Vertebrate remains from the Turonian (Upper Cretaceous) Gosau Group of Gams, Austria

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ABSTRACT

A new, systematically collected vertebrate assemblage from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria (Northern Calcareous Alps) is described here. The material consists of teeth and bones of chondrichthyan (Selachimorpha indet., *Ptychotrygon gueveli*) and osteichthyan fishes (cf. *Lepisosteus* sp., Vidalamiinae indet., Pycnodontidae indet.), amphibians (cf. *Thaumastosaurus* sp.), lizards ('Lacertilia' indet.), mosasauroids (Tethysaurinae indet.), *Theriosuchus*-like and other, peculiar crocodyliforms and theropod dinosaurs (cf. *Paronychodon* sp.). The faunal composition is most similar to the Santonian fauna of Iharkút, western Hungary, a phenomenon that can be explained by the spatial and temporal closeness of the two landmasses. The Gams assemblage is of great importance since continental vertebrates from the Cenomanian to Santonian interval of Europe are extremely scarce, and it provides a small but significant link between older and younger vertebrate faunas in the region.

Keywords: vertebrate fauna, fishes, amphibians, sauropsid reptiles, Turonian, Northern Calcareous Alps

Highlights: A new Turonian vertebrtae fauna from Gams, Austria is described. The assemblage is composed of both marine and land vertebrates. The fossils provide a link between older and younger vertebrate faunas.

1. Introduction

Early Late Cretaceous (Cenomanian to Santonian) continental vertebrate fossils are extremely rare in Europe. This is especially true for the Turonian–Coniacian interval when the sea level was one of the highest during the Phanerozoic (Csiki-Sava et al., 2015; Haq, 2014; Haq et al., 1987; Miller et al., 2003; Seton et al., 2009). Turonian remains, with a single poor exception, are restricted to scarce isolated elements (e.g. Stoliczka, 1860). In western France (Châteauneuf, Vendée) a few isolated vertebrate fossils from upper Turonian shallow-water limestones document the occurrence of indeterminate turtles, crocodylians, and possibly theropod dinosaurs (Buffetaut and Pouit, 1994; Buffetaut et al., 1991). Isolated, fragmentary remains of ornithocheirid pterosaurs from the basal members of the White Chalk Subgroup (UK) and a partial wing skeleton of a possible azhdarchoid (*Cretornis*) were reported from the Jizera Formation (Czech Republic; Averianov and Ekrt, 2015; Frič, 1881). Besides body fossils, an undescribed dinosaur tracksite from the Iberian Peninsula (Asturias, northern Spain), was mentioned by Ruiz-Omeñaca et al. (2009).

This extreme scarcity of Turonian (and practically of late Cenomanian to Santonian) continental vertebrates results in a massive knowledge gap of Early Late Cretaceous faunas, preventing the deciphering of their evolutionary history in the Cretaceous European archipelago.

Here we present a new, systematically collected vertebrate assemblage from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria (Northern Calcareous Alps, Fig. 1). The material, collected from the basal, coal-bearing layers of these Gosau Group strata, shows a mixture of marine and continental faunal elements and contributes to the better understanding of continental faunal compositions in the critical Turonian–Santonian period of the European archipelago.

Institutional abbreviations: **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MTM**, Magyar Természettudományi Múzeum, Budapest, Hungary; **NHMW**, Naturhistorisches Museum Wien, Vienna, Austria. **PIUW**, Paläontologische Institut, Universität Wien, Vienna, Austria.

2. Localities and geological setting

The Gosau Group of Gams near Hieflau (community of Landl, federal province of Styria) comprises a more than 1500 m thick succession of Upper Cretaceous to Paleogene strata (Kollmann, 1964; Wagreich et al., 2009). Sedimentation started unconformably above Triassic to Jurassic rocks of the Northern Calcareous Alps (Fig. 2). The succession can be subdivided into a terrestrial-shallow marine Lower Gosau Subgroup (Turonian–Campanian), mainly exposed in the western part of the Gams Basin, and the deepwater Upper Gosau Subgroup (Campanian– lower Eocene).

The Lower Gosau Subgroup (Wagreich and Faupl, 1994), including the sampled locality of this study, starts with reddish to grey conglomerates (Kreuzgraben Formation) of a terrestrial alluvial fan to fluvial environment (Wagreich et al., 2009, Fig. 2). These basal conglomerates are inferred to the upper Turonian, constrained by overlying upper Turonian marine strata of the Schönleiten Formation. It records marginal-marine environments with intermittent brackish influence, some coal seams (Fig. 2) in a shaly to sandy shallow water environment (Kollmann and Sachsenhofer, 1998). The following Noth Formation (Siegl-Farkas and Wagreich, 1997) includes rudist biostromes (Sanders and Pons, 1999), serpentinitic sandstones and a variety of mega- and microfossils (Kollmann, 1964; Wagreich et al., 2009), e.g. the gastropod *Trochacteon*. The following Grabenbach Formation comprises mainly grey shelf marls and shales with rare tempestite layers, including ammonites such as *Barroisiceras haberfellneri*, inoceramids and *Didymotis* of a latest Turonian to Turonian/Coniacian boundary age (Summesberger and Kennedy, 1996). The heterolithic Krimpenbach Formation (Wagreich, 2004) of late Santonian to mid-Campanian age (Summesberger et al., 1999) concludes the succession of the Lower Gosau Subgroup. The unconformably overlying Campanian to Lower Eocene Upper Gosau Subgroup consists of the Nierental Formation and the Zwieselalm Formation (Kollmann 1964; Egger et al., 2004; Wagreich et al., 2009).

The Schönleiten Formation was defined by Kollmann and Sachsenhofer (1998). It comprises up to 200 m thick, mainly gray, yellowish weathering shales and layers of densely packed sandstone; coal-bearing shales occur mainly at the base of the succession. Isolated tree trunks have been transformed into jet with a high bitumen content. The jet of the Schönleiten Formation was mined between 1418 and 1560 for making rosaries and jewels (Hable, 2016). Waste tips and an area with numerous small pits close to the Akogl road at an altitude of 700 metres are witnesses of mining in the area. It is, however, impossible to distinguish the tips of medieval mining from those of the middle of the 19th century when great efforts where undertaken to replace charcoal by fossil coal in local iron production.

2.1. Locality and palaeoenvironment

The sampled outcrop is located at the Akogl private road, about 25 m west of its first turn (Fig. 1). The base of the exposed succession is formed by a coarse, partly reddish conglomerate of the Kreuzgraben Formation which is delimited against Triassic and Upper Jurassic limestones by a younger strike-slip fault. The basal sediments of the Schönleiten Formation are almost vertically bedded.

The outcrop consists of about 1.5 m of dark coal shale within a grey shale. All new findings described in this paper come from this layer (Fig. 2). The coal-bearing shale contains randomly distributed carbonized plant remains, which originate from rooted plants, probably of conifers (Eder-Kovar, oral communication). A short abandoned mining gallery at the outcrop was obviously supposed to find mineable coal in this shale.

