al. 1996). Specimens are fragmentary and usually very robust. Several taxa have been described from the same beds: *Palaeonotopterus greenwoodi* Forey, 1997, *Calamopleurus africanus* Forey and Grande, 1998, *Oniichthys falipoui* Cavin and Brito, 2001, cf. *Mawsonia lavocati* Tabaste, 1963 (Cavin and Forey 2004), *Cladocyclus pankowskii* Forey and Cavin 2007, *Concavo-*

*tectum moroccensis* Cavin and Forey, 2008, and *Erfoudichthys rosae* Pittet et al., 2009.

### SYSTEMATIC DESCRIPTION

Subclass NEOPTERYGII Regan, 1923  
Order SEMIONOTIFORMES Arambourg and Bertin, 1958 sensu Olsen and McCune, 1991  
Family SEMIONOTIDAE Woodward, 1890, sensu Wenz, 1999  
Genus *Lepidotes* Agassiz, 1832  
*Lepidotes pankowskii* sp. nov.<sup>1</sup>

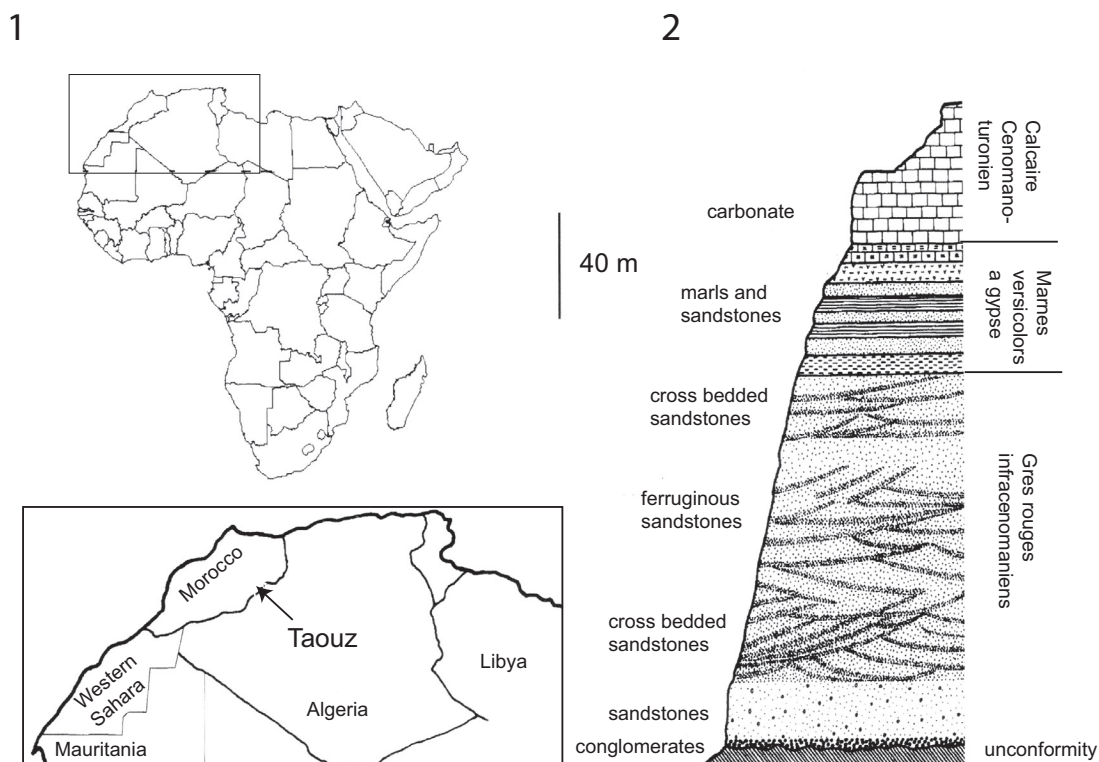
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1. The name *Lepidotes pankowskii* has appeared in Cavin (2010). This is a nomen nudum citation and does not alter the validity of name published in the current paper.

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**FIGURE 1.** 1. Type locality of †*Lepidotes pankowskii* sp. nov. The Holotype was not found in situ and the locality may only be identified as the Taouz area. 2. Section through Kem Kem beds. The holotype and additional skull roof described here undoubtedly come from the ferruginous sandstone horizon. After Forey and Grande (1998).

