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# A diverse Campanian biota from the Bozeș Formation (Petrești, Romania): Insights into the paleontology and paleoecology of a transitional sequence

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## ABSTRACT

Campanian estuarine deposits are rare across Europe, and the assemblages described herein represent a paleontologically significant exception. Systematic collection efforts conducted over the past eight years have resulted in the identification of 102 taxa spanning a broad spectrum of organisms, including calcareous nannoplankton, seeds, fruits, bivalves, gastropods, ammonites, corals, echinoids, asteroids, selachians, actinopterygians, anurans, squamates, crocodyliforms, and putative theropod dinosaurs, the latter inferred from eggshell fragments. Notably, a new percomorph fish taxon is described — *Paraplesiopoma transylvanica* n. gen. et n. sp. (Trif and Schwarzhans). In addition, amber — a rare occurrence in European Cretaceous strata — was recovered from the site. Sedimentological and paleontological evidence indicates a marked paleoenvironmental transition from fully marine to brackish, estuarine ecosystem. The presence of continental taxa within the assemblage offers valuable insights into the composition of the adjacent terrestrial ecosystems during the Campanian. This assemblage constitutes a unique mixture of autochthonous marine and aquatic elements with parautochthonous and allochtonous continental/terrestrial components, situated within the Alpine Tethyan realm, during the Late Cretaceous. Furthermore, it documents a diverse array of terrestrial organisms predating the well-known Maastrichtian vertebrate faunas of the so-called "Hațeg Island", thereby providing an important window into the pre-Maastrichtian terrestrial biota of this region.

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## INTRODUCTION

The Upper Cretaceous continental formations of Romania have garnered increasing international scientific interest over recent decades, largely due to the discovery of the so-called “dwarf dinosaurs” in the Hațeg Basin. These iconic fossils were first described in the late nineteenth and early twentieth centuries by Nopcsa (1897, 1902, 1914a, 1914b, 1915, 1923, 1925, 1929). Following these pioneering studies, research on Late Cretaceous vertebrates in Romania experienced a prolonged period of neglect, with only sporadic references in reports by geologists of the Geological Institute of Romania (e.g., Mamulea, 1953a, 1953b; Dincă et al., 1972). A revival of systematic paleontological investigations occurred during the 1980s, leading to the discovery of a remarkably diverse vertebrate assemblage. These excavations expanded the known faunal spectrum beyond dinosaurs to include mammals, pterosaurs, lissamphibians, and squamates (Grigorescu, 1983; Grigorescu and Hahn, 1987; Grigorescu et al., 1985, 1990, 1999; Jianu et al., 1997). Since then, paleontological prospecting has expanded significantly beyond the classical localities of the Hațeg Basin, with new vertebrate-bearing sites being discovered or rediscovered, thereby enlarging the known spatial distribution of fossiliferous Upper Cretaceous deposits in Romania (Csiki-Sava et al., 2016). Noteworthy additional localities include outcrops in the Sebeș region, near the village of Rusca Montană, and at Someș-Odorhei in the Jibou area, which have yielded significant fossil assemblages and have been the focus of renewed attention (Codrea et al., 2010b, 2012; Vremir et al., 2014, 2015).

The area surrounding Sebeș (Alba County, Romania) hold considerable paleontological significance, as it represents the only currently known continuous Upper Cretaceous transition from marine to continental sedimentation in Romania. This transition is preserved at the lithostratigraphic contact between the Bozeș and Sebeș formations (Vremir, 2010; Vremir et al., 2014; Csiki-Sava et al., 2016; Țabără et al., 2022; Bălc et al., 2024) (Figure 1). The site, located near the locality of Petrești, was first reported by Codrea et al. (2010a), who documented a bone fragment tentatively attributed to an indeterminate dinosaur. Subsequent investigations quickly followed, leading to the discovery of additional vertebrate remains attributed to dinosaurs, turtles, mammals, and pterosaurs. These fossils have been recovered predominantly from the Sebeș Formation, though some occurrences have also been documented within the underlying

