

Elasmobranch assemblages from a bathyal environment spanning the Cretaceous-Paleogene boundary in Austria

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Abstract

Extensive bulk-sampling of the continuous Cretaceous-Paleogene boundary section at Gams (Styria, Austria) allows for the first time the description of the elasmobranch communities inhabiting the bathyal environment of this well-known section. The sampled succession comprises six horizons from the uppermost Maastrichtian (upper part of *Nephrolites frequens* Zone CC26) and five horizons from the lowermost Danian (Zone NP1), which yielded a total of 1852 elasmobranch teeth. Although the majority of the teeth are not well preserved, this study enabled the description of at least 16 taxa of the orders Hexanchiformes, Squaliformes, Orectolobiformes, Lamniformes and Carcharhiniformes, providing a rare snapshot of elasmobranch diversity of this specific environmental setting. Beside minor diversity fluctuations between the assemblages, the extensive bulk-sampling of this section did not reveal a marked diversity decline related to the end-Cretaceous mass extinction event. However, a noteworthy correlation between the deepening upward trend of the section with the appearance of frilled and goblin sharks points to changes in palaeobathymetry, which is also reflected in the increase of the total proportion of squaliform teeth in the uppermost sampled horizon. Furthermore, teeth of the extinct triakid *Palaeogaleus* were recovered exclusively from the Danian deeper deposits, expanding the palaeoecological range of the genus down to fairly deep marine environments. In addition, this study provides the first record of the lamniform *Cretolamna* ex gr. *borealis* from the Danian of the Tethyan Realm expanding the palaeogeographic distribution of this group.

1. Introduction

The end-Cretaceous mass extinction event was the last severe ecological crisis, which caused a drastic decline of global biodiversity at 66 Ma, including several marine vertebrate and invertebrate groups (Raup and Sepkoski, 1982; MacLeod et al., 1997; Stanley, 2016). One of the most diverse and resilient groups of marine vertebrates are the cartilaginous fish (Chondrichthyes), which occupy a wide range of ecosystems. The high diversity of this group, combined with their specialisation to different feeding strategies, makes chondrichthyans as a whole less vulnerable to biotic crises (Friedman and Sallan, 2012). A comprehensive study focusing on the global impact of the end-Cretaceous crisis on elasmobranchs (sharks, rays, and skates) revealed that this event decreased the elasmobranch species richness by 62.6% (44.9% of genera

(Guinot and Condamine, 2023). Furthermore, the elasmobranch extinction pattern shows a strong degree of phylogenetic, ecological, and geographic selectivity with batomorphs, durophagous and low latitude taxa being more impacted (Guinot and Condamine, 2023). Nevertheless, little is known about the faunal turnover based on fine-scale regional analyses covering different palaeoenvironments during this crucial period of a first-order mass extinction event. In the last decades, successive fossil-rich horizons yielding elasmobranch remains from the uppermost Maastrichtian and the lowermost Danian have been sampled from only a few areas in Morocco (Noubhani and Cappetta, 1997; Noubhani, 2010) and Denmark (Adolfsson and Ward, 2014, 2015), representing two different environmental settings. With a genus-level extinction of 57% (Noubhani and Cappetta, 1997;

Adolfsson and Ward, 2014, 2015), the Moroccan assemblages demonstrate a strong impact of the K-Pg event on elasmobranchs inhabiting shallow marine ecosystems in lower latitudes. However, the extinction signal of the Moroccan section is blurred by the lack of a precise stratigraphic context and the presence of a hiatus of unknown duration across the boundary. The second investigated section that yielded elasmobranch assemblages is located in Denmark and comprises a complete K-Pg boundary succession. However, the analysed faunas derive from different localities of an intermediate to deep-water environment deposited in the Boreal Realm (Adolfsson and Ward, 2014, 2015). Compared to the Moroccan assemblages, the elasmobranchs of the deep-marine Danish Basin experienced with 23% a lower genus-level extinction (Adolfsson and Ward, 2014, 2015). A recent study of a continuous succession across the K-Pg boundary deposited in an outer neritic environment at Waidach (Austria) indicates a marked faunal turnover linked to significant changes in palaeobathymetry, which is decoupled from the end-Cretaceous extinction event (Feichtinger et al., 2023, 2024).

Sediments representing deep-marine palaeoenvironments are rarely accessible for sampling elasmobranch

assemblages, limiting our knowledge on the timing of diversification for some clades (e.g. Squaliformes). Thus, to reveal ecospace occupation, diversity, and niche adaptation to specific environments through time, fine-scale sediment processing in meaningful quantities is required. Furthermore, precise sampling of several successive horizons in combination with reliable geological and sedimentological data is vital to decipher the role of environmental forcing over the structure of past elasmobranch communities during the end-Cretaceous event. Here, we describe new dental material from a continuous K-Pg succession deposited in a bathyal setting in Gams (Styria, Austria). We provide a taxonomical overview of the elasmobranch fauna based on fine sampling of 11 successive horizons from a deepening-upward sequence spanning the K-Pg boundary.

