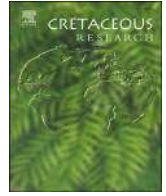




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A brackish to non-marine aquatic and terrestrial fossil assemblage with vertebrates from the lower Coniacian (Upper Cretaceous) Gosau Group of the Tiefengraben locality near St. Wolfgang im Salzkammergut, Austria

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ABSTRACT

The Turonian–Coniacian continental fossil record in Europe is scarce. Here we present a new fossil assemblage of early Coniacian age that was systematically collected from the coal-bearing Gosau Group of the Tiefengraben locality near St. Wolfgang, Austria. The diverse assemblage is composed of at least 60 taxa including sporomorphs and Normapolles-related pollen, seeds and leaves of angiosperms and gymnosperms, charophytes, gastropods, bivalves, ostracods, termites, fishes, crocodiles and dinosaurs. Concerning charophytes, ostracods, gastropods, crocodiles and dinosaurs, the discovered specimens either extend the temporal and spatial range of specific groups (in some cases as possible relict forms) or suggest the occurrence of new taxa. The discovered remains of algae, molluscs, ostracods, calcareous nannofossils and lepisosteid fish represent a mixed faunal assemblage from different palaeohabitats, from marginal marine to low salinity and freshwater or terrestrial environments. As Normapolles-related angiosperm plants dominate the flora with a relatively high number of dentate leaves, a slightly cooler microenvironment compared to other Turonian–Coniacian Central European localities is indicated. The characteristically grooved crocodylian teeth of Tiefengraben differ from the previously known Upper Cretaceous European crocodyliform teeth and suggest a more diverse crocodyliform fauna in the region. Dinosaurs are represented by teeth of at least three different theropods, the largest of which is referred here to as basal tetanurans. The fossil assemblage of this early Gosau Group occurrence is of great importance for our understanding of the continental floristic and faunistic composition of the western Tethyan archipelago during the Cenomanian–Campanian gap.

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1. Introduction

Continental vertebrate fossils from the first part of the Late Cretaceous (Cenomanian to Santonian) are extremely rare in Europe. This is mainly due to the extremely high global sea level in this period (Haq et al., 1987; Miller et al., 2003; Seton et al., 2009;

Haq, 2014) that resulted in an European archipelago situation where the deposition of continental sediments massively decreased (Mannion and Upchurch, 2011; Csiki-Sava et al., 2015). The record of the Turonian–Santonian period is the scantiest, though new discoveries from footprints to micro- and macrofossil assemblages started to fill the gap (Buffetaut and Pouit, 1994; Nicosia et al., 1999; Mezga et al., 2006; Ósi et al., 2012, 2016, 2017, 2019; Solt et al., 2020).

Similar to the Turonian (Csiki-Sava et al., 2015; Ósi et al., 2019), the Coniacian continental vertebrate record is restricted to only a few remains. Martill et al. (2008) published three possible non-azhdarchid azhdarchoid pterosaur vertebrae from the Chalk Formation of southern England. In addition, some turtle bones and two isolated crocodyliform teeth (Dalla Vecchia and Tentor, 2004), including a ziphodont one, possibly originating from a notosuchian (Dalla Vecchia and Cau, 2011), have been reported from lagoonal limestone beds of northeastern Italy. This extreme scarcity of Coniacian (and practically of late Cenomanian to Santonian) continental vertebrates results in an unfortunate knowledge gap of early Late Cretaceous faunas, preventing the deciphering of their evolutionary history in the Cretaceous European archipelago.

Consistent with the example of vertebrates, the record of invertebrates from brackish to non-marine palaeoenvironments in Europe is even less known, thus the new remains described herein have a great significance.

Here we present a new, systematically collected brackish to non-marine aquatic and terrestrial fossil assemblage including not only vertebrates but the accompanying flora and invertebrate fauna from the Gosau Group of the Tiefengraben locality, near St. Wolfgang (Northern Calcareous Alps, Austria, Fig. 1). The assemblage is early Coniacian in age, being the most diverse from this interval in

Europe so far and plays a critical role in the understanding of the evolution of brackish to non-marine aquatic as well as terrestrial ecosystems of this globally noted gap period.

2. Localities and geological setting

2.1. Sampled localities in the Gosau area

The aim of our international research project was to find as many Turonian to Santonian outcrops in the Salzkammergut area as possible to look for both macroscopic and microscopic vertebrate fossils in these sites. Most of the outcrops visited by our team are already well known (Kollmann and Summesberger, 1982), and in many cases either sedimentological or palaeontological works have been published (e.g. Summesberger and Kennedy, 1996; Wagreich, 1998; Kvacsek et al., 2008). Altogether, 11 localities have been investigated and sampled, the list and details of which are summarised in Table 1. Various rock types were sampled (e.g. marl, silty marl, clay, coal-bearing clay and silt, sandstone, reddish silt and sandstone), but only coal-bearing, silty-clayey strata yielded vertebrate fossils.

Of the 11 sampled localities, only two had the potential to contain continental vertebrate fossils since most of the outcrops are brackish to shallow marine successions. One of them is the so-called “Stoliczka-site”, a short-lived coal mine near Neualm, situated NE of Russbach am Pass Gschütt, from where Stoliczka (1860) already described and figured a crocodile tooth. Although we only had access to the reworked dump of the former coal mine, we collected 30 kg of coal-bearing rocks from there. Screen-washing of these samples resulted in only two additional crocodile teeth that are close to identical with those described by Stoliczka (1860). Due

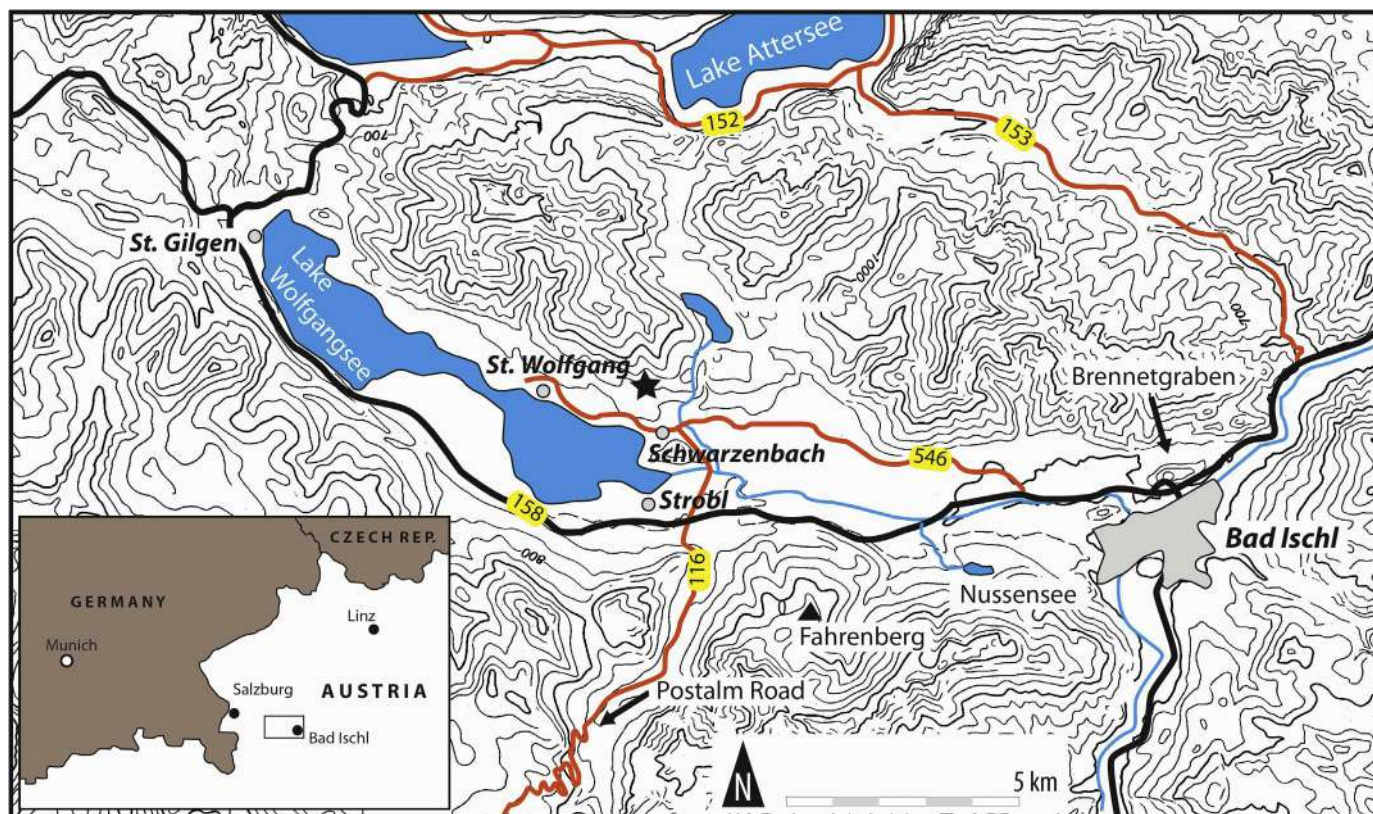


Fig. 1. Location map of several outcrops of the Lower Gosau Group in the region of St. Wolfgang (Austria) mentioned in the text. The Tiefengraben site presented in this paper is marked by the black star.

Table 1

List of the localities sampled in the Gosau area (Salzkammergut, Austria), and details of sampling with a brief summary of the discovered fossils.

Locality name	GPS coordinates	Stage	Type of sampled layer(s)	Number of sampled layer	Sample for screen-washing per layer (kg)	Fossils
Results of the 1st sampling at different localities in the Gosau area						
Neualm-"Stoliczka site" former coal-mine	47° 36' 42.02" N 13° 29' 49.25" E	Turonian	Coal-bearing clay, silt	3	3 × 10 kg	Seeds; amber fragments; termite coprolites; mollusks; few bone fragments; 3 crocodile teeth
Weissenbach Tributary	47° 40' 45.88" N 13° 28' 23.47" E	uncertain	Grey marl	1	20 kg	Mollusks; corals
'Ofenwand', Weidinger, Weissenbach, opposite the toll	47° 41' 59.88" N 13° 29' 35.13" E	Turonian	Grey silt, clayey silt	2	2 × 20 kg	–
Russbach – Radochsberg-Radosbach A	47° 34' 56.96" N, 13° 21' 51.89" E	Turonian	Grey silt and marl beds, one clayey, silty coal bed	1	20 kg	Mollusks
Russbach – Radochsberg-Radosbach B	47° 34' 58.62" N, 13° 21' 51.05" E	Turonian	Clayey bed with coalified plant fragments	1	20 kg	–
Streiteck, road-cut, type locality of Streiteck Formation	47° 35' 33.65" N, 13° 29' 13.13" E	uppermost Turonian to mid-Coniacian	Grey, silty sand	1	20 kg	–
St. Wolfgang-Tiefengraben 1	47° 44' 05.29" N, 13° 28' 47.73" E	?Coniacian–Santonian	Grey, sandy layer with coal fragments, coarse greyish-yellowish sand, clayey coal	3	3 × 25 kg	–
St. Wolfgang-Tiefengraben 2	47° 44' 05.47" N, 13° 28' 47.02" E	?Coniacian–Santonian	Coal, grey clayey silt	2	2 × 25 kg	Amber fragments
St. Wolfgang-Tiefengraben 3	47° 44' 07.19" N, 13° 28' 47.89" E	lower Coniacian	Clayly coal seam	3	20 kg	Amber fragments, termite coprolites, mollusks, 27 bone fragments, 16 fish teeth and scales, 95 crocodile teeth, 3 dinosaur teeth
St. Wolfgang-Tiefengraben 4	47° 44' 07.19" N, 13° 28' 47.89" E	Coniacian–Santonian	Sand	1	20 kg	–
Färbegraben near the Kreuzgraben type locality	–	Turonian	Red silty, clayey (lateritic) paleosol bed	1	20 kg	Mollusks
Randobach – hundred meter further towards the Neualm-"Stoliczka" site	47° 36' 21.77" N 13° 29' 35.28" E	Turonian	Grey clayey silt with some small coalified plant remains	1	20 kg	–
Randobach – a few hundred meters north from Zimmergraben, right side of the road	47° 36' 17.72" N 13° 29' 37.17" E	Turonian	Green to reddish silt, clayey silt	1	20 kg	Mollusks
Results of the 2nd sampling at St. Wolfgang-Tiefengraben 3						
St. Wolfgang-Tiefengraben 3	47° 44' 07.19" N, 13° 28' 47.89" E	lower Coniacian	Clayly coal seam	3	440 kg	13 seeds; 35 amber fragments; dozens of ostracods, 300+ termite and a dozen vertebrate coprolites; 500+ mollusks; 461 bone fragments including limb bones; 230 fish teeth, scales and bones; 466 crocodile teeth; dinosaur teeth

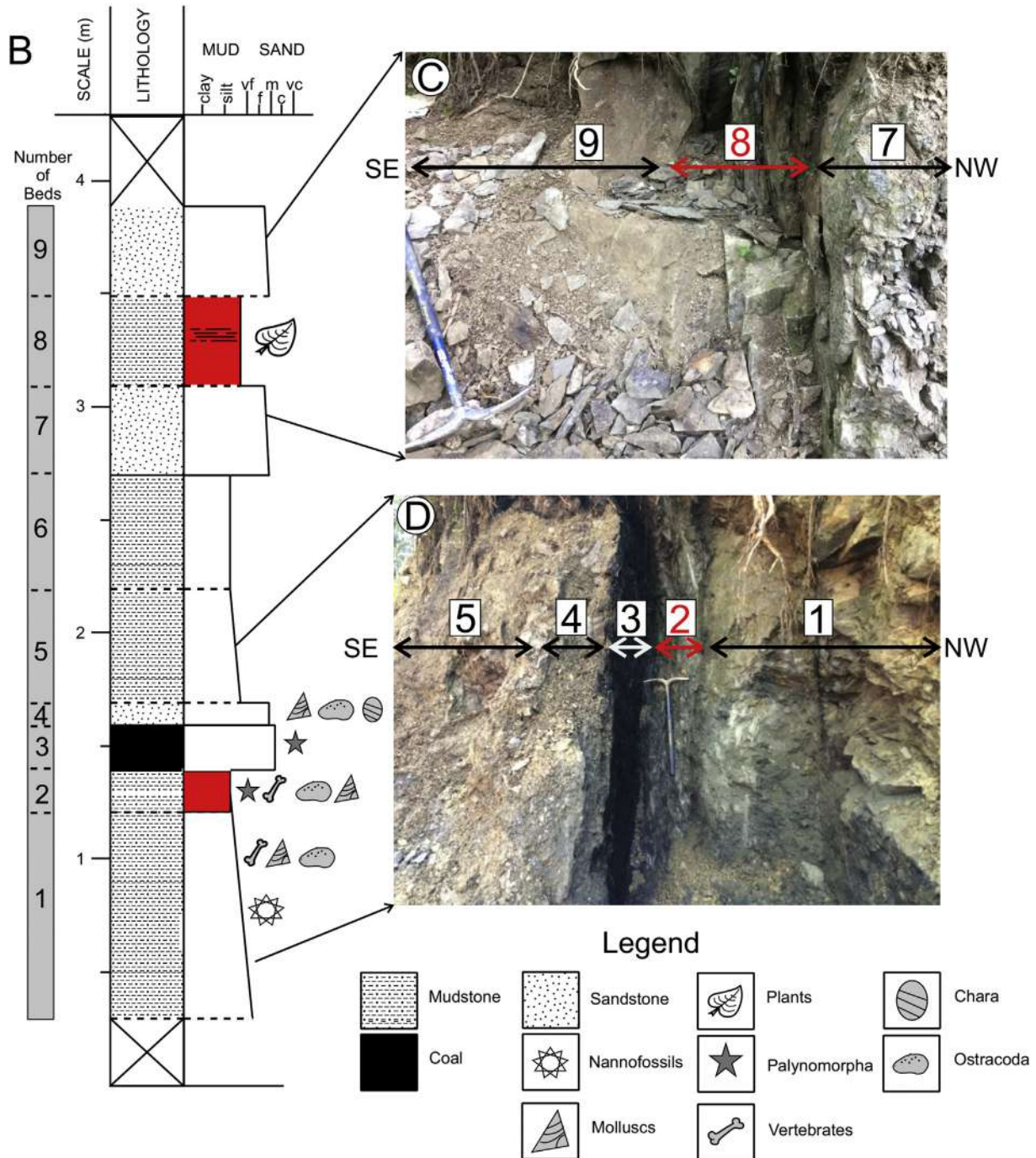
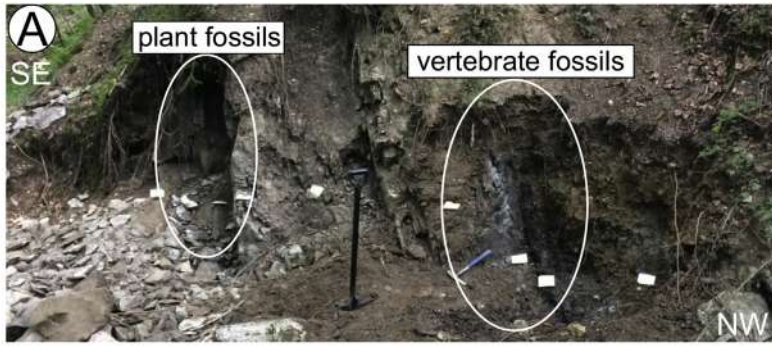
to the low number of vertebrate fossils, we did not collect more material at this site.

