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Fossil evidence of the Hammerjaw fish, *Omosudis* sp. (Teleostei, Aulopiformes) from the Middle Miocene Yokoo Formation in Nagano Prefecture, central Japan

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Abstract. A fossil palatine of an alepisauroid fish collected from the Middle Miocene Yokoo Formation in Nagano Prefecture, central Japan is described as *Omosudis* sp. Although the palatine is preserved as a fragment, the palatine teeth arranged in a single row are well-preserved. In fact, the palatine tooth characteristics are adequate as diagnostic at generic level identification. The fossil appears to be assignable to the genus *Omosudis* belonging to the family Alepisauridae by having the following characteristics: enormously large, posteriorly inclined teeth with each sharply pointed apex, apico-basal striations, a nearly straight to arcuate anterior cutting edge, a wide pulp-cavity surrounded by a thin dentine layer and a fang-like outline due to a basally elongated postapical barb. The Yokoo specimen represents the first reliable fossil record of the genus from the Middle Miocene in Japan and appears to mark the earliest occurrence of this recent genus in the Northwest Pacific region.

Keywords: Alepisauroid fish, fossil palatine, Middle Miocene, *Omosudis*, palatine tooth morphology.

Introduction

Neogene alepisauroid fishes frequently emerged from the Northern Fossa Magna

region in Nagano Prefecture, central Japan (e.g. Uyeno, 1967; Suzuki, 2008). A fossil palatine of an alepisauroid was found as a fragment from an outcrop of the Middle Miocene Yokoo Formation exposed along the Kangawa River in the Motohara area of Sanada-machi, Ueda City, Nagano Prefecture, central Japan (Figure 1). An alepisauroid belonging to the family Alepisauridae, *Omosudis* sp., was collected from the upper part of the Yokoo Formation (Figure 1). Until now, alepisauroid fish fossils have been known from only a few specimens from the Middle Miocene in Japan; *Polymerichthys nagurai* Uyeno, which was described as a new alepisauroid and placed within its own family by Uyeno (1967), from the Middle Miocene Tubozawa Formation of the Hokusetsu Subgroup in Aichi Prefecture; Alepisauroidei? from the Middle Miocene Bessho Formation in Nagano Prefecture by Uyeno (1979); and *Alepisaurus* sp., which is obviously close to *Alepisaurus ferox* Lowe, from the Middle Miocene Iseyama Formation in Nagano Prefecture by Suzuki (2005; 2008). The origin of the order of Aulopiformes clade is estimated at 140Ma in the Early Cretaceous, with a possible range into the Late Jurassic (Davis and Fielitz, 2010). The estimated divergence dates for the family Alepisauridae and the genus *Omosudis* Günther are in the Early Cretaceous. Isolated tooth fossils suggested to belong to an unidentified alepisauroid taxon have been described from the Early Cretaceous Barremian deposits of the Oliete subbasin of Alcaine in northeastern Spain (e.g. Harry, 1953; Patterson, 1993; Kriwet, 2003). The earliest definite fossil representative of the recent alepisauroid fish, *Alepisaurus paronai* D'Erasmo was discovered in the Miocene of Rosignano, Tertiary Piedmont Basin of Italy (Patterson, 1993). Alepisauroid fishes (Alepisauroidei *sensu* Davis, 2010) are known bathy- to mesopelagic predatory fishes which have diagnostic palatine and dentary teeth. As is well-known, fossil alepisauriform tooth morphologies allow for specific indentification (Kriwet, 2003). If the fossil teeth are not isolated but arranged in the palatine or dentary, identification appears to be even more probable, because it is possible to confirm that the teeth are anteriorly inclined, posteriorly inclined or not inclined. In fact, the palatine tooth characteristics indicate a meaningful taxonomic identification at the generic level. Judging from the diagnostic characterisics of the well-preserved palatine teeth, the fragment of the palatine can be

classified as a member of the family Alepisauridae, and as compared with that of extant *Omosudis lowii* Günther, the fossil is considered to belong to *Omosudis*. This specimen described here is noteworthy because, to date, it is the first reliable fossil record of *Omosudis* from the Middle Miocene in Japan and appears to mark the earliest occurrence of this recent genus in the Northwest Pacific region. This paper aims to provide palatine tooth morphologies of the fossil material assigned to *Omosudis*, and also aims to propose a better identification of fossil alepisauroids at the generic level by analyzing the palatine tooth morphology.