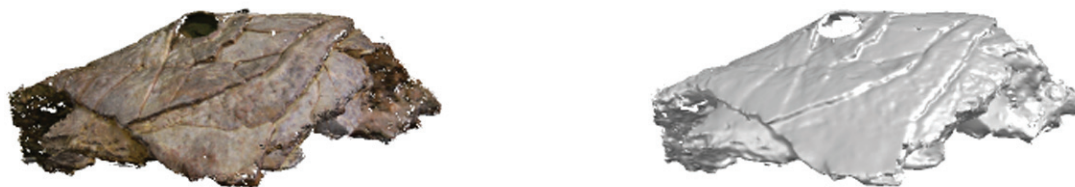
**Diagnosis.** Large *Lepidotes* reaching an estimated length of 1.6 m (based on body proportions of *L. mantelli*) in which the parietal is about half the length of the frontal; left parietal larger than the right; frontal-parietal suture interdigitate; three extrascapulars on either side of midline; orbit diameter small (12% of frontal-parietal midline length); complex suture between the nasal process of the premaxilla and the frontal; six circumorbitals with an additional small diamond-shaped circumorbital; four anterior infraorbitals; eight suborbitals with four lying in front of the orbit\*; the most anterior suborbitals articulating with the anterior infraorbitals\*; skull roof bones devoid of ganoine ornament. Lower jaw joint lying at a vertical level beneath the anterior edge of the orbit. [Asterisk denotes possible species autapomorphy.]

**Holotype.** BMNH P.66856, partial head showing skull roof, cheek bones, preopercle, interopercle, part of the opercle and posttemporal, and partial lower jaw of left side, extrascapular series of right side, vomer and crushed braincase elements. Kem Kem Beds, southeastern Morocco (see below, Locality)

**Paratype.** BMNH P.64126, skull roof and partial cheek of left side, vomer.

**Locality.** Tafilalt Region, Kem Kem Basin, south of Taouz (Figure 1). As is usual with specimens from this region the precise locality and horizon is unknown. Many specimens were found lying loose on the surface and detailed stratigraphic work has not been done. Specimens from the Kem Kem Beds of Taouz area, southeastern Morocco are well known. The vertebrate-bearing horizons in this region occur at the base of an escarpment formed by Cenomanian-Turonian carbonates. These beds have been informally divided into an upper marly unit and lower sandstone unit, recently referred to the Aoufous and Ifezouans Formations, respectively (Cavin et al. 2010). The specimen described here clearly comes from the lower sandstone unit and almost certainly from within the ferruginous sandstones (Figure 1). These beds have been dated to the Cenomanian, based on the contained shark fauna and is thought to represent a deltaic deposit (Serenio et al. 1996).

**Etymology.** Species named after Mr. Mark Pankowski of Rockville, Maryland, who kindly donated the holotype specimen to The Natural His-



**FIGURE 2.** A virtual model of *Lepidotus pankowskii* sp.nov. BMNH P.66856 [Holotype]. This model was made using a Konica-Minolta Vivid 910™ laser scanner equipped with a custom-built rotating turntable. In order to preserve as much morphological detail as possible, no attempt has been made to fill small holes in the scan or optimise the model meshes. 1. Virtual model with texture-mapped digital image of the actual specimen. This representation provides the best portrayal of the specimen including smudges, stains and other irregularities too fine to be represented as part of the scanned surface texture. 2. False-color mesh filled model showing maximum surface detail. Both files are written in the \*.icf format, which can be read by the PC version of Microsoft's Internet Explorer. The scan is also available in DXF, STL and WRL formats online which can also be used to view the scan using third-party software.

tory Museum, London. We are grateful for his patronage of palaeontology.

**Description.** Material described here is preserved in perfect three dimensions. In order to give the reader some idea of the robustness and faithfulness to life conditions, we give a rotatable laser image as Figure 2, produced by one of us (NM).