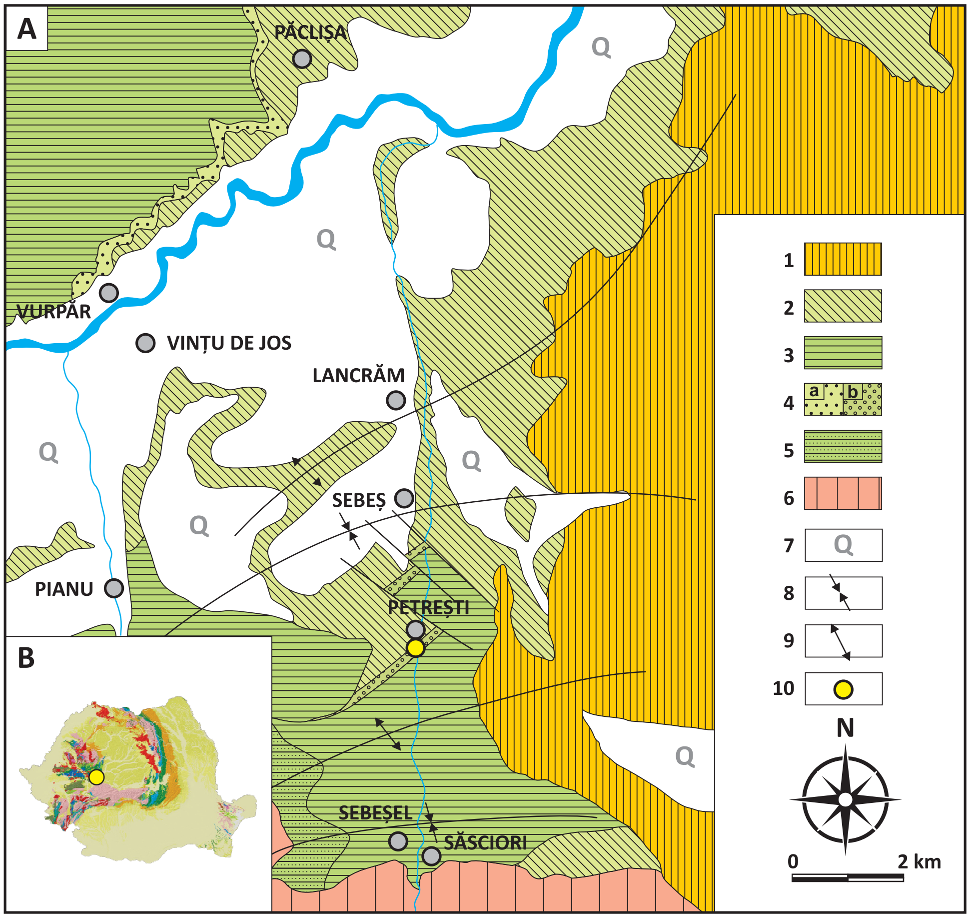

**FIGURE 1.** The position of the studied outcrop: **A,** within the southwest of the Transylvanian Basin and **B,** within the general geologic map of Romania. **1,** undifferentiated Miocene and Pliocene marine units (Sîntimbru Formation); **2,** Upper Cretaceous (uppermost Campanian–Maastrichtian–?Paleocene) continental units (Sebeș Formation); **3,** upper Santonian–upper Campanian deep marine flysch deposits (Bozeș Formation); **4,** transitional deltaic (a) or estuarian-brackish (b) facies (top Bozeș Formation); **5,** Coniacian–Santonian deltaic-fluvial deposits ("Săsciori Beds"); **6,** metamorphic basement (Getic–Supragetic nappe system); **7,** Quaternary deposits; **8,** syncline structure; **9,** anticline structure; **10,** location of the studied outcrop (modified after Vremir et al., 2014).

Bozeș Formation (Vremir, 2010; Vremir et al., 2014, 2015; Brusatte et al., 2013).

In subsequent years, research efforts focused predominantly on the Sebeș Formation, particularly at an outcrop located several kilometers north of Petrești. These investigations have yielded a diverse assemblage of vertebrate fossils, including representatives of dinosaurs, pterosaurs, birds, crocodyliforms, turtles, anuran amphibians, multituberculate mammals, and actinopterygian fishes (Csiki et al., 2010; Codrea and Jipa, 2011; Dyke et al., 2012; Vremir et al., 2014; Fernández et al., 2019; Solomon et al., 2020, 2022a, 2022b; Vasile et al., 2021, 2022; Trif and Codrea, 2022). These taxa are interpreted as components of the fauna that inhabited the so-called "Hațeg Island".