Regional geology and the alepisauroid locality

The alepisauroid fossil specimen treated in this paper was collected by the present author in recent years from an outcrop of the Yokoo Formation which is well-exposed along the Kangawa River in the Motohara area of Sanada-machi, Ueda City, Nagano Prefecture, central Japan (Figure 1). Middle Miocene deep-water sediments, which yield abundant fish remains such as isolated bones, teeth and scales, are distributed around the fossil localities. The sedimentary rocks distributed in Ueda City range in age from Early to Middle Miocene and are divided into four formations: the Oomineyama, Tarouyama, Yokoo and Iseyama Formations in ascending order (Yamagishi, 1964). The Yokoo Formation, which is the objective of the present study, is situated in the eastern margin of the Utsukushigahara Belt of the Northern Fossa Magna Region and is an equivalent stratigraphic unit to the upper part of the Uchimura Formation. The Uchimura Formation is the standard referential stratigraphy of the Northern Fossa Magna region in Nagano Prefecture (Kosaka *et al*., 1992). *Omosudis* sp. was collected from the upper part of the Yokoo Formation. The formation primarily consists of alternating beds of muddy sandstone and mudstone (Suzuki, 2007; 2012). On the basis of radiolarians and other associated fossils such as *Mizuhobaris izumoensis*, the alepisauroids-bearing strata are considered to be of Middle Miocene in age (Blow, 1969; Noda *et al*., 1986; Kubota and Kosaka, 1990; Tanabe *et al*., 2016).

Material and method

The fossil teeth are not isolated but still are arranged in the palatine and show the directions of tooth inclination. Comparative materials are specimens of *Omosudis lowii* Günther, 1887 from collections of the Fish Division and Center for Molecular Biodiversity Research National Museum of Nature and Science, Tokyo, Japan. Two relevant specimens are: NSMT-P 40156, Suriname, of western Atlantic NW Pacific; NSMT-P 93514, East of Mariana Basin. Morphological comparisons are made with *Omosudis lowii* which were described and figured by Günther (1887), Ege (1958), Rofen (1966), Rosen (1973) and Nielsen and Jespersen (1986). The Yokoo specimen described here, a fragment of a palatine with two palatine teeth (P1 and P2), is registered with the prefix USKF and housed in Uedasouzoukan, Ueda City, Nagano Prefecture, Japan (USKF-101, Figures 2 and 3). In order to discuss the morphology, it is necessary to define a few descriptive terms (Figures 4 and 5). The terminology used in this study follows that adopted by Kriwet (2003). Morphological terms in the systematic descriptions used in this paper are shown in Figure 4. The classification is referred to in Ege (1958), Rofen (1966), Rosen (1973), Nelson (2006) and Davis (2010). Figure 5 compares the important palatine tooth characteristics of extant *Omosudis* and similar alepisauroid genera.

Systematic description

Order Aulopiformes Rosen, 1973

Suborder Alepisauroidei *sensu* Davis, 2010

Superfamily Alepisauroidea *sensu* Davis, 2010

Family Alepisauridae *sensu* Davis, 2010

Genus *Omosudis* Günther, 1887

Omosudis sp.

Figures 2 and 3

Horizon and locality.-The upper part of the Yokoo Formation well-exposed at the riverside of Kangawa-River in the Motohara area of Sanada-machi, Ueda City, Nagano Prefecture, central Japan. Middle Miocene (Yamagishi, 1964; Kubota and Kosaka, 1990; Suzuki, 2007; Tanabe *et al*., 2016).

Abbreviation.-P, palatine. P1, first palatine tooth. P2, second palatine tooth.