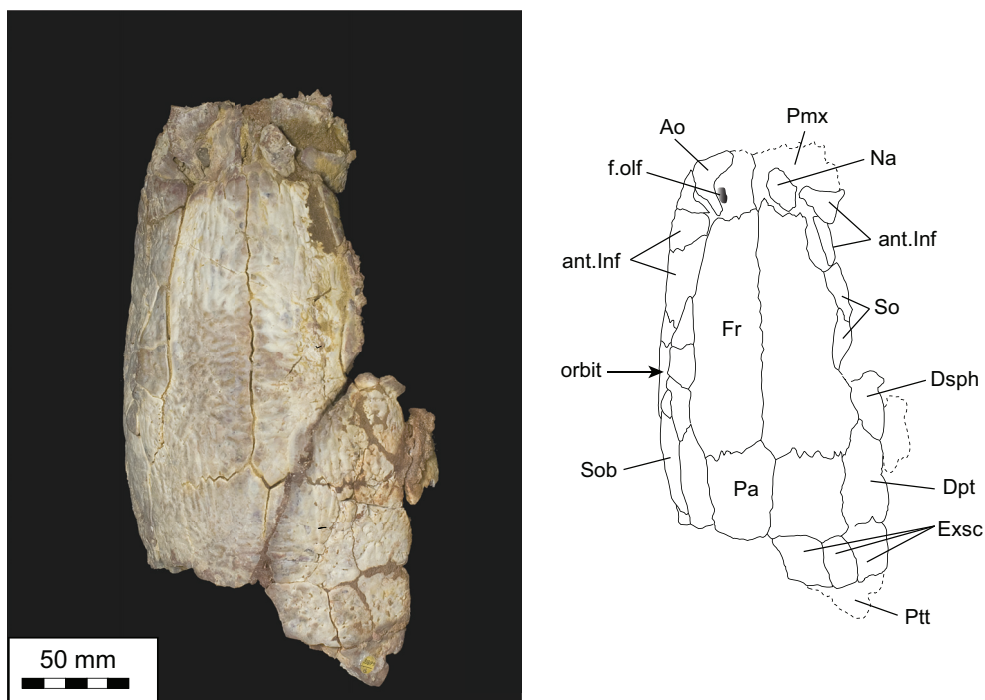
The skull roofing bones conform in shape and pattern most closely to those in *Lepidotus mantelli* and *L. maximus*. Some of the measurements are shown in Table 1. As pointed out by Jain (1983, p. 34) some of the measurements of skull roofing bones are difficult because of extreme asymmetry between ipsilateral partners as well as the irregularity of suture lines. The midline suture length (frontals and parietals combined in P.64126 (the larger of the two specimens) is 235 mm. Assuming the proportions of the entire fish to be comparable with *L. mantelli* then this skull comes from a fish of about 1.6 m total length. The holotype would have been slightly smaller.

The frontals meet one another through an almost straight mutual suture (Figure 3) as in *L. mantelli* but unlike *L. semiserratus* where it is decidedly sinuous. The suture between frontal and parietal is interdigitating and that with the dermopterotic is sinuous. The frontal is about twice as long as the larger of the parietals and the maximum width of the frontal is at the level of the dermosphenotic. Anteriorly the frontal is sutured to the premaxilla through a complex interdigitating suture such that the two bones are firmly anchored together. A band of tiny pores runs parallel and close to the lateral margin of the frontal marking the path of the supraorbital sensory canal.

The parietals are asymmetrical (a common feature in *Lepidotus* species). In the two specimens described here the left parietal is approximately 110 percent larger than the right in area. As Jain (1983) noted in species of *Lepidotus*, it is usual that in the majority of individuals of any one species either the right or left element is larger, but that there may be in a few individuals showing

**TABLE 1.** Some measurements of holotype and paratype of *Lepidotus pankowskii* sp. nov. MS, midline suture length; MFS, mutual frontal suture length; FW, maximum frontal width; FL, maximum frontal length; LPL, maximum length left parietal; RPL; maximum length right parietal; OD, maximum diameter of orbit; FW/FL, ration between the maximum frontal width and the maximum frontal length; PL/MFS, ratio between the maximum parietal length and the mutual frontal suture length; OD/MS, ratio between the maximum diameter of orbit and the midline suture length. Measurements are expressed in mm and ratios as percentages.

	MS	MFS	FW	FL	LPL	RPL	OD	FW/FL	PL/MFS	OD/MS
BMNH P.66856	204	147	52	158	66	59	26	33%	45%	12%
BMNH P.64126	235	160	60	178	85	72	27	34%	53%	11,5%



**FIGURE 3.** *Lepidotes pankowskii* sp.nov. BMNH P.66856 [Holotype] skull in dorsal view with interpretive drawing. Abbreviations: ant.Inf, anterior infraorbital; Ao, antorbital; Dpt, dermopterotic; Dsph, dermosphenotic; Exsc, extrascapular; f.olf, foramen for olfactory nerve; Fr, frontal; Na, nasal; Pa, parietal; Pmx, premaxilla; Ptt, posttemporal; So, supraorbital; Sob, suborbital.

opposite size relationships. Of course, with only two individuals we cannot be certain if this species favours larger left parietals.

The dermopterotic reaches forward to an end level with the maximum forward extent of the parietal. Because the left parietal is larger than the right, there is a compensation in the dermopterotics sizes such that the right is slightly wider than the left. Many tiny pores run in a line close to the lateral edge of the dermopterotic marking the path of the otic sensory canal.