Calcareous nannofossil data from the outcrop indicate a late Turonian age, including *Marthasterites furcatus* and *Eiffellithus eximius* (Siegl-Farkas and Wagreich, 1997). Rare planktonic foraminifera (Kollmann, 1964) suggest the *Marginotruncana schneegansi* Zone of the late Turonian, below the first occurrence of *Dicarinella concavata*. Palynology analyses report the *Subtrudopollis-Complexiopollis* Zone of Siegl-Farkas and Wagreich (1997), characterized by early angiosperms, gymnosperms, pteridophytes and some Normapolles. Pavlishina et al. (2004) resampled the outcrop and reported a rich spore association (*Deltoidospora* spp.), high abundances of *Taxodiaceaepollenites*, dinocysts in fluctuating abundances (e.g. *Spiniferites* spp., *Palaeohystrichophora infusorioides*), and Normapolles taxa like *Emscheripolli*s spp. The dinoflagellate cyst *Subtilisphaera pirnaensis* suggests Turonian age according to Pavlishina et al. (2004).

From the grey shale Schultz and Paunović (1997) recorded a jaw fragment of a pycnodontiform fish referred as *Coelodus* cf. *saturnus* (see in this paper). Besides this, fossil gastropods have been reported from the shale (Kollmann and Sachsenhofer, 1998), among them *Megalonoda reussi*, which is the stratigraphically earliest recording of a Melanopsidae gastropod. These gastropods give evidence for a brackish environment (Kollmann, 1984; Neubauer et al., 2016). This is also the case with *Cassiope*, which is common in the Late Cretaceous *Cassiope-Pirenella* assemblage of the Gosau Group of Brandenberg in Tyrol (Kowalke and Bandel, 1996).

Besides the before-mentioned taxa, *Turritella rigida* was recorded from this outcrop (Kollmann and Sachsenhofer, 1998). In modern marine environments, *Turritella* is restricted to environments below the fair weather base of the mid- to outer shelf (Allmon, 1988; Kollmann, 2005).

Other outcrops of the Schönleiten Formation show either a similar occurrence of both brackish and outer shelf taxa or exclusively of outer shelf taxa besides *Turritella* like single corals, the bivalves *Phelopteria* and *Pseudamussium* and foraminifera (Globotruncanidae) (Kollmann, 1964; Kollmann and Sachsenhofer, 1998). A fossil fauna collected by Peters (1852) and Reuss (1854) on a mining waste tip shows mainly taxa of the outer shelf but according to Reuss also *Omphalia* (=*Cassiope*). Oyster shells found together with the tree trunks and branches washed in from the mainland as drift wood and transformed into jet (Kollmann and Sachsenhofer, 1998) have probably been attached to them. This indicates a long period of drifting before they sank to the sea floor.

Summing up, it is evident that the plant fragments from the mainland and fossil mollusc remains from a brackish environment have been introduced into a shallow water depositional setting of the proximal to distal (outer) shelf. The deposition of plant and continental vertebrate material in layers suggests temporary transport of costal and terrestrial organic material by rivers into the sea, probably following major storm events. Although the grey shales containing the vertebrate fossils described herein, suggest a distal deposition there is no direct evidence concerning the position towards the mainland. A rough relief with steep slopes can be inferred, as typical for large parts of the Gosau Group of the Northern Calcareous Alps (e.g. Wagreich and Decker, 2001).

Although the vertebrate assemblage, described in this paper, is quite fragmentary (due also to the screen-washing procedure) and represents a mixture of marine and continental faunal elements, we do not think that the continental elements were reworked from older sediments based the following reasons: 1) there is no indication of abrasion as a result of physical grinding and polishing on the edges and surfaces on the teeth and the few identified bones; 2) we cannot detect weathering produced by physical and chemical agents, as seen, for example, on the Iharkút assemblage (Botfalvai et al. 2015). Based on the available taphonomical features, we assume that the vertebrate assemblage is an accumulation of bones and teeth from different (marine and terrestrial) environments in a shallow marine environment as a result of periodical river influx.

3. Material and methods

Specimens collected by our research team in 2017, as well as material obtained by screenwashing in 2014, are housed in the collections of the Natural History Museum Wien in Vienna, Austria (NHMW). The list of specimens collected in taxonomical order is in Table 1. The prefix NHMW belongs to all the catalogue numbers of the specimens, but for easier reading we only list the numbers in the text.

One ton of sample was collected from the coal-bearing basal beds of the upper Turonian Schönleiten Formation. Screenwashing and dissolution of the residue was processed partly following the Henkel process (Henkel, 1966; Martin and Krebs, 2000).

Material was dried exposed to the sun and was first washed with water through three different sieves with mesh sizes of 3 mm, 1 mm, 0.5 mm. Approximately 150 kg of residue was decanted from the largest fraction and was macroscopically sorted. In addition, 95 kg of the medium fraction (particle size between 2 and 1 mm) was also decanted. In order to dissolve the matrix of this medium fraction (in great part molluscan shell fragments), 20 % acetic acid was used. The ca. 60 kg residue of this process was then washed with water and dried. By applying a KOH solution of 65 - 80° for one hour, the dominant coalified plant fragments separated were rom the remainder of the residue. Finally, the remaining, ca. 11 kg material was washed again with water, dried and sorted under the light microscope.

Besides vertebrate fossils, two seeds (2018/0267/0000), hundreds of small amber fragments (2018/0268/0000), hundreds of termite coprolites (2018/0269/0000), and 59 ostracods (2018/0270/0000) have been also found.

4. Description and comparisons

Chondrichthyes Huxley, 1880

Selachimorpha Nelson, 1984

Selachimorpha indet.

Fig. 3A–F

Material: one tooth (2018/0252/0001), one dermal denticle (2018/0252/0002).

Description: The only here referred tooth specimen is hardly fragmentary (Fig. 3A–C). In profile view, the crown slightly bends lingually. The labial crown face is smooth, while the lingual crown face bears longitudinal striae, not extending to the cutting edge. The preserved cutting edge is smooth all along. Unfortunately, the preserved characters do not allow us to identify this single remain more accurately as an indeterminate shark tooth fragment.

A single dermal denticle has been found in the assemblage (Fig. 3D–F). The crown is drop-or arrowhead-shaped in apical view, with anteriorly bulging median keel reaching from the anterior margin to the anteroposterior half of the crown. One pair of short, lateral folds are present running parallel to the median keel.

Remarks: Various Late Cretaceous sharks had tooth morphology resembling that of the Gams shark tooth specimen, e.g. Hybodontidae, Mitsukurinidae, Scyliorhinidae (see Bourdon et al., 2011; Cappetta, 2012; Kriwet et al., 2009; Sweetman et al., 2014). The dermal denticle is similar to those of the orectolobiform *Phorcynis* (see Thies and Leinder, 2011), however, more specimens and associable dental remains are required for a certain identification.

Batomorphii Cappetta, 1980

Rajiformes Berg, 1937

Ptychotrygonidae Kriwet, Nunn and Klug, 2009

Ptychotrygon Jaekel, 1894

Ptychotrygon gueveli Cappetta, 2004

Fig. 3G–Y

Material: Four teeth (2018/0251/0001-0004).

Description: The teeth are wider than long, transversely elongate and bilaterally symmetrical. The crown is shiny and rectangular to lentoid in occlusal, whereas triangular in labial (and lingual) view, with rounded extremities. The occlusal surface is heavily ornamented. Three distinct transverse crests are present on the occlusal face, among them the middle one runs through the apex. The other two transverse crests divide above the rounded lingual (medioposterior) uvula and the labial (medioanterior) apron. The central cusp is not so well differentiated, it connects to the labial transverse crest with a short longitudinal ridge. Several short anastomosing ridges are present both labially and lingually, originating from the crown base to the mediolabial and the mediolingual transversal ridge. Some ridges, mostly those of the labial crown face connect to each other. The root is bilobate, both lobes are short, and triangular in basal view. The root is not jutting out under the crown in occlusal view. A well-developed lingual notch is present above the root.