Measurements.-Palatine first tooth (P1): tooth height 24.0mm, width of the attachment area of the underlying bone 5.0mm, Palatine second tooth (P2): tooth height 21.0mm, width of the attachment area of the underlying bone 4.0mm

Description.-The Yokoo specimen is tentatively identified as an alepisauroid palatine because of having enormously large and sharply pointed teeth arranged in a single row. This specimen is the anteriormost portion of a palatine, although it is unclear whether it corresponds to the left or right palatine (Figure 2). The preserved part of the palatine is 30.0mm in length. Its greatest depth is at least 7.0mm. The posterior part of it is missing. Four grooves are developed on the palatine surface starting from the snout tip to the dorsal edge. Two palatine teeth arranged in a single row are preserved. Each palatine tooth has initially the same morphology such as being slender, posteriorly inclined and having an enormously large, fang-like outline due to a basally elongated postapical barb (white arrows indicate in Figure 2), and a sharply pointed apex. P1 is slightly larger in size than P2. The internal structure consisting of a wide pulp-cavity (black arrows indicate in Figure 2), which is surrounded by a thin dentine layer, is recognized in P1 and P2. Each tooth height is taller than the palatine depth and has a sculpture of striations which are developed from the attachment area of the underlying bone to the apex on the tooth surface. The shape of the anterior cutting edge ranges from nearly straight to arcuate. The anterior cutting edge joins the short posterior cutting edge at the tip of the apex. The postapical barb is formed by joining the short posterior cutting edge to the long posterior cutting edge.

Discussion

Although the Yokoo specimen is only partly preserved, the palatine teeth bear some diagnostic characteristics with a close resemblance to those of extant *Omosudis*. The grooves on the palatine surface are also observable in similar fossil specimens such as *Alepisaurus* sp. belonging to the family Alepisauridae, which was collected from the Middle Miocene Iseyama Formation (Suzuki, 2008, p.44, fig.2a-b). Similar grooves are also present in the current genus *Alepisaurus* Lowe. The genus *Omosudis* Günther is the most closely related taxon of the genus *Alepisaurus* Lowe (e.g. Gregory and Conard, 1936; Gosline *et al*., 1966; Smith and Ethel, 1973; Johnson, 1982; Baldwin and Johnson, 1996). *Omosudis* Günther is distinct from similar alepisauroid genera such as *Alepisaurus* Lowe, *Anotopterus* Zugmayer and extinct *Polymerichthys* Uyeno in the general appearance of the palatine tooth (Figure 5). In fossil *Omosudis* sp., as in *Omosudis lowii*, the appearance is fang-like, but it is saber-like in *Polymerichthys*, knife-like in *Alepisaurus* and dagger-like in *Anotopterus* (Carnevale, 2007; Nazarkin, 2016). In fossil *Omosudis* sp., as in *Omosudis lowii*, a postapical barb is present, but it is absent in *Anotopterus*, *Alepisaurus* and *Polymerichthys*. In fossil *Omosudis* sp., *Omosudis lowii* and *Alepisaurus*, palatine teeth are posteriorly inclined, but they are anteriorly inclined in *Anotopterus* and *Polymerichthys*. The palatine tooth characteristics of the fossil specimen described here are strongly similar to extant *Omosudis lowii* samples (original descriptions and figures are Günther, 1887, p.201, pl.52, fig.c-c': Ege, 1958, p.13, fig.2: Rofen, 1966, p.468, fig.165, A, D, p.469, fig.166: Rosen, 1973, p.437, fig.61: Nielsen and Jespersen, 1986, p.62, fig.1-AB, p.63, fig.2-AB). *Omosudis lowii* is characterized by six diagnostic characteristics: enormously large, fang-like outline due to a basally elongated postapical barb (limited to P1 and P2), wide pulp-cavity surrounded by a thin dentine layer, nearly straight to arcuate and smooth anterior cutting edge, rounded and smooth posterior cutting edge and apico-basal striations (e.g. Lowe, 1833; Maul, 1946; Marshall, 1955; Gibbs and Wilimovsky, 1966; Rofen, 1966; Rosen, 1973; Johnson, 1974; Goody, 1976; Kriwet, 2003). It is particularly worth mentioning that the posterior cutting edge is rounded but cannot be recognized in this fossil specimen. The Yokoo specimen appears to be assignable to the genus *Omosudis* belonging to the family Alepisauridae by having the

