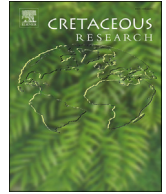




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# Revision of the Cretaceous shark *Protoxynotus* (Chondrichthyes, Squaliformes) and early evolution of somniosid sharks

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## ABSTRACT

Due to the peculiar combination of dental features characteristic for different squaliform families, the position of the Late Cretaceous genera *Protoxynotus* and *Paraphorosoides* within Squaliformes has long been controversial. In this study, we revise these genera based on previously known fossil teeth and new dental material. The phylogenetic placement of *Protoxynotus* and *Paraphorosoides* among other extant and extinct squaliforms is discussed based on morphological characters combined with DNA sequence data of extant species. Our results suggest that *Protoxynotus* and *Paraphorosoides* should be included in the Somniosidae and that *Paraphorosoides* is a junior synonym of *Protoxynotus*. New dental material from the Campanian of Germany and the Maastrichtian of Austria enabled the description of a new species *Protoxynotus mayrmelnhofi* sp. nov. In addition, the evolution and origin of the characteristic squaliform tooth morphology are discussed, indicating that the elongated lower jaw teeth with erected cusp and distinct dignathic heterodonty of *Protoxynotus* represents a novel functional adaptation in its cutting-clutching type dentition among early squaliform sharks. Furthermore, the depositional environment of the tooth bearing horizons allows for an interpretation of the preferred habitat of this extinct dogfish shark, which exclusively occupied shelf environments of the Boreal- and northern Tethyan realms during the Late Cretaceous.

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## 1. Introduction

The fossil record of dogfish sharks, the Squaliformes, dates back to the Barremian (Early Cretaceous) (Thies, 1981) with a diversification event in the Late Cretaceous (Adnet and Cappetta, 2001; Flammensbeck et al., 2018). Extant squaliforms comprise five to six extant families (Somniosidae/Oxynotidae, Etmopteridae, Dalatiidae, Centrophoridae, and Squalidae (Straube et al., 2015)) with a predominantly deep-dwelling lifestyle (Compagno, 1984). Deep-

marine sediments from the Cretaceous bear teeth of the oldest squaliforms and span the time of the first major diversification of this group, highlighting the important role of studying marine sediments from this crucial time, but are rarely sampled, causing an incomplete fossil record for this group (Kriwet and Klug, 2009). For deciphering the diversity and evolution of deep-sea sharks through time, extensive bulk-sampling is necessary to collect reliable data to improve our understanding of especially small taxa and their palaeogeographic distribution (Underwood, 2006; Guinot et al., 2012; Underwood et al., 2015).

In northwestern Europe, the diversity of Squaliformes increased towards the upper Campanian (Guinot, 2013), which may have been triggered by a significant sea-level rise (Jarvis et al.,

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2002; Haq, 2014), providing possibilities for range expansions and adaptations (Adnet and Cappetta, 2001). This study presents new fossil dental material from the Campanian and Maastrichtian of the northern Tethyan and Boreal realms from Austria and Germany, which possess a unique tooth morphology among early squaliform sharks. These fossils are characterised by a tooth morphology previously assigned to *Protoxynotus misburgensis* Herman, 1975 and *Paraphorosoides ursulae* (Thies and Müller, 1993), both from the Campanian of the Boreal realm of Germany (Fig. 1). *Paraphorosoides ursulae* was originally assigned to the genus *Palaeomicroides* Thies and Müller, 1993, but was subsequently replaced by the genus name *Paraphorosoides* by Kriwet et al. (2006) since the name *Palaeomicroides* was preoccupied. Although lower jaw teeth of both genera (*Protoxynotus* and *Paraphorosoides*) share strong similarities (e.g., strongly labio-lingual compressed, triangular erected cusp, lingual strong sinusosity of the enameloid, extended labial apron, and medio-lingual foramen) and although both were coeval during the Campanian, they were assigned to two different families. Upon description of *Protoxynotus*, Herman (1975) highlighted the similarities to teeth of the extant genus *Oxynotus* Rafinesque, 1810 of the family Oxynotidae. However, Thies and Müller (1993), discussed similarities with the extant genus *Euprotomicroides* Hulley and Penrith, 1966, which belongs to the Dalatiidae. Later, Kriwet et al. (2006) indicated strong similarities with teeth of *Oxynotus* and *Scymnodon* Barbosa Du Bocage and De Brito Capello, 1864, both genera of the Somniosidae/Oxynotidae clade. Based on molecular data, the phylogenetic interrelationships of Squaliformes estimate the families Squalidae, Dalatiidae, Etmopteridae and Oxynotidae to be monophyletic. However, the Oxynotidae nest within the Somniosidae, rendering the latter paraphyletic (e.g., Straube et al., 2015; Flammensbeck et al., 2018). Herein, we follow Straube et al. (2015) and consider Oxynotidae as part of the Somniosidae clade.

In order to determine the family-level affiliation of *Protoxynotus*, *Paraphorosoides* and the new material, we performed a phylogenetic analysis to estimate the phylogenetic placement of this unique tooth morphology within Squaliformes using a combination

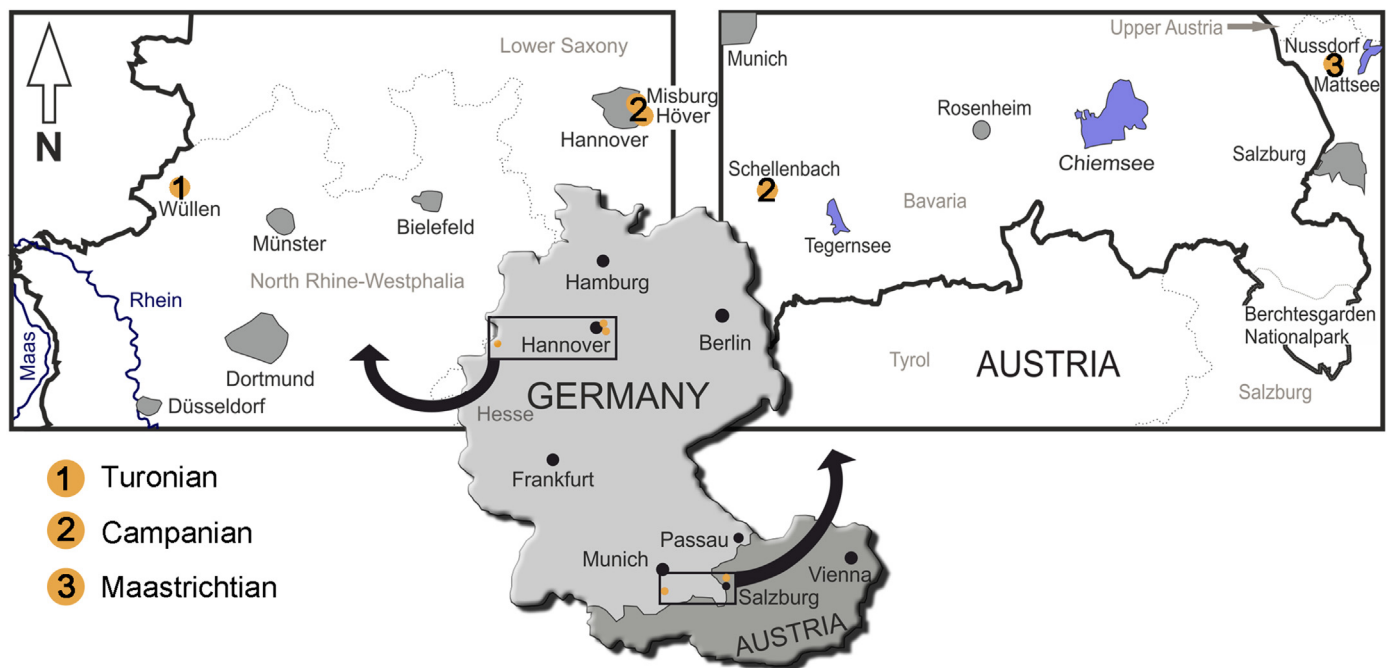
of morphological data from both extant and fossil taxa as well as DNA sequence information from extant species. Additionally, we provide photographs and discuss differences and similarities of all documented teeth of this morphology, which led us to revise the genera *Protoxynotus* and *Paraphorosoides*.