While research on the Sebeș Formation has increasingly focused on macrofossils, investigations of the underlying Bozeș Formation and the intervening transitional estuarine interval have primarily concentrated on microfossil assemblages. These studies have emphasized calcareous nannoplankton, palynomorphs, and have incorporated organic geochemical analyses to reconstruct paleoenvironmental conditions (e.g., Bălc and Chira, 2002; Bălc et al., 2007, 2012, 2024; Țabără et al., 2022). Nevertheless, historical studies have also documented certain macrofossil groups from the Bozeș Formation, notably mollusks and isolated plant remains (Staub, 1889; Pálfy, 1902).

Given the rarity of such transitional estuarine environments in Romania, we conducted an extensive, multidisciplinary investigation over an eight-year period to better understand the sedimentological and paleontological characteristics of this unique Upper Cretaceous sequence. Fieldwork was carried out along the right bank of the Sebeș River, near the village of Petrești, a northern suburb of the city of Sebeș (Alba County). This site yielded a diverse assemblage of invertebrate fossils, as well as both terrestrial and aquatic microvertebrate remains, eggshell fragments, plant seeds, leaf impressions, and amber — all of which form the basis of this study.

## GEOLOGICAL SETTING

The studied section is situated in the Sebeș area, in the southwestern part of the Transylvanian Basin, between the Metaliferi Mountains (a subunit of the Apuseni Mountains) and the Șureanu Mountains (part of the Southern Carpathians) (Krézsek and Bally, 2006) (Figure 1).

The Transylvanian Basin is a Late Cretaceous–Paleogene sedimentary basin that developed atop a complex structural substrate comprising a Paleozoic crystalline basement, ophiolitic assemblages, island-arc volcanic units, and Triassic to mid-Cretaceous sedimentary sequences (Săndulescu and Visarion, 1978; Paraschiv, 1979; Bortolotti et al., 2004; Krézsek and Bally, 2006). The basin's sedimentary infill is subdivided into four major tectonostratigraphic megasequences: Upper Cretaceous, Paleogene, Lower Miocene, and Middle to Upper Miocene (Krézsek and Bally, 2006). Of particular relevance to this study are the Upper Cretaceous deposits, which comprise the marine Bozeș Formation and the overlaying continental Sebeș Formation. These units record a rare, continuous marine-to-continental transition, making the region a key area for reconstructing Late Cretaceous paleoenvironmental dynamics in the Carpathian realm.

During the Late Cretaceous, numerous sedimentary basins developed across the region, accumulating a wide range of deposits from deep- and shallow-marine to continental settings. The latter are frequently characterized by red beds (Willingshofer et al., 2001; Krézsek and Bally, 2006). In the Sebeș area, the marine succession is represented by the Bozeș Formation, a typical flysch unit with an estimated thickness of approximately 3000 m. This formation comprises a varied lithological assemblage, including sandstones, calcareous sandstones, silty marls, microconglomerates, and conglomerates, particularly in its upper intervals (Dimian and Popa-Dimian, 1964; Bălc et al., 2007). Initially, the Bozeș Formation was assigned a Santonian to early Maastrichtian age based on macrofossil evidence (Dimian and Popa-Dimian, 1964; Tomescu et al., 1969). However, more recent biostratigraphic analysis utilizing calcareous nannoplankton, foraminiferal, and palynological assemblages have revised this age to the mid- to late Campanian (Bălc et al., 2007, 2024; Țabără et al., 2022). While certain ammonite taxa previously suggested a possible Maastrichtian age (Macovei and Atanasiu, 1934; Tomescu et al., 1969), this interpretation remains unconfirmed by current biostratigraphic frameworks (Bălc et al., 2007). At the top of the Bozeș Formation, within the Petrești section, a relatively thin but distinct brackish-estuarine interval is preserved, marking a transitional phase between marine and continental deposition (Vremir et al., 2014, Bălc et al., 2024).