following characteristics: enormously large, posteriorly inclined teeth with each sharply pointed apex, apico-basal striations, a nearly straight to arcuate anterior cutting edge, a wide pulp-cavity surrounded by a thin dentine layer and a fang-like outline due to a basally elongated postapical barb. In any case, important characteristics correspond to original descriptions, figures and comparative materials of *Omosudis lowii*. The essential diagnostic characteristic for assignment of the fossil to *Omosudis* are P1 and P2 that are fang-like in shape due to a basally elongated postapical barb. Other fish that also have fang-like teeth such as the genera of *Muraenesox* McClelland (Muraenesocidae), *Leptostomias* Gilbert (Stomiidae), *Evermannella* Fowler (Evermannellidae) and *Trichiurus* Linnaeus (Trichiuridae) differ in that their palatine or dentary teeth include a short postapical barb that only develops near the tip of the apex (e.g. Rosen, 1973; Johnson, 1982; Long, 1991; Carpenter, 1999; Nakabo, 2002; Kriwet, 2003; Nelson, 2006) (Figure 6). The morphological resemblance between the fossil *Omosudis* and extant *Omosudis lowii* indicates their close relationship. Importantly, the palatine teeth described here show the reliable evidence of similarity. That is, the presence of a basally elongated postapical barb, thought to have functioned as a specialized feeding mechanism, is a diagnostic characteristic of *Omosudis*. Moreover, the presence of a postapical barb has often been assumed as one of several diagnostic characteristics of some extant alepisauroids. Nevertheless, it seems justified to assign the Yokoo specimen to *Omosudis*.

In some extant alepisauroids, especially *Alepisaurus*, *Anotopterus* and *Omosudis*, reclining replacement teeth exist within a single row (Marshall, 1955; Gibbs and Wilimovsky, 1966; Rofen, 1966; Rosen, 1973; Johnson, 1974; Kriwet, 2003). However, the replacement teeth cannot be recognized in the Yokoo specimen because this is the anteriormost portion of a palatine.

Concluding remarks

In conclusion, it is evident from the discussion above that the presence of articulated dental remains, even if they are fragmentary specimens, provide better information to

identify fossil alepisauroid remains than isolated teeth. It should be emphasized that the diagnostic characteristics of fossil teeth being arranged in a single row can be used for assigning fossil alepisauriform teleosts, even though the isolated fossil tooth morphology can allow for specific identification at the generic level. This paper provides verifiable palatine tooth morphologies of the fossil material assigned to *Omosudis*. The method in this paper allows utilization of incomplete specimens. It remains unclear whether the fossil *Omosudis* sp. is the same species as *Omosudis lowii*. Species level identification currently remains difficult because of exceedingly rare occurrences and insufficient preservations. However, this is the first reliable fossil record from the Middle Miocene in Japan and appears to mark the earliest occurrence of this recent genus in the Northwest Pacific region.

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【Figure captions】

Figure 1. Map showing the fossil locality of USKF-101 (marked by ★). Using the topographical map “Sanada” scale 1:25,000 published by the Geospatial Information Authority of Japan.