2. Geographical and geological settings

The investigated Cretaceous-Paleogene boundary section is referred to as “Gams 2” in Kollmann (2009) or as Gamsbach section in Egger et al. (2009), the latter being followed in the present study. The Cretaceous-Paleogene boundary of the Gamsbach section (E 14°51’50” N

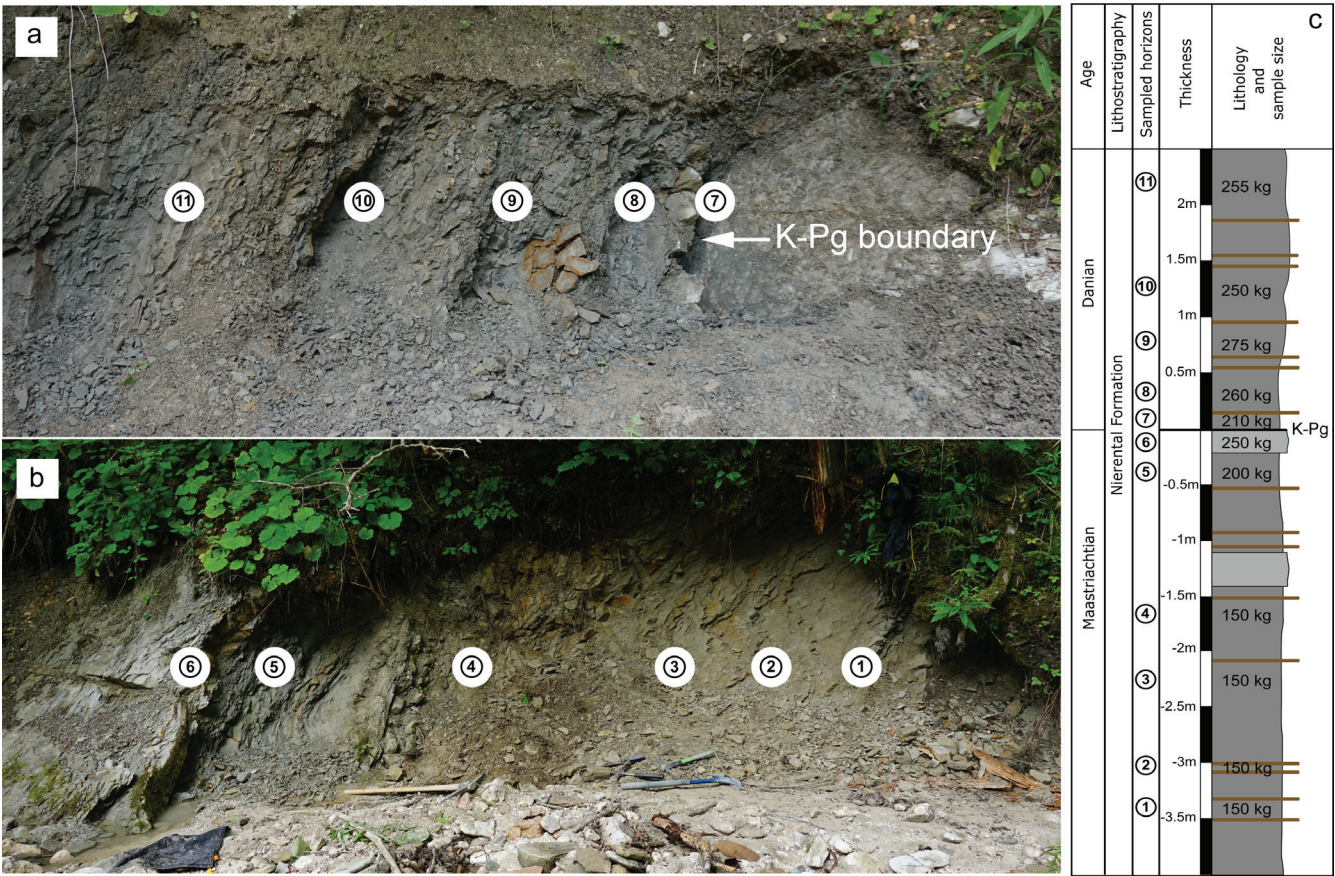


Figure 1: Lithostratigraphic overview of sampled horizons from the continuous Gamsbach section in Gams. **a:** Grey to reddish silty marls and marlstones of the Danian succession, comprising horizons 7–11 (Zone CC 26). **b:** Marlstones and marly limestones of the Maastrichtian succession, comprising horizons 1–6 (Zone NP1). **c:** Lithostratigraphic profile of the section, including the position of the intercalated turbidites and the sample size for each sampled horizon.

47°39'51") is accessible along the Gamsbach river east of the old Haid sawmill in Gams, Styria. The succession belongs to the Gosau Group (Nierental Formation) and was deposited in the northwestern Tethyan Realm at an estimated palaeolatitude of 20° to 30° N (Wagreich and Faupl, 1994; Haubold et al., 1999; Stampfli et al., 2002; Pueyo et al., 2007). The Gosau Group comprises sediments of an unstable environment with a rapid shift from shelf to bathyal settings triggered by strong tectonic subsidence during the early Campanian, which terminated the shallow marine facies of the Lower Gosau Subgroup (Wagreich, 1993; Wagreich and Faupl, 1994). The base of the adjacent Upper Gosau Subgroup (Maastrichtian - Eocene) comprises deep-water sediments of Maastrichtian age represented by light grey to brownish hemipelagic marlstones and marly limestones alternating with sandy turbidites. The base of the Danian is marked by a thin (0.2–0.4 cm) layer of yellowish clay with an iridium anomaly (Egger et al., 2009; Grachev et al., 2009) identified as being diagnostic for the Cretaceous-Paleogene transition (Alvarez et al., 1980). In addition, the K-Pg boundary of the Gamsbach section was identified by analyses of calcareous nannoplankton and foraminifera (Egger et al., 2009; Korchagin and Kollmann, 2009). Similar to the Knappengraben locality, which represents another accessible K-Pg succession in this area (Egger et al., 2004), the lowermost Danian (horizon 7, Zone NP1 (Egger et al., 2004, 2009)) of the Gamsbach section contains reworked planktonic foraminifera from the uppermost Maastrichtian. The deepening of the palaeoenvironment (Egger et al., 2004) continued into the early Danian with a change of lithology to dark grey to reddish silty marls and marlstones after the boundary clay. Although the section represents a deepening-upward sequence, the sediment was deposited above the local calcite compensation depth (Krenmayr, 1996).