Remarks: Because of their low frequency and small size, teeth of *Ptychotrygon* are rarely found without using micropaleontological methods, e.g. screenwashing (McNulty and Slaughter, 1972). According to Cappetta (2012) and Kriwet et al. (2009), the genus *Ptychotrygon* ranges from the Albian to the Maastrichtian with about 20 nominal species. Most species differ only in the ornamentation of the occlusal surface of their teeth (Schubert et al., 2016).

All Gams specimens bear the significant dental characters of the type material of *P. gueveli*, reported by Cappetta (2004) from the Turonian of France. The Gams teeth clearly differ from the teeth of *P. triangularis* and *P. ledouxi* (note that Meyer (1974) synonymized the latter two species) in having markedly more developed occlusal ornamentation (see Becker et al., 2010; Cappetta, 1973; Hamm and Cicimurri, 2011; McNulty and Slaughter, 1972; Schubert et al., 2016; Williamson et al., 1993). Since its formal description (Cappetta, 2004), the present study provides the second report of *P. gueveli*.

The massive teeth characteristic for the genus are well adapted to processing small invertebrates like crustaceans, bivalves, annelids and even small fish they were able to catch. Species of *Ptychotrygon* are considered as inhabitants of shallow marine, coastal waters or even of estuarines (Kriwet, 1999).

Chondrichthyes indet.

Fig. 3Z, A’

Material: two dermal denticles (2018/0253/0001-0002).

Description: Two dermal denticles sharing the same morphology are referred to indeterminate chondrichthyans. In apical view the crown is oval to rectangular, and weakly ornamented by crenulae around the outline. The base of both specimens is rather poorly preserved, and in basal view a small circular foramen of the basal canal is visible.

Remarks: The Gams chondrichthyan denticles are similar to the figured denticles of Thies and Leidner (2011, pl. 26, figs B–D). Because of the low number and poor preservation of the denticles, they can not be undeniably attributed to any chondrichthyan. Until more specimens, or associable skeletal or dental elements are found, here we describe them only as indeterminate chondrichthyan denticles.

Osteichthyes Huxley, 1880

Actinopterygii Cope, 1887

Lepisosteiformes Hay, 1929

Lepisosteidae Cuvier, 1825

Lepisosteus Lacépède, 1803

cf. *Lepisosteus* sp.

Fig. 4A–D

Material: six teeth (2018/0254/0001-0006), two ganoid scales (2018/0254/0007-0008)

Description: The teeth are of simple morphology and relatively poorly preserved. Some specimens still have some portions of the tooth base preserved, showing fine apicobasal striations (referring to plicidentine tooth structure). Though the very tip of the best preserved specimen (2018/0254/0001, Fig. 4A, B) is missing, a few isolated acrodine caps were also found, showing simple, conical tip. This feature is characteristic for *Lepisosteus*, unlike *Atractosteus*, which has lanceolate fang tips (Sigé et al., 1997; see also figures of Grande, 2010 and Kammerer et al., 2006).

Three fragmentary ganoid scales have been also found. These scales are flat, exposing a bony base, covered by a shiny, continuous layer of ganoine. Although all scales are fragmentary, their preserved portions refer to a rhomboid outline in external view. Following Gayet and Meunier (1986, 2001) and Gayet et al. (2002), the parameters of the ganoine tubercles spreading on the external surface of the scales distinguish the lepisosteid genera from one another. Among the Gams ganoid scales specimen 2018/0254/0007 (Fig. 4C, D) exhibits a ganoine-surface well-preserved enough for taking measurements on the structure of the microsurface. Seventy-four tubercles and 169 inter-tubercular spaces have been measured, the average diameter of the tubercles is 5.669 μm, while the average inter-tubercular distance is 4,686 μm. Comparison of our results with measurements on other lepisosteid scales shows that the parameters of the microornamentation of 2018/0254/0007 also indicates a close relation to *Lepisosteus* (see Fig. 4E).

Remarks: Gars (family Lepisosteidae) are a well-known group of primitive neopterygians, with a fossil record going back to the Kimmeridgian (Late Jurassic) (Brito et al., 2017a). Lepisosteids are common elements of Late Cretaceous vertebrate assemblages in Europe, and even worldwide (Szabó et al., 2016a, fig. 1 and table 1). The family is represented by seven living species of two genera, *Atractosteus* and *Lepisosteus* (Grande, 2010). All extant lepisosteid species are piscivorous predators, inhabiting freshwater habitats mainly (Grande, 2010), however, all living species of *Lepisosteus* (*Lepisosteus oculatus*, *L. osseus*, *L. platostomus* and *L. platyrinchus*) occasionally occur in brackish and marine environments (Grande, 2010; Lee et al., 1980; Parker and McKee, 1984; Scott and Crossman, 1973; Smylie et al., 2016 and references therein; Suttkus, 1963).

Amiiformes Hay, 1929

Amiidae Bonaparte, 1838

Vidalamiinae Grande and Bemis, 1998

Vidalamiinae indet.

Fig. 5A–D

Material: three teeth (2018/0255/0001-0003).

Description: All here referred tooth remains comprise the enameloid caps only, representing a typical amiiform morphology. They are triangular and flattened, both faces are smooth and shiny, and slightly transparent at the cutting edges. The cutting edges are smooth all along, the very tip is pointed. In profile view, the teeth are slightly curved lingually (this might depend on the position of the tooth in the dental arcade). All Gams vidalamiine teeth bear slightly translucent enamel.

Remarks: Vidalamiine amiiforms are large-sized predatory fishes reported from various Mesozoic localities of Europe (Grande and Bemis, 1998; Martín-Abad and Poyato-Ariza, 2013; Szabó and Ősi, 2017). Their only report from the Late Cretaceous of Europe comprises two vertebral centra from the Santonian Csehbánya Formation of Iharkút (Hungary) (Szabó and Ősi, 2017). The Gams teeth are identical to the Vidalamiinae teeth figured by Brinkman et al. (2013, fig. 10.8A, B; 2017, fig. 5A), Brito et al. (2017b, fig. 4E, F) and Grande and Bemis (1998, figs 286F and 288H) both in size and morphology. Since the Gams vidalamiine material is restricted to isolated teeth, a generic determination would not be established. Nevertheless, the Gams report of Vidalamiinae represents the second occurrence of the subfamily from the Late Cretaceous of Europe. According to Grande and Bemis (1998), some vidalamiine taxa inhabited brackish and marine environments (and frequently entered drainages), while others may have preferred freshwaters with connection to the marine habitats, so their occurrence in these environments is not surprising.

Pycnodontiformes Berg, 1937

Pycnodontidae Poyato-Ariza and Wenz, 2002

Pycnodontidae indet.

Fig. 5E–R

Material: one fragmentary right prearticular (NHMWien 1996z0 189/000 1.), 33 molariform teeth (2018/0256/0000, 2018/0256/0001-0002), 4 incisiform teeth (2018/0256/0000, 2018/0256/0003-0004), 17 branchial teeth (2018/0256/0000, 2018/0256/0005).