The second and most productive locality, presented in this paper, is in one of the trenches of the Tiefengraben, along the Tiefenbach, near St. Wolfgang (Fig. 1). Among other sampled sites in Tiefengraben (see Table 1), we numbered this place as Tiefengraben 3, but since this was the only potential site in Tiefengraben here we refer the site to as *Tiefengraben*. The locality can be reached along a narrow asphalt road, which branches off in a northwestern direction west of Schwarzenbach village towards the rustic snack stations Mostbauer and Holzerbauer. The fossil site is located along a side creek of the Tiefenbach stream in the forest of the "Gschwandtnerbauer" estate (GPS: 47° 44' 07.19" N, 13° 28' 47.89" E), and yielded a rich brackish to non-marine aquatic and terrestrial floral and faunal assemblage that is described in this paper.

2.2. Geology and stratigraphy of the Tiefengraben fossil site near St. Wolfgang im Salzkammergut

2.2.1. General geology

Upper Cretaceous strata of the Northern Calcareous Alps (NCA) of Austria are summarised under the lithostratigraphic term Gosau Group (Wagreich and Faupl, 1994). The area around St. Wolfgang and Lake Wolfgangsee forms a classical site of Cretaceous fossils, known since Ehrlich (1850) and Reuss (1854). The Late Cretaceous palaeotopography in this northern Salzkammergut region, part of the central NCA in Austria, was characterised by several small, tectonically truncated and therefore isolated depressions, the Gosau basins. These basins mainly comprise rocks of Turonian to Maastrichtian age (in the eponymous area of Gosau, as well as near Russbach am Pass Gschütt, sedimentation even lasted till the



Eocene), and stretch from Lake Wolfgangsee in the west to the east of Lake Traunsee.

During the early phase of Alpine orogeny, after Early Cretaceous thrusting and faulting, these basins slowly deepened, initially accommodating terrestrial, brackish and marginal marine deposits [Lower Gosau Subgroup (LGS), Turonian–Santonian], and later deeper marine sediments (Upper Gosau Subgroup, Campanian–Eocene). Rocks of the former subgroup, in which the present sampling campaign took place, are characterised by conglomerates, sandstones and marls that are often richly fossiliferous. Locally, terrestrial and limnic sediments are intercalated, especially near the base of the basin fill, occasionally comprising coal deposits of varying thickness, some of which were mined between the early 19th and the mid-20th century. One of these small coal deposits was the Tiefengraben mine close to the village of St. Wolfgang im Salzkammergut.

2.2.2. Previous research

According to Ehrlich (1850), who presented the first detailed geological and palaeontological study on the Lake Wolfgangsee region, the tectonically disturbed Tiefengraben sequence comprises, from bottom to top, sandstones, marly shales with coal-layers, and bituminous limestone. Among other fossils Ehrlich also collected fossil plants in the coal mine dump, from which Franz Unger determined ten taxa in the same publication. Eight of these were already known from the Bohemian Lower Quader Sandstone while two were new species (Ehrlich, 1852). Later, Unger (1867: 650) described the flora in detail, although without mentioning the exact locality from which the material was obtained (“in schisto argilloso formationis gosaviensis ad St. Wolfgangum Austriae superioris” – i.e., Tiefengraben). More than 150 years later, Kvaček et al. (2008) started to restudy the macroflora of the Tiefengraben locality.

The basic studies of Ehrlich (1850, 1852, 1854) were followed by the voluminous monograph of Reuss (1854), which represents one of the most concise sources of information on the geology and palaeontology of the Gosau Group of the Lake Wolfgangsee area to date, in particular also on the Tiefengraben coal deposit. Commenda (1900) mentioned that the fossil plants from Tiefengraben are represented by ferns and conifers (*Araucarites*), and also by leaves of various dicotyledons. In addition, two rhombic ganoid scales (originally described by Reuss (1854) as “*Palaeoniscus*-like”, but this identification needs revision) have been found. The most recent geological maps with explanatory texts on the Lake Wolfgangsee region are those by Leischner (1960), and in particular by Plöschinger (1973) and Plöschinger et al. (1982a, b).

Only limited modern studies exist so far concerning the stratigraphic age of the various other coal-bearing Gosau localities of the northern Salzkammergut region. The westernmost coal-bearing beds of the LGS in the northern Salzkammergut region are accessible in scattered outcrops in the surroundings of St. Gilgen, east of Lake Wolfgangsee (Fig. 1). Woldrich (1868) documented the sequence at the Plomberg underground coal mine, while Hradecká et al. (2008) and Szente et al. (2010) reported a sequence of grey marls of the LGS with poorly preserved plant fossils exposed in the Kohlbachgraben north of St. Gilgen. Here, foraminifers, calcareous nannofossils and palynomorphs indicated a Turonian, respectively Turonian/Coniacian boundary age.

Hradecká et al. (2006) studied the nearby road cuts at “Station Billroth”, which, according to Švábenická (in Hradecká et al., 2006)

show a mid-Turonian age, i.e., nannofossil zone UC8 sensu Burnett et al. (1998), with *Eiffellithus eximius* and *Lucianorhabdus malmformis*. The presence of *Braarudosphaera bigelowii* points to a shallow marine environment. The study of the foraminifers and palynomorphs is, with some reservations, in agreement with this age, or younger ages. The grey marls sampled in two exposures near the locality “Station Billroth” also yielded poorly preserved microfossils as well as a moderately diverse colonial coral and rudist assemblage indicating a Turonian age.

Similar ages have been reported from the Strobl/Weissenbach locality about 6 km southeast of St. Wolfgang, where ammonites indicate a late Turonian to early Coniacian age (Summesberger and Kennedy, 1996). The ammonite-bearing grey marls lie above conglomerates and thin coal seams, thus indicating an upper Turonian age of the coal. Nannofossils corroborate this age (Wagreich, 1998), with the presence of *Marthasterites furcatus* and *Lithastrinus septenarius* (nannofossil zone UC9 of Burnett et al., 1998).

The best exposures of strata of the LGS in the surroundings of Bad Ischl are the sections devoid of coal close to Lake Nussensee, i.e., Coniacian–Santonian marls of the Sophiental-section along the stream Nussenseebach (Wagreich, 1998), and of the coal-bearing marls in the Brennetgraben creek east of Bad Ischl with upper Turonian ammonites (Summesberger and Kennedy, 1996), and Turonian–Coniacian microfossils (Hradecká et al., 2006). The Brennetgraben is also well known as one of the few localities in Austria where pitch coal was found (Kollmann and Sachsenhofer, 1998; Bechtel et al., 2001).

In the Eisenbach creek east of Lake Traunsee, the easternmost occurrence of the LGS in the northern Salzkammergut region is exposed. The sequence shows a variety of environments along the creek, from fully marine, fossiliferous, grey silty marls and sandstones to occasionally coal-bearing freshwater and/or brackish bituminous black shales (Weber, 1960). Calcareous nannoplankton investigations by Švábenická (in Schlagintweit et al., 2003) and Hradecká et al. (2005) confirm a mid-Turonian to Coniacian age of the oldest part of the sequence. In the coal-bearing marls amber has also been found (Reuss, 1851; Vávra, 2005). Rantitsch et al. (1995) studied the organic geochemistry of the coal. In the “Eisenbach-Gosau”, small-scale coal mining also took place in times of need.

2.2.3. Sedimentological description of the exposed successions of the Tiefengraben site

The observed section is a natural outcrop formed by erosive processes along an intermittent small stream. Unfortunately, the slope of the gully is covered by a few metres thick debris and thus only a 4 m thick section on the right side of the ravine was cleaned and investigated in detail during the field work (Fig. 2).

The observed sedimentary section (including the fossiliferous beds) contains a series of three fining-upward units, made up of sandstone, organic rich mudstone and coal seams. Dipping of the exposed beds along the creek is almost vertical with a strike of 210° SSW. The coarse-grained sedimentary rocks consist predominantly of medium to fine-grained sandstones, where fining-upward trends within beds are common, and their tops are always grading into mudstone. The sandstone bodies have flat, non-erosive bases and their thickness is usually few decimetres (30–50 cm). The firmly cemented sandstone beds only contain highly fragmented and unidentified remains of plants and molluscs, while vertebrate fossils were not found. However, there is a few centimetres thick, non-cemented, organic rich sandstone bed above the coal bed (Bed 4 see

Fig. 2. Geological setting and the fossil-rich beds within the lower Coniacian Gosau beds (Lower Gosau Subgroup) of Tiefengraben, St. Wolfgang, Austria: A) Photo of the investigated section; B) Schematic stratigraphical section of site Tiefengraben III at St. Wolfgang, showing main lithofacies and fossil content. C) photo of the lower part of the section with the bone-bearing bed marked in red; D) photo of the upper part of the section with the leaf fossil enriched bed marked in red. Abbreviation: SE = southeast and NW = northwest. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 2), which yielded a rich mollusc assemblage (see below). The orientation of these shells (besides the direction of fining-upward trends) indicates that the beds become younger from the northwest to the southeast in the exposed section.

The fine-grained sedimentary rocks of the observed section can be subdivided into two groups. The first group includes mostly monotonous, rarely slightly laminated, dark coloured, organic-rich mudstone beds containing mollusc shells, plant debris and vertebrate fossils (in the lower part of the section), while the second group includes laminated, light coloured mudstone beds rich in plant fossils, which are more dominant towards the top of the section.

A valuable vertebrate fossil assemblage was collected from an only a few centimetres thick, dark, organic-rich mudstone bed, located immediately below the coal bed (Bed 2 see Fig. 2). This bed is a slightly laminated, dark grey calcareous mudstone and claystone with a relatively high concentration of siderite and gypsum. Organic material in this bed is dominantly unrecognizable plant debris. The mollusc shell fossils are also present in a relatively large quantity in this bed, with their size varying from identifiable 0.2–0.5 cm remains to unrecognizable fragments while, rarely, larger sized gastropod shells (from 1 to 3 cm) are also preserved. The other fossil-rich bed is situated at the top of the exposed section, yielding a rich and diverse plant fossil assemblage (Bed 8 see Fig. 2). The plant-bearing bed is a light grey to light brown, finely laminated, firmly cemented, calcareous mudstone located between two sandstone beds. The collected plant fossils are not well-preserved (in most cases leaves and leaf fragments), but other fossils (e.g. vertebrates) were not found in this bed.

The observed sedimentary succession, dominated by dark coloured, organic rich mudstone beds intercalated with thin, fine-grained sandstone and coal beds, indicates a dominantly wet, marshy palaeoenvironment within the transition zone between the terrestrial and the marine habitats.

2.2.4. Stratigraphy and age of the Tiefengraben fossil locality

Concerning the stratigraphic age of the Tiefengraben coal and the adjacent sandy marl layers with fossil plants, only a limited number of studies exist, e.g. those of [Stojaspal and Lobitzer \(1976\)](#), [Hradecká et al. \(2006, 2008\)](#) and [Kvaček et al. \(2008\)](#). [Plöching \(1973\)](#) and [Plöching et al. \(1982a, b\)](#) considered the non-marine rocks of the Tiefengraben locality of Coniacian–Santonian age. Ammonites at St. Wolfgang prove a late Turonian age of marine marls below coral- and rudist-bearing strata ([Summesberger and Kennedy, 1996](#)).

The recent palynological study from the bone-bearing bed (Bed 2, see Fig. 2) shows the following stratigraphically meaningful results: the sporomorph assemblage is dominated by angiosperm pollen of the Normapolles-group while other groups are less abundant. Concerning the age, the genus *Semioculopollis* first appears in the Coniacian and *Vacuopollis* near the late Turonian–Coniacian boundary, thus the age of this sample can be near the Turonian–Coniacian boundary, probably early Coniacian according to palynology.

In the same wall of the gully, some 30 m southeast from the excavated fossil site, the presence of calcareous nannofossils indicates a marine intercalation. This part of the LGS is stratigraphically older as the fossil site presented here because the beds become younger from the southeast to the northwest in the exposed section (see above). The nannofossil assemblage included *Quadrum gartneri* and *Quadrum intermedium*, which, without the presence of *Micula staurophora*, point to a Turonian to early Coniacian age. Poorly preserved *Quadrum* cf. *gartneri* was also found some 50 cm below the bone-bearing bed (Bed 1 see Fig. 2). In correlation to the surrounding sections at St. Gilgen, Strobl-

Weissenbach and Bad Ischl, a possible stratigraphic range of the Tiefengraben Gosau-Group succession from mid-/upper Turonian to Coniacian is inferred.

Assuming the information from palynomorphs, plant macrofossils, and marine microfossils, the depositional age of the fossil-bearing strata of Tiefengraben is close to the Turonian–Coniacian boundary. According to the earliest appearance of the Normapolles *Semioculopollis*, the age of the fossiliferous section is most probably early Coniacian.

3. Material, methods, and preservation

The palaeontological material, collected and screen-washed from the Tiefengraben locality in 2019, is housed in the Palynological Collection of the Institute of Geology, Czech Academy of Sciences (CAS), Department of Palaeobiology and Palaeoecology, Prague (residues and slides of palynomorphs) as well as in the Geoscience Collection of the Oberösterreichische Landes-Kultur GmbH (OLL; formerly Oberösterreichisches Landesmuseum) in Linz, Upper Austria (all other fossils). Scanning electron microscope images of the fossils were taken at the Botanical Department of the Hungarian Natural History Museum (MTM) in Budapest, and at the Department of Geology of the University of Vienna (charophytes). The list of collected taxa are summarized in [Table 2](#) and the catalogue number of the specimens are listed in [Supplementary Table 1](#).

3.1. Palynology and plant micro-, macro- and mesofossils

Dark grey calcareous mudstone, claystone and coal seam samples were treated using a standard palynological extraction technique involving HCl-HF-HCl, KOH and acetolysis or heavy liquid ZnCl₂. The residue was mounted in glycerine jelly, and 5–10 slides were studied from each sample. The slides have been examined with a light microscope (Leica DM2500) and for the microflora photos, the software IM50 was used.

Plant macrofossils including leaves and seeds have been collected during the manual cracking up of a well-layered silt to fine sand bed (Bed 8 see, Fig. 2). The surface of the specimens was covered with glycerine to avoid destruction of the cuticula-bearing parts. While plant microfossils are basically in good condition, macro- and meso-specimens are sometimes fragmentary and moderately well preserved.

3.2. Invertebrates

Molluscs were prepared either mechanically or, in case of small specimens, by screen-washing. For ostracod analyses, samples were collected from three grey silty beds (Beds 1, 2 and 4; see Fig. 2) of the Tiefengraben locality. For each sample, about 1 kg of air-dried mudstone was processed with hydrogen-peroxide to extract the carbonate skeletal microfauna and microflora (ostracod, molluscs and charophyte gyrogonites). The preservation potential of the studied ostracod specimens is poor given that most of the valves and carapaces are pyritised, broken and filled with sediment. In many cases, the originally thin-shelled ostracods are present only as casts. Though some of the mollusc specimens are slightly compressed, they are generally well preserved, clearly showing the characteristic morphological traits.

3.3. Vertebrates

After the first successful probes of sampling, an additional 450 kg sample was collected from the coal-bearing bed (Bed 2, Fig. 2) of the LGS at the locality Tiefengraben near St. Wolfgang. Screen-washing and dissolution of the residue was processed

Table 2

List of discovered taxa and their preferred environment or ecology from the lower Coniacian Gosau beds of Tiefengraben at St. Wolfgang, Austria.