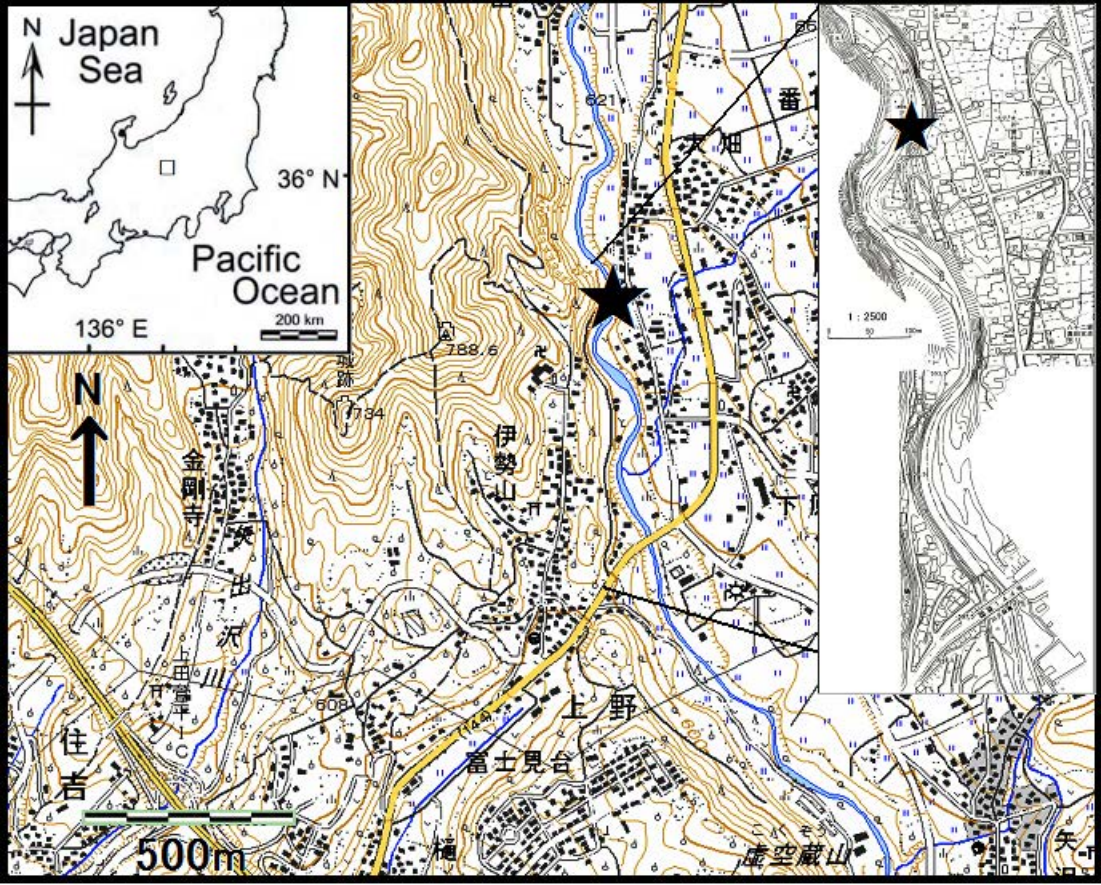
Figure 2. The fossil palatine of *Omosudis* sp., USKF-101. Scale bar indicates 10 mm. Black arrows indicate the wide pulp-cavities of the two teeth. White arrows indicate the basally elongated postapical barbs.

Figure 3. Drawing of the fossil palatine of *Omosudis* sp., USKF-101.

Figure 4. Schematic drawing of a fang type palatine tooth, showing descriptive terms used in this paper. Terms mostly from Kriwet (2003).

Figure 5. Brief correlation of diagnostic palatine tooth characteristics of *Omosudis* and the similar alepisauroid genera. — indicates that the characteristic does not exist.