All of the roofing bones show an ornament pattern of low vermiculating ridges. Ganoine appears to be absent from all skull bones. The absence of ganoine is unlike other species of *Lepidotes*. Most Jurassic species of the genus have an extensive covering of ganoine on the skull bones. Cretaceous species tend to have ganoine covering restricted to isolated tubercles on the roofing and cheek bones. In the species described here even that restricted ornament appears to be absent. We should add that weathering may have removed all traces; therefore we are cautious in claiming that this species is totally devoid of ganoine ornament.

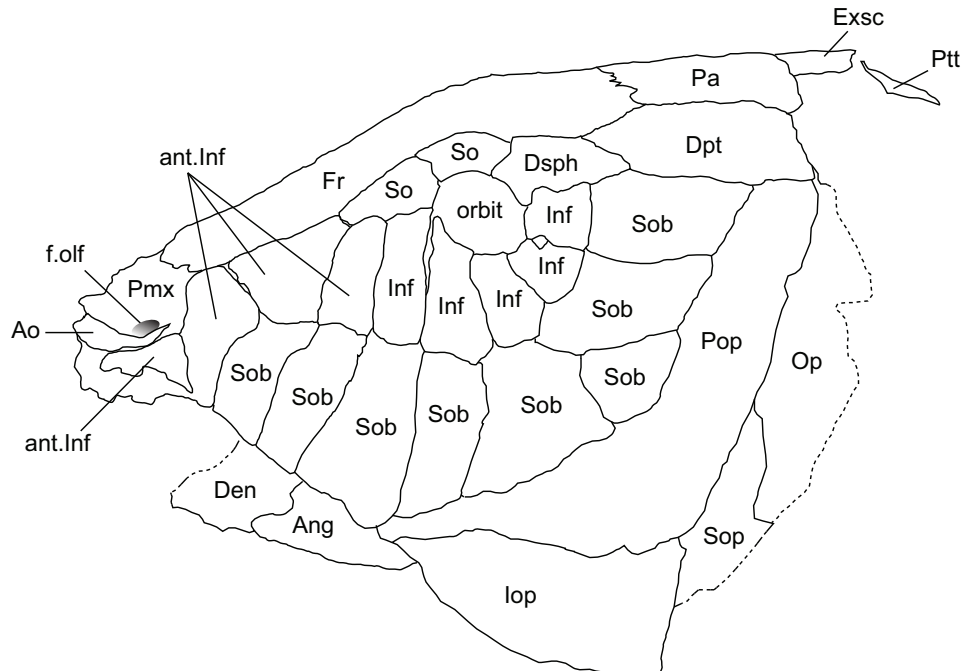
There are three extrascapulars on either side of the midline (only those of the right side are preserved in the holotype). The medial and lateralmost are both larger than the middle of the series, and in BMNH P.64126 the medial is larger than the lateralmost (in the holotype the medial is broken so the relative size is unknown). The medial extrascapular is sutured to the parietal, the lateralmost with the dermopterotic while the middle element sutures with both the parietal and the dermopterotic.

In both specimens the dorsal tip of the posttemporal can be seen to project beneath the middle member of the extrascapular series and in BMNH P.64126 can be seen to reach the medial extrascapular.

In BMNH P.64126 there are fragments of a median scale plus the first of the lateral scales.

At the anterior end of the skull parts of the premaxillae can be seen in both specimens, but they are much better preserved in the holotype. Here they are extremely large and stout (Figure 4). The anterior part of the premaxilla is broad and much thickened. Although the anterior edge is broken, the root canals for about 10 teeth in each premax-





**FIGURE 4.** *Lepidotes pankowskii* sp.nov. BMNH P.66856 [Holotype] skull in left lateral view with interpretive drawing. Abbreviations: Ang, angular; ant.Inf, anterior infraorbital; Ao, antorbital; Den, dentary; Dpt, dermopterotic; Dsph, dermosphenotic; Exsc, extrascapular; f.olf, foramen for olfactory nerve; Fr, frontal; Inf, infraorbital; lop, interopercle; Pop, preopercle; Op, opercle; Pa, parietal; Pmx, premaxilla; Ptt, posttemporal; So, supraorbital; Sob, suborbital; Sop, subopercle.

illa can be seen. The nasal process is broad and long, and the dorsal surface of the posterior end of the process is tightly united by an interdigitating suture to the underside of the frontal such that this joint is immovable. An interdigitating suture is characteristic of *Lepidotés* (although this feature is also seen in other holosteans). The nasal process is perforated by the large olfactory foramen. The premaxillae of either side remain separate.

Remains of the right nasal can be seen in the holotype where it lies in situ. It is small and irregular in shape although the true shape is unknown because the anterolateral edge is broken. A line of pores crosses the nasal indicating the path of the supraorbital canal.