3. Material and methods

The dental material reported here was collected by bulk sampling of six horizons (1–6) in the latest Maastrichtian and five horizons (7–11) situated immediately above the Cretaceous-Paleogene boundary (Fig. 1). The teeth were extracted from a total amount of 2 300 kg of sediment, collected during a field campaign by two of the authors (IF, MK) and volunteers in 2021–2022. The rock samples were dried, dissolved in diluted hydrogen peroxide (5%) and Rewoquat®, and sieved down to a mesh size of 320 µm. The recovered fossils comprise 2590 ichthyoliths, which include 1852 elasmobranch teeth, 76 dermal denticles, and 662 undetermined bony fish teeth. The majority of the teeth recovered are not well preserved, which hampered species identification. Of the 1852 teeth recovered, 541 (~30%) are identified at order level. Among them, 57 (~3%) teeth are identified at family level and 50 (~3%) at genus level. All specimens are stored in the Natural History Museum Vienna (NHMW/2023/0254/0000 – NHMW/2023/0264/0000).

4. Results and discussion

4.1. Inferences of diversity fluctuations between the assemblages

The eleven sampled horizons from the continuous K-Pg Gamsbach section at Gams in Austria yielded at least 16 elasmobranch taxa of the orders Hexanchiformes, Squaliformes, Orectolobiformes, Lamniformes, and Carcharhiniformes (Fig. 2). Despite the high number of ichthyoliths recovered from all horizons, very few specimens were well-preserved enough to allow identification below the family level. Therefore, the faunal list and number of taxa reported here likely understate the taxonomic richness of the sampled assemblages. Nevertheless, the first description of elasmobranch teeth from this K-Pg boundary section contributes significantly to the reconstruction and interpretation of the ecological history of this prominent and extensively studied section and provides important information over elasmobranch distribution around the K-Pg event.

Investigation of the eleven sampled horizons revealed diversity fluctuations between the recovered assemblages. However, heterogeneity in diversity should be interpreted with caution, as this pattern might depict an artefact of preservation rather than reflecting a real pattern. The lowermost horizon 1 yielded isolated cusps of Hexanchidae, as well as tooth fragments of undetermined Squaliformes, and Lamniformes. Horizon 2 contained teeth of *Protoxynotus* sp. (Fig. 3n–o), one lower jaw tooth of *Centroscyrnus* sp. (Fig. 3t–u), and cusps of undetermined Squaliformes and Lamniformes. Horizon 3 produced no well-preserved teeth suitable for genus-level identification, but the assemblage is rich in indeterminable cusps of Squaliformes (Fig. 3y) and Lamniformes (Fig. 2). Horizon 4 comprises teeth of Hexanchidae, *Protoxynotus*, one upper jaw tooth of *Centroscyrnus* (Fig. 3r–s), and isolated cusps of Squaliformes and Lamniformes. With at least four different genera, horizon 5 produced the most diverse latest Maastrichtian assemblage, comprising teeth of the genera *Rolfodon* (Fig. 3a–c) and *Protoxynotus*, cusps of Mitsukurinidae and Chlamydoselachidae, one enigmatic tooth of a hitherto unknown putative carcharhiniform (Fig. 4q), and cusps of Squaliformes and Lamniformes.

Horizon 7 represents the boundary clay and thus, the assemblage of the lowermost Danian. This yielded cusps of the families Hexanchidae, Chlamydoselachidae and Mitsukurinidae, and tooth fragments of Squaliformes, Lamniformes, and Carcharhiniformes (Fig. 2). In horizon 8, teeth of the genus *Palaeolageus* sp. (Fig. 4n–o) are associated with cusps of the families Chlamydoselachidae and Mitsukurinidae, as well as fragmented cusps of Squaliformes, Lamniformes, and Carcharhiniformes (Fig. 2). Adjacent horizon 9 yielded four identifiable taxa: *Chlamydoselachus* sp. (Fig. 3f–h), *Rolfodon* sp. (Fig. 3d–e), *Cretolamna* ex gr. *borealis* (Priem, 1897) (Fig. 4a–b), and *Palaeogaleus* sp. (Figs. 4d–m), along with cusps of the families Chlamydoselachidae and Mitsukurinidae (Fig. 4c), and fragments of Squaliformes, Lamniformes,