Figure 6. Schematic drawings of fang type short postapical barb teeth. A. Palatine or dentary tooth of *Muraenesox cinereus* (Muraenesocidae) (redrawn from Carpenter, 1999). B. Palatine or dentary tooth of *Leptostomias robustus* (Stomiidae) (redrawn from Nakabo, 2002). C. Palatine or dentary tooth of *Evermannella balbo* (Evermannellidae) (redrawn from Johnson, 1982). D. Palatine or dentary tooth of *Trichiurus lepturus* (Trichiuridae) (redrawn from Long, 1991).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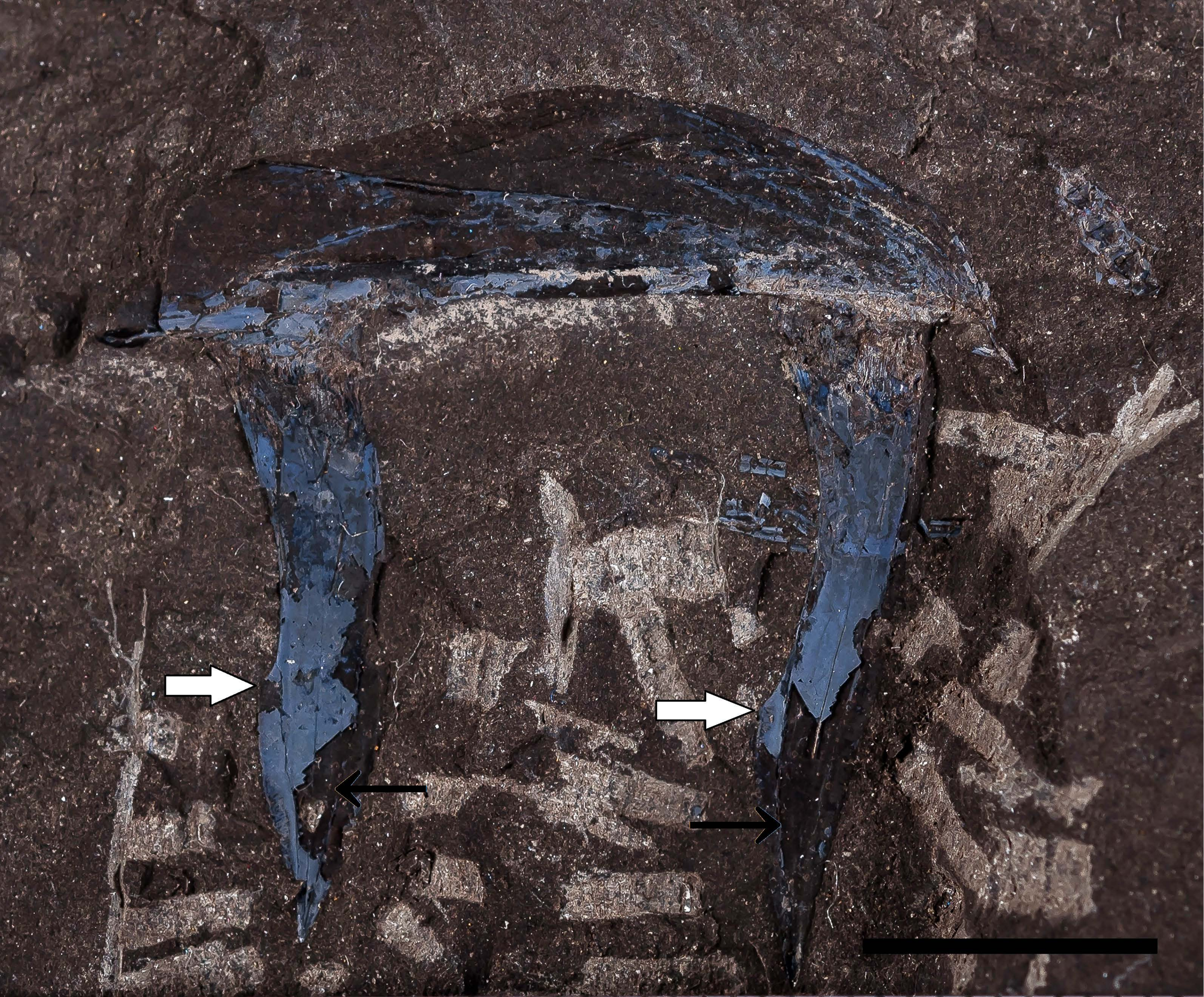
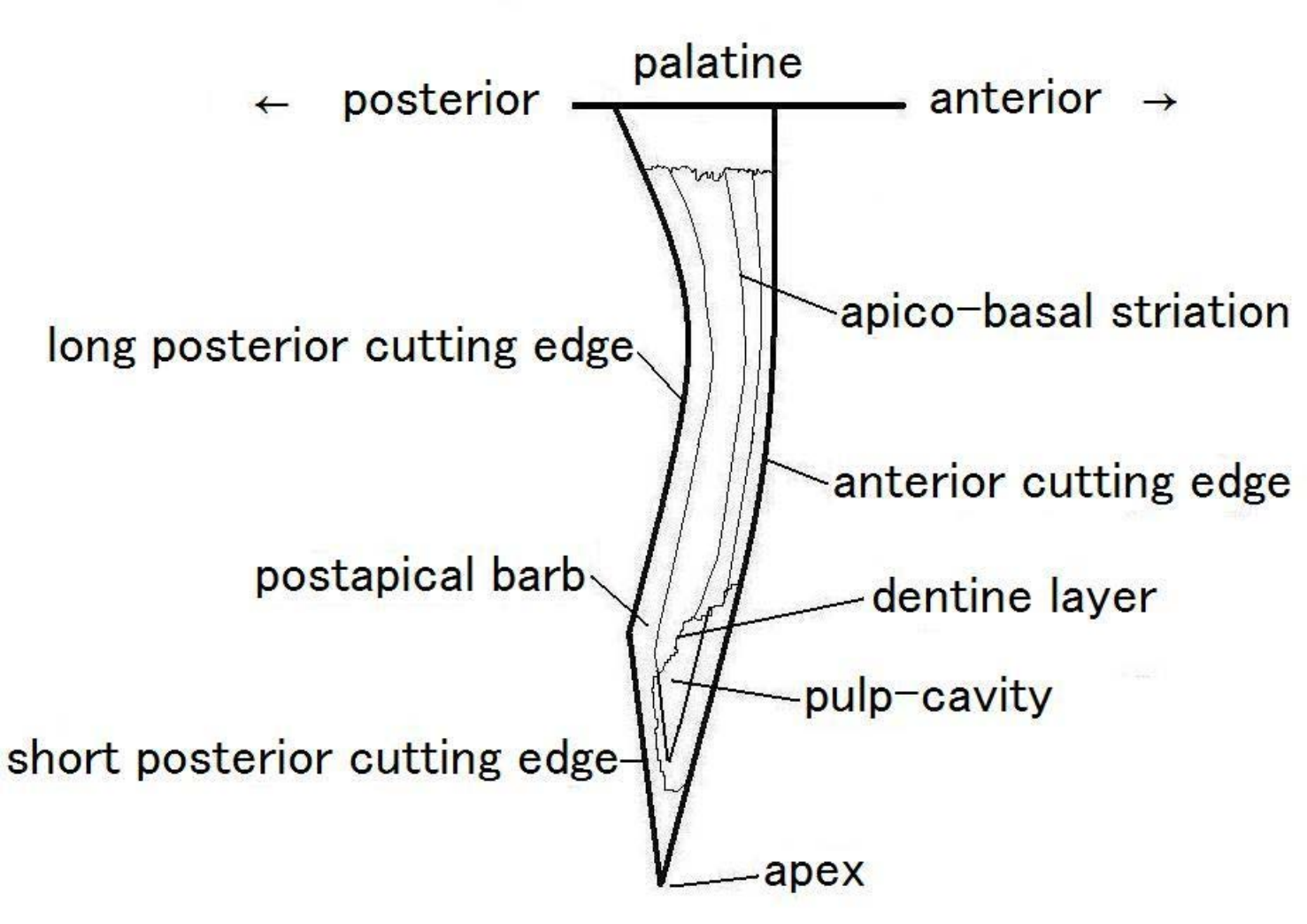
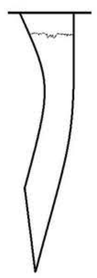
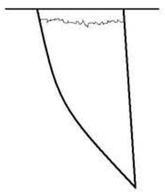
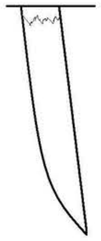
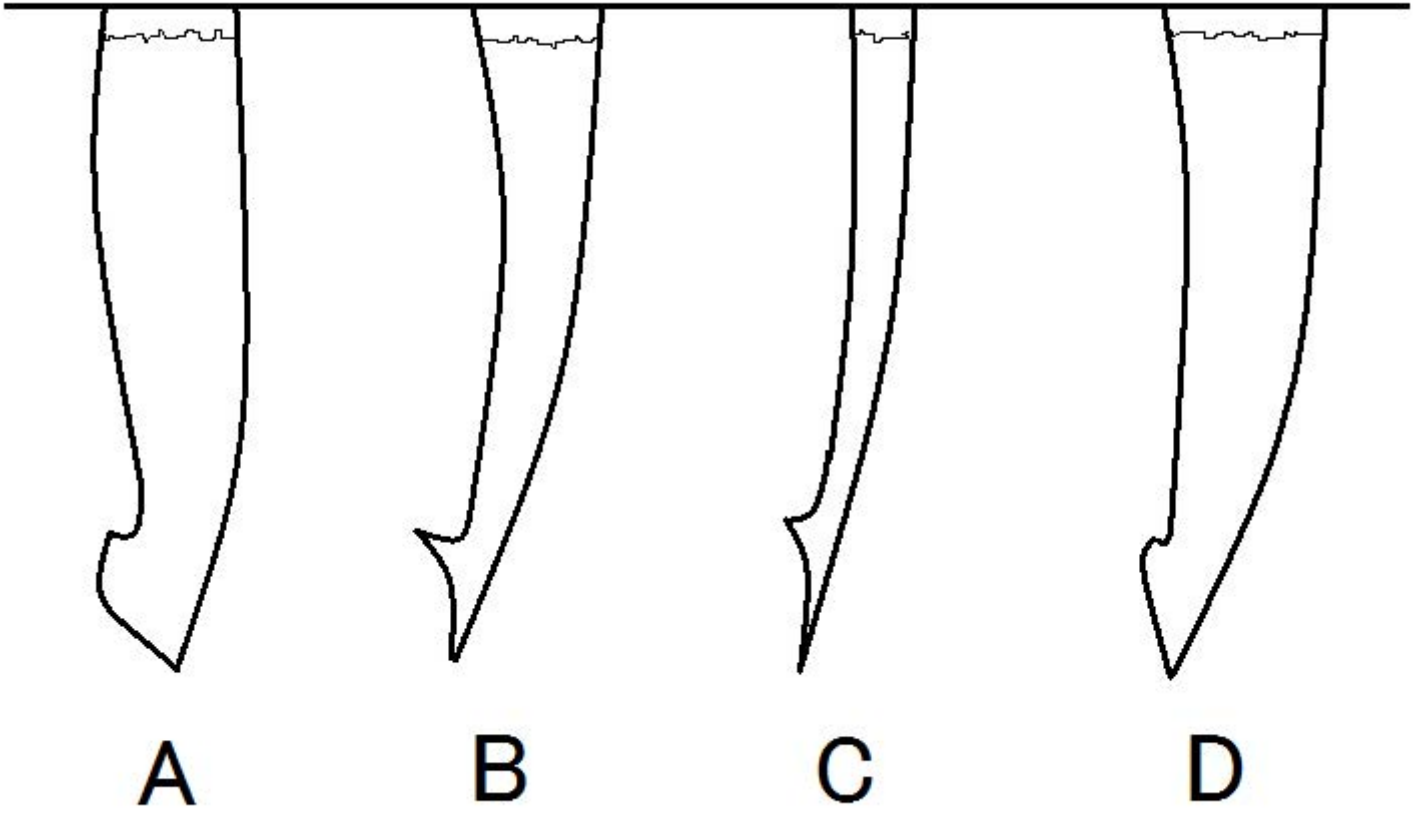