## 2. Material and methods

### 2.1. Material

The isolated teeth used herein for the analyses and re-evaluation of the genus *Protoxynotus/Paraphorosoides* come from different localities in Germany and Austria. The stratigraphic oldest tooth derives from the upper Turonian and was collected by one of us (JL) in 1998. This single lower jaw tooth was found in an abandoned quarry near Wüllen (Münsterland, Northwest Germany; see Ladwig (2002) for a geological overview) and was donated to the Natural History Museum Vienna with the inventory number NHMW/2021/0162/0001 in 2021.

Additional lower jaw teeth from Schellenbach (Pattenau Formation, lower Campanian) near Bad Tölz in Bavaria, Germany consisting of one complete tooth, one partly preserved crown, and one well-preserved root, were described and included in our analyses. The teeth were collected at the locality described by Ohmert (2011; fig. 4, p. 41) as Schellenbach “Süd-Schuppe”, from the base of the Pattenau Formation (*elevata* zone). The lithology of this basal layer consists of clayey marlstone that was dissolved in diluted hydrogen peroxide to extract the teeth. The teeth were collected by one of us (SS) in 2017 and donated to the NHMW Vienna in 2021 with the inventory numbers NHMW/2021/0162/0002 – NHMW/2021/0162/0004. Additionally, the holotypes of *Paraphorosoides ursulae* (inventory number IGPH 1992-I-11) and *Protoxynotus misburgensis* (Kat.-Nr. kca 8), stored at the Federal Institute for Geosciences and Natural Resources, respectively from the Campanian of Höver near Hannover and Misburg (Germany), were analysed and newly illustrated.



**Fig. 1.** Geographic overview of localities that yielded the specimens studied. The Turonian material comprises one tooth of *Protoxynotus* aff. *misburgensis* (NHMW/2021/0162/0001) from Wüllen (Germany). Fossils from the Campanian comprise 18 teeth of *Paraphorosoides ursulae* (IGPH 1992-I-9 – 26) from Höver (Germany) and two teeth of *Protoxynotus misburgensis* (Kat.-Nr. kca 8–9) from Misburg (Germany). New dental material includes three teeth (NHMW/2021/0162/0002 – 0004) from the Campanian of Schellenbach (Germany) and seven teeth (NHMW/2021/0116/0001 – 0007) from the Maastrichtian of Waidach (Austria).

The stratigraphic youngest dental material comprises three complete and four fragmentary teeth (inventory numbers NHMW/2021/0116/0001 – 0007). These teeth were extracted from 250 kg of sediment from the uppermost Maastrichtian exposed in the Waidach section (Gerhartsreit Formation) near Nussdorf (Salzburg, Austria) collected during a field campaign by IF and JP in 2021. The teeth were sampled from a horizon situated 1.25 m below the hiatus, which spans the Cretaceous – Palaeogene boundary as described by Mohamed et al. (2013). The clayey marlstone was dried, dissolved in diluted hydrogen peroxide (3%) and screen washed down to a mesh size of 320 µm. Teeth with the inventory numbers NHMW/2021/0116/0001 – 0007 and NHMW/2021/0162/0001 – 0004 are stored in the Natural History Museum Vienna (NHMW) and teeth with the inventory numbers IGPH 1992-I-9 – 26 are deposited in the collection of the Institute for Geology and Palaeontology at the University of Hannover (IGPH), Germany. Based on their morphology, the specimens were preliminarily assigned to *Protoxynotus* (Table 1). For a geographic overview of all records, see Fig. 1.

The new taxonomic name introduced in the present work has been registered in ZooBank: LSIDurn:lsid:zoobank.org:act:494ED7DE-8CB9-474B-AFEF-282422CF68A.

## 2.2. Phylogenetic placement – character matrix and phylogenetic analysis

In an effort to estimate the phylogenetic position of *Protoxynotus* and *Paraphorosoides* among Squaliformes, we first coded the dental characters for the *Paraphorosoides* type material from Thies and Müller (1993) and the newly described material from the Waidach section (Table 1) following the procedure described in Pollerspöck and Straube (2021). The type material from *Protoxynotus misburgensis* was excluded because the type series comprises only a single symphyseal tooth (holotype) and a single fragmented lower lateral tooth (paratype), which are not well-preserved. No new characters were added but the matrix of Pollerspöck and Straube (2021) was extended with further fossil taxa of the species *Protocentrophorus steviae* Cappetta, Morrison and Adnet, 2019, *Etmopterus cahuzaci* Adnet, 2006,

*Squaliodalatiya savoiei* Cappetta, Morrison and Adnet, 2019, and *Cretascymnus westfalicus* Müller and Schöllmann, 1989 to comprise fossil representatives assigned to extant lineages. Overall, the dataset comprises morphological characters from both fossil and extant species as well as DNA sequence information from Straube et al. (2015) for part of extant species. The morphological characters of extant species are derived from the data used in Shirai (1992), Flammensbeck et al. (2018), and Pollerspöck and Straube (2021) and comprises 72 dental characters (35 lower jaw, 34 upper jaw, 3 concern heterodonty) and 79 anatomical characters. Extant species represented exclusively with morphological data are *Cirrhigaleus barbifer*, *Centrophorus squamosus*, *Mollisquama parini*, *Euprotomicroides zantedeschia*, *Heteroscymnoides marleyi*, *Squaliolus laticaudus*, *Centrosymnus owstoni*, *Scymnodalatiya albicauda*, *Somniosus rostratus*, *Etmopterus spinax*, and *Oxynotus bruniensis*. The newly included fossil material comprises upper and lower jaw teeth from *P. ursulae*, *P. steviae*, *E. cahuzaci*, *S. savoiei*, *C. westfalicus* and lower jaw teeth from the newly described *Protoxynotus* species from Waidach. In our next step, dental characters 3, 9, 11, 14, 24, 44, 49, and 59 in the tooth character matrix from Pollerspöck and Straube (2021) were coded based on Thiele's (1993) equation to avoid miscategorising. Our subsequent phylogenetic analysis was performed in RAXML ver. 8.2.12 (Stamatakis, 2014) using the -g option constraining the tree topology for all extant species with DNA data to match the squaliform phylogeny from Straube et al. (2015). We guided the phylogenetic estimate with topology constraining to provide a scaffold for the extant squaliform phylogeny and test if extant taxa without DNA data cluster within their respective families. The dataset was partitioned, comprising a partition for the morphological characters (123 alignment patterns) and one for the DNA sequence information (19,556 alignment patterns). The multistate morphological data based on six distinct characters were analysed using the Markov k model of character evolution as a substitution matrix (Lewis, 2001). The DNA data was analysed under the general time-reversible nucleotide substitution and GAMMA rate heterogeneity models.