The circumorbital and cheek bones are best preserved on the left side of the holotype (Figure 4). There is close agreement with the pattern of the remaining bones seen in BMNH P.64126. The orbit is very small compared with the length of the head, the maximum diameter being equal to about 12 percent mid-suture length of the skull roof. It appears to be considerably larger in most other species of *Lepidotés* examined here (e.g., in *L. semiserratus* this ratio is 30% while in *L. mantelli* it is 25%), except for *L. roxoi* (see Gallo and Brito 2004, figure 3) and probably *L. latifrons* (see reconstruction of the skull in Jain and Robinson 1963, figure 1).

There are eight bones bordering the orbit. The two above the orbit are usually designated as supraorbitals, a large element at the posterodorsal position can be called the dermosphenotic since it carries the infraorbital sensory canal onto the roof where it presumably joins with the otic sensory canal, and five further elements border the posterior and anterior margins of the orbit. The two circumorbitals lying behind the eye are each equidimensional; those beneath the eye are deeper than wide. The supraorbitals and the dermosphenotic are sutured with the skull roofing bones. The elements behind and beneath the eye are marked with a prominent ridge along the orbital margin. This ridge may suggest the path of the main lateral line canal but it should be pointed out that there is a series of tiny pores scattered close to the distal margin of these bones that may mark the surface exits of the infraorbital sensory canal.

Lying in front of the circumorbital series there are five more bones in the holotype, and these represent the anterior infraorbital and antorbital series (terminology of López-Arbarello and Sferco in press). In BMNH P.64126 only the most posterior of these is preserved. There are four anterior

infraorbitals, two of them lie against the lateral edge of the frontal such that there is no gap between the skull roof and the anterior infraorbital series (cf., new semionotiform from Germany López-Arbarello and Sferco in press). The next anterior infraorbital is a small triangular bone while the anteriormost is a curved element that lies above the nasal process of the premaxilla and is usually called the antorbital. Pores, presumably related to the infraorbital sensory canal, can be seen in all of the infraorbitals. They are most prominent in the anteriormost element as a line of closely spaced pores lying near the lateral edge of the antorbital.

Between the dermosphenotic and the circumorbital behind the eye there is a tiny diamond-shaped bone that must be considered as part of the circumorbital series. It is found in both specimens where it is similarly developed and must be considered as a characteristic for the species.

There is a series of eight suborbitals, seven of which are sutured to the bones of the infraorbital and antorbital series. At least three lie in front of the vertical level beneath the anterior margin of the orbit. The three most anterior suborbitals sutured with the four anterior infraorbitals, which is a unique feature among semionotiforms. The most posterior of the suborbitals is sutured to the dermosphenotic and the dermopterotic. A small suborbital lies at the posteroventral extent of the cheek series but it fails to reach the circumorbital series.

Parts of the opercular bones are preserved on the left side of the holotype. The preopercle is prominent. It has an elongate vertical limb meeting a horizontal limb through an angle of about 120°. The horizontal limb reaches forward to the level of the jaw articulation. Scattered pores mark the path of the preopercular sensory canal.

The interopercle is deep and appears tightly sutured to the whole horizontal limb of the preopercle. Behind this level parts of the subopercle and opercle can be seen, and all appear closely sutured to one another. The ascending process of the subopercle is broad, as is the case in *Lepidotés maximus* or *L. laevis* (contrary to *L. mantelli* or new semionotiform from Germany, López-Arbarello and Sferco in press).

A small part of the left lower jaw is preserved in the holotype but little useful information can be gleaned except that the jaw joint is located at a vertical level beneath the anterior margin of the orbit. The angular is deep and shows a complex sinusoidal suture with the dentary (the anterior part of which is missing, so it is not possible to see the

depth of the symphysis – a feature of some importance in distinguishing some *Lepidotes* species from others). Many small pores mark the path of the mandibular sensory canal running close to the ventral edge of the jaw.

### COMPARISONS AND DISCUSSION

The species described here is referred to the genus *Lepidotes* based on the following combination of characters that can be seen in the specimens: asymmetrical parietals; more than two anterior infraorbitals; a series of more than two suborbitals extending ventral to the orbit; close overlap between the opercle, interopercle, subopercle and propercle. Although all these features are present in the type species *Lepidotes elvensis*, none of these characters alone is unique to *Lepidotes* species, and indeed the genus is in urgent need of revision.