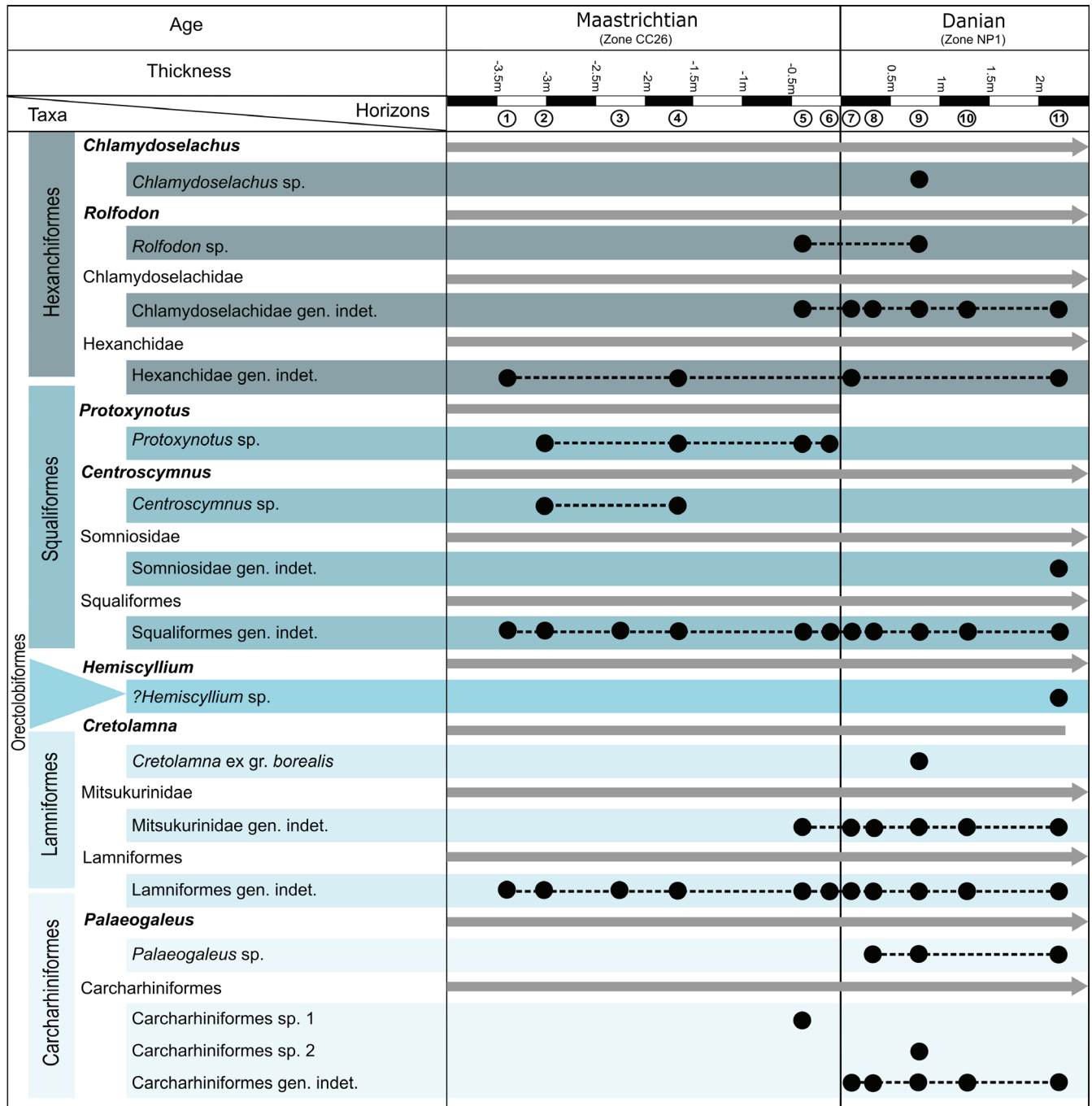


Figure 2: Stratigraphic range of the reported elasmobranchs within the Gamsbach section at Gams. Dashed lines indicate ghost lineages of taxa, grey lines indicate global occurrence of taxa modified from Guinot & Condamine (2023).

Carcharhiniformes, and one tooth of Carcharhiniformes sp. 2 (Fig. 4p). This association from horizon 9 shows the highest diversity among the Danian assemblages sampled. Horizon 10 contained in addition to cusps of the families Chlamydoselachidae and Mitsukurinidae fragmented cusps of the orders Squaliformes, Lamniformes and Carcharhiniformes (Fig. 2). The assemblage of horizon 11 comprises teeth of Hexanchidae (Fig. 3i), ?*Hemiscyllium* (Fig. 3z–z'), *Palaeogaleus*, and one upper jaw tooth of Somniosidae indet. (Fig. 3v–x), along with undeterminable teeth of Chlamydoselachidae, Mit-

sukurinidae, Squaliformes, Lamniformes, and Carcharhiniformes.

The latest Maastrichtian fauna comprises a total number of three identified genera and at least nine species (*Rolfodon* sp., Chlamydoselachidae, Hexanchidae, *Protoxynotus* sp., *Centroscyrnus* sp., Squaliformes indet., Mitsukurinidae indet., Lamniformes indet., and Carcharhiniformes sp. 1). Taxic richness increased in the earliest Danian fauna where the five sampled horizons yielded five identified genera and at least 11 species, comprising teeth of *Chlamydoselachus* sp., *Rolfodon* sp., Hexanchi-