In our analysis, *Echinorhinus brucus* was defined as outgroup and 1000 rapid bootstrap inferences were executed to attain node

**Table 1**

All documented records, including new dental material. Abbreviations: Turonian (Turon); Campanian (Campan); Maastrichtian (Maast); Number (N).

Species (original description)	Species (revised)	Stage	Country	Locality	Type material	N	Jaw	Inventory numbers	Figure	References
<i>Protoxynotus misburgensis</i>	<i>Protoxynotus misburgensis</i>	Turon	Germany	Wüllen	no	1	Lower	NHMW/2021/0162/0001	Fig. 3J–K	Ladwig (2002)
<i>Paraphorosoides ursulae</i>	<i>Protoxynotus misburgensis</i>	Camp	Germany	Höver	Holotype	1	Lower	IGPH 1992-I-11	Fig. 3B–C	Thies & Müller (1993)
<i>Paraphorosoides ursulae</i>	<i>Protoxynotus misburgensis</i>	Camp	Germany	Höver	Paratypes	2	Upper	IGPH 1992-I-9 – 10	Fig. 3D–G	Thies & Müller (1993)
<i>Paraphorosoides ursulae</i>	<i>Protoxynotus misburgensis</i>	Camp	Germany	Höver	Paratypes	3	Lower	IGPH 1992-I-12 – 13	NA	Thies & Müller (1993)
<i>Paraphorosoides ursulae</i>	<i>Protoxynotus misburgensis</i>	Camp	Germany	Höver	no	22	Lower	IGPH 1992-I-15 – 36	NA	Thies & Müller (1993)
<i>Protoxynotus misburgensis</i>	<i>Protoxynotus misburgensis</i>	Camp	Germany	Misburg	Holotype	1	Lower	Kat.-Nr. kca 8	Fig. 3A	Herman (1975)
<i>Protoxynotus misburgensis</i>	<i>Protoxynotus misburgensis</i>	Camp	Germany	Misburg	Paratype	1	Lower	Kat.-Nr. kca 9	NA	Herman (1975)
New material	<i>Protoxynotus misburgensis</i>	Camp	Germany	Schellenbach	no	1	Lower	NHMW/2021/0162/0002	Fig. 3H–I	This study
New material	<i>Protoxynotus misburgensis</i>	Camp	Germany	Schellenbach	no	2	Lower	NHMW/2021/0162/0003 – 0004	NA	This study
New material	<i>Protoxynotus mayrmelnhofi</i> sp. nov.	Maast	Austria	Waidach	Holotype	1	Lower	NHMW/2021/0116/0001	Fig. 3L–M	This study
New material	<i>Protoxynotus mayrmelnhofi</i> sp. nov.	Maast	Austria	Waidach	Paratypes	2	Lower	NHMW/2021/0116/0002 – 0003	Fig. 3N–Q	This study
New material	<i>Protoxynotus mayrmelnhofi</i> sp. nov.	Maast	Austria	Waidach	Paratypes	4	Lower	NHMW/2021/0116/0004 – 0007	NA	This study

support values which were plotted on the most likely tree topology (Fig. 2). The character catalogue and the alignment of characters used for the analysis are available as online [Supplementary materials 1 and 2](#).

### 3. Results

#### 3.1. Tooth morphology and systematic implications

Visual inspection of fossil specimens listed in [Table 1](#) allowed the identification of similarities with teeth of extant genera *Zameus* [Jordan and Fowler, 1903](#) and *Oxynotus* [Rafinesque, 1810](#) of the Somniosidae/Oxynotidae clade and with the poorly known dalatiids *Euprotomicroides* [Hulley and Penrith, 1966](#) and *Mollisquama* [Dolganov, 1984](#) especially the overall tooth morphology of the lower jaw teeth with a long-erected cusp, which is flanked by a distal heel. An additional shared character is the well-developed labial apron of lower jaw teeth and the pronounced dignathic heterodonty with small, needle-like upper jaw teeth.

However, lower jaw teeth of *Protoxynotus* and *Paraphorosoides* differ distinctly from all above-mentioned genera in the rounded root outline of the basal face, which is more or less angular in all somniosid and dalatiid teeth, except for *Somniosus* (Somniosidae). Additionally, lower jaw teeth of the material listed in [Table 1](#) display a strong to faint sinuosity of the enameloid at the lingual crown base, which is absent in all dalatiid teeth but developed in some extant and extinct somniosids, e.g., *Somniosus pacificus* [Bigelow and Schroeder, 1944](#), *Somniosus rostratus* ([Risso, 1827](#)), *Zameus squamulosus* ([Günther, 1877](#)), and *Cretascymnus westfalicus* [Müller and Schöllmann, 1989](#) and in teeth of *Oxynotus*. Considering the tooth morphology of living Dalatiidae, all teeth possess a bifurcating apron enclosing a large medio-labial foramen. The only exception is represented by teeth of *Euprotomicroides* that develop a large foramen basally to the apron. Consequently, teeth of *Euprotomicroides* are exceptional within the Dalatiidae based on this morphological character. However, a basally situated foramen adjacent to the apron is not developed in teeth of *Protoxynotus* and *Paraphorosoides* but present in some genera of the family Somniosidae (e.g., *Scymnodalatius Taniuchi and Garrick, 1986*, *Scymnodon Barbosa Du Bocage and De Brito Capello, 1864*, and *Zameus* [Jordan and Fowler, 1903](#)).

Notwithstanding some minor intraspecific variations, some striking differences and similarities among the 72 coded dental characters used for the phylogenetic analysis should be mentioned. These include character 24, which exclusively concerns *Oxynotus*. The crown to root ratio (Character 24) is noticeably high in teeth of the latter due to the low cusp height. Thus, teeth of *Oxynotus* differ due to the nearly equal crown to root ratio of the other mentioned genera, including *Protoxynotus* and *Paraphorosoides*. Another important character separating *Oxynotus* from all other considered genera is the strongly developed apron in the upper jaw teeth, which is absent in *Paraphorosoides*, *Zameus*, and *Euprotomicroides*. Additional noteworthy characters refer to *Euprotomicroides*, which exclusively shares the imbricate arrangement pattern of teeth within the jaw (Character 23) with *Protoxynotus* and *Paraphorosoides*. However, the teeth of *Euprotomicroides* differ from all discussed genera due to the absence of a lingual groove (Character 34). A unique character of lower jaw teeth of *Protoxynotus* and *Paraphorosoides* is the strongly developed sinuosity of the enameloid at the lingual crown base (Character 36).