The Sebeș Formation conformably overlies the Bozeș Formation and has been interpreted as Maastrichtian in age (Vremir et al., 2014, 2015). An alternative stratigraphic framework and sedimentological interpretation was proposed by Codrea and Dica (2005), who suggested the presence of a distinct lithostratigraphic unit. However, this interpretation has since been refuted. The lithological units proposed in that model are now regarded as facies variations within a single depositional system, reflecting lateral changes due to variable sediment sources (for a detailed discussion see Vremir, 2010; Vremir et al., 2015). In the Petrești section, the Sebeș Formation is characterized by transitional wetland to lacustrine deposits, as well as fluvial mudstones and channel-fill sediments (Vremir et al., 2014).

The study site corresponds to the uppermost stratigraphic interval of the Bozeș Formation, encompassing its final meter prior to the transition into the overlying Sebeș Formation. The succession consists of alternating sandy marls, marls, and sandstones, with a total measured thickness of 27 m. At its base, the sequence begins with approximately 5 m of fully marine deposits, characterized by compacted sands grading into sandstones and yielding a diverse assemblage of marine invertebrates, including corals, gastropods, bivalves, ammonites, rudists, asteroids, and echinoids. These marine beds are overlain by approximately 22 m marls, sandy marls, and sandstones interpreted as representing a transitional estuarine depositional environment. Within this composite section, five discrete fossiliferous horizons have been identified (designated LV1 through LV5), with individual thicknesses ranging from 0.2 to 0.4 m (LV1 to LV4), and up to 5 m in the case of LV5 (Figure 2).

These deposits are overlain by a thick succession of well-consolidated conglomerates and sand-