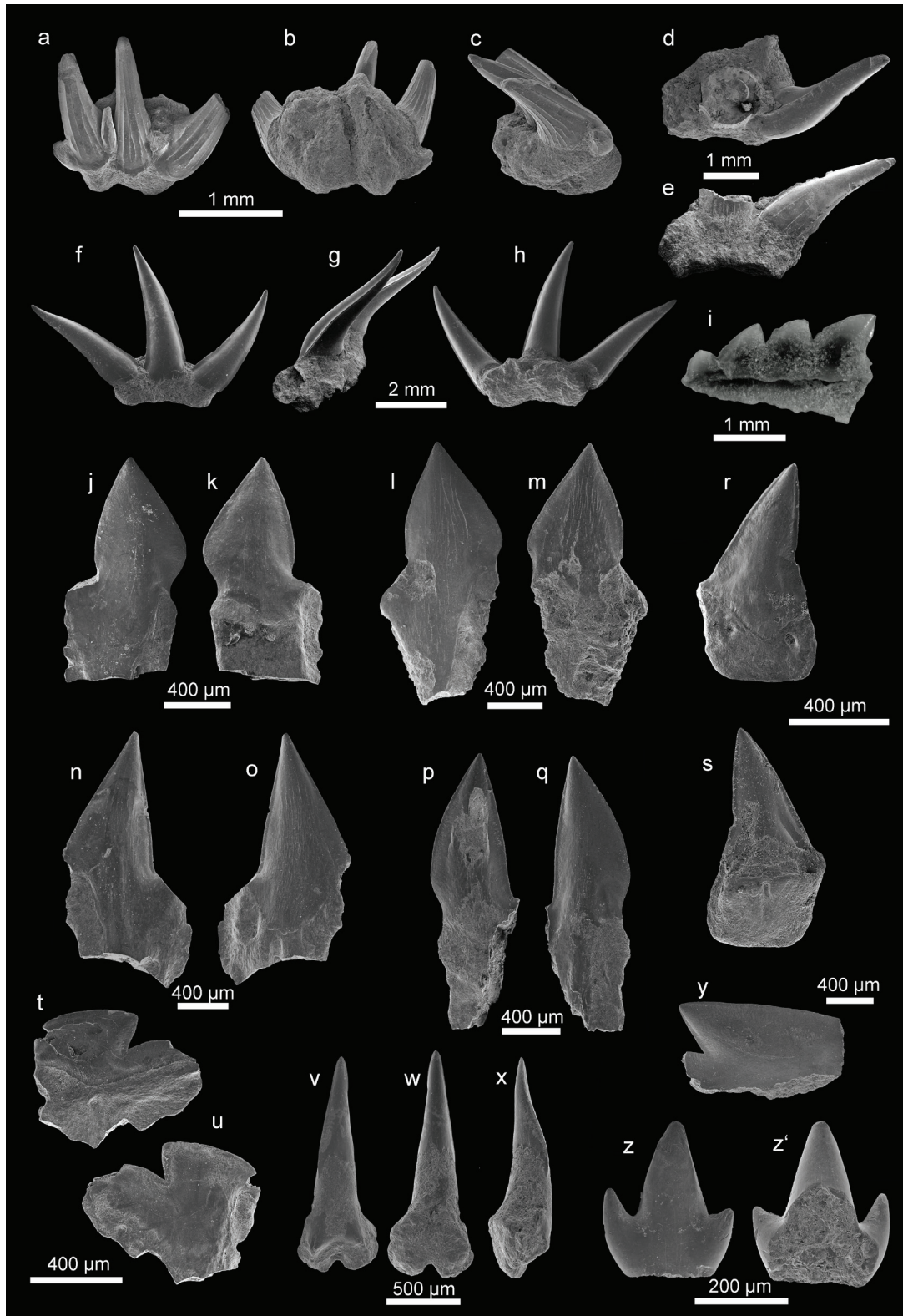


Figure 3: Teeth of Chlamydoselachidae, Hexanchidae, Somniosidae, Hemiscylliidae, and Squaliformes indet. from the Gamsbach section. **a–c:** *Rolfodon* sp. (NHMW/2023/0260/0001; horizon 5), **a:** labial, **b:** basal, **c:** profile views. **d–e:** *Rolfodon* sp. (NHMW/2023/0256/0001; horizon 9), **d:** occlusal, **e:** labial views. **f–h:** *Chlamydoselachus* sp. (NHMW/2023/0256/0002; horizon 9), **f:** labial, **g:** profile, **h:** lingual views. **i:** Hexanchidae gen. indet. (NHMW/2023/0254/0001; horizon 11), lingual view. **j–k:** *Protoxynotus* sp.: **j–k:** (NHMW/2023/0259/0001; horizon 6), **j:** labial, **k:** lingual views. **l–m:** (NHMW/2023/0259/0002; horizon 6), **l:** labial, **m:** lingual views. **n–o:** (NHMW/2023/0263/0001; horizon 2), **n:** labial, **o:** lingual views. **p–q:** (NHMW/2023/0259/0004; horizon 6), **p:** lingual, **q:** labial views. **r–s:** *Centroscymnus* sp., upper jaw tooth (NHMW/2023/0261/0001; horizon 4), **r:** labial, **s:** lingual views. **t–u:** *Centroscymnus* sp., lower jaw tooth (NHMW/2023/0263/0003; horizon 2), **t:** lingual, **u:** labial views. **v–x:** Somniosidae indet., upper jaw tooth (NHMW/2023/0254/0003; horizon 11), **v:** labial, **w:** lingual, **x:** profile views. **y:** Squaliformes indet., lower jaw tooth (NHMW/2023/0262/0001; horizon 3). **z–z':** ?*Hemiscyllium* sp. (NHMW/2023/0254/0002; horizon 11), **z:** labial, **z':** lingual views. Scale bars: 2 mm: **f–h**; 1 mm: **a–e**, **i**; 500 µm: **v–x**; 400 µm: **j–u**, **y**; 200 µm: **z–z'**.

dae, Squaliformes indet., ?*Hemiscyllium* sp., *Cretolamna* ex gr. *borealis*, Mitsukurinidae indet., Lamniformes indet., *Palaeogaleus* sp., Carcharhiniformes sp. 2, and Carcharhiniformes indet. It is noteworthy that highly fragmented cusps assigned to Chlamydoselachidae indet. likely represent teeth of the genus *Chlamydoselachus* and thus, are not considered to account for an additional species recovered from the Danian. Conversely, the fragmented chlamydoselachid cusps from the Maastrichtian are mentioned as an additional species, as they are distinctly distinguishable from *Rolfodon* and thus, represent a second, probably new genus or species within the Chlamydoselachidae.