Considering the upper jaw teeth, it is striking that the root face of *Euprotomicroides* and *Mollisquama* is pierced by numerous, large foramina openings on the labial and lingual faces with additional foramina on the basal face. This is in contrast with teeth of *Zameus* and *Paraphorosoides*, which upper jaw teeth possess merely one central lingual foramen with an additional one in teeth of *Zameus*

and two on teeth of *Paraphorosoides*, which are laterally positioned. Teeth of *Zameus* possess one to two very small foramina or a groove, which extends to the root base and *Paraphorosoides* possesses only one central labial opening. It is also noteworthy that this type of bilobate root morphology of the upper jaw teeth is exclusively developed in *Paraphorosoides*, *Zameus*, and *Euprotomicroides*.

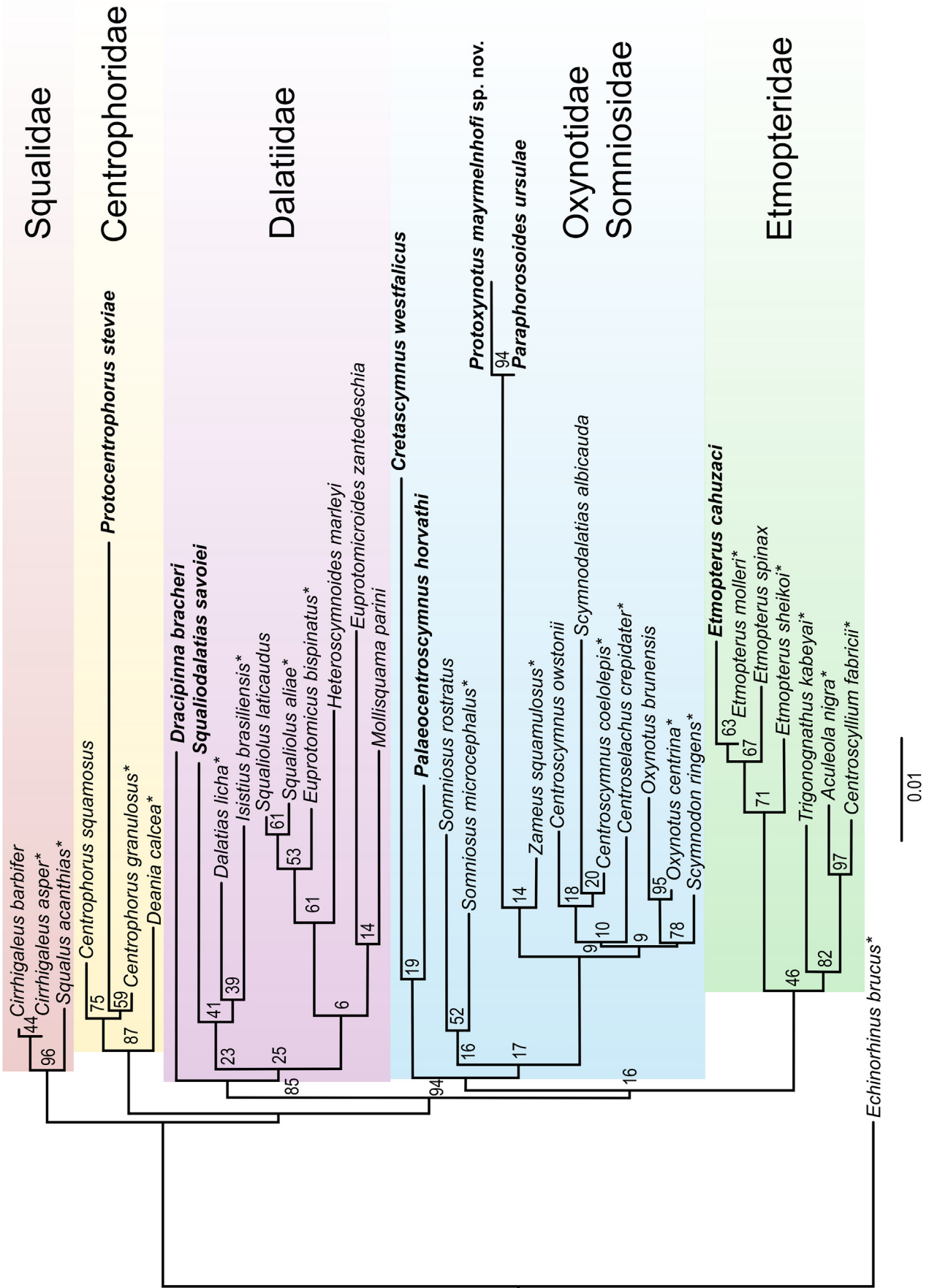
These observations suggest that the Somniosidae and Dalatiidae share numerous dental characters, which complicates the identification of the family-level placement of *Protoxynotus* and *Paraphorosoides*. The coding of the 72 dental characters used in this study provides a well-founded database for a phylogenetic analysis, although morphological variation of fossil material regarding uncertainties of tooth position, sex, and ontogenetic state should be considered.

#### 3.2. Phylogenetic placement of *Protoxynotus* and *Paraphorosoides*

Due to constraining the phylogenetic inference to the topology for all extant species with DNA sequence information, the topology resulting from our analysis ([Fig. 2](#)) shows major clades as in [Straube et al. \(2015\)](#). Squaliformes split into five clades representing families Squalidae, Centrophoridae, Dalatiidae, Etmopteridae and Somniosidae, including Oxynotidae. Computed node support is notably low, however, extant species represented in the dataset with morphological characters only cluster in reasonable positions within their respective families. *Cirrhigaleus barbifer* is sister to *C. asper* in the Squalidae, *C. squamosus* is sister to the clade comprising *C. granulatus* and fossil *P. steviae*, and *S. laticaudus* is sister to *S. aliae*. The *Euprotomicrus* and *Squaliolus* clade is sister to *H. marleyi*. *Euprotomicroides zantedeschia* and *M. parini* form a clade sister to genera *Squaliolus*, *Euprotomicrus*, and *Heteroscymnoides*. Further, *C. owstoni*, *S. albicauda* and *O. bruniensis* cluster within the Somniosidae/Oxynotidae clade with *O. bruniensis* sister to *O. centrina*. Within Etmopteridae, *E. spinax* is sister to a clade comprising *E. molleri* and fossil *E. cahuzaci* ([Fig. 2](#)). Newly added fossil taxa represented in our dataset with dental characters only show similar patterns, i.e. *P. steviae* cluster among Centrophoridae, *S. savoiei* is sister to the *Dalatius/Isistius* clade, *C. westfalicus* clusters within Somniosidae and *E. cahuzaci* is sister to *E. molleri* within Etmopteridae ([Fig. 2](#)). Some taxa are placed on rather long branches. Our target taxa *Protoxynotus* clusters with *Paraphorosoides*. This split is rather highly supported by bootstrapping compared to other nodes in the phylogeny and is positioned sister to the velvet belly sleeper shark *Zameus squamulosus* ([Fig. 2](#)). This sister group relationship is only weakly supported by bootstrapping. *Protoxynotus mayrmelnhofi* sp. nov. is the taxon with the most missing data due to the absence of upper jaw teeth, resulting in an exceptionally long branch of *Paraphorosoides/Protoxynotus*. Generally, the low support values are likely caused by the large amount of missing data for the fossil taxa and resulting uncertainty of phylogenetic placement. Within the set of 1000 bootstrapping trees (support material 3), taxa represented by morphological data only, especially fossil taxa represented by dental morphological characters only, frequently change the position in the trees, affecting the bootstrap support of other, deeper phylogenetic nodes, for example on family level. This is also true for *Protoxynotus* and *Paraphorosoides*. However, both taxa form a clade in the majority of bootstrapping trees and are also not estimated to be closely related specifically to *Oxynotus* or *Euprotomicroides*.