There are well over 150 nominal species described from deposits ranging from the Rhaetic through Cenomanian. Almost any large Mesozoic fish showing thick rhomboid scales, thick skull bones and robust grasping and crushing teeth runs the risk of being identified as a species of *Lepidotes*. Many of these nominal species are based on very fragmentary material, poorly construed and must be considered as *nomina dubia*. Others are different parts of the same species, and some have been associated (see Woodward 1895). Yet others have been given specific names simply because of their geographic or stratigraphic locations. Clearly this situation only emphasises the need for a comprehensive review that must also include species referred to the genus *Semionotus* (another common species-rich taxon often confused with *Lepidotes*). An added dimension to this taxonomic uncertainty is the fact that the type species of the genus is *Lepidotes elvensis* (Blainville 1818) from the Lower Jurassic of Germany, France and England. This form differs considerably from many Upper Jurassic and Cretaceous species referred to the genus in the pattern of skull roof bones, numbers of extrascapulars, cheek bones, dentition and depth of mandibular symphysis (see Jain and Robinson 1963, Jain 1983). It is very likely therefore that many of the later species, including the taxon described here, will have to be referred to new genera. However, since this cannot be decided until much more revisionary work has been completed we keep this taxon in the genus, preferring this action to creating additional names that may not be justified.

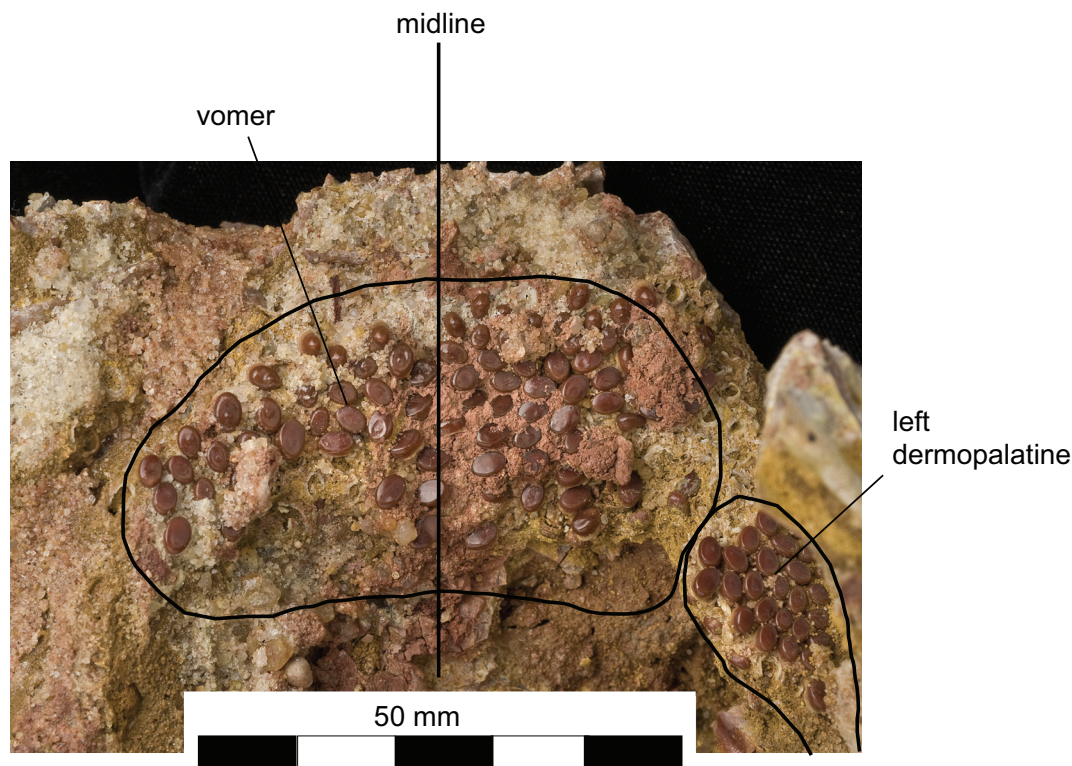
Despite the taxonomic uncertainty regarding the limits of the genus the taxon described here resembles strongly some of the Upper Jurassic and Lower Cretaceous species that show strongly tritoral dentitions such as the Upper Jurassic *L. laevis* Agassiz, 1837, *L. toombsi* Jain and Robinson, 1963, *L. maximus* Wagner, 1863, *L. decoratus* Wagner, 1863, or Lower Cretaceous *L. degenhardtii* Branco, 1885, *L. mantelli* Agassiz, 1833, and *L. souzai* Woodward, 1908.

A tritoral dentition was recognised by Jain (1983) with the following characteristics: 1, co-ossified vomers; 2, long tooth-bearing area on vomer; 3, coronoids thick with large tooth-bearing areas; 4, deep jaw symphysis; 5, inner teeth short (i.e., not pedicillate) with low convex or flat surfaces. *Lepidotes pankowskii* shows characteristics 1, 2 and 5 (Figure 5). The jaw symphysis is unknown in this species. The coronoids are also unknown but it is possible to speculate that, if found, they would bear a large tooth-bearing area because the opposing dentition upon the dermopalatine shows teeth arranged in at least six longitudinal rows.