4.2. Remarks on palaeoecology, palaeogeography, and stratigraphic range of the elasmobranchs recovered

4.2.1. Hexanchiformes

The majority of the identified genera show wide palaeogeographic and stratigraphic ranges. The genus *Rolfodon* (Hexanchiformes, Chlamydoselachidae) is known from the Santonian and Campanian of Antarctica (Richter and Ward, 1990; Kriwet et al., 2006), the Campanian of Angola and Canada (Antunes and Cappetta, 2002; Cappetta et al., 2021), the Maastrichtian of Japan (Tanimoto and Tani, 1998), the Danian of New Zealand (Consoli, 2008), with additional records in younger strata (see Cappetta, 2012). The second documented genus of the family Chlamydoselachidae, *Chlamydoselachus*, is known from the Santonian of Japan (Kitamura, 2019) and from the Campanian of Canada (Cappetta et al., 2021), the Maastrichtian of Japan (Goto et al., 1999), Antarctica (Cione et al., 2018), and Austria (Feichtinger et al., 2023), with additional records in younger strata (see Cappetta, 2012). Both known extant chlamydoselachid species, *Chlamydoselachus anguineus* Garman, 1884 and *C. africana* Ebert and Compagno, 2009, have a bathydemersal and benthopelagic lifestyle. The presence of chlamydoselachids in the bathyal palaeoenvironments of Gamsbach agrees with the ecology of extant representatives of this family.

The recovered hexanchid teeth are generally very badly preserved, however, the teeth show most similarities with that of the genus *Hexanchus*. The fossil record of the cosmopolitan genus *Hexanchus* (Hexanchiformes, Hexanchidae) extends back to the Santonian (Davis, 1887; Cappetta, 1980, 2012). Records from the Maastrichtian are documented from the USA (Case and Cappetta, 1997; Case et al., 2017), Syria (Bardet et al., 2000), Morocco (Noubhani and Cappetta, 1997), Egypt (Cappetta, 1991), Brazil (Rebouças and Santos, 1956), and Austria (Feichtinger et al., 2023). The genus is also known from the Danian of Denmark (Adolfssen and Ward, 2014, 2015), Sweden (Siversson, 1995), and Morocco (Noubhani and Cappetta, 1997) and comprises three extant representatives, which all possess a bathydemersal lifestyle inhabiting water depths down to 2500 m (Compagno et al., 2005).

4.2.2. Squaliformes

The extinct genus *Protoxynotus* represents a small somniosid shark with a fossil record ranging from the Turonian to the latest Maastrichtian and a palaeogeographic distribution restricted to the Boreal and Tethyan Realms. This genus is exclusively known from intermediate to deep marine environments in Germany, Lebanon and Austria (see Feichtinger et al., 2022a, b).

The second somniosid genus, *Centroscyrnus*, is known from the Campanian of Canada and Germany (Cappetta, 2012; Cappetta et al., 2021), the Campanian and Maastrichtian of Sweden (Siverson, 1993a) and Germany (Herman, 1982) and with one record in the Danian of Denmark (Adolfssen and Ward, 2014; for stratigraphically younger records see Cappetta, 2012). The tooth morphology of the fossil species *C. praecursor* Müller and Schöllmann, 1989 known from the Campanian to the earliest Danian, is very close to that of the teeth reported in this study. The extant representatives of *Centroscyrnus* have a bathydemersal lifestyle with a depth range down to 3700 m (Compagno et al., 2005), and the record of this genus from bathyal deposits at Gamsbach agrees with this distribution.

4.2.3. Orectolobiformes

The extant genus *Hemiscyllium* (Hemiscylliidae) has a stratigraphic record starting in the Campanian with occurrences in the USA, Canada, Spain, and Germany (Cappetta, 2012; Cappetta et al., 2021). The records in the Maastrichtian are from the USA (Case et al., 2001), Morocco (Noubhani and Cappetta, 1997), Jordan (Cappetta et al., 2000), Senegal (Guinot et al., 2023), Germany (Zacke, 2003), and Denmark (Adolfssen and Ward, 2014, 2015). Although the genus was palaeogeographically widespread during the Late Cretaceous, teeth of *Hemiscyllium* are extremely rare during the Paleocene, being only reported from the Danian of Denmark (Adolfssen and Ward, 2014, 2015) and the Danian of the Limhamn Quarry in Sweden (Siverson, 1993b), where 1% of all recovered elasmobranchs belong to *Hemiscyllium* (Siverson pers. com.). Given the state of preservation, the assignment of this tooth to *Hemiscyllium* is only tentative. The habitat of all nine extant species is reef-associated, ranging down to a water depth of 50 m (Compagno et al., 2005), which contrasts with the palaeoecology of some Late Cretaceous representatives. The genus *Hemiscyllium* was reported from intermediate to deep-water environments of the Campanian of Hornby Island, Canada (Cappetta et al., 2021), Maastrichtian of Jasmund Peninsula, Germany (Zacke, 2003), and latest Maastrichtian-earliest Danian of Stevns Klint, Denmark (Adolfssen and Ward, 2014, 2015). However, some records include shallow marine environments down to 50 m (e.g., Case, 1991; Noubhani and Cappetta, 1997; Underwood and Mitchell, 1999) indicating higher adaptability to cope with different environments compared to modern representatives.