Description: Schultz and Paunović (1997, fig. 5) reported *Coelodus plethodon* from the Turonian of Gams bei Hieflau based on a fragmentary right prearticular (NHMWien 1996z0 189/000 1.; Fig. 5E) with six teeth (three teeth of the principal prearticular tooth row and three teeth of the first lateral prearticular tooth row) preserved in their original arrangement. The medioventral region of the prearticular bears no teeth. Part of the coronoid process is also preserved.

Isolated molariform teeth discovered by screenwashing are elongate to roundish, or sometimes weakly rectangular in occlusal view (Fig. 5F–J). They display various stages of functional wear, however, unworn teeth of pycnodontids are usually ornamented by various grooves and crenulae. Isolated incisiform teeth are flattened labiolingually and rectangular in lingual (and labial) view. They represent two morphotypes: one with convex (Fig. 5K–M), and one with concave cutting edge (Fig. 5N–P). Following Szabó et al. (2016b), the two morphotypes possibly represent dentary and premaxillary incisiform teeth. The branchial teeth are fragmentary, they comprise only the bent, claw-like, slightly translucent, flattened apical portion (Fig. 5Q, R).

Remarks: Pycnodontiform fishes are characteristic elements of Late Cretaceous vertebrate assemblages worldwide. Their well-developed, specialized, heterodont dentition is suited for feeding on hard-shelled preys (e.g., various molluscs). Besides thousands of macroscopic mollusc specimens, a large number of such invertebrate taxa have been sorted from the screenwashed residue of the Schönleiten Formation.

Isolated pycnodontiform remains extremely similar to the Gams specimens have been reported from the Santonian Ajka Coal and Csehbánya formations (Ajka and Iharkút, Hungary) (Ősi et al., 2016, fig. 5A, C–E; Szabó et al., 2016b, figs 5, 6). The latter material also includes well-preserved prearticular and vomerine remains, which allowed us to describe the Iharkút material as cf. *Coelodus* sp. (Szabó et al., 2016b). The arrangement and general morphology of the teeth of specimen NHMWien 1996z0 189/000 1. are comparable with those of *Coelodus* (after Kriwet, 2005; characters 43–44 and 48–51 of Poyato-Ariza and Wenz, 2002), however, the specimen is too poorly preserved for a generic determination. The number of prearticular tooth rows, the number of teeth on main prearticular tooth row, and most of the characters of the coronoid process (characters 45–47 of Poyato-Ariza and Wenz, 2002) cannot be described because of the general condition of the specimen. Altogether, the Gams pycnodontiform material is too fragmentary for a generic description. Following the high intrageneric and intraspecific variability of the pycnodontiform dentition (Kriwet, 2005), here we find it more appropriate to describe the Gams pycnodontiform material, including NHMWien 1996z0 189/000 1., only as Pycnodontidae indet.

Actinopterygii indet.

Fig. 5S, T

Material: one vertebral centrum (2018/0257/0001).

Description: A single, incomplete vertebra is referred to an indeterminate actinopterygian. It consists of about one third of an amphicoelous centrum, the preserved portions refer to a circular outline. Numerous bony bars are extending between the anterior and posterior articular faces of the centrum.

Remarks: The centrum is similar to that of elopiform fishes (see Blanco et al., 2017, fig. 3E–J, L, M; Brinkman, 2014, pp. 34–35; Brinkman and Neuman, 2002, figs 1.19–1.27, Brinkman et al., 2013, fig. 10.14.C; Szabó and Ősi, 2017, fig. 11). The poor preservation of the here referred specimen does not allow us to identify it on lower rank.

Amphibia Gray, 1825

Lissamphibia Haeckel, 1866

Anura Fischer von Waldheim, 1813

Neobatrachia Reig, 1958

Ranoides Frost et al., 2006

Natatanura Frost et al., 2006

Familia incertae sedis

cf. *Thaumastosaurus* sp.

Fig. 6A–E

Material. One fragmentary left maxilla (2018/0258/0001).

Description. This robust bone has a distinctive pit-and-ridge structure on its labial surface. Pits are irregular and relatively deep and are surrounded with flattened and high-pitched ridges. The distribution of pits is relatively consistent. In lingual view, the horizontal lamina is well developed and rounded with a long edge in its lower third. However, the posterior end of the pterygoid process is broken but the remaining part is clearly remarkable projecting lingually. Behind the pterygoid process, a slightly oval foramen opens posterodorsally. The dorsal and ventral parts of this bone are broken off.

Remarks. The combination of a robust bone with a distinctive pit-and-ridge ornamentation on its labial surface, and the well-developed, rounded horizontal lamina is specific for *Thaumastosaurus*-like neobatrachian frogs (e.g. Holman and Harrison, 2002, 2003; Laloy et al., 2013; Rage and Roček, 2007; Roček and Lamaud, 1995). The irregular but rather circular pits on the labial surface of this specimen differ from the elongated pits of *Thaumastosaurus wardi* and *T. sulcatus* (Holman and Harrison, 2002, 2003). The oval foramen behind the well-developed pterygoid process is also present in *Thaumastosaurus bottii* (e.g. Roček and Lamaud, 1995) but in this species it is significantly larger. In other *Thaumastosaurus*-like neobatrachian frogs this anatomical feature is not mentioned. The broken tooth plate and dorsal margin do not allow the study of these parts of this maxilla.

Anura indet.

Fig. 6F-G

Material. Fragmentary presacral vertebra (2018/0259/0001).

Description. Only the centrum of this vertebra is preserved bearing a well-developed medial keel on its ventral surface (Fig. 6E).

Remarks. The only feature observed is an intense medial keel on the ventral surface of the centrum which also appears on vertebrae III and IV of the "mummified" specimen (MNHN QU 17279) of *Thaumastosaurus* described from the Quercy Phosphorites, the Eocene of France (Laloy et al. 2013). This suggests that this bone might belong to *Thaumastosaurus* but the aforementioned problems do not allow a more precise determination.

Sauropsida Goodrich, 1916

Squamata Oppel, 1811

'Lacertilia' indet.

Fig. 6H-K

Material. Fragmentary possible dentary (2018/0260/0001).

Description. A small (1 mm long, 1.5 mm high) fragment (Fig. 6H) bears two pleurodont teeth and another, damaged tooth position. The small size suggests that the specimen is from a juvenile individual. Judging from the curvature of the labial surface of the bone it is most probably a dentary fragment (Fig. 6I). The portion of the bone with the subdental shelf and the Meckelian canal is missing. The teeth are heavily worn or abraded, relatively closely packed and extend with about one fourth, one fifth of their height above the lateral wall of the bone (Fig. 6H–K). In lingual view the teeth have an elongated shaft that is slightly narrower at the base than the crown. No resorption pits are visible. The tooth crowns seem to be slightly curved backwards. They appear to have a blunt mid-cusp that is elevated above the mesial and distal areas. This mesial ’shelf’ is situated more basally than the distal one. In the case of the tooth in the mesial position this gives the mesial side of the crown an ’excavated’ appearance. This is also visible from mesial view on that tooth and on both teeth in occlusal view. However, in mesial view the teeth are the widest at mid-height of the shaft and taper gradually both in basal and apical directions with both the labial and lingual sides being convex. As a result the apex is blunt wedge-shaped in this view. The teeth are not curved in lingual direction but project straight apically from their bases in mesial view.