#### 3.3. Systematic palaeontology

The dental terminology and systematic scheme employed here follow [Cappetta \(2012\)](#). Subclass Elasmobranchii [Bonaparte, 1838](#) Cohort Euselachii [Hay, 1902](#)



Subcohort Neoselachii [Compagno, 1977](#)  
 Superorder Squalomorphii [Compagno, 1973](#)  
 Order Squaliformes [Compagno, 1973](#)  
 Family Somniosidae [Jordan, 1888](#)

Genus *Protoxynotus* [Herman, 1975](#)

[Fig. 3A–Q](#)

Type species: Symphyseal tooth of *Protoxynotus misburgensis* [Herman, 1975](#), by monotypy ([Herman, 1975](#): 296), upper Campanian (Upper Cretaceous), Misburg near Hannover, Germany.

**Revised diagnosis.** Small teeth not exceeding a height of 2.3 mm. Strong dignathic heterodonty with small needle-like upper teeth and asymmetrical, strongly labio-lingually compressed lower teeth. Upper jaw teeth with bilobate root and sigmoid cusp in profile view. Characteristic lower teeth with triangular main cusp with smooth cutting edge flanked by a distal heel. Lingual crown base with strong sinuosity of enameloid, slight bulge below bears a medio-lingual foramen. Bulge flanked by a pair of margino-lingual foramina, central foramen occasionally present. A nutritive groove continues from the medio-lingual foramen (or central foramen, if present) towards the labial root edge. Labial face with extended apron and one or more pairs of margino-labial foramina. Tooth interlocking devices developed as latero-external depressions along the entire root height.

**Remarks.** This genus was erected by [Herman \(1975\)](#) based on two incomplete teeth, which have been interpreted as ancestral tooth morphology of the extant genus *Oxynotus*. In his genus diagnosis, [Herman \(1975\)](#) described the following morphological characters indicating an oxynotid affiliation: (1) the contour of the teeth; (2) the number of lingual foramina; (3) the lingual nutritive groove; (4) the occurrence and shape of the apron and lingual extension of enameloid; (5) the crown contour with an incipient serration. According to [Herman's](#) diagnosis, the genus *Protoxynotus* differs from *Oxynotus* by the distinctly smaller size and the lower height of the root with barely developed labial foramina and a basal foramen. However, the incomplete lower jaw teeth allow only an insufficient description and the documented serration of the cusp appears to be an artefact due to poor preservation rather than a real morphological character. Based on the strongly fragmented teeth of the type series, we provide an emended genus diagnosis based on dental material from the Turonian, Campanian, and Maastrichtian, also including upper jaw teeth ([Fig. 3](#)). This partly new described dental material shares considerable similarities with the fragmented teeth described by [Herman \(1975\)](#) and with the teeth described as *Paraphorosoides ursulae* by [Thies and Müller \(1993\)](#): (1) strong labio-lingual compressed teeth with teardrop-shaped contour of cusp; (2) distal heel (only the notch, separating the heel from the main cusp, is preserved); (3) strong sinuosity of the enameloid of lingual crown base and apron; (4) large medio-lingual foramen below crown, accompanied by a pair of mesial and distal foramina; (5) lingual nutritive groove.

Based on this unique tooth morphology, we argue that the dental material previously described as *Paraphorosoides* represents teeth of the genus *Protoxynotus*, thus *Paraphorosoides* is considered as junior synonym of *Protoxynotus*.

Species *Protoxynotus misburgensis* [Herman, 1975](#)

\*1975 *Protoxynotus misburgensis* n. gen. n. sp. — [Herman, p. 296](#), pl. 1, fig. 1a-b.

1993 *Palaeomicroides ursulae* n. sp. — [Thies and Müller, p. 97](#), figs. 8–13.

v2002 *Protoxynotus misburgensis* [Herman 1975](#) — [Ladwig, p. 36](#), fig. 1a-b.

2006 *Paraphorosoides ursulae* — [Kriwet, Thies and Müller, p. 487](#), [Fig. 3H–I](#).

**Material.** One complete tooth (NHMW/2021/0162/0002), one partly preserved crown (NHMW/2021/0162/0003), and one well-preserved root (NHMW/2021/0162/0004), all antero-lateral teeth from the lower jaw.

**Locality.** Schellenbach near Bad Tölz, Bavaria, Germany.

**Stage.** Lower Campanian (Upper Cretaceous); Pattenau Formation.

**Description.** Lower jaw teeth are strongly labio-lingually compressed with a total height of 2.3 mm and a width of 1.0 mm. The mesial and distal cutting edges are sharp and distally convex, but mesially straight. The base of the mesial cutting edge possesses a pronounced curvature and narrows strongly at the crown-root junction. Both crown faces are slightly convex labially and lingually, and the triangular cusp is distally flanked by a heel. The enameloid of the lingual crown face extends towards the base (sinuosity of the enameloid) but does not reach the medio-lingual foramen that is situated near the lingual face and pierces a pronounced medio-lingual bulge. This foramen is accompanied by one margino-lingual foramen at each side, the distal one being slightly displaced in apical direction. A nutritive groove extends from the medio-lingual foramen towards the labial root edge, where it divides the root into two lobes. The labial face bears an apron that reaches nearly the base of the root and is also accompanied by at least three margino-labial foramina at each side.

**Remarks.** These newly documented teeth share similarities with lower jaw teeth of *P. misburgensis* from the Campanian of Misburg (holotype; [Fig. 3A](#)) and with teeth originally assigned to *P. ursulae* from Höver ([Fig. 3B–C](#)) as well as with the single tooth from the Turonian of Wüllen ([Fig. 3J–K](#)). Although the overall tooth morphology is similar, the crown morphology differs between specimens, which might represent a variation within the jaw or gynandric heterodonty. The mesial and distal cutting edges are convex on the symphyseal tooth from Misburg ([Fig. 3A](#)). Antero-lateral teeth from Höver ([Fig. 3B–C](#)) possess a convex distal but a slightly concave mesial crown contour, whereas antero-lateral teeth from Schellenbach exhibit a convex distal and straight mesial cutting edge ([Fig. 3H–I](#)). The oldest record of this species, which is represented by one isolated tooth from the Turonian of Wüllen, possesses a rather straight mesial and distal contour of the cutting edges ([Fig. 3J–K](#)). Based on the combination of the unique tooth morphological characters (e.g., erected and teardrop-shaped cusp, strong sinuosity of the enameloid of lingual crown base, medio-lingual bulge, one medio-lingual foramen, and one pair of mesial and distal foramina) and the palaeogeographic occurrence of *P. misburgensis* and *P. ursulae*, we include the latter in the species *P. misburgensis*.