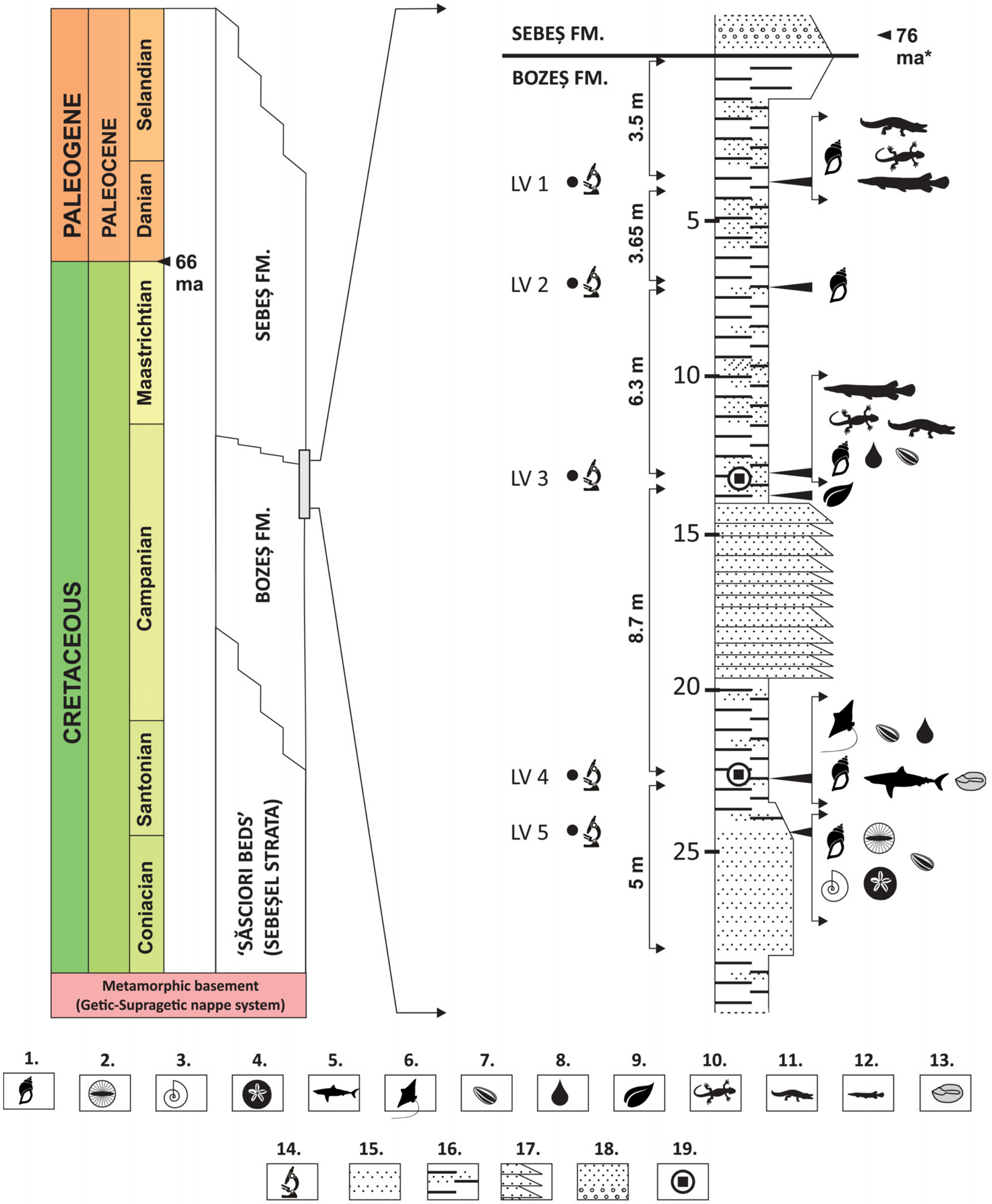

**FIGURE 2.** Stratigraphy of the studied outcrop. Legend: **1,** gastropods and bivalves; **2,** corals; **3,** ammonites; **4,** echinoderms; **5,** shark teeth; **6,** batoid teeth; **7,** seeds; **8,** amber; **9,** leaf impression; **10,** amphibians; **11,** crocodyliforms; **12,** gar fish; **13,** otoliths; **14,** calcareous nannoplankton samples; **15,** compacted sands; **16,** marls and sandy-marls; **17,** sandstones; **18,** conglomerates and sands; **19,** pyrite nodules; * indicates the level where the ~76 Ma U–Pb absolute age on detrital zircon was reported by Bălc et al. (2024).

stones, which are interpreted as representing the lowermost stratigraphic interval of the Sebeș Formation (see Figure 3).

## MATERIALS AND METHODS

The site was systematically investigated between 2016 and 2024. Fieldwork and sampling for both macro- and micropaleontological analyses were conducted across five stratigraphic levels.

**FIGURE 3.** The Petrești outcrop. **A,** the right bank of the Sebeș River with the marked positions of the sampled levels. **B,** close up view of a gastropod cluster *(Cassiope obvoluta)* from LV1. **C,** large piece of carbonized wood in LV3. **D,** plant remains (cf. *Sphenopteris ungeri)* at the base of LV3. **E,** *Cunnolites* sp. coral in LV5. **F,** large inoceramid (?*Platyceramus* sp.) detached from LV5.

To assess the fossil content, a total of 272 kg of marl and sandy marl was collected from these levels, where fossil concentrations were visually noted to be higher. The samples underwent a disaggregation procedure involving controlled drying to a residual humidity of 5–10%, followed by rapid rehydration using water heated to 100°C. The resulting disaggregated sediment was then wet-sieved using a 0.5 mm mesh. The residue retained on the sieve was subsequently dried and examined under a stereomicroscope. This protocol enabled the recovery of a diverse assemblage of microfossils, including microvertebrate remains, plant seeds, eggshell fragments, small mollusks, and amber.

An additional collection technique was employed specifically for the recovery of fragile mollusk specimens. Large, intact fragments of wet sediment were carefully extracted in the field and transported to the laboratory under controlled conditions to maintain their original moisture content. In the laboratory, mollusk specimens were meticulously extracted from the matrix using fine needles and scalpels. To facilitate the cleaning and to stabilize the fragile shell structures, a 5% polyvinyl acetate (PVA) solution was applied with a fine brush to remove residual sediments and consolidate any existing fractures. The treated specimens were then allowed to dry gradually at ambient room temperature.

The otoliths classification follows the phylogenetic framework of Betancur-R. et al. (2017), while the morphological terminology is based on Koken (1884), with modifications by Chaine and Duvergier (1934) and Schwarzhans (1978). All otoliths are illustrated from the right side; left-side specimens were mirrored digitally and are clearly indicated as such in figure captions.