Remarks. This morphology is rather unusual. It does not seem to be an agamid or a chameleon which have an acrodont type of tooth implantation. Iguanids usually have simple, tricuspid or polycuspate teeth. Anguimorph teeth have labiodistally located resorption pits and basal crenulations. Geckos on the other hand, possess more simple teeth with cylindrical shafts and peg-like crowns. However, the Gams specimen can belong to a scincomorph, though this cannot be ascertained because it lacks diagnostic characters due to its fragmentary nature (Estes, 1983; Estes et al., 1988).

This is not unlikely since a wide variety of taxa assigned to this group has been reported from the Upper Cretaceous localities of Europe, though a similar tooth crown morphology has not been described yet in any of them (Blain et al., 2010; Codrea et al., 2002; 2012; 2017; Csiki et al., 2008; Folie and Codrea, 2005; Gheerbrant et al., 1997; Makádi, 2006; 2013a; 2013b; Makádi and Nydam, 2015; Rage, 1999; 2013; Venczel and Codrea, 2015; Vullo and

Néraudeau, 2008; Vullo et al., 2011). The Gams lizard jaw fragment is too fragmentary to be assigned unequivocally to any groups but might be a scincomorph.

Remarks. The taxonomic name ’Lacertilia’, though now considered paraphyletic and obsolete, is used for the sake of simplicity to designate non-ophidian and non-amphisbaenian squamates.

Mosasauroidea Camp, 1923

Tethysaurinae Makádi, Caldwell et Ősi, 2012 *sensu* Makádi et al., 2012

cf. Tethysaurinae indet.

Fig. 6L-O

Material. 14 teeth (2018/0261/0001-0014).

Description. Several small tooth crown fragments (Fig. 6L-O) have been recovered from the screenwashing residue which are neither fish nor archosaurian teeth. However, they are most similar to the teeth of tethysaurine and halisaurine mosasauroids, especially the tethysaurine *Pannoniasaurus* from the Santonian Iharkút continental vertebrate locality, Hungary (Makádi, et al., 2012).

The tooth fragments are conical and curved linguodistally (Fig. 6L, M), though a few fragments seem to curve in the opposite direction. This suggests that the teeth, though curved backwards and inwards altogether, had a slight S-shaped curvature, similarly to *Pannoniasaurus* and *Halisaurus arambourgi* (Bardet et al, 2005; Makádi et al., 2012; L.M. personal observation). The cross-section of the teeth is subcircular, with the labial side being less convex than the lingual one (Fig. 6N) as in *Pannoniasaurus* (L.M., personal observation).

Two carinae are present on the teeth, of which the mesial carina is stronger than the other, similarly to *Pannoniasaurus* (Makádi et al., 2012). Since the other carina has a labiodistal position in most mosasaurs with carinated teeth, tethysaurines or other (e.g. Makádi et al., 2012; Massare, 1987; Páramo, 1994; Páramo-Fonseca, 2000; Polcyn and Bell, 2005), a similar arrangement is suggested also in the case of the Gams specimens. Basically, all tethysaurines (*Russellosaurus*, *Yaguarasaurus*, *Pannoniasaurus*, *Romeosaurus*) but *Tethysaurus* (which does not have carinae at all) seem to have this condition (Bardet et al., 2003; Makádi et al., 2012; Palci et al., 2013; Páramo, 1994; Páramo-Fonseca, 2000; Polcyn and Bell, 2005). *Halisaurus*, on the other hand has mesially and distally positioned carinae (Bardet et al, 2005).

The surface of the crowns bears fine longitudinal striae (Fig. 6L, M, O) like in *Pannoniasaurus, Russellosaurus, Romeosaurus sorbinii* and *Halisaurus* (as well as in the non-tethysaurine and non-halisaurine *Plioplatecarpus, Platecarpus* and *Clidastes*) (Bardet and Pereda Suberbiola, 2002; Bardet et al, 2005; Makádi et al., 2012; Palci et al., 2013; Polcyn and Bell, 2005). These are more pronounced on the ?lingual side of the crown (i.e. on the area encompassed by the carinae lingually) and less developed labially as in *Russellosaurus* and *Pannoniasaurus* (Polcyn and Bell, 2005; L.M. personal observation). Regarding other tethysaurines, *Yaguarasaurus* has striations lingually and smooth crown labially (Páramo, 1994; Páramo-Fonseca, 2000). However, in contrast to *Pannoniasaurus*, the longitudinal striae on the Austrian specimens do not extend on the carinae, thus they seem to lack the pseudo-serrations of the teeth of the former. The striae running onto the carinae and forming pseudo-serrations were described neither in *Russellosaurus* and *Yaguarasaurus,* nor in *Halisaurus* (Bardet and Pereda-Suberbiola, 2002; Bardet et al, 2005; Páramo, 1994; Páramo-Fonseca, 2000; Polcyn and Bell, 2005) and seem to be unique in *Pannoniasaurus*. *Tethysaurus* on the other hand, has striation only on the lower half of the crown and only in larger specimens (Bardet et al., 2003). *Romeosaurus fumanensis* has no striations at all (Palci et al., 2013).

Since teeth are not sufficient for more exact taxonomical determination, the Gams specimens are assigned as cf. Tethysaurinae indet.

Remarks. The taxonomic name Tethysaurinae is used sensu Makádi et al. (2012) („the most recent common ancestor of *Pannoniasaurus inexpectatus* and *Russellosaurus coheni* and all its descendants") for the sake of simplicity. In the phylogeny of Palci et al. (2013), the Gams teeth can belong to either their Tethysaurinae or Yaguarasaurinae, though the former seems more probable because of more similarities with *Pannoniasaurus* and because of palaeogeographical considerations.

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Neosuchia Benton and Clark, 1988

Neosuchia indet.

Fig. 7

Material. 83 isolated teeth (2018/0262/0000-0008).

Description. Crocodyliform teeth are the most common elements in the screenwashed material. Although based on crown height/width proportions different morphotypes can be distinguished, the characteristic features on all teeth (e.g. the presence and morphology of the carinae, see below) indicate their referral to a single taxon.

The first morphotype (40 teeth) is apicobasally high with a crown height/mesiodistal width proportion higher than 1.3 (Fig. 7A–H). This tooth crown type has an oval, in some cases almost rounded cross section (Fig. 7D, H). Crowns are slightly or in some cases markedly bent lingually resulting in a slightly concave lingual surface. Tooth crown is slightly constricted basally. Both the lingual and labial surfaces bear parallel, longitudinal ridges, though those of the labial side are not as well developed as seen on ‘atoposaurid’ teeth from the Upper Jurassic of Germany (Thies et al., 1997). Ridges on the mesiodistal surfaces are slightly curved towards the carinae but do not reach the carinae, resulting in a non-ziphodont’ texture (according to Legasa et al., 1994 and Prasad and de Broin, 2002, Fig. 7B, G, J). Carinae are not well-distinguished, mesiodistally projecting crests, as typically seen in crocodylomorph teeth but rather ledge-like structures with significant lingual shelves (Fig. 7C, E). Thus, these carinae are not observable from labial view (Fig. 7C) but only in any other directions. Wear facets cannot be observed on these type of teeth, though most of them are fragmentary with the apical end frequently missing. This morphotype might have been situated in the anterior alveoli and/or in the hypertrophied positions as e.g. in other *Theriosuchus*-like neosuchians (see e.g. Martin et al., 2010; Schwarz et al., 2017).