Higher-level taxon	Genus/species or higher-level taxon	Fossils	Ecology/autochthonous environment
Fungi	<i>Pluricellaesporites</i> sp.	Spores	Saprophytic
Fungi	<i>Diporicellaesporites</i> sp.	Spores	Saprophytic
Algae	<i>Ovoidites</i> sp.	Palynomorphs	Freshwater
Charophyta	<i>Mesochara voluta</i>	Gyrogonites	brackish-water
Pteridophyta	<i>Cyathidites australis</i>	Spores	Underwood
Gymnospermae	<i>Taxodiaceapollenites vacuipites</i>	Pollen	Wetland forest
Gymnospermae	<i>Taxodiaceapollenites hiatus</i>	Pollen	Wetland forest
Gymnospermae	<i>Taxodiaceapollenites</i> sp.	Pollen	Wetland forest
Gymnospermae	<i>Ephedripites</i> sp.	Pollen	Underwood
Gymnospermae	<i>Classopollis</i> sp.	Pollen	?
Gymnospermae	<i>Cycadopites</i> sp.	Pollen	Terrestrial
Gymnospermae	Gymnospermae indet.	Seed, branch fragments	Forests
?Gymnospermae	?Gymnospermae indet.	Amber fragments	Forests
Angiospermae	<i>Plicapollis</i> sp.	Pollen	Forests
Angiospermae	<i>Vacuopollis</i> sp.	Pollen	Forests
Angiospermae	<i>Semioculopollis</i> sp.	Pollen	Forests
Angiospermae	<i>Interporopollenites</i> sp.	pollen	forests
Angiospermae	<i>Trudopollis</i> sp.	Pollen	Forests
Angiospermae	<i>Minorpollis</i> sp.	Pollen	Forests
Angiospermae	<i>Complexiopollis</i> sp.	Pollen	Forests
Angiospermae	<i>Psilatricolporites</i> sp.	Pollen	Forests
Angiospermae	<i>Juglandiphyllites</i> sp.	Leaves	Riparian vegetation
Angiospermae	<i>Dryophyllum</i> sp.	Leaves	Forests
Angiospermae	<i>Cinnamomoides</i> sp.	Leaves	Forests
Angiospermae	<i>Laurophyllum</i> sp.	leaves	Woodland
Angiospermae	<i>Celastrophyllum</i> cf. <i>johannae</i>	Leaves	Wetland forest
Angiospermae	<i>Dicotylophyllum</i> sp.	Leaves	?
Angiospermae	Monocot indet.	Leaves	Riparian vegetation
Angiospermae	cf. <i>Caryanthus</i> sp.	Fruit	Forests
Angiospermae	cf. <i>Quedlinburgia</i> sp.	Fruit	Forests
Angiospermae	Angiospermae indet.	Reproductive organ	Forests
Gastropoda	<i>Pyrgulifera</i> sp.	Shells	Freshwater
Gastropoda	? <i>Pachymelania</i> sp.	Shells	Freshwater
Gastropoda	?Thiaridae, gen. et sp. nov.	Shells	Freshwater
Gastropoda	?Rissoidae, gen. et sp. indet.	Shells	Freshwater
Gastropoda	<i>Ariomphalus</i> sp.	Shells	Freshwater
Gastropoda	<i>Physa</i> s. l. sp.	Shells	Freshwater
Gastropoda	<i>Terebraliopsis articulata</i>	Shells	Brackish-water
Gastropoda	Gastropoda A, gen. et sp. indet.	Shells	Freshwater
Gastropoda	Gastropoda B, gen. et sp. indet.	Shells	Freshwater
Bivalvia	<i>Polymesoda</i> sp.	Shells	Brackish-water
Bivalvia	? <i>Mytilopsis</i> sp.	Shell fragment	Freshwater
Bivalvia	" <i>Cyclas</i> " <i>gregaria</i>	Shells	Brackish-water
Ostracoda	<i>Damonella</i> sp.	Carapace	Non-marine
Ostracoda	<i>Cetacella</i> sp.	Carapace	Non-marine
Ostracoda	<i>Neocyprideis</i> cf. <i>iberiacus</i>	Carapace	Brackish-water
Ostracoda	<i>Neocyprideis</i> cf. <i>coudouxensis</i>	Carapace	Brackish-water
Ostracoda	<i>Darwinula</i> ? sp.	Carapace	Freshwater
Ostracoda	<i>Heterocypris</i> sp.	Carapace	Freshwater to oligohaline
Arthropoda	' <i>Microcarpolithes</i> ' <i>hexagonalis</i>	Coprolites	Forests
Pisces	<i>Lepisosteus</i> sp.	Teeth, postcranial elements	Brackish to freshwater
Pisces	Actinopterygii indet.	Vertebrae	?
?Testudines	?Testudines indet.	Plate fragments	?
Mosasauroidae	Tethysaurinae indet.	Teeth	Brackish to freshwater
Crocodyliformes	<i>Neosuchia</i> indet. 1	Teeth	Semiaquatic
Crocodyliformes	<i>Neosuchia</i> indet. 2	Teeth	Semiaquatic
Dinosauria	?Tetanurae indet.	Teeth	Terrestrial
Dinosauria	Maniraptora indet. 1	Teeth	Terrestrial
Dinosauria	Maniraptora indet. 2	Teeth	Terrestrial
Vertebrata	?Pisces indet.	Coprolites	?aquatic

partly following the Henkel process (Henkel, 1966; Martin and Krebs, 2000; Ósi et al., 2019). The remaining, ca. 40 kg material (large, medium and small fractions sorted by 3 mm, 1 mm and 0.5 mm meshes, respectively) was washed again with water, dried and sorted under a stereo microscope.

All of the vertebrate remains are isolated, suggesting the presence of dispersal processes during the deposition of vertebrate remains. The material can be divided into two main parts. The first group includes unidentifiable bone and tooth pebbles. High rates of abrasion and the spherical shape of these remains indicate that

they were transported over a great distance with the bed-load sediment from the source area. The second group contains the identified vertebrate remains, which exhibit a relatively good preservation, though few of them were slightly abraded and fractured, indicating short-term transportation before accumulation. Altogether, the investigated vertebrate material includes isolated remains (characterized by different density, shape and abrasion state) from terrestrial and aquatic/semiaquatic animals, indicating that this collection represents an attritional, multitaxic, allochthonous assemblage.

4. Description and comparison of the biotic elements

4.1. Palynomorphs

4.1.1. Bed 2 – The bone-bearing bed

Palynomorphs consist of very rare pteridophyte spores of the Selaginellaceae family assigned here to *Echinatisporites varispinosus*, fungal spores of *Pluricellaesporites psilatus*, poorly preserved angiosperm pollen of *Minorpollis* sp. (Normapolles group), and some reticulate pollen of *Retitricolpites* sp. A marine admixture is represented only by some broken dinoflagellate cysts and agglutinated microforaminiferal linings.

4.1.2. Bed 3 – Coal seam

A relatively rich palynomorph assemblage was found in this coal-bearing bed (Fig. 3). Angiosperm pollen of the biostratigraphically important Normapolles group (Góczán, 1964; Góczán et al., 1967; Góczán and Siegl-Farkas, 1990) dominated this assemblage (80% of the palynomorphs) consisting of the genera *Plicapollis*, *Vacuopollis*, *Semioculopollis* (Fig. 3G–H), *Interporopollenites* (Fig. 3I–J), *Trudopollis* (Fig. 3K), *Minorpollis*, *Complexiopollis* (Fig. 4A). A similar angiosperm assemblage, but with marine admixture, was described by Svobodová et al. (2012) from the Turonian–Coniacian of St. Gilgen am Wolfgangsee. Of other angiosperm pollen, *Psilatricolporites* sp. is present (4%). Pteridophyte spores (11%) are represented only by *Cyathidites australis*. Gymnosperm pollen (4%) consist of several species of *Taxodiaceapollenites* (*T. vacuipites*, *T. hiatus*, *Taxodiaceapollenites* sp., Fig. 3E), as well as of a single specimen of each *Ephedripites* cf. *multistriatus* (Fig. 3F), *Classopollis* sp. and *Cycadopites* sp. Some non-marine algal-derived palynomorphs (1%), here referred to as *Ovoidites* sp. (Fig. 3A), and fungal spores of *Pluricellaesporites* and *Diporicellaesporites* (Fig. 3C), have also been found (Fig. 4A). Fungal spores are abundant in strata with organic matter such as wood fragments, cuticles or other tissues, and reflect the presence of saprophytic fungi. No marine microplankton was detectable in the observed material.

4.2. Micro-, macro- and mesoflora

The charophyte microflora recovered from Bed 4 is a monospecific assemblage of small specimens of *Mesochara voluta*, as confirmed by the unipartite basal plate (Fig. 5G). The well-preserved gyrogonites (Fig. 5A–D) are quite abundant and devoid of any corrosion features.

The macrofossil plant assemblage collected from Bed 8 of the investigated section (Fig. 6) is rich in dicotyledon angiosperm leaves. The most common is foliage of juglandoids (*Juglandiphyllites*, *Dryophyllum*), which could be assigned to the Normapolles complex (Friis et al., 2011, Fig. 4B). *Dryophyllum* is the most abundant genus of the section (Fig. 6A–C, G–I) with 24 specimens (34%). All of their leaves (leaflets) have a dentate margin. Two leaf shapes are present, an elongated, narrow form as well as an elliptic to ovate shape. Leaves (leaflets) of *Juglandiphyllites* are the second most common form being represented by 9 specimens (13%, Fig. 6F). Further angiosperm foliage is assigned to lauroids (*Laurphyllum*, *Cinnamomoides*, Fig. 6E) with 7 specimens (10%). Several other large-leaved dicots of unknown affinity are interpreted as *Celastrorhynchium* cf. *johannae* (5 specimens, Fig. 6D); those without details of venation preserved are determined as *Dicotylophyllum* sp. (13 specimens, 18%). Only one small fragment of a monocot leaf was found (Fig. 4B, 6L). Absence of pteridophytes and conifers, and the rare occurrence of monocots, stand in marked contrast to the flora from another outcrop of the St. Wolfgang region. The flora described by Kvaček et al. (2007) was interpreted as representing

swampy, coal-forming vegetation. Out of 52 well-preserved specimens, 27 are entire-margined leaves and 25 dentate (Fig. 4C). Leaf laminas are generally of medium size, although this can be misleading because *Dryophyllum* and *Juglandiphyllites* might represent leaflets of larger compound leaves.

The studied flora is similar to the Coniacian flora of Sudetes in Poland (Halamski and Kvaček, 2015; Kvaček et al., 2015; Halamski et al., 2020) and that of the Bohemian Cretaceous Basin (Halamski and Kvaček, 2016; Halamski et al., 2018). All these floras share a similar number of juglandoid angiosperms (*Juglandiphyllites*, *Dryophyllum*) and putative lauroids (*Laurphyllum*). Both above-mentioned Coniacian floras from Central Europe differ from the studied flora, however, in containing ferns, conifers (*Geinitzia*), platanoids (*Ettingshausenia*) and monocots (*Pandanites*, *Smilacites*).

Earlier palaeobotanical studies of Turonian sandstones from St. Wolfgang and Turonian–Coniacian of St. Gilgen (Kohlbachgraben) provided impressions of strap-like leaves of the halophytic gymnosperm *Dammarites albens* (Szente et al., 2010; Kvaček and Lobitzer, 2012), which were not recorded in the studied section. Coniacian vegetation associated with a coal seam from St Wolfgang (but in a different horizon) provided an assemblage of numerous fossil plants, consisting of conifers, dicotyledon leaves and monocots. The taphocoenosis next to the coal seam was dominated by pandanus leaves of *Pandanites trinervis* (Kvaček et al., 2007). The Santonian Iharkút flora (Bodor et al., in prep.) is also Normapolles dominated and the Iharkút locality has a bed where plant fossils of a juglandaceous wetland forest were preserved but dentate leaves are missing. The Campanian Grünbach flora from the Gosau Group of Grünbach near Vienna, representing largely swamp vegetation, is less similar to the studied Tiefengraben taphocoenosis, sharing only a few taxa (e.g. *Celastrorhynchium*) (Herman and Kvaček, 2010).

The mesoflora of the St. Wolfgang-Tiefengraben site is moderately well preserved and rare (Fig. 6O–Q). Besides the Normapolles related fruits here referred to as cf. *Caryanthus* sp. (Fig. 6N), specimens of the angiosperm cf. *Quedlinburgia* sp. (Fig. 6M) and gymnosperm seed fragments were also determinable.

A few dozens of amber fragments (their size ranging up to 2 mm) have also been found in the screen-washed material. The pieces are mostly splinters but some of them preserve their original, rounded teardrop shape.

4.3. Molluscs

Gastropod and bivalve fossils have been collected from Beds 1, 2 and 4 of the section (Fig. 7). The preservation of gastropods is usually good or mediocre. Due to the friable nature of the shells, however, internal features of bivalves could be studied only in a few cases.

Beds 1 and 2 have yielded a relatively diverse mollusc assemblage dominated by gastropods both in abundance and diversity. Among them, small-sized (usually less than 2 cm in height) specimens of *Pyrgulifera* sp. (Fig. 7A–G) are by far the most frequent. *Pachymelania*? sp. (Fig. 7H–K) and an indeterminate form (Fig. 7A, C) were encountered more rarely. In addition, washing residue of Bed 2 was found to contain a surprisingly rich and well-preserved mesofauna comprising gastropods representing at least five taxa, reaching less than 2 mm as maximum size. The assemblage consists of a hitherto apparently undescribed thiarid? (Fig. 7P–T), a rissoid? (Fig. 7U and V), *Ariomphalus* sp. (Fig. 7W–Y), *Physa* s. l. sp. (Fig. 7Z–AB) and an indeterminate form (Fig. 7AD). Bivalves are rare in Beds 1 and 2, and are represented only by shell fragments in the studied material. Only *Mytilopsis*? sp. could be, although tentatively, identified. The specimen in question is a fragment of

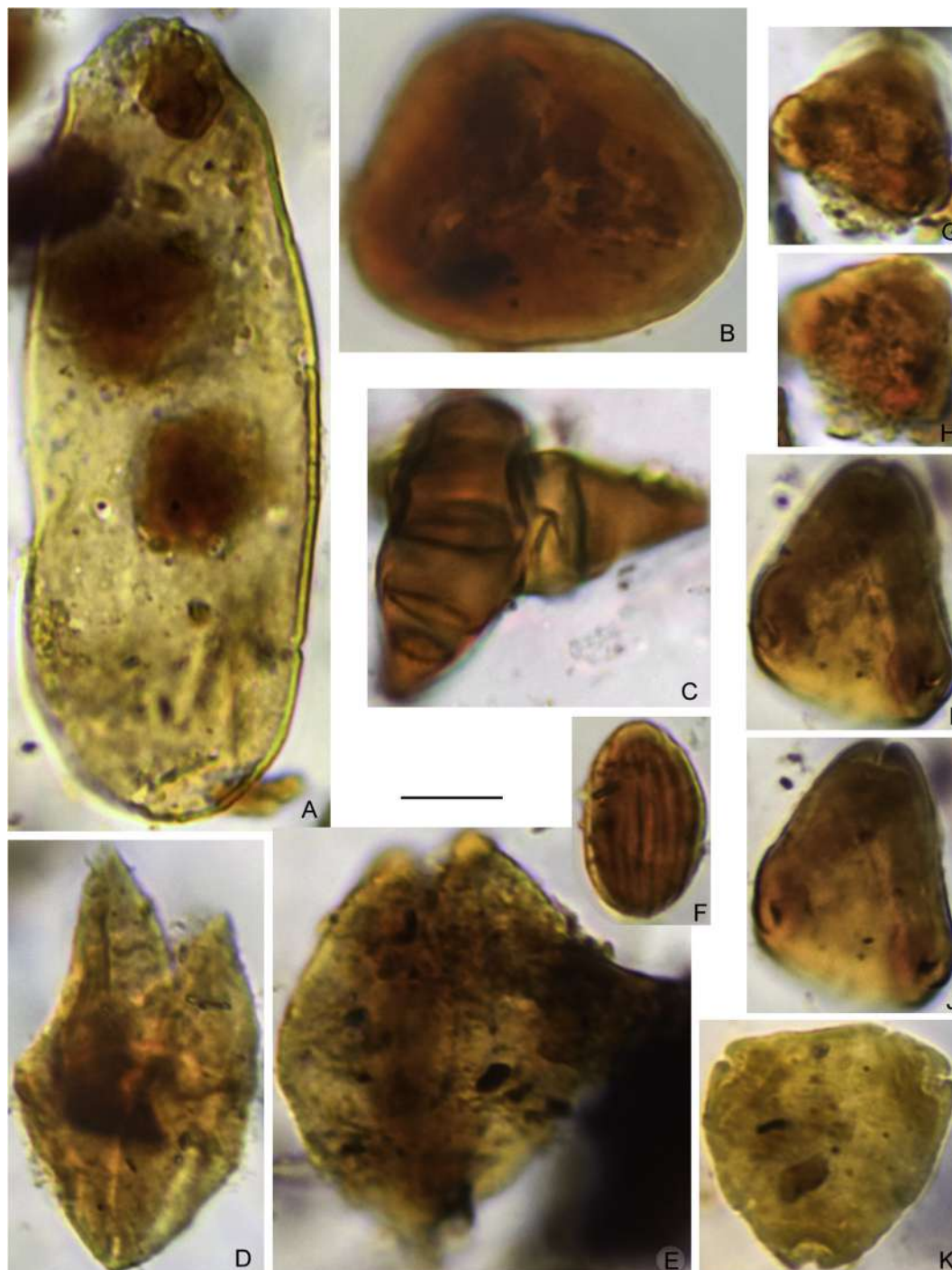


Fig. 3. Palyno- and sporomorphs from the lower Coniacian Gosau beds (Lower Gosau Subgroup) of Tiefengraben at St. Wolfgang, Austria. A, *Ovoidites* sp., B, *Deltoidospora* cf. *ordinata*, C, *Diporicellaesporites* sp., D, *Taxodiaceapollenites vacuipites*, E, *Taxodiaceapollenites* sp., F, *Ephedripites* cf. *multistriatus*, G–H, *Semiculopollis* cf. *minutus*, I–J, *Interporopollenites* sp., K, *Trudopollis* sp. Scale bar equals 10 μ m.

the umbonal region of a left valve bearing an internal septum as well as an apophysis (Fig. 7AE). Thus, it can be considered as one of the earliest known representatives of the family Dreissenidae.