Macroscopic specimens, including mollusks, corals, and echinoids, were photographed using a Nikon D5300 digital camera fitted with a Sigma 105 mm macro lens. Microvertebrate remains and plant seeds were imaged with an AmScope 10X Plan Achromatic objective mounted on a 200 mm host lens. To enhance image sharpness and depth field, focus staking was performed using CombineZP software (version1.0). Eggshell fragments were examined and photographed using a TescanVega II SBH Scanning Electronic Microscope.

Calcareous nannoplankton analysis was conducted on five samples collected from the uppermost part of the marine sequence to refine the biostratigraphic age of the studied section. Smear slides were prepared following the standard technique outlined by Bown and Young (1998), and analyzed under a light microscope (Axiolab A) at 1000x magnification. Four traverses were completed per slide (~700 fields of view), and all identifiable taxa were counted to determine relative abundance. Selected specimens were imaged using an AxioCam ERCc5s digital microscope camera for illustration.

Fossil specimens exceeding 1 mm in maximum dimension were measured using a Profi Scale Precise PS 7215 electronic caliper, which has a reported measurement accuracy of ±0.01 mm. Smaller specimens were measured digitally using ImageJ software (version 1.54g), calibrated with a graphical scale included in each image alongside the specimen.

All collected specimens have been deposited in the Paleontological Collection of the Natural History Museum in Sibiu, part of the Brukenthal National Museum, and are referenced hereafter with the abbreviation NHMS.

Cluster analysis was conducted using Past software (version 0.45), employing the paired group (UPGMA) algorithm and Jaccard similarity index to assess taxonomic associations among the fossil assemblages.

**Abbreviations used in the text:** LV1 — level 1; LV2 — level 2; LV3 — level 3; LV4 — level 4; LV5 — level 5; OL — otolith length; OH — otolith height; OT — otolith thickness; OsL — ostium length; OsH — ostium height; CaL — cauda length; CaH — cauda height; U/D — umbilical width to shell diameter ratio; NHMS — Natural History Museum, Sibiu.

## RESULTS AND DISCUSSION

### 1. Flora

### Microflora — Calcareous Nannoplankton

The calcareous nannofossil assemblage is characterized by poor to moderate preservation and comprises 36 species, exhibiting very low relative abundances (ranging from 0.02 and 0.21 specimens per field of view). Both species richness and total abundance decrease progressively from sample LV5 to sample LV1, with the number of recorded species declining from 22 to 7. Detailed counts and species occurrences for each stratigraphic level are provided in Table 1.

The most dominant taxon within the assemblage is *Watznaueria barnesiae* (Black in Black and Barnes, 1959; Perch-Nielsen, 1968), representing between 29.6 and 55.5% of the total assemblage. Other common species include *Retecapsa crenulata* (Bramlette and Martini, 1964; Grün in Grün and Allemann, 1975), *Eiffellithus eximius* (Stover 1966; Perch-Nielsen, 1968), *Prediscosphaera cretacea* (Arkhangelsky, 1912; Gartner, 1968), and *Cribrosphaerella ehrenbergii* (Arkhangelsky, 1912; Deflandre in Piveteau, 1952).

Key taxa identified within the recovered calcareous nannofossil assemblage, relevant for biostratigraphic age determination, include *Broinsonia parca constricta* (Hattner et al., 1980), *Reinhardtites anthophorus* (Deflandre, 1959; Perch-Nielsen, 1968), and *Eiffellithus eximius.*