The second morphotype (27 teeth) is intermediate between the former apicobasally high crowns and the lowest, bulbous crowns. This morphotype has a more or less equilateral triangle shape in labiolingual view. Labiolingually they are more compressed and the crown height/mesiodistal width proportion is between 1.0 and 1.3 (Fig. 7I–L). Labiolingual ornamentation and carinae are similar to that of morphotype 1, though they have less developed carinae.

The third morphotype (16 teeth) is low-crowned, and tooth crowns are labiolingually strongly compressed, and the crown height/mesiodistal width proportion is less than 1.0 (Fig. 7O). Labiolingual ornamentation is similar to that of morphotype 1 and 2, but the carinae, though definitely present in contrast to the *Bernissartia* teeth from the Early Cretaceous of Denmark (Schwarz-Wings et al. 2009), are less pronounced. Most of these teeth are strongly worn apically, suggesting some crushing function of these low-crowned posterior teeth (Fig. 7M, N, S).

Remarks. The generally similar morphology of the three morphotypes suggests that these teeth belong to a single taxon but represent different tooth positions within the tooth row. Dental features, such as the presence of quite heterodonty in the tooth row, labiolingulally flattened, pseudoziphodont teeth and low-crowned, bulbous posterior crushing teeth, are most reminiscent of the teeth of *Theriosuchus*-like forms present in many Cretaceous continental vertebrate faunas.

Crocodyliform teeth have been already described from two different Gosau occurrences of the Northern Calcareous Alps. One tooth (NHMW 1859-L-6420) is from the most probably upper Turonian-Coniacian (Pavlishina et al., 2004; Summesberger and Kennedy, 1996) Gosau Group beds of Rußbachtal (Neualpe) near Gosau (Stoliczka, 1860; Buffetaut, 1979), whereas some others (PIUW 2349/62-65) are from the lower Campanian of Muthmannsdorf (Buffetaut, 1979; Seeley, 1881). Buffetaut (1979) described the Muthmannsdorf teeth as Alligatoridae indet. and referred the Rußbach specimen as being very similar to those. The tooth from Rußbach, however, has some features that might rather refer it to *Theriosuchus*-like neosuchians, as is the case in the Gams specimens. As Stoliczka (1860) described and figured, the labial side is flatter than the lingual one and the fine enamel ridges on the lingual side curve towards the carinae resulting in a kind of pseudoziphodont carinae since they are not serrated. On the other hand, the Rußbach tooth is not constricted at the base of the crown, in contrast to all the specimens from Gams. The similarity and a close taxonomic relationship of the Rußbach tooth and those from Gams would not be surprising, since they are from almost contemporaneous sediments and were buried on the same margin (though with 80 km distance) of the Northern Calcareous Alps (Wagreich and Faupl, 1994).

Some of the Muthmannsdorf teeth are also similar to those from Gams. The stocky posterior tooth illustrated by Buffetaut (1979:table 2. fig. 4) is very similar to one of the Gams specimens illustrated on Fig. 7Q–S, though the ornamentation might be somewhat more prominent in the latter. Furthermore, the specimen illustrated by Buffetaut (1979: Table 2. fig. 5) is very similar to that illustrated on Fig. 7G–H, though the latter has rather anastomosing than parallel enamel ridges and more developed lingual shelves along the carinae. Here we suggest that some of these teeth (at least the ones compared here) might belong to some *Theriosuchus*-like crocodyliforms.

Remarks. Though various new material has been recently published, the systematic position and taxonomic composition of Atoposauridae is still highly controversial (Martin et al., 2010; 2014; Schwarz et al., 2017; Tennant et al., 2016; Turner, 2015; Venczel and Codrea in prep.), and individual tooth morphology does not help to solve the problem. The extreme heterodonty and individual tooth morphology described in the above specimens are present in *Theriosuchus*-like forms, but some of them (e.g. the posterior crushing teeth) are also reminiscent of the teeth of some other neosuchians, e.g. bernissartids (Schwarz-Wings et al., 2009). Thus, here we tentatively refer these teeth to Neosuchia indet. until more complete material helps to clarify their status.

Crocodyliformes indet.

Fig. 8A–D

Material. One tooth (2018/0263/0001).

Description. A quite unusual, single tooth crown was recovered from the screenwashed material. The massive crown is slightly constricted and higher than labiolingually wide with oval shaped cross-section basally (Fig. 8D). The most striking feature of this tooth is a shoulder-like cingulum basally around the whole crown (Fig. 8A–D). This cingulum borders a main conical cusp that bears weakly worn unserrated carinae both mesially and distally (Fig. 8B, D). The carinae, however, do not extend on the surface of the cingulum. The crown is ornamented by two different types of ridges: the main cusp lingually bears parallel, relatively widely spaced longitudinal ridges extending from its base to the apex, while the cingulum, where it is not worn, bears finer and denser, anastomosing ridges. The apex of the crown is heavily worn.

Remarks. This crown morphology markedly differs from all the tooth types discovered in the Gams material suggesting a different taxon. Based on the true enamel on the crown surface, the constricted crown and the presence and the arrangement of mesial and distal carinae we refer this tooth to Crocodyliformes indet. Its crown morphology, however, differs from that of other crocodyliforms suggesting that it might represent a new form. Whereas the stocky central cusp has a typical crocodyliform morphology with a slightly smaller lingual side of the cusp than the labial one and weakly lingually bending carinae, the massive shoulder-like cingulum is rather reminiscent of the bulbous crushing teeth of the some neosuchians, such as *Acynodon adriaticus* (Delfino et al., 2008) or *Allognathosuchus* (Lucas and Estep, 2000; Rossmann, 2000). This specimen looks like a transitional form between a traditional, conical tooth and a lower, bulbous crushing tooth might suggestsome hylaeochampsid affinity, a group with various types of heterodont dentition including bulbous forms, that was quite wide-spread in the Cretaceous European archipelago (Rabi and Ősi, 2010; Turner and Brochu, 2010).

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Paronychodon Cope, 1876

cf. *Paronychodon* sp.

Fig. 8E–G

Material. One tooth (2018/0264/0001).

Description. A middle part of a small, slightly distally curved tooth has D-shaped cross section. Mesial and distal carinae are present but unserrated. Whereas the lingual surface is flat and ornamented by two-three shallow apicobasal grooves, the labial side is strongly convex and smooth (Fig. 8E–G).

Remarks. The combination of traits present on this small tooth is most reminiscent to the teeth of the enigmatic *Paronychodon* described from various Cretaceous localities (e.g. Canudo and Ruiz-Omeñaca, 2003; Cope, 1876; Currie et al., 1990; Sahni, 1972; Sankey et al., 2002, 2005) including the Santonian Iharkút vertebrate locality in Hungary. *Paronychodon*-like teeth were mainly reported from Upper Cretaceous (Senonian) sediments, but some older occurrences might also occur (see e.g. Canudo and Ruiz-Omeñaca, 2003; Zinke, 1998; Zinke and Rauhut, 1994). These Late Jurassic (Guimarota, Portugal) or Early Cretaceous (Galve, Spain) specimens have, however, serrated carinae, so, according to Currie et al. (1990) and Sankey et al. (2002), they might represent other theropods. Whatever is the case, the Turonian specimen from Gams, Austria clearly widens the range of these bizarre theropod teeth.

Theropoda indet.

Fig. 8H–T

Material. Four isolated teeth (2018/0265/0001-0004).