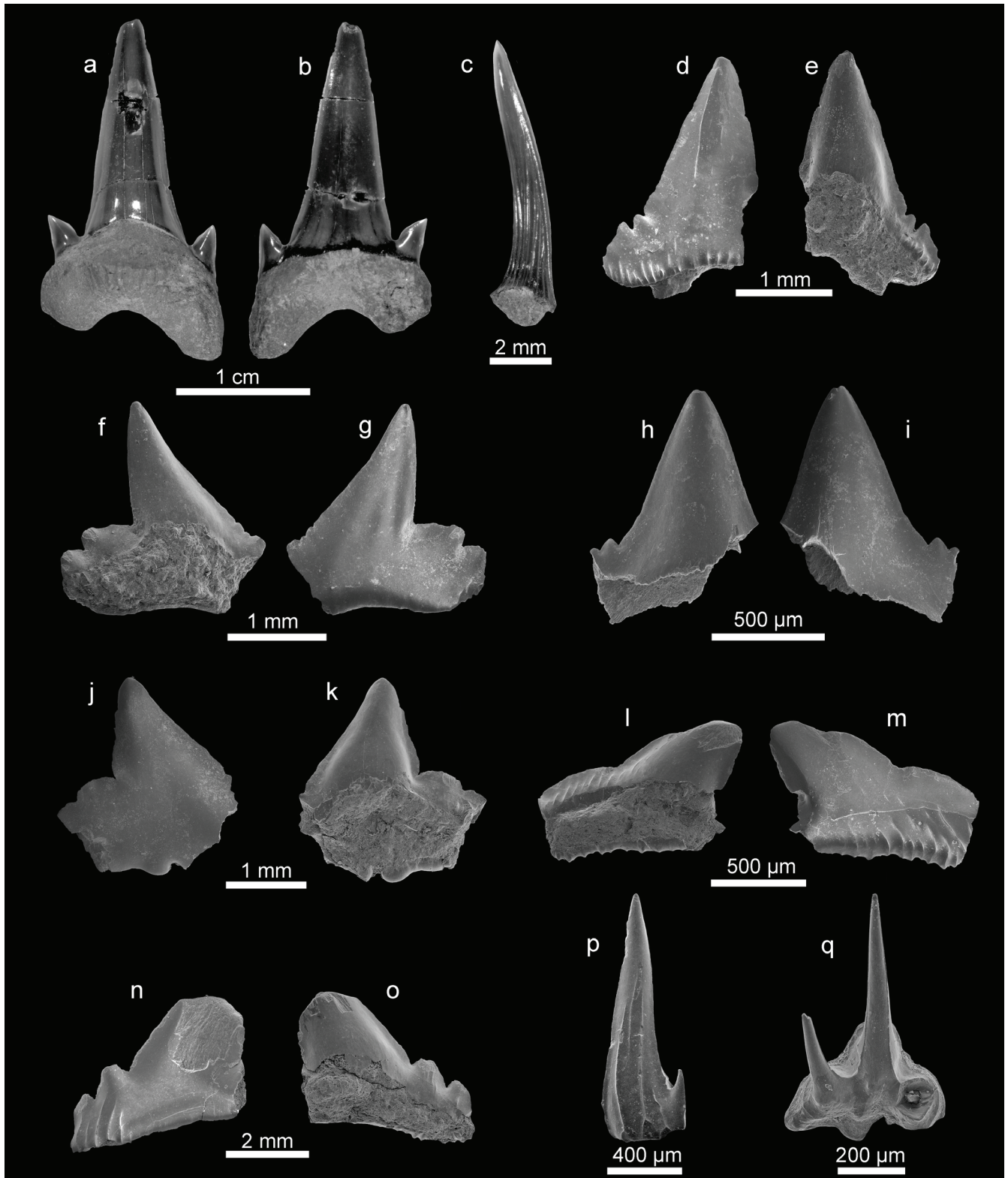


Figure 4: Teeth of Otodontidae, Mitsukurinidae, Triakidae, and Carcharhiniformes from the Gamsbach section. **a–b:** *Cretolamna* ex gr. *borealis* (NHMW/2023/0256/0003; horizon 9), **a:** lingual, **b:** labial views. **c:** Mitsukurinidae (NHMW/2023/0256/0004; horizon 9), profile view. **d–o:** *Palaeogaleus* sp.: **d–e:** (NHMW/2023/0256/0006; horizon 9), **e:** labial, **f:** lingual views. **f–g:** (NHMW/2023/0256/0007; horizon 9), **f:** lingual, **g:** labial views. **h–i:** (NHMW/2023/0256/0008; horizon 9), **h:** lingual, **i:** labial views. **j–k:** (NHMW/2023/0256/0009; horizon 9), **j:** labial, **k:** lingual views. **l–m:** (NHMW/2023/0256/0010; horizon 9), **l:** lingual, **m:** labial views. **n–o:** (NHMW/2023/0257/0001; horizon 8), **n:** labial, **o:** lingual views. **p:** Carcharhiniformes sp. 2 (NHMW/2023/0256/0005; horizon 9), labial view. **q:** Carcharhiniformes sp. 1 (NHMW/2023/0260/0002; horizon 5), occlusal view. Scale bars: 1 cm: **a–b**; 2 mm: **c**; 1 mm: **d–g, j–k**; 400 µm: **p**; 200 µm: **q**.

4.2.4. *Lamniformes*

The extinct species *Cretolamna borealis* (Otodontidae) is known from the Santonian of Japan (Shimada et al., 2010; Siversson et al., 2015) followed by an expansion of its palaeogeographic range during the Campanian (Glikman, 1980; Averianov and Popov, 1995; Vullo, 2005; Siversson et al., 2015). Siversson et al. (2015) reassessed the validity of this species and considered one of the specimens used by Priem (1897) when erecting the species *Lamna borealis* as not belonging to the species *Cretolamna borealis*. According to Siversson et al. (2015) this specimen from the Danish Faxø quarry (NP3 Zone, Danian), along with others from the Danian (NP3 Zone) horizons of the Limhamn quarry, Sweden, differs from *C. borealis* in the morphology of lateral cusplets and basal edge of the root. The specimen recovered from the earliest Danian horizon 9 of Gams differs from all known *Cretolamna borealis* specimens reported so far by the morphology of the lateral cusplets and the morphology of the labial face of the crown and root (M. Siversson pers. com.) and are here included in *Cretolamna* ex gr. *borealis*.