Among these tritoral species the cheekbone series varies, Jain (1983) noted that within the *Lepidotes* species that he considered (usually the better known Jurassic and Cretaceous species) there is a group containing species in which there are 2 – 6 suborbitals (Jain 1983 named these bones cheekplates) arranged in a single row. This is in contrast to a group containing species with 8 – 10 suborbitals (= cheekplates of Jain 1983). *Lepidotes pankowskii* falls into this latter group with at least eight suborbitals.

Jain further recognised that among those species with the higher number of suborbitals some had the bones arranged in a single row (e.g., *L. mantelli*) while others had a mosaic of bones (e.g., *L. souzai*), rather similar to *Pliodetes nigeriensis* Wenz, 1999. *Lepidotes pankowskii* complies most closely with those of the first group with the exception that there is one suborbital wedged between the distal ends of two suborbitals. A similar pattern is shown by *Lepidotes maximus* (Jain 1985: plate 2, figures A, B). Figure 6 illustrates the cheek of *L. pankowskii* alongside examples of two other tritoral species recognised by Jain and Robinson (1963).

In all species studied so far, the suborbital series extends as far forward as the anterior level of the orbit. *Lepidotes pankowskii* differs in that this series extends well anterior to this level such that the anteriormost suborbital reaches close to the ethmoid region. Furthermore, the most anterior suborbitals in *L. pankowskii* are peculiarly sutured



**FIGURE 5.** *Lepidotes pankowskii* sp.nov. BMNH P.66856 [Holotype]. Ventral view of snout region to show vomerine and dermopalatine dentition.

to the anterior infraorbitals. This feature is unique among the species of *Lepidotes* and among semionotiforms in general.

Another feature noted by Jain (1983) and Woodward (1895) is the increase in the numbers of extrascapulars in later occurring species. Most of the non-tritoral species show a single pair of extrascapulars (e.g., *L. semiserratus* Agassiz, 1837, *L. deccanensis* Sykes 1851) while the tritoral species tend to show more (*L. maximus* – four pairs, *L. mantelli* – three or four pairs *L. souzai* – three pairs). *Lepidotes pankowskii* shows three pairs.

A final observation noted by both Woodward (1895) and Jain (1983) is the fact that in later species the orbit decreases in relative size. The orbit of *Lepidotes pankowskii* is particularly small and may result in the apparent increased preorbital length and, perhaps the high number of anterior infraorbitals characteristic of this species.

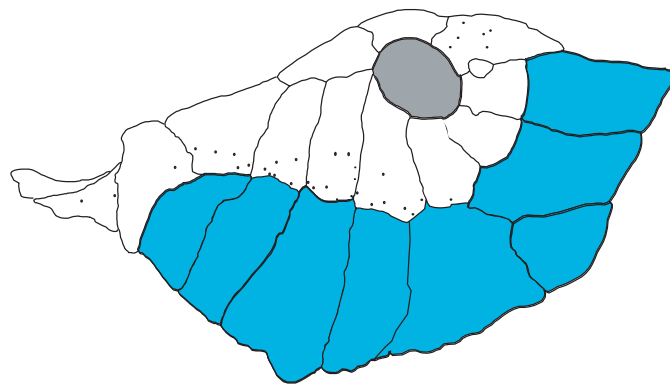
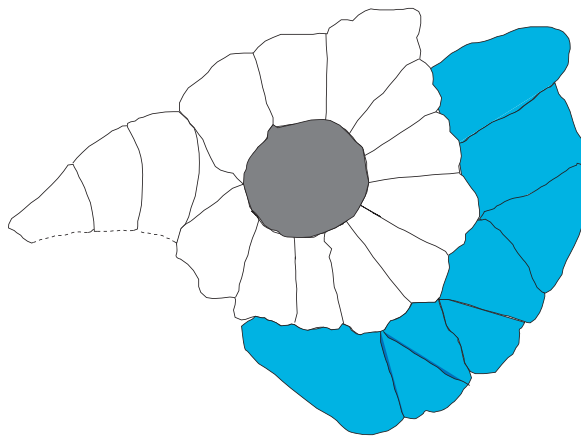
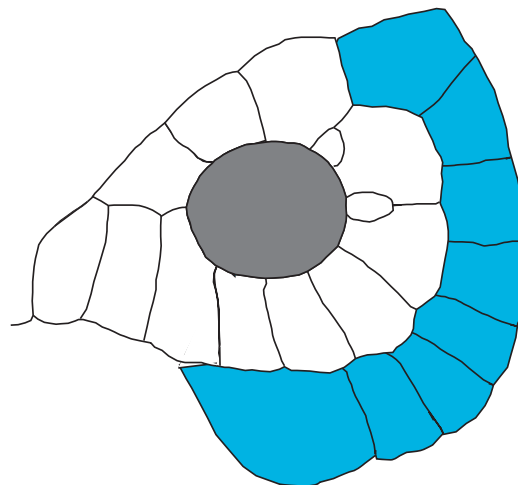
In sum *L. pankowskii* appears most closely similar to tritoral species such as *L. mantelli* and *L. maximus* in the dentition, disposition of the cheek plates and the number of extrascapulars. It remains distinct in the high number of anterior