Description. Two of the four teeth (2018/0265/0001-0002, Fig. 8I, Q) are very similar in crown morphology, though the larger one has less distal curvature (Fig. 8Q). Both teeth have a labiolingually compressed crown with serrated mesial and distal carinae. Whereas the denticles of the mesial serration are very low, the distal denticles are pointed and more prominent (Fig. 8H, O). Labiolingually the crown surface bears shallow grooves reaching the base of the crown. Mesial to the distal serrated carina a prominent self is present (Fig. 8I, Q). A third tooth fragment (2018/0265/0003) is from the apical half of the crown (Fig. 8L–N). The distal carina is well serrated, while the mesial one is avoid of serration. In contrast to specimens 2018/0265/0001-0002, the labial and lingual surfaces are smooth and not ornamented with ridges.

Remarks. Of the four specimens, 2018/0265/0001-0002 (Fig. 8I, Q) most probably represent the same taxon, but the third specimen with only distal serration and the lack of longitudinal ridges (Fig. 8L) might belong to a different form. Features of 2018/0265/0001-0002 are most reminiscent of some maniraptoran teeth (Currie et al., 1990), but more complete material is needed for exact measurements on the crowns and the denticles to provide a better taxonomical assignment.

5. Discussion

As it is expected from the deposits and the invertebrate fossil record, the vertebrate fauna from Gams contains dominantly marine (fishes, mosasauroids) to semi-aquatic (crocodyliforms) forms. In similar Cretaceous vertebrate assemblages (see Csiki-Sava et al., 2015 for an overview) turtle fossils, mostly plate fragments, are characteristic and abundant elements . This might have been the case in Gams as well. Dozens of small (up to 3–4 mm), sometimes rectangular, sometimes slightly rounded pieces of bone fragments (2018/0266/0000) with densely spongious texture are frequent elements among the screenwashed material. These bones might represent turtle plates but are too fragmentary for a better taxonomical assignment. Ankylosaurs may be also part of this assemblage. Various small bone fragments having irregularly surfaces and typical spongious cross-section might belong to ankylosaurian osteoderms. The occurrence of ankylosaurs in costal, semi-aquatic, brackish marine habitat would not be surprising, since the bones of many European taxa (see e.g. *Europelta* from Spain, Kirkland et al., 2013; *Struthiosaurus* from southern France, Garcia and Pereda-Suberbiola, 2003; *Hungarosaurus* and *Struthiosaurus* from Hungary, Botfalvai et al., 2015; Ősi and Makádi, 2009) have been recorded from -sediments deposited in moist, coastal to riverside environments (Arbour et al., 2015). The next nearby, but younger (early Campanian) finding of *Struthiosaurus* comes also from coaly, largely non-marine Gosau Group deposits of Muthmannsdorf at the eastern margin of the Northern Calcareous Alps (Bunzel, 1870; Hofer et al., 2011).

The diverse fish material represents various trophic levels, however, durophagous feeders (including ptychotrygonids and pycnodontids) are dominant, a phenomenon that well correlateswith the extremely rich mollusc fauna (Kollmann and Sachsenhofer, 1998).

The presence of tiny amphibian remains (along with the theropod dinosaur fossils) unambiguously indicates that the depositional environment of these coal-bearing bedswould have been relatively close to terrestrial and freshwater environments. The affinity of the Gams amphibians, is, however, quite surprising, although neobatrachians are represented by *Hungarobatrachus szukacsi* in the Santonian of Hungary (Iharkút, Bakony Mountains) (Szentesi and Venczel, 2010). The genus *Thaumastosaurus* belongs to African originated natatanuran ranoids (e.g. Laloy et al., 2013; van der Meijden et al., 2007) currently known by four species (*T. bottii*, *T. gezei*, *T. sulcatus* and *T. wardi*) from the middle and late Eocene of France and England (e.g. Holman and Harrison, 2002, 2003, Roček and Lamaud, 1995; Roček and Rage, 2000). If our identification is correct, the fossil specimen from the Turonian of Gams (Austria) represents the oldest and first-Mesozoic *Thaumastosaurus*-like neobatrachian frog on the European continent.

The systematic range of Gondwanan-originated natatanuran ranoids is highly controversial among researchers (see e.g. Laloy et al., 2013; Rage and Roček, 2007). Nevertheless, depending on the systematic position, a Gondwanan origin is highly plausible and would not be surprising in the light of the occurrence of various Gondwanan-originated vertebrate groups in the European Cretaceous archipelago (see e.g. Buffetaut et al., 1988; Csiki-Sava et al., 2015; Ősi et al., 2015; Pereda-Suberbiola, 2009; Rabi and Sebők, 2015; Vullo and Néraudeau, 2008; Vullo et al., 2009).

The similarities of a few mosasauroid teeth from Gams with those of tethysaurines (especially *Pannoniasaurus*) and halisaurines suggest the presence of another tethyosaurid in brackish marine environments of the European Cretaceous archipelago during the Turonian .

6. Conclusions

The Turonian vertebrate fauna from Gams is an important piece in the puzzle of the Late Cretaceous faunal composition of the Cretaceous European archipelago since it provides a small but significant link among older (pre-Cenomanian) and younger (Santonian to Maastrichtian) faunas of the region. The palaeogeographic position of the fauna is also noteworthy since, except for the Campanian Muthmannsdorf fauna and a crocodyliform tooth from the Gosau type locality of Neualpe, no land vertebrates have been reported from the Cretaceous landmasses of the Northern Calcareous Alps before.

The faunal elements of the Gams assemblage are most similar to the Santonian vertebrate fauna from Iharkút, western Hungary (Ősi et al., 2012). Pycnodontid, vidalamiine and lepisosteid fishes, tethysaurine mosasauroids, *Theriosuchus*-like crocodyliforms and *Paronychodon*-like theropods are all present in Iharkút as well, a phenomenon that is probably related to the spatial closeness of the Northern Calcareous Alps and the Transdanubian Central Range during the Late Cretaceous (Csontos and Vörös, 2004; Dercourt et al., 2000; Kázmér and Kovács, 1985; Wagreich and Siegl-Farkas, 1999). Whereas the latter existed as a landmass most probably already from the Coniacian (or perhaps earlier) to Santonian (Botfalvai et al., 2016; Haas, 2012), land surfaces on the Northern Calcareous Alps existed from the late Turonian to Campanian times (Wagreich and Faupl, 1994) due to mid-Cretaceous tectonic deformation and thrusting. Hopefully, further excavations in other Gosau deposits deposited in this critical Turonian–Santonian period will extend our knowledge on the composition of the continental vertebrate fauna in the western Tethyan archipelago.

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FIGURE CAPTIONS

Figure 1. Location map of the Gams locality (Austria).

Figure 2. Geological setting and the bone-yielding horizon within the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria. Modified after Summesberger et al. (2009).