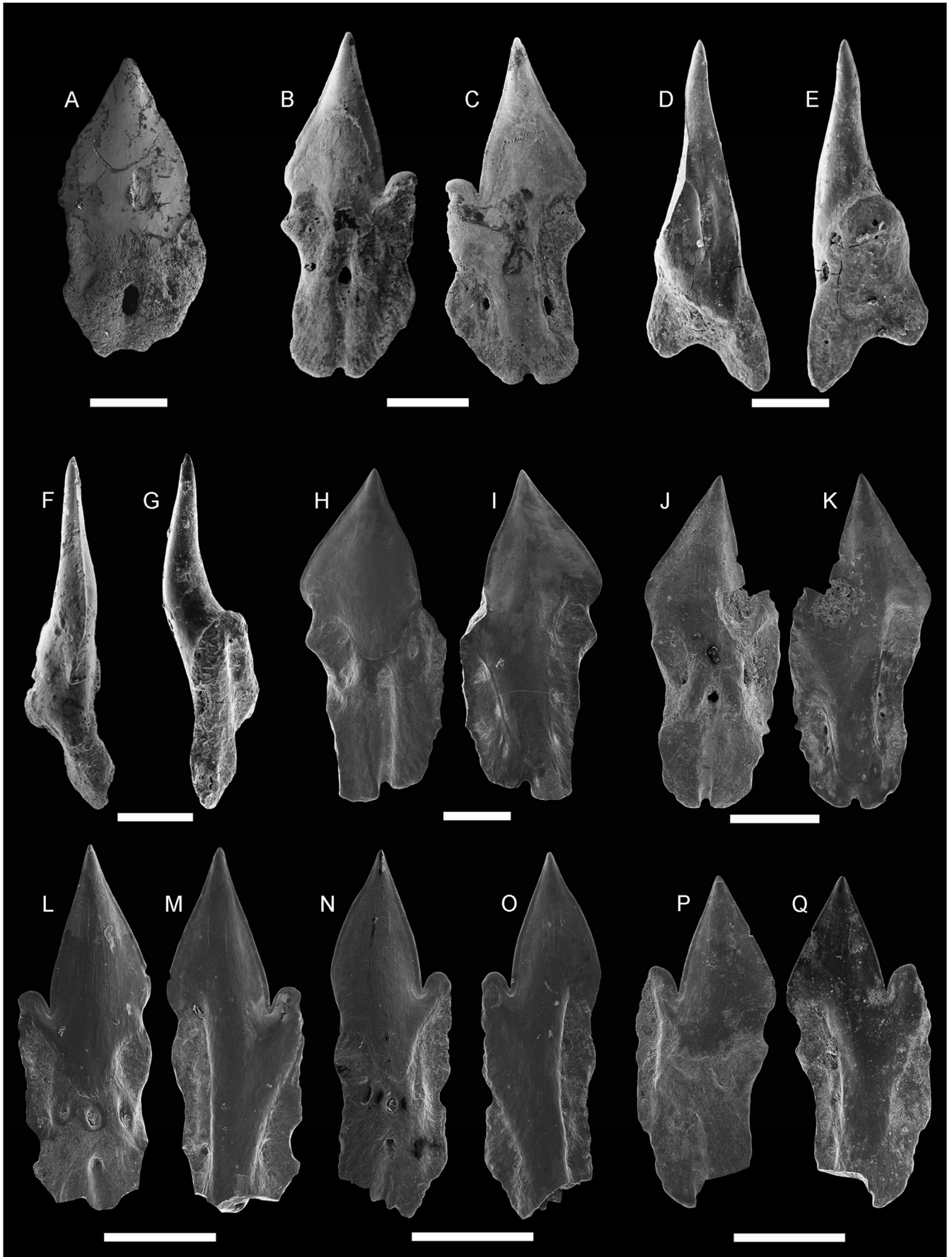
Species *Protoxynotus mayrmelnhofi* sp. nov.

[Fig. 3L–Q](#).

**Type locality.** E13°00'27", N47°56'34"; Waidach section near Nussdorf, Austria.

**Stage.** Upper Maastrichtian (Upper Cretaceous); Gerhartsreit Formation.

**Fig. 2.** Maximum likelihood based phylogenetic analysis nests *Protoxynotus* within the Somniosidae/Oxynotidae clade as sister taxon to *Zameus*. *Paraphorosoides ursulae* is considered to be synonymous with *Protoxynotus misburgensis*. Analyses based on morphological (incl. tooth) characters and DNA data. Numbers at branching points indicate node support values, which were generated from 1000 bootstrap replicates (Supplement data 2). Bold font indicates extinct taxa. Extant taxa with available DNA data are marked with an asterisk. *Echinorhinus brucus* was chosen as outgroup.



**Derivation of name.** Dedicated to the Mayr-Melnhof Company, the landlord of the forest where the teeth were collected.

**Holotype.** One complete, well-preserved antero-lateral tooth from the lower jaw (NHMW/2021/0116/0001).

**Paratypes.** Two complete and four fragmentary-preserved teeth (NHMW/2021/0116/0002 – 0007).

**Diagnosis.** Labio-lingually compressed, asymmetrical but delicate teeth not exceeding a height of 1.8 mm and a width of 0.5 mm. Teardrop-shaped and smooth cusp flanked by a well-rounded distal heel. Broad extension (sinuosity) of enameloid towards the base on lingual face with basally adjacent pronounced bulge, exhibiting one medio-lingual foramen and a central foramen. Nutritive groove on basal face running from the labial root edge to the central foramen. A pair of margino-lingual foramina is present on the edges of the lingual bulge, slightly higher than the medio-lingual foramen. Labial crown possesses a long apron, bordered laterally by several margino-labial foramina.

**Description.** This new species is characterised by a teardrop-shaped, pointed cusp with a well-developed but smooth cutting edge, which continues from the cusp to the distal, well-rounded heel. A sharp notch separates the distal heel from the cusp, which is extremely labio-lingually compressed. The elongated cusp is also labio-lingually flattened but biconvex. The mesial cutting edge tapers where the crown narrows strongly above the crown-root junction. The transition from the enameloid covered crown to the root is strongly arched towards the base of the root (sinuosity of enameloid) but does not reach the medio-lingual foramen. A distinct bulge is developed where the medio-lingual foramen opens. The medio-lingual foramen is mesially and distally accompanied by a pair of margino-lingual foramina of the same size at each side. A central foramen is present at mid-height between the sinuosity of enameloid and the labial root edge, in lingual view. A nutritive groove extends from the central foramen towards the labial root edge. The tooth interlocking devices, developed as mesial and distal depressions, are distinctly observable. The labial crown face possesses a bulged apron, which tapers towards the base. The apron is flanked by a few small margino-labial foramina at each side.

**Remarks.** Teeth of the new erected species *Protoxynotus mayrmelnhofi* sp. nov. can be differentiated from the type species *P. misburgensis* by the number of lingual foramina. Teeth of *P. mayrmelnhofi* sp. nov. exhibit both central and medio-lingual foramina and thus, differ from teeth of *P. misburgensis*, which lack a central foramen.