Bed 4 has yielded a mollusc assemblage different from that of Beds 1 and 2 in both composition and diversity. Among gastropods, the most frequent elements are the fragments of the potamid? *Terebraliopsis articulata*, reaching 4 cm in height in some cases (Fig. 7L–O). The Tiefengraben specimens correspond well to the figures and description given by Zekeli (1852, p. 113, pl. 23,

FIGS. 4 a, b) based on material collected by Heinrich Ernst Beyrich in the region of St. Wolfgang. Thus, the Tiefengraben is close to, or identical with, the type locality of this species. Poorly preserved, small-sized and hitherto unidentified gastropods also occur in Bed 4 in very low numbers. Washing residue of the bioclast-rich part of Bed 4 was found to contain a gastropod assemblage dominated by juvenile specimens of *Pyrgulifera*, a genus apparently lacking in the macrofauna. Height of the specimens hardly exceeds 1 mm.

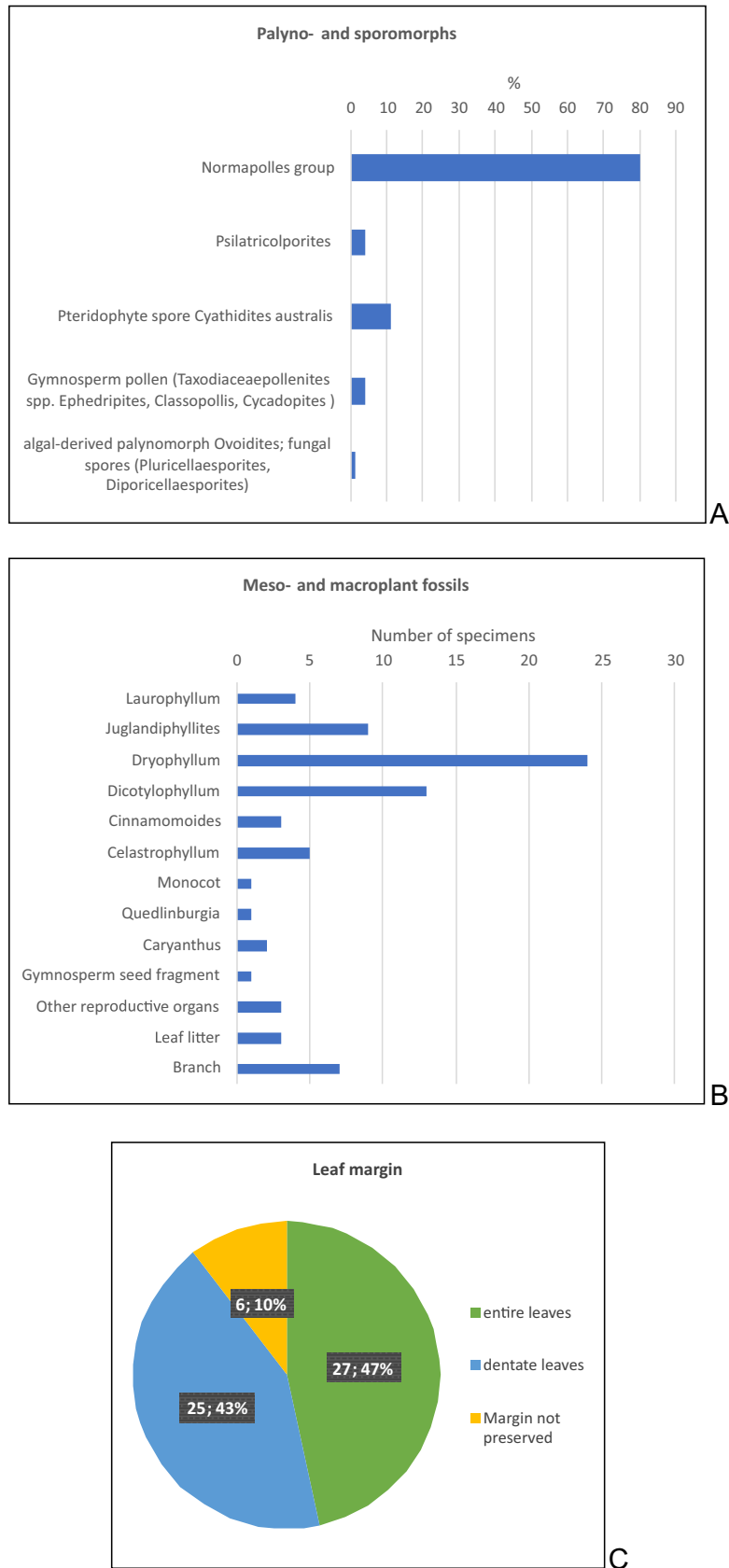


Fig. 4. Abundance of the different palyno- and spore-morphs (A) as well as meso- and macro-plant fossils (B), and the proportion of the different types of leaf margins (C).

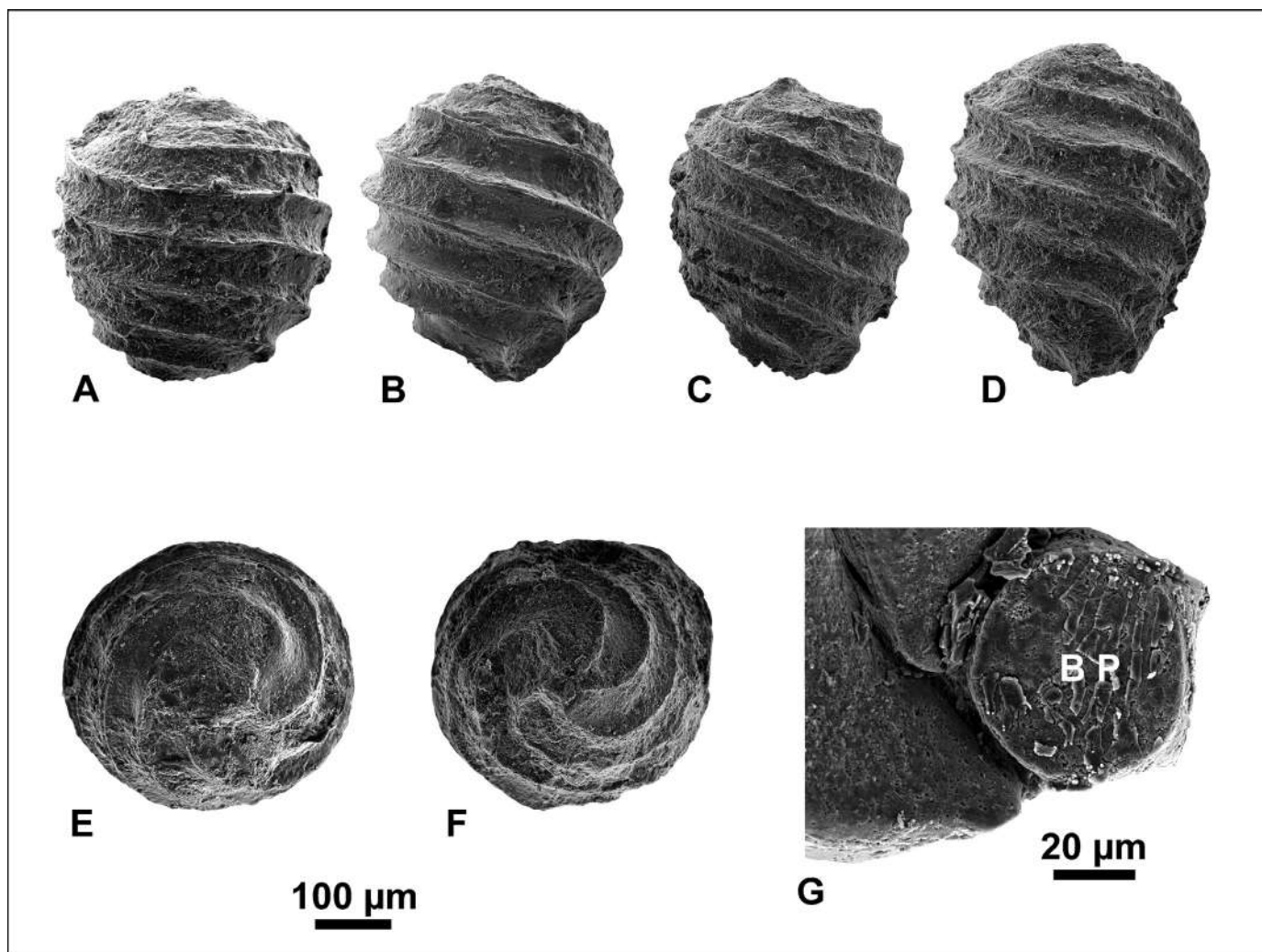


Fig. 5. Specimens (OLL 2021/2) of the charophyte *Mesochara voluta* (Characeae) from Tiefengraben, Bed 4. A–D, lateral views of gyrogonite; E, apical view; F, basal view; G, detail of the simple (unipartite) basal plate (BP) as seen from the inside of an empty gyrogonite.

The largest and most conspicuous element of the Tiefengraben mollusc fauna is a thick-shelled cyrenid (i. e. corbiculid) bivalve from Bed 4 and identified tentatively as *Polymesoda* sp. (Fig. 7AH–AL). Identification of cyrenid bivalves requires knowledge of internal characteristics, especially the details of the hinge, of which only cardinal regions of a right and a left valve could be studied in the Tiefengraben specimens until now. Both were found to possess three cardinals, two of which appear to be bifid. The Tiefengraben specimens seem to differ from “*Cyrena* (*Corbicula*) *solitaria*” introduced by Zittel (1865, p. 133, pl. 4, FIG. 5) partly on the basis of specimens collected at “Billmannsgraben located to the East of St. Wolfgang” by their larger size and more variable outline, as well as by the bifid appearance of cardinal teeth. It cannot be excluded, however, that these apparent differences are of ecophenotypic nature or due to the imperfect state of preservation. Unfortunately, it proved to be impossible to trace the location of “Billmannsgraben” until now. The Tiefengraben specimens also strongly resemble *Geloina* previously interpreted as a subgenus of *Polymesoda*. According to Schneider et al. (2020), however, cardinal teeth of *Geloina* are not bifid. In addition to the aforementioned form, small-sized cyrenid bivalves representing “*Cyclas*” *gregaria* Zittel (1865, p. 134, pl. 4, FIG. 7) were also encountered (Fig. 7AF and AG). Due to the lack of information on the hinge, an assignment of this form to any of the known cyrenid genera was not attempted.

4.4. Ostracods

Seven ostracod taxa were identified. We identified five non-marine species of three families, *Damonella* sp. (Fig. 8D–E) and *Cetacella* sp. (Fig. 8A), Candonidae gen. et sp. indet. (Candonidae), *Darwinula*? sp. (Darwinulidae), and *Heterocypris* sp. (Cyprididae, Fig. 8G), as well as two brackish-water species of the family Cytherideidae, *Neocyprideis* cf. *iberiacus* (Fig. 8F) and *N.* cf. *coudouxensis* (Fig. 8C). The species of *Cetacella*, *Damonella* and *Heterocypris* are likely to be new, as potentially also *Darwinula*? sp., and thus all require further investigation. Bed 1 produced mainly small-sized, thin-shelled ostracod carapaces identified as *Damonella* sp., with some similarities to *D. pygmaea* (Berriasian to Barremian of England, UK; Anderson, 1985), as well as a few specimens of the finely striated *Cetacella* sp., and Candonidae sp. indet. Bed 2 (the bone-bearing bed) yielded fragments and damaged valves of the small-sized *Neocyprideis* cf. *iberiacus*, *Cetacella* sp., and *Darwinula*? sp., as well as representatives of the large *Heterocypris* sp. The studied specimens of *Neocyprideis* seem to be juveniles based on their size, outline and thin shell. The ostracod fauna of Bed 4 is dominated by specimens of the species of *Neocyprideis*: *N.* cf. *coudouxensis* and *N.* cf. *iberiacus*. Besides these specimens, a few valves of *Damonella* sp. and *Darwinula*? sp. (Fig. 8L) also occur in the studied material.

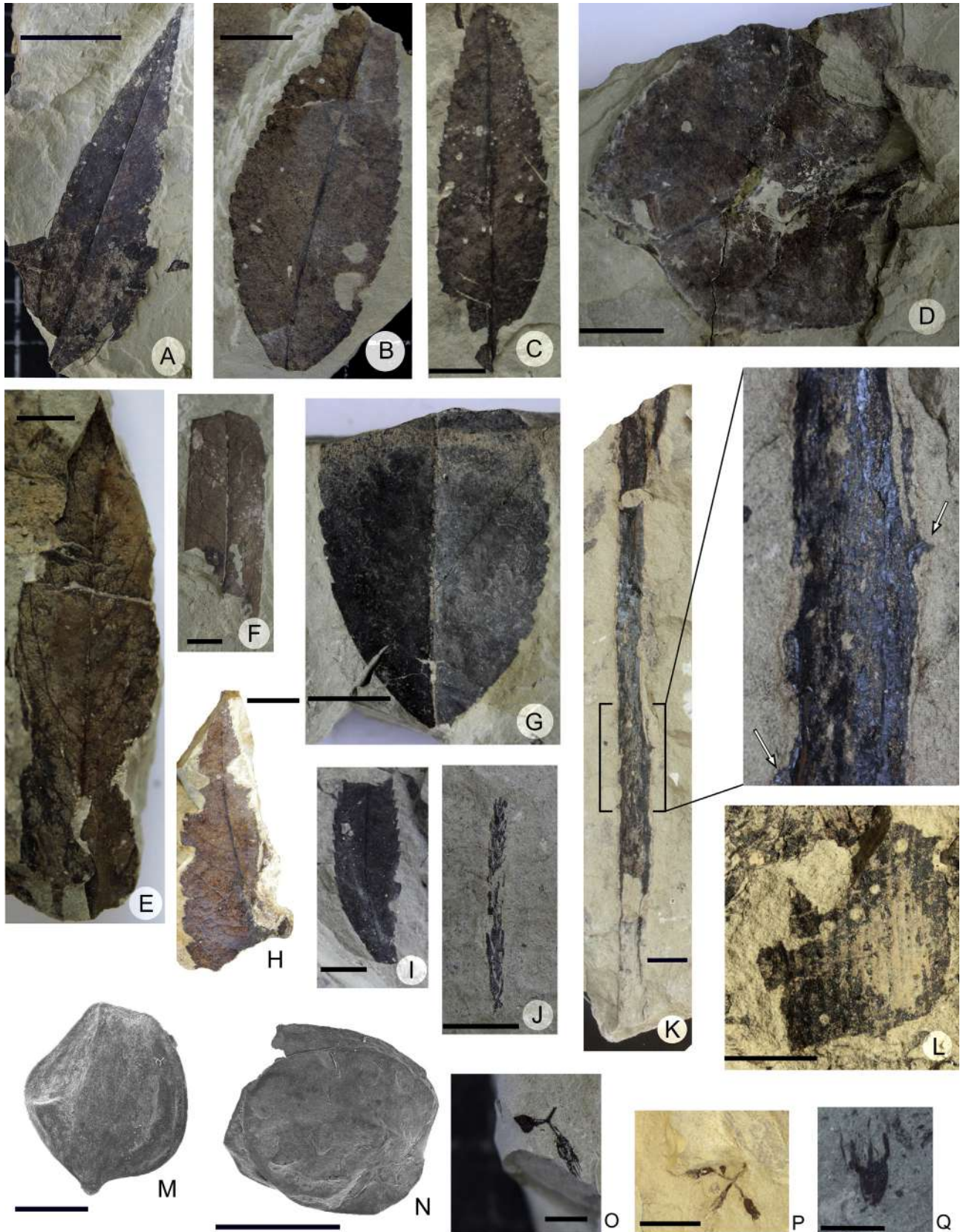


Fig. 6. Meso- and macro-plant fossils from the lower Coniacian Gosau beds (Lower Gosau Subgroup) of Tiefengraben (Bed 8) at St. Wolfgang, Austria. A, *Dicotylophyllum* sp. leaf (OLL 2021/4A); B, *Dryophyllum* sp. leaf or pinnule (OLL 2021/5A); C, *Dryophyllum* sp. leaf or pinnule (OLL 2021/5B); D, *Celastrorphyllum* sp. *johannae* (OLL 2021/10A); E, *Cinnamomoides* sp. leaf (OLL 2021/11A); F, *Juglandiphylloides* sp. leaf fragment (OLL 2021/12A) with brochidodromous venation; G, *Dryophyllum* sp. leaf fragment (OLL 2021/5C); H, *Dryophyllum* sp. leaf fragment (OLL 2021/5D) with trace of insect damage; I, *Dryophyllum* sp. leaf fragment (OLL 2021/5E); J, possible gymnosperm branch (OLL 2021/7); K, branch with presumable spikes (indicated by arrows); L, monocot leaf fragment (OLL 2021/14); M, cf. *Quedlingburgia* seed (OLL 2021/15); N, cf. *Caryanthus* fruit (OLL 2021/16); O, P, angiosperm reproductive organ with possible flying apparatus (OLL 2021/17–18); Q, angiosperm fruit (OLL 2021/19A). Scale bars equal 2 cm for A, D, K; 1 cm for B, C, G, H, L, P; 5 mm for E, F, I, J, O, Q; 2 mm for N; 1 mm for M.