palatine
← posterior
anterior →
apico–basal striation
long posterior cutting edge
anterior cutting edge
postapical barb
dentine layer
pulp–cavity
short posterior cutting edge
apex

	Similar alepisauroid genera				
	This study	Extant			Extinct
Characteristics \ Genera	***Omosudis* Günther**	*Anotopterus* Zugmayer	*Omosudis* Günther	*Alepisaurs* Lowe	*Polymerichthys* Uyeno
Tooth-typies and schematic drawings	**fang** 	dagger 	fang 	knife 	saber 
Appearance	**slender**	massive	slender	slender	slender
Tooth height for palatine depth	**high**	high	high	high	high
Inclined	**posteriorly**	anteriorly	posteriorly	posteriorly	anteriorly
Apex	**pointed**	pointed	pointed	pointed	pointed
Postapical barb	**present (limited to P1 and P2)**	absent	present (limited to P1 and P2)	absent	absent
Anterior cutting edge	**nearly straight to arcuate**	arcuate	nearly straight to arcuate	nearly straight to arcuate	straight
Posterior cutting edge	—	arcuate	—	nearly straight to arcuate	nearly straight to arcuate
Long posterior cutting edge	**nearly straight to arcuate**	—	rounded	—	—
Short posterior cutting edge	**straight**	—	straight	—	—
Apico-basal striations	**present**	present	present	present	present
Replacement tooth	**unknown**	present	present	present	present
Wide pulp-cavity	**present**	present	present	present	unknown
Reference(s)		Rofen (1966)	Rosen (1973)	Gibbs and Wilimovsky (1966) Suzuki (2008)	Uyeno (1967) Carnevale (2007) Nazarkin (2016)


A
B
C
D