**TABLE 1.** Taxonomic and stratigraphic distribution of fossils from the Petrești Section.

| Category | Identification | Number of specimens | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|---|---|
| **Calcareous nannoplankton** | *Amphizygus brooksii* | 4 |  | x | x | x |  |
|  | *Amphizygus minimus* | 2 |  | x |  | x |  |
|  | *Arkhangelskiella cymbiformis* | 4 | x |  | x |  | x |
|  | *Biscutum constans* | 1 | x |  |  |  |  |
|  | *Broinsonia parca constricta* | 3 |  |  |  | x | x |
|  | *Broinsonia parca parca* | 1 |  |  |  |  | x |
|  | *Calculites ovalis* | 1 |  | x |  |  |  |
|  | *Chiastozygus amphipons* | 7 |  | x | x | x | x |
|  | *Chiastozygus bifarius* | 3 |  |  |  | x | x |
|  | *Chiastozygus litterarius* | 1 |  | x |  |  |  |
|  | *Cretarhabdus striatus* | 1 |  |  |  |  | x |
|  | *Cribrosphaerella ehrenbergii* | 1 |  | x | x | x | x |
|  | *Cylindralithus coronatus* | 1 |  |  |  |  | x |
|  | *Eiffellithus eximius* | 20 | x | x | x | x | x |
|  | *Eiffellithus gorkae* | 2 |  |  |  |  | x |
|  | *Eiffellithus turriseiffelii* | 35 |  | x |  | x |  |
|  | *Eprolithus floralis* | 1 |  |  |  |  | x |
|  | *Gartnerago segmentatum* | 1 |  |  |  | x |  |
|  | *Helicolithus trabeculatus* | 3 |  | x |  | x | x |
|  | *Lithastrinus grillii* | 1 |  |  | x |  |  |
|  | *Loxolithus armilla* | 4 |  |  | x | x |  |
|  | *Lucianorhabdus maleformis* | 5 |  | x |  | x | x |
|  | *Manivitella pemmatoidea* | 2 |  |  |  | x | x |
|  | *Micula staurophora* | 12 | x | x | x | x | x |
|  | *Placozygus fibuliformis* | 1 |  |  |  | x |  |
|  | *Prediscosphaera cretacea* | 22 | x | x | x | x | x |
|  | *Reinhardtites anthophorus* | 7 | x | x |  |  | x |
|  | *Retecapsa crenulata* | 33 | x | x | x | x | x |
|  | *Rhagodiscus achlyostaurion* | 2 |  | x |  |  |  |
|  | *Russellia laswellii* | 1 |  |  |  |  | x |
|  | *Staurolithites sp.* | 1 |  | x |  |  |  |
|  | *Tranolithus orionatus* | 14 | x | x | x | x | x |
|  | *Watznaueria barnesiae* | 174 | x | x | x | x | x |
|  | *Watznaueria quadriradiata* | 1 |  |  | x |  |  |
|  | *Zeugrhabdotus bicrescenticus* | 2 |  |  | x |  | x |
|  | *Zeugrhabdotus diplogrammus* | 3 |  | x | x |  |  |
| **Mesoflora** | Taxon 1 | 1 |  |  |  | x |  |
|  | Taxon 2 | 1 |  |  |  | x |  |
|  | Taxon 3 | 1 |  |  |  | x |  |
|  | Taxon 5 | 1 |  |  |  | x |  |
|  | Taxon 6 | 1 |  |  |  | x |  |
|  | Taxon 7 | 1 |  |  |  | x |  |
|  | Taxon 8 | 1 |  |  |  | x |  |