4.5. Termite coprolites

Besides coprolites assigned to vertebrates (see below), hundreds of small (up to 1 mm), hexagonal, rod-shaped, carbonised specimens have been found in the screen-washed material (Fig. 8H, J, K). These fossils, mostly as isolated elements or aggregated in clumps (Fig. 8J), are interpreted to be termite coprolites. The morphology of these specimens is most similar to “*Microcarpolithes*” *hexagonalis* (Vangerow, 1954; for its nomenclature see; Friis, 1983; Colin et al., 2011; Knaust, 2020). Almost identical termite coprolites have been mentioned from the Turonian–Santonian of the South Bohemian basins in the Czech Republic (Knobloch, 1964, 1971), the Coniacian/Santonian of Poland (Heřmanová et al., 2020), the Santonian of Iharkút, Hungary, the lower Campanian of Grünbach, Austria (JM and AŐ, pers. observation), and the Maastrichtian of the Hațeg Basin, Romania (Vasile et al., 2013), and suggest a wide distribution of wood-foraging termites on the Late Cretaceous Central European islands.

4.6. Vertebrates

4.6.1. Fishes

Lepisosteiform fish (gars or garpikes) are represented by 28 teeth, one branchial tooth, 172 ganoid scales, 9 hemitrichia, 16 fringing fulcra or rudimentary elements, and 2 unidentified ganoid elements. Most teeth have the tooth base preserved, showing a fine apicobasal striation (referring to plicidentine tooth structure). All broken specimens show a circular cross-section outline. The acrodine cap of the complete specimens is conical (Fig. 9A and B). The single branchial tooth (Fig. 9C) is flattened and shiny, its crown is triangular and slightly bent. Portions of the base are also preserved. Most ganoid scales are fragmentary, however, while the complete specimens are of rhomboidal outline (Fig. 9D–H). Based on Grande (2010), the scales represent lateral line scales and mid-abdominal flank scales. They are composed of a relatively thick bony base and a continuous layer of shiny ganoin on the external surface. The better-preserved scales possess an anterodorsal process and remains of a weakly developed dorsal peg. Hemitrichia (Fig. 9I–L) are minute, half tube-like elements, with squared external (and internal) view and C-shaped cross-section. They bear a ganoin ornamentation of parallel, lentoid ridges. Fringing fulcra and rudimentary rays anteriorly line the fins of lepisosteids (Grande, 2010). The suggested fringing fulcra or rudimentary elements (Fig. 9M–P) are elongate and rod-like, and have a rectangular–subrectangular, drop-shaped, or circular to sub-circular outline in cross-section view. Their ganoin ornamentation is arranged in a single or in multiple linear layers along the longer axis of the specimens. Hemitrichia, possibly fringing fulcra or rudimentary ray elements of lepisosteids, which are identical to the Tiefengraben specimens have been figured by Blanco et al. (2017, FIG. 3L, M) and Szabó and Ősi (2017, FIGs. 2A–D, F–L, O–Q). The ganoin ornamentation of the indeterminate ganoid elements (Fig. 9Q) is built up of elongate to lentoid units of ganoin on their outer surface. A similar bone element referred to as *Atractosteus* sp. has been published in Szabó and Ősi (2017, FIG. 4A, B).

Only plicidentine teeth with conical tips have been found, which is a characteristic feature of the genus *Lepisosteus*. It is noteworthy that *Atractosteus*, the other lepisosteid genus known from the Mesozoic of Europe, has lanceolate fang tips (Sigé et al., 1997; Szabó et al., 2016a; Ősi et al., 2019; see also figures in; Grande, 2010). The single branchial tooth is different from those of pycnodontiform fishes (also an abundant actinopterygian group in the Mesozoic of Europe) in being shorter, less curved and more triangular-shaped (see figures in Kriwet, 2005; Ősi et al., 2019; Szabó et al., 2016b).

We tentatively refer this element also to lepisosteid fishes, as this is the dominant fish group of the Tiefengraben vertebrate fauna, while no remains referable to pycnodontid fishes have been found. The ganoin surface of the scales was investigated with a scanning electron microscope. The measured diameter of the ganoin tubercles and the measured inter-tubercular spaces also suggest that the Tiefengraben lepisosteid remains are closely related to genus *Lepisosteus* (after Gayet and Meunier, 1986, 2001; see Fig. 10, and Table 3). Based on this, and in combination with the conical shape of the teeth, we describe here the Tiefengraben lepisosteid material as cf. *Lepisosteus* sp.

Two fragmentary amphicoelous vertebral centra have an hour-glass shape in cross-section (Fig. 9S and T). The anterior and posterior articular surfaces show concentrically arranged growth-lines. The preserved portions point to a circular outline in anterior (and posterior) view for both specimens. In one of the specimens (Fig. 9S and T), numerous bony bars seem to extend on the side of the centrum.

Due to their low number and poor preservation, the two fragmentary fish centra cannot be determined more accurately than Actinopterygii indet. They surely do not belong to lepisosteids, as these primitive actinopterygians have opisthocoelous centra (Grande, 2010; Szabó et al., 2016a).

4.6.2. Mosasauroids

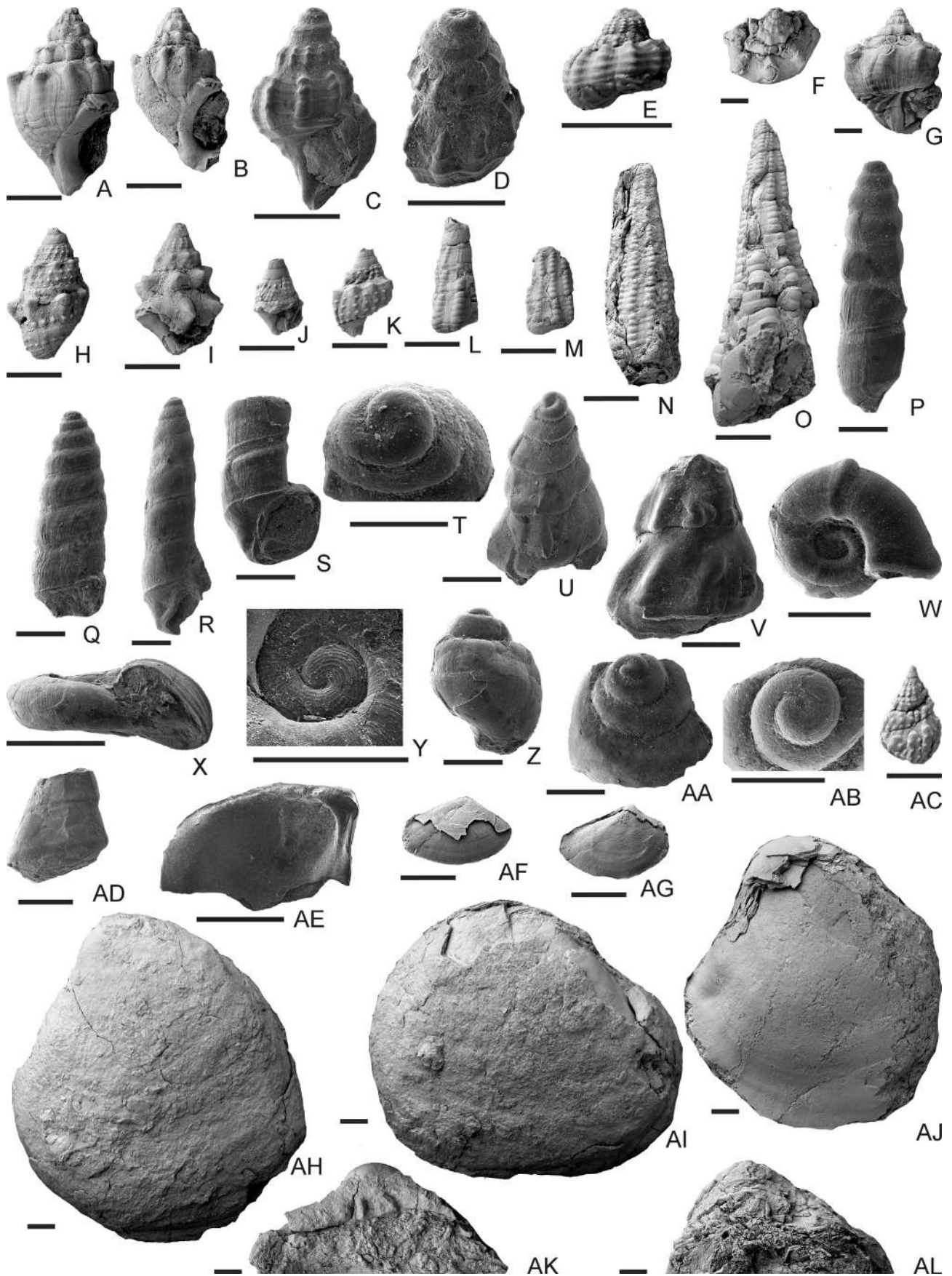
Two small fragmentary tooth crowns have been identified as indeterminate tethysaurine mosasauroid teeth, very similar to the ones reported recently from the Gosau Group of Gams, Austria (Ősi et al., 2019). The more complete (and larger) fragment (Fig. 11O) seems to be an apical tooth portion with a worn tip, while the other preserves only a smaller mid-portion of a crown. Also, significant wear made some parts of the teeth not eligible for study. The fragments curve linguodistally as in most mosasaurs and other reptiles, and the slight S-shaped curvature (if it was present) that is typical of *Pannoniasaurus* is not visible due to the fragmented nature of the specimens. However, the cross-section of the preserved part of the teeth is subcircular, with a less convex labial side as in *Pannoniasaurus* (Makádi et al., 2012).

The teeth are broken, worn and preserved in a way that allows only one of the presumed two carinae to be visible on each tooth: the smaller fragment preserves a mesial carina while the larger one shows a labiodistal one. This contrasts with *Halisaurus* that has mesial and distal carinae, and is also unlike *Tethysaurus* where the carinae are missing, but is consistent with the rest of tethysaurines *sensu* Makádi et al. (2012). Also, the labiodistal carina appears to be less developed, similarly to *Pannoniasaurus* and the teeth from Gams (Páramo, 1994; Páramo-Fonseca, 2000; Bardet et al., 2003; Bardet et al., 2005; Polcyn and Bell, 2005; Makádi et al., 2012; Palci et al., 2013; Ősi et al., 2019).

The intact surfaces of the crowns bear apicobasally extending fine striae that anastomose with each other (Fig. 11O) as in *Halisaurus*, *Pannoniasaurus*, *Romeosaurus* and *Russellosaurus*. They seem to be more developed on the lingual sides similarly to the Gams tethysaurine teeth, as well as to those of *Pannoniasaurus* and *Russellosaurus*. However, these striae on the Tiefengraben specimens, just as in the Gams teeth, do not extend onto the carinae, and, as a result, they lack the pseudo-serrations seen on the teeth of *Pannoniasaurus* (Bardet and Pereda Suberbiola, 2002; Bardet et al., 2005; Polcyn and Bell, 2005; Makádi et al., 2012; Palci et al., 2013; Ősi et al., 2019).

4.6.3. Crocodiles

Crocodiles are represented by teeth (their size ranging between 1 and 6 mm) and possibly a small (preserved length: 10 mm) distal end of a metapodium. Crocodile teeth are by far the most frequent



vertebrate fossils in the Tiefengraben (see Table 1), belonging to at least two different taxa. Based on their morphological features here we refer them to as Neosuchia indet. 1 and 2 until more complete material is available for a more precise taxonomical assignment.

Neosuchia indet. 1 (more than 400 teeth) is characterised by conical, labiolingually slightly flattened tooth crowns having mesiodistally positioned, unserrated carinae (Fig. 11F–J). Crowns are constricted basally and slightly bent lingually resulting in a slightly concave lingual surface. Carinae are ledge-like structures with lingual shelves (thus they cannot be observed in labial view). Apicobasally oriented, parallel enamel ridges ornament both the lingual and labial surfaces but labially they are not so pronounced. Of this taxon, three morphotypes can be distinguished that most probably represent different positions in the tooth row. The more anterior teeth (Fig. 11F) have greater crown height/mesiodistal width proportion than the more bulbous, posterior teeth (Fig. 11G–J). The higher, more anteriorly positioned teeth are most similar to the Neosuchian teeth from the Turonian of Gams (Ósi et al., 2019, FIG. 7J, K) and the teeth from the Santonian of the Ajka Coal Formation (Ósi et al., 2016), although the lingual shelves of the carinae are not as wide mesiodistally as those of the Gams specimens.

Some of the posterior, low-crowned teeth are mesiodistally strongly elongate and labiolingually narrow (Fig. 11I–J), similarly to the posterior teeth of some *Theriosuchus*-like (e.g. Martin et al., 2010, 2014; Venczel and Codrea, 2019) and bernissartiid (Buffetaut and Ford, 1979) forms, and are almost identical with some of the neosuchian teeth from Gams (Ósi et al., 2019, FIG. 7O, P). These specimens are slightly different from the massive, bulbous crowns with oval cross-section of Neosuchia indet. 1 (Fig. 11G and H) and might represent a different taxon.

Neosuchia indet. 2 (29 teeth) is characterised by conical, labiolingually slightly flattened tooth crowns bearing mesiodistally positioned, unserrated carinae and apicobasally fine enamel ridges with parallel orientation on the lingual surface (Fig. 11A–E). The main distinguishing feature of these crowns are the 4–6, deep, apicobasally oriented grooves along the lingual and usually on the basal half of the labial crown surfaces. These deep grooves result in a cumulus-like cross-section of these crowns (Fig. 11D). According to different tooth positions, two morphotypes, representing anteriorly positioned, higher, pointed crowns (Fig. 11A–B) and posterior, lower crowns (Fig. 11C), existed in this taxon as well. To our knowledge, similar, deeply grooved crowns are not present in the typical European Late Cretaceous crocodiles (e.g. allodaposuchids, hylaeochampsids, *Theriosuchus*-like forms sensu Tennant et al., 2016), while they nevertheless exist in some other groups of mesoeucrocodylians. From the Gondwanan landmasses, the uruguayosuchid *Araripesuchus wegeneri* (Buffetaut, 1981; Sereno and Larsson, 2009), the peirosaurid *Hamadasuchus rebouli* from the Albian–Cenomanian Kem Kem beds (Buffetaut, 1994; Larsson and Sues, 2007), and the baurusuchid *Gondwanasuchus* (Marinho et al., 2013) possess crowns with longitudinal grooves, though some of these taxa have zipodont teeth, which is not characteristic of Neosuchia indet. 2 from Tiefengraben. From the northern hemisphere, the miniature paralligatorid *Wannchampsus kirpachi* from the Lower Cretaceous of North America (Adams, 2014) has crowns with grooves, though they are zipodont, and the grooves

are not as deep as those on the Tiefengraben teeth. In addition, a mesoeucrocodylian zipodont tooth from the Albian bauxite of Hungary has a fluted crown as well (Ósi et al., 2015).

4.6.4. Dinosaurs

Dinosaurs are represented by seven fragmentary isolated theropod teeth belonging to at least three different taxa. The largest tooth (preserved apicobasal length: 5 mm; Fig. 11P) is labiolingually slightly compressed, oval in cross-section, and has slightly concave, serrated distal and serrated convex mesial carinae. Distal serration is more pronounced than the mesial in having mesiodistally more elongate denticles. The serration density on the distal carina is 3–4 denticles in 1 mm. No fluting, grooves or enamel ridges can be observed. This tooth differs from the typical, labiolingually flattened paravian teeth in that it has strong growth lines, and no shelves along the carinae or longitudinal fluting on the crown. The cross-section, the fine wrinkles on the crown surface, and the serration density makes this tooth most reminiscent of the smaller tetanuran teeth described from the Santonian of Hungary and the Campanian of Muthmannsdorf, Gosau Group of Austria (Ósi et al., 2010), thus we tentatively refer this tooth to Tetanurae indet.

Based on their morphological traits, we assign the remaining teeth to maniraptorans and distinguish two taxa. Maniraptora indet. 1 is represented by probably four, small (preserved apicobasal length: 4 and 2 mm), labiolingually compressed tooth fragments. One of the larger specimens is more pointed, both of its carinae are serrated but the mesial serration is weaker (Fig. 11K–N). The smaller tooth fragment bends more distally than the previous one and does not have mesial serration. A slightly concave shelf extends along the carinae in both specimens, and on the basal half of the lingual and labial sides of the larger specimen an apicobasally extensive shallow depression is present (Fig. 11L). These teeth are almost identical with some theropod teeth from the Turonian of Gams (Ósi et al., 2019, FIG. 8I, L, Q). As it was noted for the Gams teeth, these features of the tooth crown are most reminiscent of some maniraptoran teeth (Currie et al., 1990). Two further specimens might belong to this taxon as well. One of them has a similar shape, distal serration and unserrated mesial carinae as those seen in the previous specimens but it is too fragmentary for a more detailed comparison. A fourth specimen might belong to this taxon and is probably an anterior tooth having a more rounded cross section. Its crown slightly bends lingually (not distally) and bears weakly developed mesial and distal serrations which do not reach the base of the crown. The crown is ornamented by a few shallow and wide longitudinal grooves (sensu Hendrickx et al., 2015) on all sides, and it appears that much of the enamel is already missing from the crown.