Figure 3. Fish remains from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria. A-C, Selachimorpha indet. tooth (2018/0252/0001):A, lingual view; B, in profile view; C, in labial view. D-F, Selachimorpha indet. placoid scale (2018/0252/0002): D, apical view; E, in lateral view; F, in anterior view. G–Z, *Ptychotrygon gueveli* (G-K: 2018/251/0001, L–P: 2018/251/0002, Q–U: 2018/251/0003, V-Y: 2018/251/0004); G, L, Q, V: in occlusal view; H, M, R: in basal view; I, N, S, W: in lingual view; J, O, T, X: in labial view; K, P, U, Y: in profile view. Z-A’, Chondrichthyes indet. dermal denticle (2018/253/0001): Z, in apical view; A’, in profile view. Scale bars: A–C, G–Y: 1 mm; D–F, Z, A’: 500 µm

Figure 4. Fish remains from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria. A-B, cf. *Lepisosteus* sp. tooth (2018/0254/0001) in two different views; C, cf. *Lepisosteus* sp. ganoid scale (2018/0254/0007) in external view (white rectangle shows the position of fig. D); D, scanning electron microscopic photograph of the ganoine tuberculation of the same scale specimen; E, measurements of the diameter of the ganoin tubercles and the inter-tubercular distances on the scales of extant and extinct lepisosteids, including the Gams material. Abbreviations: F, fossil; K, Cretaceous; T, Tertiary; Q, Quaternary; R, Recent (modified after Gayet et al., 2002). Scale bars: A–C: 1 mm; D, 50 µm

Figure 5. Fish remains from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria. A-D, Amiiformes indet. tooth (2018/0255/0001): A, in labial view; B, in profile view, C, in lingual view; D, in opposite profile view. E, Pycnodontidae indet. right prearticular (NHMWien 1996z0 189/000 1.) in occlusal view. F-G, Pycnodontidae indet. molariform tooth (2018/0256/0001): F, in occlusal view; G, in profile view. H, Pycnodontidae indet. molariform tooth (2018/0256/0002) in occlusal view. I, Pycnodontidae indet. molariform tooth (2018/0256/0003) in occlusal view (white rectangle shows the position of Fig. J); J, close-up of the occlusal surface of the same specimen, showing scratches, attributed to functional wear. K-M, Pycnodontidae indet. incisiform tooth (2018/0256/0004): K, in labial view; L, in occlusal view; M, in lingual view. N-P, Pycnodontidae indet., incisiform tooth (2018/0256/0005): N, in labial view; O, in occlusal view; P, in lingual view. Q-R, Pycnodontidae indet. branchial tooth (2018/0256/0006): Q, in occlusal view; R, in lateral view. S-T, Actinopterygii indet. vertebra (2018/0257/0001): S, in lateral view; T, in articular view. Scale bars: A–D, H, I, K–T: 1 mm; E: 10 mm; F, G, J: 500 µm

Figure 6. Amphibian and squamate remains from the from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria. A–E, cf. *Thaumastosaurus* sp. maxilla fragment (2018/0258/0001): A-B, in labial; C, in lingual; D, in posterior; E, in ventral view. F–G, Anura indet. fragmentary vertebral centrum (2018/0259/0001) in ventral view. H–K, ’Lacertilia’ indet. jaw fragment (2018/0260/0001) in H, lingual; I, in mesial; J, in labial; K, in occlusal view. L–O, cf. Tethysaurinae indet. tooth fragment (2018/0261/0001) in L, lingual; M, labial, N, in occlusal; O, in mesial view. Anatomical abbreviations: cn, condylus; ct, cotylus ; lh, horizontal lamina; pp, pterygoid process; vk, ventral keel. Scale bars: A–E: 1 mm; F–O: 500 µm

Figure 7. *Theriosuchus*-like crocodyliform teeth from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria. A-D, anterior or middle tooth (2018/0262/0001) in A, mesial/distal view; B, in lingual view; C, in apical view; D, in basal view. E-F, anterior tooth (2018/0262/0002) in E, apical view; F, in lingual view. G-H, anterior or middle tooth (2018/0262/0003) in G, lingual view; H, in basal view. I-J, middle tooth (2018/0262/0004) with slightly heart-shaped base in I, apical view; J, in lingual view. K-L, middle tooth (2018/0262/0005) in K, lingual view; L, in basal view. M-N, posterior tooth (2018/0262/0006) in M, apical view; N, details of the worn apex. O-P, posterior tooth (2018/0262/0007) in O, lingual view; P, in apical view. Q-S, posterior tooth (2018/0262/0008) in Q, lingual/labial view; R, in mesial/distal view; S, in apical view. Scale bars: A-D: 2 mm; E-M, O-S: 1 mm; N: 250 μm.,

Figure 8. Unidentified crocodyliform tooth and theropod dinosaur teeth from the upper Turonian Schönleiten Formation of Gams bei Hieflau, Austria. A-D, Crocodyliformes indet. tooth (2018/0263/0001) in A, lingual view; B, in mesial/distal view;, C, in labial view; D, in apical view. E-G, cf. *Paronychodon* sp. tooth (2018/0264/0001) in E, lingual view; F, in basal view; G, in apical view. H-K, Theropoda indet. tooth (2018/0265/0001) morphotype 1: H, distal serration in lingual/labial view; I, tooth in lingual/labial view; J, mesial serration in lingual/labial view; K, tooth in basal view. L-N, Theropoda indet. tooth (2018/0265/0003) morphotype 2: L, in lingual/labial view; M, distal serration in lingual/labial view; N, tooth in basal view. O-T, Theropoda indet. tooth (2018/0265/0002) morphotype 3: O, distal serration in lingual/labial view; P, tooth in distal view; Q, tooth in lingual/labial view; R, tooth in basal view, S, tooth in mesial view; T, mesial serration in lingual/labial view. Scale bars: A, B, C, D, I, K, P, Q, R, S: 1 mm; E, F, G, L, N, T: 500 μm; J, O: 250 μm; H, M: 200 μm.

Table 1. List of taxa discovered from the Turonian Gams locality (Austria).

Taxon	**Referred specimens**	**Inventory Numbers**	**Ecology**
Pisces		**NHMW**	**for references see text**
Ptychotrygon gueveli	4 teeth	2018/0251/0001-0004	marine
Selachimorpha indet.	1 tooth, 1 dermal denticle	2018/0252/0001-0002	dominantly marine
Chondrichthyes indet.	2 dermal denticles	2018/0253/0001-0002	dominantly marine
cf. *Lepisosteus* sp.	6 teeth, 2 ganoid scales	2018/0254/0001-0008	brackish to freshwater
Vidalamiinae indet.	3 teeth	2018/0255/0001-0003	marine
Pycnodontidae indet.	33 molariform, 4 incisiviform, 17 branchial teeth	2018/0256/0000-0006	marine to freshwater
Actinopterygii indet.	1 vertebral centrum	2018/0257/0001	undefinable
Amphibia			
cf. *Thaumastosaurus* sp.	1 fragmentary left maxilla	2018/0258/0001	freshwater
Anura indet.	1 fragmentary presacral vertebra	2018/0259/0001	freshwater
Squamata			
Lacertilia indet.	1 fragmentary possible dentary	2018/0260/0001	terrestrial
cf. Tethysaurinae indet.	14 teeth	2018/0261/0001-0014	marine to freshwater
Crocodyliformes			
Neosuchia indet.	83 isolated teeth	2018/0262/0000-0008	freshwater to terrestrial
?Crocodyliformes indet.	1 tooth	2018/0263/0001	freshwater to terrestrial
Dinosauria			

cf. *Paronychodon* sp.	1 tooth	2018/0264/0001	terrestrial
Theropoda indet.	4 teeth	2018/0265/0001-0004	terrestrial
Vertebrata indet.	224 bone and tooth fragments	2018/0266/0000	undefinable