The elongated needle-like cusps with well-developed cutting edges and strong lingual crown folds (Fig. 4c) are characteristic of teeth of the family Mitsukurinidae. The family comprises the extinct genera *Anomotodon*, *Scapanorhynchus*, *Striatolamia*, and *Woellsteinia* with a fossil record dating back to the Early Cretaceous (Biddle, 1993; Cappetta, 2012). The extant genus *Mitsukurina* evolved during the Paleogene and represents a rare, but typical deep-water inhabitant in modern oceans (Compagno et al., 2005). A preferred deep-water habitat for this group is also reflected by the higher abundance of the teeth with increasing water depth in the Danian horizons at Gams. In the Waidach section, the mitsukurinids *Anomotodon plicatus* and *Anomotodon* sp. were only recovered from Maastrichtian horizons with no records of Mitsukurinidae in the Danian (Feichtinger et al., 2024), which is likely due to the shallowing upward trend of the section.

4.2.5. *Carcharhiniformes*

The extinct genus *Palaeogaleus* (Triakidae) possesses a wide palaeographic and stratigraphic range. Records from the Maastrichtian comprise the USA, Morocco, Spain, Netherlands, Belgium, France, Germany, and Denmark (Cappetta, 2012; Adolfssen and Ward, 2014; Hoganson et al., 2019). The genus crossed the K-Pg boundary and is known from the Danian of the USA (Ward and Wiest, 1990), Morocco (Noubhani and Cappetta, 1997), Denmark (Adolfssen and Ward, 2014, 2015), Sweden (Nilsson, 2003), and Austria (Feichtinger et al., 2024). For stratigraphically younger records see Cappetta (2012). The Triakidae represents a diverse group of small- to medium-sized sharks inhabiting a wide range of environments, hampering palaeoecological inferences based on modern representatives. However, most *Palaeogaleus* specimens from the Maastrichtian or Danian derive from shallow-marine environments or intermediate water depths (e.g., Herman,

1977; Noubhani and Cappetta, 1997; Cappetta and Corral, 1999; Nilsson, 2003; Adolfssen and Ward, 2014; Case et al., 2017; Hoganson et al., 2019). This is in accordance with the appearance of *Palaeogaleus* spp. in the Danian of the Waidach section, which is linked to a shallowing trend of the succession across the K-Pg boundary (Feichtinger et al., 2024). Although the apparition of *Palaeogaleus* in the Danian at Gams and Waidach is contemporaneous the depositional environment differs significantly, which is interpreted as outer neritic at Waidach and bathyal at Gams pointing towards a high adaptability to different environmental settings of the extinct genus *Palaeogaleus* after the K-Pg crisis.

5. Conclusions

The composition of the elasmobranch assemblages recovered from eleven successive horizons spanning the Cretaceous-Paleogene boundary of the Gamsbach section reflects a deep-marine environmental setting, which is congruent with previous palaeoecological reconstructions from the Gams basin. The observed heterogeneity in diversity between the assemblages may partly be a result of the preservation of the teeth and limited morphological characters available for taxonomic identification. Notwithstanding this, some trends in the evolution of the faunal composition are observed, which are possibly related to the increase of water depth throughout the section. These include the successive appearance of frilled sharks (*Rolfodon* sp., *Chlamydoselachus* sp., and *Chlamydoselachidae* indet.) and goblin sharks (Mitsukurinidae), which suggests an increase in water depth. This trend is also reflected in the high total proportion of triangular, labio-lingually compressed tooth cusps in the uppermost sampled horizon, which presumably represent teeth of Squaliformes. None of the two somniosid squaliform genera identified in the Maastrichtian horizons at Gams were found in the Danian samplings. While the typical deep-water inhabitant *Protosynodus* (Somniosidae, Squaliformes) went extinct at the end-Cretaceous, *Centroscymnus* is known to cross the K-Pg boundary in other marine realms. However, teeth of the latter might be present among the large number of unidentifiable, triangular, labio-lingual compressed teeth recovered from the Danian assemblages of this section. Except for one enigmatic species of the order Carcharhiniformes (*Carcharhiniformes* sp. 1), all other representatives of this order (*Palaeogaleus* sp., *Carcharhiniformes* sp. 2, and *Carcharhiniformes* indet.) derived from the Danian assemblages pointing to the preference of deep-marine conditions of this section. This contrasts especially with the ecological range of the cosmopolitan genus *Palaeogaleus*, which was previously known to inhabit shallower marine environments. In addition, the occurrence of *Heimysyllium* in a bathyal environment provides further evidence for the wide palaeoecological range of this genus, of which all extant representatives are reef-associated. Furthermore, this study provides the first record of the

lamniform species group *Cretolamna* ex gr. *borealis* from the Danian in the Tethyan Realm.

Despite the poor preservation of the 1852 elasmobranch teeth recovered, this study documents at least 16 taxa that thrived in or migrated through a bathyal environment, which sediments are rarely accessible for extensive bulk sampling. Based on the rarity of fossil-bearing bathyal outcrops, this study contributes significantly to revealing the palaeoecological range of certain deep-sea elasmobranch species during this crucial period spanning a first-order mass extinction event.

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