Maniraptora indet. 2 has a labiolingually compressed, distally curved fragmentary crown (Fig. 11Q–S). The mesial and apical parts of the crown are broken, thus the presence or absence of the mesial carina is unknown. The distal carina, at least on the basal part, seems to be absent. The main distinguishing features of the crown are the shallow basal depression at the crown–root junction both labially and lingually, and the wide, apicobasally oriented grooves resulting in a “wavy” crown surface (Fig. 11Q–S). To our knowledge, similar teeth have not been reported in Late Cretaceous European theropod faunas. Only the teeth of *Paronychodon* (e.g. Zinke and

Fig. 7. Molluscs from the lower Coniacian Gosau beds of Tiefengraben at St. Wolfgang, Austria. A–G, *Pyrgulifera* sp. (OLL 2021/43A, OLL 2021/43B, OLL 2021/43C, OLL 2021/43D, OLL 2021/43E, OLL 2021/43F). H–K, *Pachymelania?* sp. (OLL 2021/44A, OLL 2021/44B, OLL 2021/44C, OLL 2021/44D). L–O, *Terebraliopsis articulata* (OLL 2021/49A, OLL 2021/49B, OLL 2021/49C, OLL 2021/49D). P–T, *Thiaridae?*, gen. et sp. nov. (OLL 2021/45A, OLL 2021/45B, OLL 2021/45C, OLL 2021/45D, OLL 2021/45E). U, V, *Rissoidea?*, gen. et sp. indet. (OLL 2021/46A, OLL 2021/46B). W–Y, *Ariomphalus* sp. (OLL 2021/47A, OLL 2021/47B, OLL 2021/47C). Z–AB, *Physa* s. l. sp. (OLL 2021/48A, OLL 2021/48B OLL 2021/48C). AC, Gastropoda A, gen. et sp. indet. (OLL 2021/50). AD, Gastropoda B, gen. et sp. indet. (OLL 2021/51). AE, *Mytilopsis?* sp. (OLL 2021/53). AF, AG, “*Cyclas*” *gregaria* (OLL 2021/54A, OLL 2021/54B). AH–AL, *Polymesoda* sp. (OLL 2021/52A, OLL 2021/52B, OLL 2021/52C, OLL 2021/52D). A–K and P–AE have been collected from Beds 1 and 2; L–O and AF–AL from Bed 4. Scale bars represent: 500 μ m (D, P–V, AA, AB, AD); 1 mm (C, W, X, AE); 5 mm (A, B, E–O, AC, AF–AL).

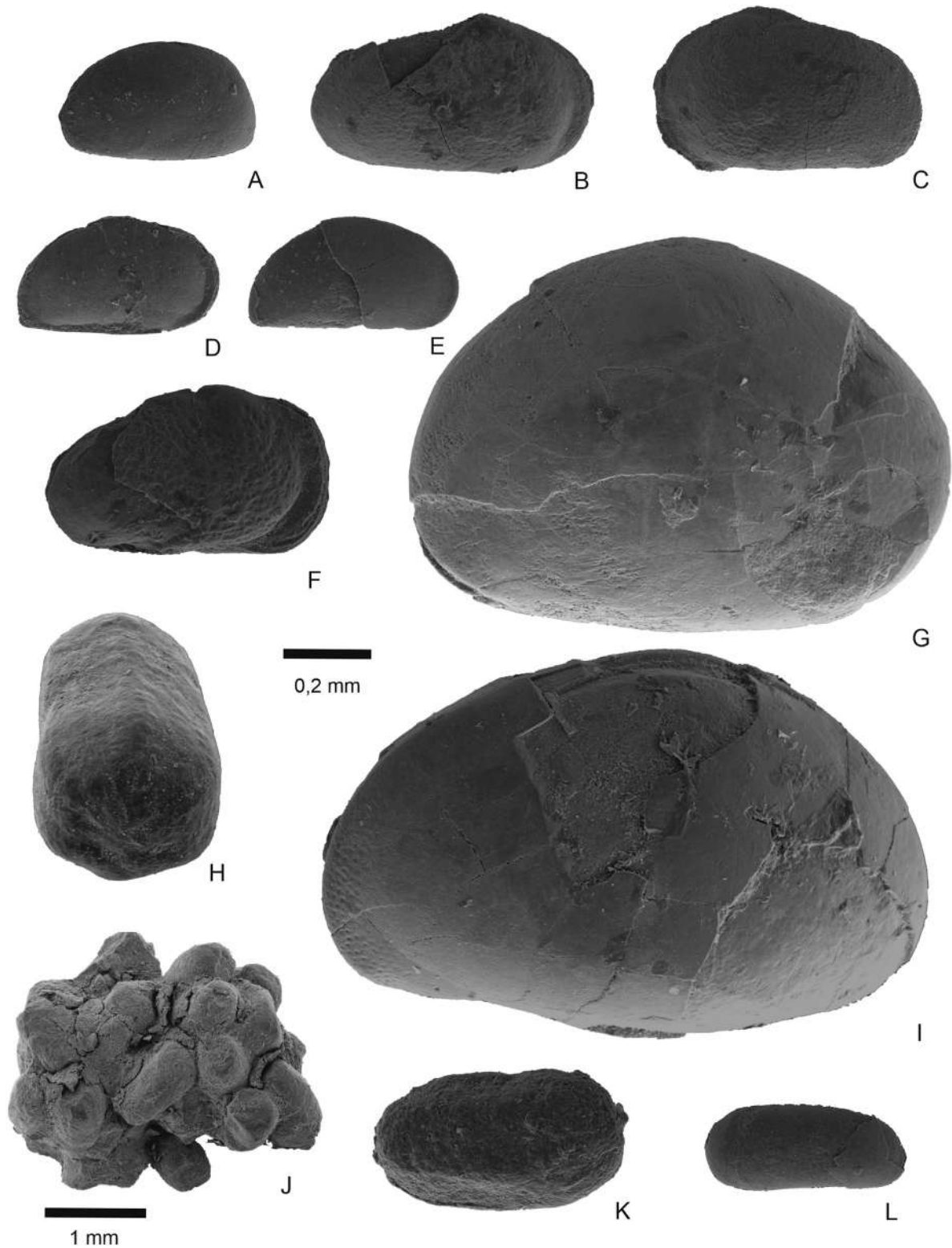


Fig. 8. Ostracods and termite coprolites from the lower Coniacian Gosau beds of Tiefengraben at St. Wolfgang, Austria. A, *Cetacella* sp., (OLL 2021/22Y) RV in lateral view from Bed 2. B, *Neocyprideis* cf. *coudouxensis* (OLL 2021/22Q) RV in lateral, C, *Neocyprideis* cf. *coudouxensis* (OLL 2021/22T) LV in lateral view from Bed 4. D–E, *Damonella* sp., (OLL 2021/22G, OLL 2021/22H) C in right view from Bed 1. F, *Neocyprideis* cf. *iberiacus* (OLL 2021/22K) C in right view from Bed 4. G, *Heterocypris* sp. (OLL 2021/22A) C in right view from Bed 2. H, termite coprolite (OLL 2021/22U) in apical view. I, *Heterocypris* sp. (OLL 2021/22B) C in left view from Bed 2. J, termite coprolite aggregate (OLL 2021/V) from Bed 4. K, termite coprolite (OLL 2021/U) in lateral view from Bed 4., L, *Darwinula?* sp. (OLL 2021/22S) C in left view from Bed 4.

Rauhut, 1994) and *Euronychodon* (Antunes and Sigogneau-Russell, 1991) are characterised by longitudinal grooves on at least one side of the crown. A possible *Paronychodon* tooth has been also reported from the Turonian of Gams (Ósi et al., 2019) but this specimen has a D-shaped cross-section, as typically seen in both of these enigmatic taxa. In addition, *Euronychodon*, does not have the longitudinal grooves on the basal part of the crown. On the other hand, a similar morphology with labiolingual grooves and unserrated carinae is characteristic of unenlagiine theropods, such as *Buitreraptor* from South America (Gianechini et al., 2011).

The fourth possible taxon has a small (preserved apicobasal length: 1.5 mm), labiolingually compressed crown with unserrated carinae (at least on its preserved part, Fig. 11T). Its surface is smooth and neither the concave shelf on its basal part nor longitudinal grooves can be observed, similarly to a theropod tooth from the Santonian Ajka Coal Formation (Ósi et al., 2016: FIG. 5P–Q). This tooth might be a juvenile representative of Maniraptora indet. 2 or perhaps belongs to a different group of theropods, since unserrated teeth occur in a variety of theropod clades, including unenlagiine dromaeosaurs (*Buitreraptor* Makovicky et al., 2005), ornithomimosaur (*Pelecanimimus* Pérez-Moreno et al., 1994), and enantiornithine birds (Chiappe and Walker, 2002).

4.6.5. Other vertebrate fossils

The vertebrate material from Tiefengraben contains various microscopic and a few macroscopic bone fragments, some of which are more informative than others. Some specimens are strongly reminiscent of cube-shaped fragments of turtle shells. Their inner and outer surfaces are parallel to each other, relatively smooth and slightly weathered, and they do not bear any diagnostic pattern of outer bone texture. The inner texture is densely spongy as is typically seen in turtle shell elements.

Besides unidentified bone fragments, an approximately 2 cm long bone bearing a simple, convex articulation surface has been found. The shaft is not hollow, it has an oval cross-section, and shallow ridges extend along its shaft, perhaps for the attachment ligaments or muscles. It might be from a limb element (e.g. metapodium) but is not diagnostic enough to ascertain its more precise anatomical position. In addition, a small (preserved length: 7 mm) limb bone fragment, being most similar to a distal end of a femur having a mediolaterally widened epiphysis, has been found in the screen-washed material.

4.6.6. Coprolites

More than a dozen fragmentary coprolites (length between 5 and 25 mm) have been found, which, based on their size and shape, supposedly belong to vertebrates. Each has a cylindrical shape with a circular or oval cross section. The light brown colour and the finer grain size of the matrix of the coprolites show significant differences from the embedding rocks. Some specimens are spirally wound. Bones were preserved in two specimens, one of them is a cylindrical bone fragment, while in the other specimen bones are reminiscent of a mass of ganoid scales. They do not bear cracks on their surface. These coprolites are similar to those from the Santonian of Iharkút, Hungary (Segesdi et al., 2017). Their shape, and the fish-scale content of one of these coprolites suggest that their producers might have belonged to an aquatic group as those from Iharkút but this hypothesis needs to be proved by further analyses (i.e., mineral content, further inclusions, taphonomical characters).

5. Discussion

5.1. Temporal and spatial distribution of the biotic components

The specimens of brackish to non-marine aquatic and terrestrial floras and faunas collected from Upper Cretaceous sites in Europe is

uneven and highly incomplete in many respects (see e.g. Bandel and Riedel, 1994; Sames and Horne, 2012; Csiki-Sava et al., 2015; Halamski et al., 2020). This situation is particularly characteristic for the 17 million years long late Cenomanian–middle Campanian gap period, from which we hardly know a complex biotic record in Europe. Of the Turonian–Coniacian period, only plant fossils from Bohemian (Czech Republic) and Silesian (Poland) sites (e.g., Halamski et al., 2020), as well as crocodiles and dinosaurs from the Turonian of France (Buffetaut and Pouit, 1994) and the Turonian of Styria, Austria (Ósi et al., 2019) have been documented. From the Santonian, besides few specimens discovered in France (Buffetaut and Pouit, 1994), the Iharkút site (Hungary) is the only one from where a diverse, well-documented biota that comprises paly-nomorphs, macro- and mesoplants, ostracods, molluscs and vertebrates is known (Bodor and Baranyi, 2012; Ósi et al., 2012; Botfalvai et al., 2015). From the lower Campanian, the Grünbach biota from eastern Austria (plant, invertebrate and vertebrate fossils) is the most diverse assemblage of the European archipelago (Seeley, 1881; Herman and Kvaček, 2007, 2010). In addition, the finds of the less diverse Villeveyrac locality in southern France, which includes pollen, charophytes, ostracods, and vertebrates, is worth to be mentioned (Freytet, 1970; Feist and Freytet, 1983; Buffetaut et al., 1996; Garcia and Pereda Suberbiola, 2003). Thus, the lower Coniacian set of 60 taxa presented here is particularly important in understanding the temporal and spatial distribution of taxa characteristic of these environments.

5.1.1. Algae and plants

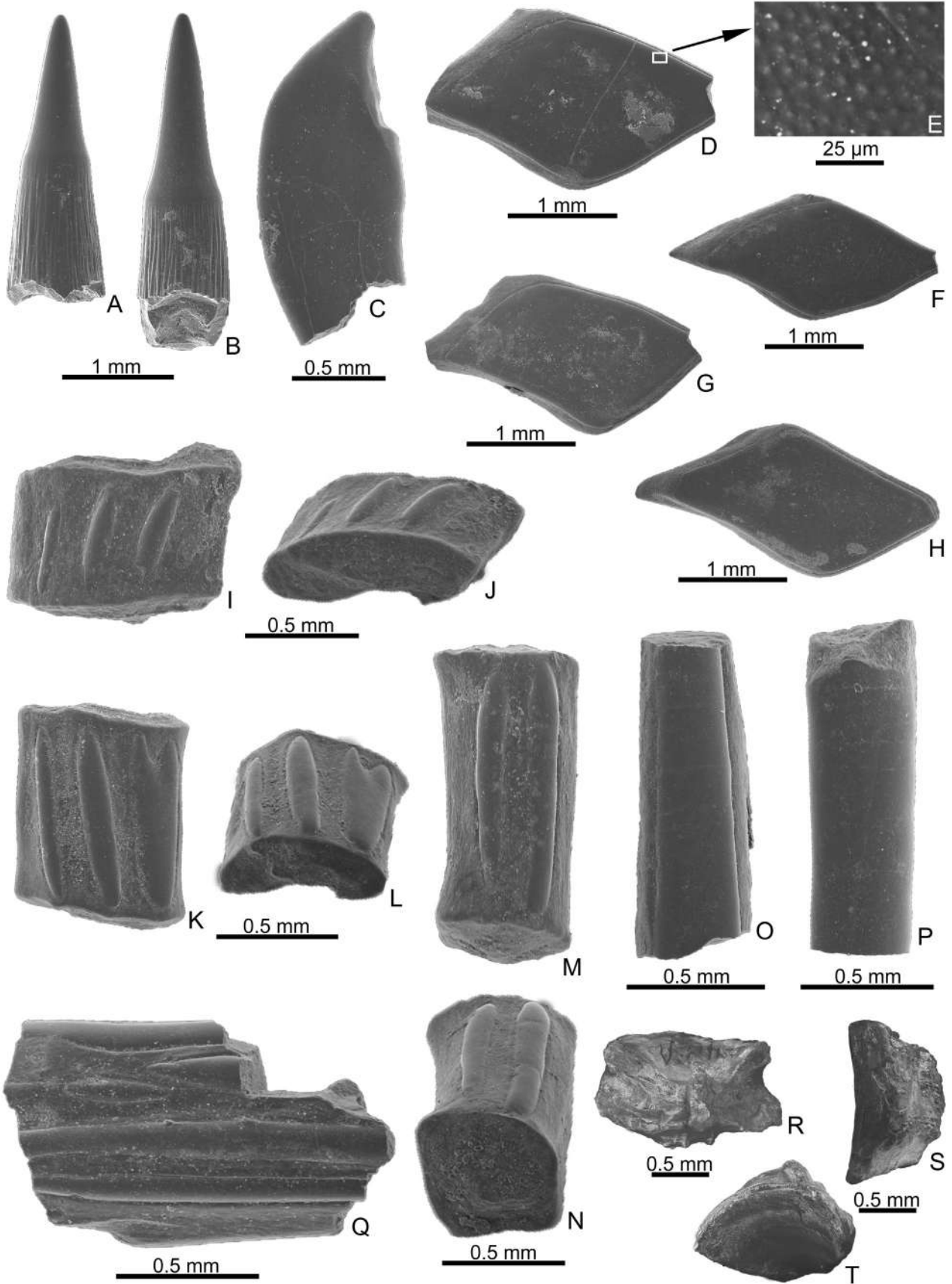
The abundance of gyrogonites of *Mesochara voluta* as well as their association with brackish-water ostracods (species of *Neocyprideis*) in the studied sample suggest that this particular flora is autochthonous.

Mesochara voluta has been reported from Middle Jurassic to Lower Cretaceous deposits from all over the world (e.g., Tiss et al., 2019 and references therein for review) as well as the Upper Cretaceous of China (Wang, 1965). Our specimens are morphologically identical to multiple and well-known records of *M. voluta* – with the exception of their decreased average size, which is palaeoenvironmentally induced (see section 5.2 below for details) – justifying our taxonomic identification.

From the palaeobiogeographical and stratigraphical point of view, this is the first record of the species *M. voluta* from the Upper Cretaceous of Europe as well as the second record of charophytes from the Turonian–Santonian of this continent. Indeed, the only other European charophyte record from this time interval has been reported by Feist (1981) from the Turonian of France. Therefore, the Gosau basins could be considered as a refuge of elements from the early Mesozoic charophyte flora in Europe that survived the Turonian crisis.