infraorbitals, the anterior extent and relationships of the suborbitals, and the small size of the orbit.

The order Semionotiformes sensu Olsen and McCune (1991) is a monophyletic group including the lepisosteids, macrosemiids and semionotids. The monophyly of the Lepisosteidae and the Macrosemiidae are widely accepted, but the semionotids most probably represent a non-monophyletic assemblage including all semionotiforms that cannot be referred to one of the two monophyletic families (see López-Arbarello and Sferco (in press) for a brief historical overview). Nonetheless, the record of semionotid fishes in Africa is patchy and intriguing (López-Arbarello 2004, López-Arbarello et al. 2008).

The oldest record in this continent is *Semionotus capensis* in the Early Jurassic Clarens Formation of South Africa (Woodward 1888), followed by *Lepidotes congolensis* in the Middle Jurassic Stanleyville Beds of the Lualaba Series in the Democratic Republic of Congo (Hussakof 1917, Saint-Seine 1955) and *Lepidotes tendaguruensis* in the Late Jurassic Upper Saurian Beds of Tendaguru (Arratia and Schultze 1999). With the exception of *S. capensis*, which is represented by numerous, relatively complete and rather well-preserved spec-



*L. pankowskii**L. maximus**L. mantelli*

**FIGURE 6.** Comparison of cheekbone patterns in three tritoral species of *Lepidotes*. *Lepidotes maximus* based on Jain (1985), *L. mantelli* based on Woodward (1916). See text for discussion.

imens, the other two species are only known from disarticulated bones or only a few and incomplete specimens respectively. Scales or teeth of *Lepidotes* have been reported from the Late Triassic-Early Jurassic Adigrat Sandstones, the Middle to early Late Jurassic Tiouraren Formation in Niger, and the Late Jurassic Mughher Mudstone Formation

in Ethiopia (Moody and Sutcliffe 1991, Goodwin et al. 1999, Murray 2000, Rauhut and López-Arbarello 2009). Similarly, several isolated scales or teeth of *Lepidotes* have been mentioned throughout the Cretaceous (e.g., in the Albian Cocobeach Series of Gabon, the Albian Loia Beds and Albian to Early Cenomanian Bokungo Beds in

the Democratic Republic of Congo, and the Hama Koussou Basin of Cameroon; more detailed information in Murray 2000), but articulated remains are very rare. Apart from *Lepidotes pankowskii* n. sp. described herein, complete and well-preserved specimens previously identified in *Lepidotes* and currently recognized as a different taxon, *Pliodetes nigeriensis*, are known from the Aptian of Gadoufaoua in Niger (Wenz 1999). Additional complete and well-preserved material identified as *Lepidotes manni* of probably Early Cretaceous age is reported from the Babouri-Figuil Basin in Cameroon, but this species is poorly understood and currently under study (Olga Otero, personal commun. 2010).

Therefore, the only well-preserved material of semionotids is sparsely recorded from the Early Jurassic to the Cenomanian and represents quite different taxa. Even the species of *Lepidotes*, *L. tendaguruensis* and *L. pankowskii* are probably not closely related. *Lepidotes tendaguruensis* is strikingly similar to *L. minor* (ALA personal observations) from the Purbeck of England, which resembles *Semionotus* in several features (McCune 1986). As previously discussed, *L. pankowskii* is most probably closely related to the large tritoral forms known from the Late Jurassic and Early Cretaceous of central Europe.

*Lepidotes pankowskii* furthermore represents the youngest confident record of a semionotid globally. Other Cenomanian or younger fossils identified in *Lepidotes* or simply referred to as semionotids consist of isolated bones or, more frequently scales or teeth. Although at least some of these fossils might actually represent semionotids, many of them might turn out to be lepisosteids after thorough revision.

#### ACKNOWLEDGMENTS

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