## 4. Discussion

### 4.1. Phylogenetic position of *Protoxynotus* and the early evolution of squaliform dentition

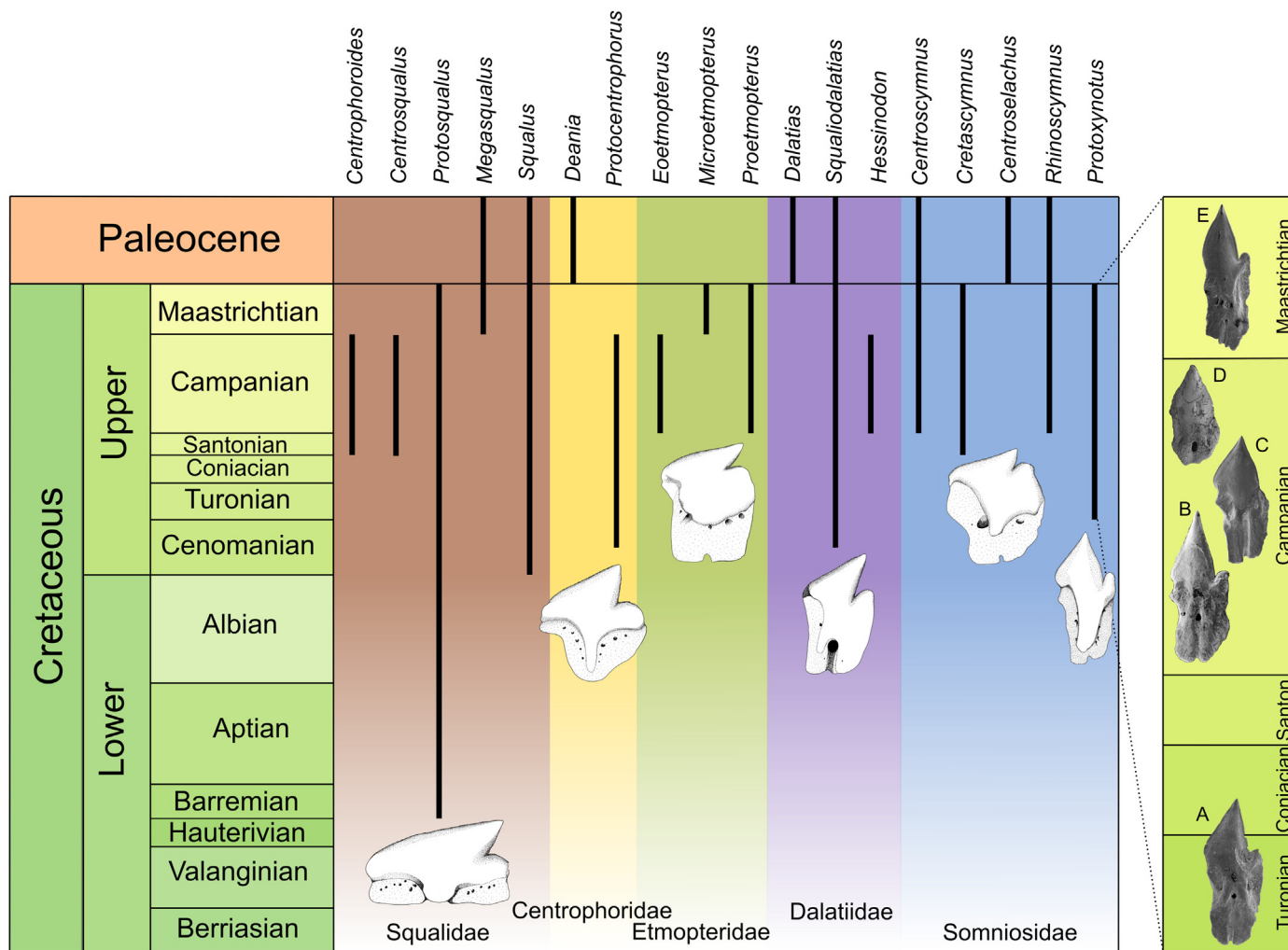
The phylogenetic placement of *Protoxynotus* and *Paraphorosoides* was a subject of discussion in previous studies (Herman, 1975; Thies and Müller, 1993; Ladwig, 2002; Kriwet, Thies and Müller, 2006; Kriwet and Klug, 2009; Flammensbeck et al., 2018) and both genera have been previously attributed to two different families (Somniosidae/Oxynotidae and Dalatiidae). In his

genus description, based exclusively on two lower jaw teeth, Herman (1975) argued for the similarities to teeth of the extant genus *Oxynotus* (Somniosidae/Oxynotidae). Based on the description of lower and upper jaw teeth of *Paraphorosoides* by Thies and Müller (1993), which we now include in *Protoxynotus*, an affiliation with *Oxynotus* is rejected due to the presence of a pronounced apron in upper jaw teeth of the latter, which is not developed in upper jaw teeth of *Paraphorosoides*. Thies and Müller (1993) suggested an attribution of *Paraphorosoides* to the family Dalatiidae based on the similarities with lower jaw teeth of the extant genus *Euprotomicroides* (Dalatiidae) but did not discuss similarities or differences to *Protoxynotus*. However, the presence of a lingual nutritive groove in lower jaw teeth of *Paraphorosoides*, which is absent in teeth of *Euprotomicroides* but common among somniosids (e.g., *Centroscymnus*, *Scymnodalatis*, *Scymnodon*, *Somniosus*, and *Zameus*) and *Protoxynotus*, support the placement within the somniosids which is also reflected in the phylogenetic analysis (Fig. 2). The attribution to the somniosids is further supported by the limited number of small foramina openings in upper jaw teeth of *Paraphorosoides*, which is a shared character with upper jaw teeth of *Zameus* (Somniosidae). In contrast, upper jaw teeth of *Euprotomicroides* are strongly pierced by numerous large foramina distributed labially, lingually and on the basal root face. Considering all discussed morphological differences and similarities of teeth of *Paraphorosoides* and *Protoxynotus* to *Euprotomicroides* of the dalatiids and to certain somniosids (e.g., *Zameus*, *Somniosus*), the attribution of both genera in question to the somniosids is eligible as supported by our phylogenetic analysis, which shows a sister-group relationship of *Paraphorosoides* with *Protoxynotus* (Fig. 2).