Our data give new insights on the evolution of charophytes from a stratigraphic interval which in Europe had previously been considered to be represented by a hiatus and, thus, as a gap in our knowledge (Riveline et al., 1996; Martín-Closas and Soulié-Marsche, 2016). Outside Europe, Turonian–Santonian charophytes have only been described from two localities: a low-diversity brackish flora from South America (Argentina, Uliana and Musacchio, 1978), and a very high-diversity freshwater (lacustrine) flora from Asia (North China, Li et al., 2019).

Most of the pollen and sporomorph material at Tiefengraben, as well as the plant macro- and mesofossils, show a composition typical for European sites. For example, pollen (e.g. *Trudopollis*), seed (e.g. *Caryanthus*), and leaf (e.g. *Juglandiphyllites*) fossils representing the Normapolles Province are known from many other sites on the continent (Knobloch and Mai, 1984; Szente et al., 2010; Friis et al., 2011; Bodor and Baranyi, 2012; Halamski and Kvaček,



2015; Heřmanová et al., 2016; Polette and Batten, 2017; Halamski et al., 2020). However, *Quedlinburgia* from the Tiefengraben section is a novelty in the Gosau Group Cretaceous because it was previously known only from the Albian and Santonian of western Hungary and from the Santonian and Maastrichtian of central Germany (Knobloch and Mai, 1984).

5.1.2. Invertebrates

Serious gaps can be recognised in the spatial and temporal distribution of the invertebrate groups discussed here, to which the faunal elements of the Tiefengraben locality serve as a particularly important addition. Among molluscs, there are forms that appear in strata of similar or even older age in Europe (Fabre-Taxy, 1948; Herm, 1977; Fürsich, 1994; Bandel, 1996). However, *Ariomphalus* was previously known only from the Santonian Ajka Coal Formation in Hungary (Bandel and Riedel, 1994), so the findings described here extend the temporal range of this genus to the early Coniacian, and its spatial distribution from the Transdanubian Mountains to the Northern Calcareous Alps. For *Mytilopsis*, the Tiefengraben specimen represents the first documented record from the Mesozoic; previously this genus was only known from the Cenozoic (Kennedy, 2011).

Non-marine Cretaceous ostracod faunas in Europe are well known from the Lower Cretaceous (mainly Berriasian to Barremian) “Purbeck-Wealden” non-marine depositional facies (e.g., Martin, 1940; Wolburg, 1971; Kilenyi and Neale, 1978; Anderson, 1985 and references therein; Colin and Oertli, 1985), and from continental Campanian to Maastrichtian deposits. Late Cretaceous brackish and non-marine faunas are, however, almost exclusively based on records from southern France and the Iberian Peninsula (summarised in Babinot et al., 1996; Garcia et al., 2000; Babinot, 2003). Unique occurrences are limnic ostracod faunas from the Santonian to Campanian of the Western Carpathians, and from the Maastrichtian dinosaur-bearing rocks of the Hațeg Basin in Romania (Pipík, 2009; Silye et al., 2014). In Europe, Turonian–Coniacian brackish-water ostracods of the genus *Neocyprideis* have only been reported from Spain (for a review see Babinot et al., 1996). With the occurrence of this genus in the lower Coniacian of the Tiefengraben we here extend the earliest record of this genus to the Alpine region. Similarly, we extend the Late Cretaceous spatial distribution of species of *Heterocypris*, living from the Cenomanian to the present day (Cabral et al., 2008), to Central Europe as well.

The occurrence of species of *Damonella* and *Cetacella* at the Tiefengraben site are a novelty for the Upper Cretaceous of Central Europe, both in time and space. So far, these forms are only known from the Upper Jurassic (e.g., Helmdach, 1971; Dépêche, 1985; Ainsworth et al., 1989; Gramann and Luppold, 1991) and Lower Cretaceous strata of the “Purbeck-Wealden” interval (e.g., Kilenyi and Allen, 1968; Anderson, 1985; Horne, 1995; Rodriguez-Lázaro, 1995; El Albani et al., 2004; Schudack and Schudack, 2012), with the exception of a few records of *Cetacella* from the Maastrichtian of India (Whatley, 2012, and references therein). The findings from Tiefengraben provide the first evidence to indicate the Late Cretaceous existence of species of *Damonella*, and of species of *Cetacella* in Europe, and also represent their very first record in the Alpine region. This suggests that they might have been relict forms that, like some vertebrate groups (see below), might have survived in certain areas of the western Tethyan archipelago, or were re-

introduced from adjacent palaeogeographic areas since many non-marine ostracods can be passively transported by larger animals over long distances on supraregional to intercontinental scales, crossing migration barriers (Sames and Horne, 2012).

The “mid-Cretaceous faunal turnover” in the non-marine ostracod faunal composition (Sames and Horne, 2012) is barely understood to date. Resulting from the mid-Cretaceous transgressions (loss of habitat) and climate changes (detailed effects on the respective ostracods are not well-understood, though temperature was probably important), many of the common or even dominant faunal elements of the “Purbeck-Wealden” became locally extinct (particularly in the circum-Atlantic areas but surviving in India and Asia). At the same time, more “modern” faunal elements appeared, closer relatives of which still exist today. The mid-Cretaceous eustatic sea-level rise also resulted in the considerable reduction of non-marine and terrestrial deposits leading to a respective gap in the non-marine record worldwide, in Europe from the Aptian to the Cenomanian and beyond. With respect to non-marine ostracods, the Tiefengraben fauna emphasizes the importance of every single one of the few sporadic mid-to Late Cretaceous non-marine records in Europe and their contribution to the understanding of the mid-Cretaceous faunal turnover.

Hexagonal “*Microcarpolithes*” coprolites have been described from a number of Lower and Upper Cretaceous sites in Western Europe (for a review see Colin et al., 2011). Finds from the Coniacian of Tiefengraben, the Santonian of Iharút (Vasile et al., 2013, 2014), and the lower Campanian of Muthmannsdorf show well the widespread distribution and ecological importance of these wood-destroying termites in the land areas of the Late Cretaceous Alpine region.

5.1.3. Vertebrates

Lepisosteid fishes are common elements of Late Cretaceous vertebrate assemblages across Europe (see Szabó et al., 2016a, FIG. 1). The presence of tethysaurine mosasaurs fits well in the faunistic composition of this region. Occurrence of the group in the Turonian of Morocco (Bardet et al., 2003) and Austria (Gams) (Ósi et al., 2019), the Santonian of Hungary (Makádi et al., 2012), and the Campanian–Maastrichtian of southern France (Buffetaut et al., 1999; Laurent, 2003; Garcia et al., 2015), shows the much wider distribution of the group in the western Tethyan archipelago. However, representatives of the group are unknown from the Campanian–Maastrichtian of Transylvania, Austria (Muthmannsdorf) and Spain (Csiki-Sava et al., 2015). Nonetheless, the growing number of occurrences of these minuscule remains of tethysaurines indicates that the group was more widespread than previously thought.

Although in most cases crocodile remains cannot be determined by teeth at the genus level, Neosuchia indet. 1 presumably represents a neosuchian or early eusuchian form, and the teeth described here are most reminiscent of some neosuchian (Ósi et al., 2016, 2019) as well as allodaposuchid teeth from other European localities (Rabi and Delfino, 2012; Martin et al., 2016). In contrast, teeth belonging to crocodile Neosuchia indet. 2 do not resemble the teeth of European Late Cretaceous crocodiles, and this type of teeth has not yet been reported from the Turonian (Stoliczka, 1860; Buffetaut, 1979; Ósi et al., 2019) and lower Campanian (Buffetaut, 1979) of Austria. The strong grooves seen on the lingual and labial sides of the teeth suggest a relationship with other mesoeucrocodylian groups (e.g., paralligatorids).

Fig. 9. Fish remains from the lower Coniacian Gosau beds (Bed 2) of Tiefengraben at St. Wolfgang, Austria. A–N, cf. *Lepisosteus* sp. A, B, teeth (OLL 2021/26A, OLL 2021/26B). C, pharyngeal tooth (OLL 2021/26D) in lateral view. D–H, scales (OLL 2021/26E, OLL 2021/26F, OLL 2021/26G, OLL 2021/26H) in external view; white rectangle shows the position of fig. E. I–L, hemitrichia (OLL 2021/26J, OLL 2021/26K; I and K: external view, J and L: profile or cross-view). M–P, fringing fulcra or rudimentary elements (OLL 2021/26M, OLL 2021/26N, OLL 2021/26O; M, O, P: external view, N, profile or cross-view). Q, indeterminate ganoid element (OLL 2021/26Q) in outer view. R–T, Actinopterygii indet. centra (OLL 2021/27A and OLL 2021/27B; R: cross-section view, S: side view, T: articular view).

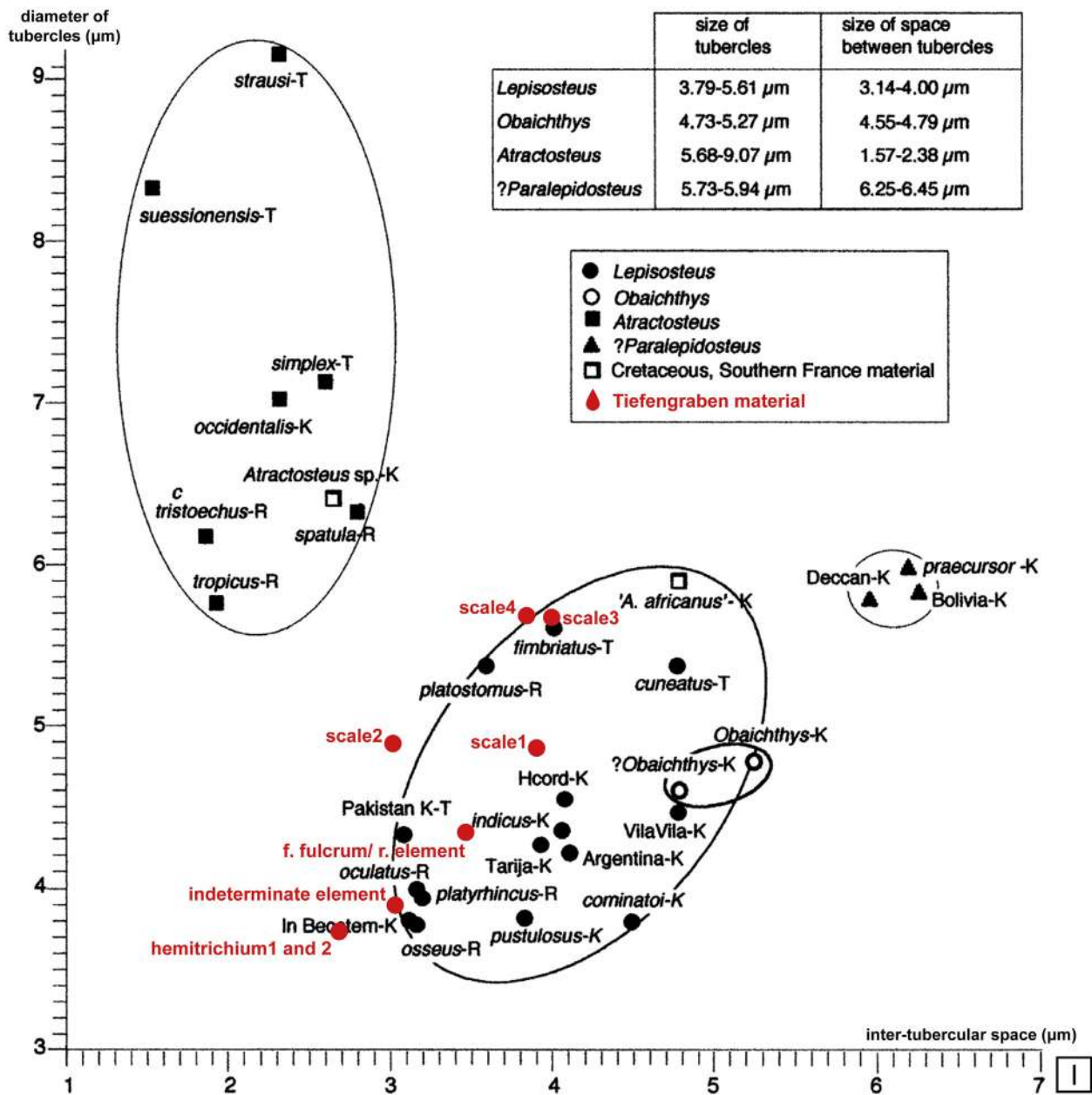
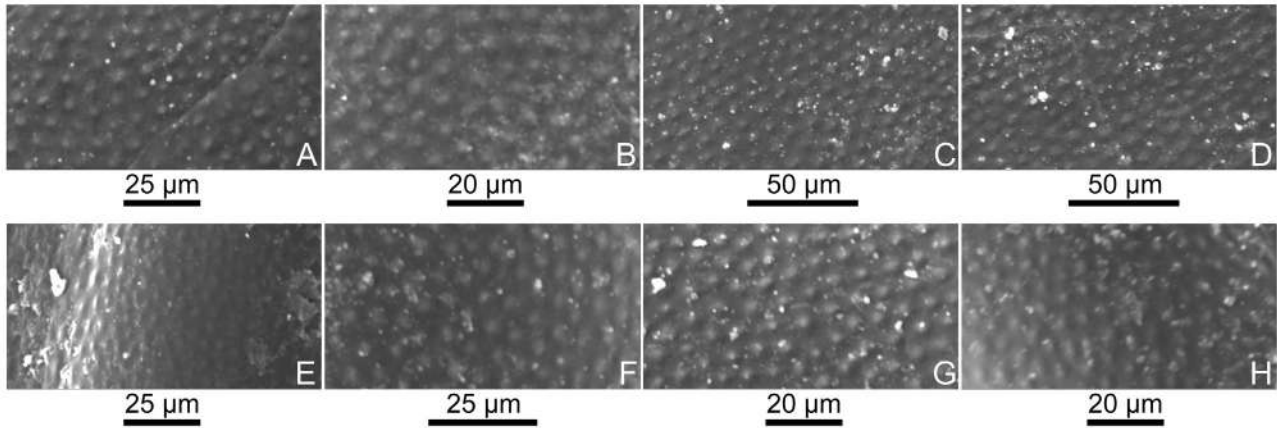


Table 3Measured parameters of the ganoid scales here referred to as cf. *Lepisosteus* sp., discovered from the lower Coniacian Gosau beds of Tiefengraben at St. Wolfgang, Austria.

Specimen		Number of measured ganoinc tubercles	Number of measured inter-tubercular spaces	Average ganoinc tubercle diameter (μm)	Average inter-tubercular space (μm)
Scales	tg3003_2	77	194	4.86	3.9
	tg3004_2	42	91	4.89	3.04
	tg3005_2	154	412	5.68	4
	tg3006_2	96	193	5.69	3.84
Hemitrichia	tg3011	55	124	3.75	2.69
	tg3012	41	97	3.76	2.7
F. fulcrum/r. element	tg3009	83	211	4.34	3.46
Indeterminate element	tg3008	47	96	3.9	3.02

Interestingly, dinosaurs are represented only by theropods. The remains of ankylosaurians, as common elements of coal-bearing strata (Seeley, 1881; Garcia and Pereda-Suberbiola, 2003; Kirkland et al., 2013; Ósi et al., 2016), are not yet known. However, fragmentary pieces of ankylosaurian armour elements found in the Turonian of Gams, Austria (Ósi et al., 2019) suggest that this group was clearly present in the Gosau Group from the Turonian to the Campanian (Pereda-Suberbiola and Galton, 2001). Basal tetanurans, like some ostracods, also seem to be relicts: the tooth described here most closely resembles the tetanuran teeth found in the Lower Cretaceous Wealden (e.g., “*Megalosaurus dunkeri*” known from the Barremian of the Isle of Wight). The youngest finds of such basal tetanuran teeth are from the ?Coniacian–Santonian of Borod, Transylvania (Nopcsa, 1902; Csiki-Sava et al., 2015), the Santonian of Iharkút, and the lower Campanian of the Muthmannsdorf sites (Ósi et al., 2010). Based on teeth, basal tetanurans are not yet known from the Campanian–Maastrichtian of Western Europe and the Maastrichtian of Transylvania (Csiki and Grigorescu, 1998; Pereda-Suberbiola, 1999; Smith et al., 2002; Csiki-Sava et al., 2015; Torices et al., 2015), suggesting that this group might have disappeared from the European archipelago until the late Campanian and represent a relict lineage of theropods (Ósi et al., 2010). In the late Campanian–Maastrichtian, abelisauroids (Buffetaut et al., 1988; Tortosa et al., 2014) and groups of coelurosaurians (dromaeosaurids, troodontids, ornithomimosaurids, alvarezsaurids; Le Loeuff and Buffetaut, 1998; Allain and Taquet, 2000; Csiki-Sava et al., 2015; Torices et al., 2015) dominated. Of the theropod teeth in the Tiefengraben, Maniraptora indet. 1 and 2 presumably represent the dromaeosaurid clade, a common member of Late Cretaceous European faunas. However, the wavy-edged tooth morphology is unknown in the above-mentioned clade, suggesting that it may represent a hitherto unknown form in Europe. On the other hand, *Paronychodon* teeth reported from Gams (Turonian; Ósi et al., 2019), Iharkút (Santonian), Transylvania (Maastrichtian) and Spain (Campano–Maastrichtian; Canudo and Ruiz-Omeñaca, 2003; Csiki-Sava et al., 2015; Torices et al., 2015), have not been found at the Tiefengraben site, which is presumably a sampling bias rather than a faunistic character.