Interestingly, the tooth-based fossil record of squaliform sharks indicates the Squalidae as the oldest family of the order (Fig. 4). Within the family, the genus *Protosqualus* Cappetta, 1977 is documented from the Barremian (Thies, 1981) to the Maastrichtian (Cione et al., 2018) and *P. albertsi* Thies, 1981 is considered as the most ancient squaliform (Flammensbeck et al., 2018). The Squaliformes did not diversify until the Late Cretaceous (Adnet and Cappetta, 2001; Straube et al., 2015; Flammensbeck et al., 2018), with the appearance of the first representatives of the families Centrophoridae, (e.g., *Protocentrophorus* Adnet, Cappetta, and Mertiniene, 2008) and Dalatiidae (e.g., *Squaliodalatis*) in the Cenomanian (Dalinkevicius, 1935; Adnet et al., 2008), the Somniosidae/Oxynotidae clade with *Protoxynotus* in the Turonian (Ladwig, 2002), and the Etmopteridae (e.g., *Eoetmopterus*) in the Campanian (Müller, 1989). This implies that the elongated and erected lower jaw teeth of *Protoxynotus* with bilobate, needle-like upper jaw teeth represents the oldest record of this type of dignathic heterodonty among the Squaliformes. Considering the evolution and appearance of the different morphotypes, it is striking that the most ancient Squalidae (*Protosqualus*, oldest record in the Barremian) did not display a dignathic heterodonty. Dignathic homodonty is still characteristic in extant Squalidae, which have strongly labio-lingual compressed teeth with low roots and a massive but short labial apron (e.g., Underwood et al., 2016, fig. 2a). The evolution of a well-pronounced dignathic heterodonty within the order is first documented with *Protocentrophorus* (Centrophoridae) and *Squaliodalatis* (Dalatiidae) in the Cenomanian. However, a

**Fig. 3.** A *Protoxynotus misburgensis* (Kat.-Nr. kca 8), symphyseal lower jaw tooth, lingual view, Upper Campanian, Misburg near Hannover, Germany (Holotype from Herman, 1975). B–C *Protoxynotus misburgensis* (IGPH 1992-I-11), lower jaw, Lower Campanian, Höver near Hannover, Germany (Holotype of *P. ursulae* from Thies and Müller, 1993), B lingual, C labial. D–G *Protoxynotus misburgensis* (IGPH 1992-I-9 – 10), upper jaw, Lower Campanian, Höver near Hannover, Germany (Paratypes of *P. ursulae* from Thies and Müller, 1993): D–E (IGPH 1992-I-9), D labial, E lingual; F–G (IGPH 1992-I-10) profile. H–I *Protoxynotus misburgensis* (NHMW/2021/0162/0002), lower jaw, Campanian, Schellenbach near Bad Tölz, Germany: H lingual, I labial. J–K *Protoxynotus misburgensis* (NHMW/2021/0162/0001), lower jaw, lower middle Turonian, Wüllen near Ahaus, Germany: J lingual, K labial. L–Q *Protoxynotus mayrmelnhofi* sp. nov. L–M Holotype (NHMW/2021/0116/0001), lower jaw: L lingual, M labial; N–O Paratype (NHMW/2021/0116/0002), lower jaw: N lingual, O labial; P–Q Paratype (NHMW/2021/0116/0003), lower jaw: P lingual, Q labial, Upper Maastrichtian, Waidach near Nussdorf, Austria. Scale bars equal 500 µm (B–C, H–I, J–K, L–M, N–O, P–Q), 250 µm (A), and 200 µm (D–E, F–G).





**Fig. 4.** Stratigraphic column with first (FOD) and last (LOD) occurrence dates based on genus level (no indication of ghost lineages; References in Supplementary material 3). Paleocene records are limited to the Danian stage. Line drawings of lower jaw teeth indicate characteristic tooth morphology of families. A *Protoxynotus misburgensis* (NHMW/2021/0162/0001), Upper Turonian, Wüllen (Germany). B *Protoxynotus misburgensis* (IGPH 1992-I-11), Lower Campanian, Höver (Germany). C *Protoxynotus misburgensis* (NHMW/2021/0162/0002), Campanian, Schellenbach (Germany). D *Protoxynotus misburgensis* (Kat.-Nr. kca 8), Upper Campanian, Misburg (Germany). E *Protoxynotus mayrmelnhofi* sp. nov. (NHMW/2021/0116/0002), Upper Maastrichtian, Waidach (Austria).

noteworthy change in morphology from strong distally inclined to erected cusps, which may indicate a change in function, first appeared in *Protoxynotus*, with its oldest known occurrence in the Turonian. Although upper jaw teeth of this genus are only known from the Campanian (Thies and Müller, 1993, figs. 8–9; Fig 3D–G), we assume that they escaped collection due to their small size and thus, were already present in the oldest representative of this genus in the Turonian.

Based on our current knowledge, which is largely hampered by an incomplete fossil record, we highlight the rapid adaptation of the dogfish sharks to new feeding strategies from dignathic homodonty as ancestral state (Squalidae) to different forms of dignathic heterodonty (Centrophoridae, Dalatiidae, Etmopteridae, and Somniosidae) during the Late Cretaceous (Fig. 4). Thus, *Protoxynotus* represents one of the oldest dignathic heterodont squaliform genera and hitherto the first genus with an assumed novel functional adaptation in its cutting-clutching type dentition with needle-like upper jaw teeth and compressed but erected lower jaw teeth.

#### 4.2. Palaeoecology and distribution

Teeth of *Protoxynotus* were documented from different environmental settings from the Boreal and Tethyan realms. The habitat of the oldest known record from the upper Turonian (Wüllen, Münsterland, Northwest Germany) from the Boreal realm is interpreted as shallow subtidal setting but corresponds to a transgressive phase of the western margin of the Münster Basin (Ernst et al., 1998). *Protoxynotus misburgensis* from the Campanian was also found within stratae of two transgressive phases (Neumann et al., 2002) of the *lingua/quadrata* and *conica/papillosa* subzones of the Boreal realm at Höver (Near Hannover, Northern Germany) and within the sediments from the transgrading Pattenau Formation of the Northern Helvetic Shelf (Ohmert, 2006, 2011) in Schellenbach near Bad Tölz, Bavaria (Southern Germany), which belongs to the Tethyan realm. The stratigraphic youngest occurrence of *Protoxynotus* (*P. mayrmelnhofi* sp. nov.) from the Maastrichtian derived from neritic sediments deposited in the Southern Helvetic Shelf at Waidach near Salzburg (Austria) (Mohamed et al., 2013)

also representing the Tethyan realm. Combining all available ecological data, it is assumed that *Protoxynotus* inhabited neritic shelf environments restricted to the Boreal- and northern Tethyan realms. Considering the environmental conditions of the Waidach section in Austria, in which sediments are described as dysoxic to suboxic (Mohamed et al., 2013), *Protoxynotus* may not have been a bottom-dwelling shark.

## 5. Conclusion

The squaliform genera *Protoxynotus* and *Paraphorosoides* have been previously attributed to two different clades (Somniosidae/Oxyntidae and Dalatiidae). A phylogenetic analysis allows for a family placement of both genera within the Somniosidae/Oxyntidae clade. Based on the morphological similarities of both genera, a detailed re-evaluation of the type series enabled a new taxonomic placement of *Paraphorosoides ursulae*, which is now included in *Protoxynotus misburgensis*. Thus, *P. ursulae* is now considered as a subjective junior synonym of *P. misburgensis*. The revision of the genus *Protoxynotus* allows further an emended genus diagnosis. Additionally, we document new dental material from the Campanian (Germany) and the Maastrichtian (Austria), which resulted in the description of a new species, *Protoxynotus mayrmelnhofi* sp. nov. This species represents the youngest record of the genus *Protoxynotus*, which ranges from the Turonian to the Maastrichtian. This detailed study indicates that *Protoxynotus* occupied the Boreal- and northern Tethyan realms of the Late Cretaceous and was most likely not a bottom-dwelling shark with a highly specialised dognathic heterodonty.

## Data availability

No data was used for the research described in the article.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2022.105331>.