5.2. Palaeoecological inferences

5.2.1. Aquatic environments

The perception of the former palaeoenvironment of the Tiefengraben Gosau Group is greatly characterised by the diversity of salinity tolerance of the different taxa present. Based on the fossil

record presented here, environments with different salinities seem to have alternated during short time intervals (physically through a few tens of cm of sedimentary layers). Thus, a purely and stable marine environment had not yet developed during the deposition of these fossil-bearing beds, although these are present in nearby outcrops based on the occurrence of calcareous nannofossils. In addition, samples from the coaly claystone of Bed 3 resulted in a few finds of rare marine remnants, such as unidentifiable fragmented dinoflagellate cysts and organic linings of agglutinated foraminifera, suggesting marine influence to a certain degree.

Among molluscs, the palaeoecology of *Pyrgulifera*, which proved to be the dominant element of the macro-invertebrate assemblage of Beds 1 and 2, may be informative. On the basis of the study of a large amount of material yielded by the Santonian Ajka Coal Formation of Hungary, Bandel and Riedel (1994) concluded that “Probably each individual of *Pyrgulifera* tolerated freshwater as well as brackish water” (l. c., p. 16.). This interpretation is supported by the overall fossil assemblage of the Ajka Coal Formation where *Pyrgulifera* can be found abundantly along with definitely freshwater fossils such as unionid bivalves (Tausch 1886) and characeans (Rákosi, 1989). Recently, a moderately diverse freshwater ostracod assemblage has been identified from that succession by Mizsei et al. (2020). Moreover, Upper Cretaceous *Pyrgulifera* was also reported to be associated with “freshwater genera” by Vega et al. (2019).

As inferred from the palaeoenvironmental interpretation of the few associated faunal elements hitherto identified, *Pyrgulifera* sp. encountered in the Gosau beds exposed at the Tiefengraben also lived in a freshwater environment. *Pachymelania?* sp., *Ariomphalus* sp. and *Physa* s.l. sp. represent freshwater families Thiaridae, Valvatidae and Physidae, respectively (e. g. Gray, 1988). Thus, the mollusc assemblage of Beds 1 and 2 indicates a freshwater or slightly brackish sedimentary environment.

In Bed 1 the ostracod assemblage is dominated by the genus *Damonella*, a typical “Purbeck–Wealden” ostracod that occurs in great abundance in Berriasian–Barremian Purbeck Beds of England and France that were deposited under non-marine and episodically fully marine conditions (e.g., Kilenyi and Neale, 1978; Anderson, 1985; Colin and Oertli, 1985; Horne, 2002). Based on Horne’s (2002) concept, *Damonella* were commonly present with *Darwinula* in the „S-phase” association, suggesting a non-marine environment with a permanent waterbody under humid climate conditions. The representatives of the genus commonly occur in Aptian and Albian lacustrine rocks of the Jatobá and Araripe basins (Brazil), together with other low-alkalinity freshwater taxa such as *Cypridea*, *Neuquenocypris* and *Rhinocypris* (Tomé et al., 2014).

The appearance of *Heterocypris* and *Cetacella* in Bed 2, beside darwinulids and the subordinate specimens of *Neocyprideis*, indicates

Fig. 10. Measurements of the ornamentation of fish scales. A–H, close-up of the ganoinc surfaces of various ganoinc elements (A: OLL 2021/26E, B: OLL 2021/26F, C: OLL 2021/26G, D: OLL 2021/26H, E: OLL 2021/26J, F: OLL 2021/26K, G: OLL 2021/26M, H: OLL 2021/26Q). I: measurements of tubercle diameters and the inter-tubercular distances on ganoinc elements of extant and extinct lepisosteids, including the Tiefengraben material (red colour); modified after Gayet et al. (2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

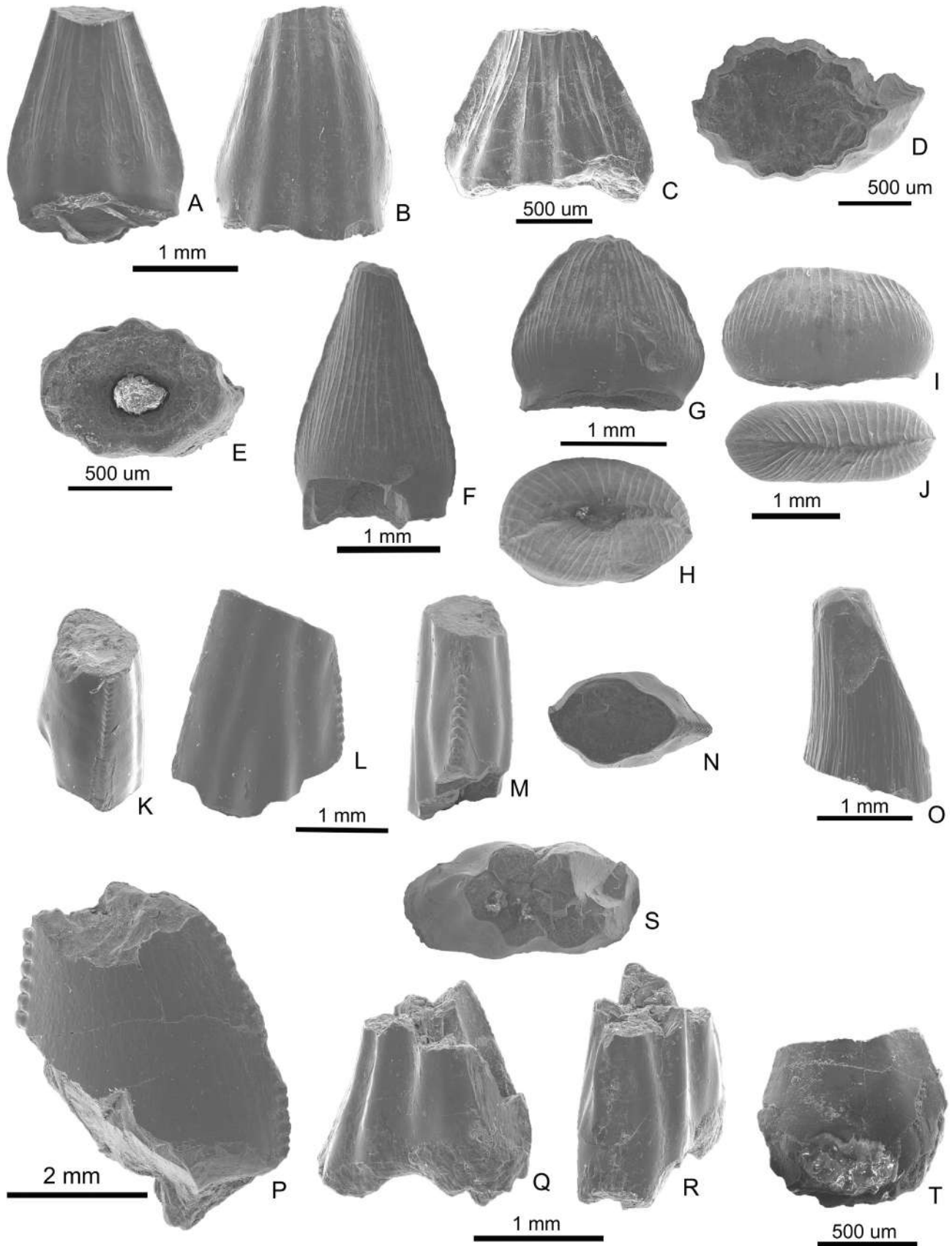


Fig. 11. Sauropsid fossils from the lower Coniacian Gosau beds (Lower Gosau Subgroup) of Tiefengraben (Bed 2) at St. Wolfgang, Austria. A, *Neosuchia* indet. 2. crocodile tooth (OLL 2021/31A) in lingual, B, labial view. C, *Neosuchia* indet. 2. crocodile tooth (OLL 2021/31B) in lingual view. D, *Neosuchia* indet. 2. fragmentary crocodile tooth (OLL 2021/31C) in apical view. E, *Neosuchia* indet. 2. crocodile tooth (OLL 2021/331D) in basal view. F, *Neosuchia* indet. 1. crocodile anterior tooth (OLL 2021/30A) in lingual view. G, *Neosuchia* indet. 1.

a mixed assemblage where brackish (*Heterocypris*, *Neocyprideis*) and non-marine forms (*Cetacella*, *Darwinula*) could have accumulated together. *Heterocypris berthouli*, described from middle Cenomanian deposits of Portugal, occurred in lagoonal brackish depositional environments (Cabral et al., 2008). However, extant species of *Heterocypris* can tolerate wide salinity ranges, including freshwater to oligohaline (0–0.5 psu) and hypersaline conditions, with a very large geographical distribution in several continents and islands (e.g., Ganning, 1971; Baltanás et al., 1990; Malmqvist et al., 1997). The marine ancestors of *Heterocypris* probably successively adapted to lower salinities via brackish environments. *Cetacella* was one of the most characteristic taxa in Late Jurassic to Early Cretaceous (Kimmeridgian to Berriasian), non-marine environments of the Tethyan Realm (e.g., Martin, 1958; Wienholz, 1968; Ainsworth, 1985; El Albani et al., 2004; Schudack, 2009; Schudack and Schudack, 2012).

In contrast, as inferred from the gastropod and bivalve fauna, Bed 4 was deposited in a brackish-water environment where salinity was considerably higher than in the case of Beds 1 and 2. Recent *Polymesoda* and *Geloina* inhabit brackish-water environments such as estuarine swamps as well as tropical/subtropical mangrove forests and lagoons, respectively (e.g. Spijkerman et al., 2015). Medium-sized to large, smooth and usually thick-shelled, shallow-infaunal suspension-feeding bivalves, such as *Polymesoda* sp. from Bed 4, are characteristic elements of Mesozoic and younger oligo- and mesohaline benthic associations (Fürsich, 1994). According to Kowalke (2005) corbiculids, considered as characteristic brackish-water bivalves in the Cenozoic, as well as potamidid gastropods were already confined to coastal habitats in the Cretaceous, and are widespread faunal elements in coastal swamp and lagoonal sedimentary units of the Gosau Group (see also Herm, 1977; Kowalke and Bandel, 1996). It should be mentioned, however, that relationships of *Terebraliopsis* and other extinct genera to recent potamidid “mud whelks” are, according to Reid et al. (2008), questionable. Presence of abundant juvenile *Pyrgulifera* shells, in conjunction with the apparent lack of adult ones, may indicate that salinity increased during the deposition of Bed 4 and exceeded the upper tolerance limit of *Pyrgulifera*.

Accordingly, the charophyte flora described here supports as well the brackish-water setting for the respective Bed 4, as notably indicated by the associated mollusc remains (see above). Indeed, in contrast to the majority of species of the genus, the species *Mesochara voluta* reported here was adapted to brackish-water environments, as suggested by the few other coeval charophyte-bearing localities described: one from Europe (France, Feist, 1981) and one from South America (Argentina and Brazil, Uliana and Musacchio, 1978). Furthermore, the polymorphism and notably the reduced size observed in the studied characean specimens – on average 200 µm less than those of the same species described from Middle Jurassic to Lower Cretaceous localities – seems to be the result of salinity and temperature stress, i.e., notably the warm climate prevailing during the earlier Late Cretaceous. This has already been documented in characean species from the Turonian of France (Feist, 1981), from the Maastrichtian of Spain (Vicente et al., 2016), and experimentally confirmed on recent charophytes by Sanjuan et al. (2017).

Based on the ostracod assemblages (see summary in Section 5.1.2.), the *Neocyprideis*-dominated assemblage from Bed 4 of the Tiefengraben section indicates a marginal marine, brackish estuarine or lagoonal environment that is in accordance with the

conclusions drawn from the mollusc remains and the charophytes. Nevertheless, the presence of the non-marine ostracod *Darwinula?* sp., land plant fossils, termite coprolites, and dinosaur teeth definitely indicates that the non-marine and terrestrial palaeoenvironments were situated in proximity to the depositional area, from where rich and diverse non-marine and terrestrial remains were transported into the brackish environment and mixed with the autochthonous assemblages. The transport of thin-shelled non-marine ostracods by rivers might have occurred via saltation or in suspension, which might have been helped by the formation of (decay) gas bubbles within the closed carapace directly after death in the case of intact carapaces (e.g. Kilenyi and Allen, 1968; Kilenyi, 1971).

To sum up, the early Coniacian aquatic palaeoenvironment of the Tiefengraben area during deposition of these fossil-bearing beds was quite diverse, with dominantly freshwater environments during deposition of Beds 1 and 2, and rather shallow, marginal marine estuarine environments with different degrees of freshwater input in the case of Bed 4. Molluscs and ostracods, as two excellent indicators of water salinity, are mostly in congruence with this conclusion, though both groups are represented by forms of higher salinity tolerance. Freshwater input influencing salinity conditions might have been controlled by seasonal humidity changes.

5.2.2. Terrestrial environment

Terrestrial biotic elements from Tiefengraben are represented by remains of plants, termite coprolites, crocodiles and dinosaurs that reveal some basic palaeoenvironmental conditions existing on land. Based on the moderately diverse and abundant plant fossils and the clear terrestrial influx of sediments, the plant taphocoenosis suggests a river flood plain vegetation, probably representing a gallery forest intermixed with “upland” vegetation. Prevailing small-leaved dicots, very rare monocots, as well as the absence of pteridophytes and conifers argue for mesophytic conditions without permanent wetlands or swamps. This terrestrial habitat seems to have been slightly different from that of St. Gilgen, another slightly older (Turonian) site near St. Wolfgang, from where a mesophytic/xerophytic flora was reported (Szente et al., 2010). The relatively high amount of dentate (not entirely margined) forms in this new site suggests that the climate might have been slightly cooler than in the comparative (Turonian–lower Campanian) Central European localities (Kvaček and Herman, 2004; Herman and Kvaček, 2010; Szente et al., 2010; Kvaček et al., 2015; Halamski and Kvaček 2015, 2016).

The coprolites here referred to as “*Microcarpolithes*” also yield some palaeoecological information. The high number of these pellets in the screen-washed residue suggests that these insects could have been frequent components of the ecosystem, and they supposedly played a significant role in the trophic webs as decomposers and recyclers, similar to that seen in recent representatives (Adl et al., 2011). The taxonomic affinity of the wood material that could have been the food resource of these termites is still unknown. In other Cretaceous localities, termite coprolites are frequently found in amber, suggesting that resin producers, most probably araucarians, could have been the primary source of food for these insects (Colin et al., 2011). Of the fossil plant record from Tiefengraben, only some poorly preserved seeds are indicative of gymnosperms. Additionally, the small pieces of amber might have originated from this group as well.

crocodile posterior tooth (OLL 2021/30B) in lingual, H, apical view. I, Neosuchia indet. 1. crocodile posterior tooth (OLL 2021/30C) in lingual, J, apical view. K, Maniraptora indet. 1 tooth (OLL 2021/33A) in mesial, L, labial/lingual, M, distal, N, apical view. O, cf. Tethysaurinae indet tooth (OLL 2021/29A). P, Tetanurae indet. tooth (OLL 2021/32) in labial/lingual view. Q, Maniraptora indet. 2 tooth (OLL 2021/34) in labial/lingual, R, oblique distal, S, apical view. T, Maniraptora indet. 1? tooth (OLL 2021/33B) in labial/lingual view.

Though the record of land vertebrates is restricted mainly to teeth, two crocodiles with different tooth morphology and at least three different theropod dinosaurs can be recognised. The crown and denticle size of the largest tooth fragment, here referred to as basal tetanuran, indicates that the complete crown reached at least a height between 1 and 2 cm suggesting a 1.5–2.5 m long animal. Basal tetanurans were the largest representatives of theropods in the Santonian of Iharkút and in the early Campanian Grünbach fauna, and it seems that members of this group were the top-predators in early Coniacian times in other regions of the Austro-alpine landmass as well.

6. Conclusions

Most sedimentary rocks of the Upper Cretaceous Gosau sequences were formed under strong marine influence (Wagreich and Faupl, 1994), whereas intervals of non-marine to terrestrial strata are relative poorly known from the Alpine areas. The preserved elements of the Tiefengraben biota documented here provide a unique insight into the brackish, freshwater and terrestrial environments of the Northern Calcareous Alps in such lower (lower Coniacian) Gosau Group occurrences. In addition, the finds presented here fill a gap in understanding the continental faunal composition during the Cenomanian–Campanian hiatus, a phenomenon that is typical of Europe and that spans about 20 million years (Mannion and Upchurch, 2011; Csiki-Sava et al., 2015). The fossils of some relict faunal elements further strengthen the role of the western Tethyan archipelago in preserving some basal and much earlier (Early Cretaceous) lineages. On the other hand, it also shows good congruence with the Turonian–Campanian finds known from other Central European localities in terms of both the flora and fauna. The discovery of the assemblage from Gams (Turonian; see Ósi et al., 2019) and Tiefengraben (lower Coniacian, this paper) clearly demonstrates that a further quest for additional localities, excavations and screen-washing can fill the Late Cretaceous hiatus heretofore existing in the continental faunas of the Gosau Group Provinces and Europe.

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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.2021.104938>.

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