**TABLE 1** (continued).

| Category | Identification | Number of specimens | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|---|---|
| | Taxon 9 | 1 | | | | x | |
| | Taxon 10 | 1 | | | | x | |
| | Taxon 12 | 1 | | | | x | |
| | Taxon 13 | 1 | | | | x | |
| | Taxon 15 | 1 | | | | x | |
| | Taxon 16 | 1 | | | | x | |
| | Taxon 17 | 1 | | | | x | |
| **Macroflora** | cf. *Sphenopteris ungeri* | 4 | | | x | | |
| **Amber** | Amber | 36 | | | x | x | |
| **Cephalopods** | *Pachydiscus (Pachydiscus)* cf. *haldemsis* | 3 | | | | | x |
| **Gastropods** | *Pirenella alvincziense* | 10 | x | | x | | |
| | *Pleurocera* sp | 112 | x | x | x | | |
| | *Pyrgulifera boeckhi* | 2 | x | x | x | | |
| | *Campylostylus galloprovincialis* | 90 | x | x | x | | |
| | *Neritoplica* sp. | 1 | x | | | | |
| | *Parateinostoma* sp. | 1 | x | | | | |
| | *Pirenella* sp. | 50 | x | | x | | |
| | *Cassiope obvoluta* | 1 | x | | | | |
| | *Onkospira* sp | 1 | | | | x | |
| | *Melanopsis crastina* | 70 | x | x | x | | |
| | ?*Rhabdocolpus* sp. | 261 | | | | x | |
| | *Acteonoidea* indet | 1 | | | | x | |
| | *Pseudamaura alkenyeriensis* | 1 | | | | | x |
| | *Trichotropis* sp. | 1 | | | | | x |
| | *Ageria* sp. | 1 | | | | | x |
| | Voluthidae indet. | 1 | | | | | x |
| | *Acteonella renauxana* | 1 | | | | | x |
| | ?*Nairiella* sp. | 1 | | | | | x |
| | *Neritopsis spinosa* | 3 | | | x | | |
| | *Deianira bicarinata* | 2 | | | x | | |
| **Bivalves** | *Venericardia* sp. | 4 | | | | x | |
| | ?*Corbula* sp. | 11 | x | | x | x | |
| | ?*Exogyra* sp. | 12 | | | | x | |
| | ?*Platyceramus* sp. | 4 | | | | | x |
| | *Granocardium* sp. | 1 | | | | | x |
| | *Panopea* sp. | 1 | | | | | x |
| | *Pycnodonte* sp. | 1 | | | | | x |
| | *Pinna* sp. | 3 | | | | | x |
| | *Sauvagesia* sp. | 2 | | | | | x |
| | Anomiidae indet. | 1 | | | | | x |
| **Echinoids** | Hemiasteridae indet. 1 | 1 | | | | | x |
| | Hemiasteridae indet. 2 | 1 | | | | | x |

**TABLE 1** (continued).

| Category | Identification | Number of specimens | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|---|---|
| **Asteroids** | Asteroidea indet. | 1 | | | | | x |
| **Corals** | *Cunnolites* sp. | 6 | | | | | x |
| | *Aulosmilia* sp. | 2 | | | | | x |
| **Insects ichnofossils** | *Knoblochia cretacea* | 3 | | | x | x | |
| | *Microcarpolithes hexagonalis* | 5 | | | x | x | |
| **Elasmobranchii** | aff. Lamniformes indet. | 1 | | | | x | |
| | *Paratrygonorrhina amblysoda* | 1 | | | | x | |
| **Actinopterigii** | *Atractosteus* sp. | 2 | | | x | | |
| | *Lepisosteus* sp. | 6 | | x | x | | |
| | *Paralbula casei* | 5 | | | | x | x |
| | *Enchodus* cf. *petrosus* | 3 | | | | x | |
| | *Paraplesiopoma transylvanica* | 6 | | | | x | |
| **Herpetofauna** | ?Alytidae indet. | 1 | x | | | | |
| | Anura indet. | 3 | x | | x | | |
| | Scleroglossa indet. | 1 | x | | | | |
| | cf. *Doratodon* sp. | 1 | | | x | | |
| | Allodaposuchidae indet. | 1 | x | | | | |
| **Dinosaurs** | Maniraptoran theropods eggshells | 3 | x | x | | | |

All of these species are illustrated in Figure S1 of Supplementary materials, Section A. It is noteworthy, however, that several biostratigraphically diagnostic taxa typically indicative of the Campanian are absent from the assemblage, thereby limiting the resolution of age assignment. Nevertheless, based on the presence of the aforementioned taxa, the age of the deposits can be constrained. The first occurrence of *Broinsonia parca constricta* marks the base of the UC $14_b$ Biozone (Burnett, 1998), corresponding to approximately 81.4 Ma (Young et al., 2022), thus indicating a maximum (oldest possible) age no earlier than the early Campanian. Furthermore, the last occurrence of *Reinhardtites anthophorus* and *Eiffellithus eximius* fall within the $UC15_e$ subzone of Burnett (1998), dated to the later part of the late Campanian, thereby providing a minimum (youngest possible) age constraint. Consequently, the stratigraphic interval under study is tentatively assigned to a timespan between the early and late Campanian.

Our results are consistent with the findings of Bălc et al. (2024), who also reported the presence of calcareous nannoplankton assemblages in the uppermost part of the Bozes Formation. This concordance between studies enhances the robustness of the proposed age model. Our study reinforces the conclusions of Bălc et al. (2024) and independently confirms the assignment of this stratigraphic interval to the Late Campanian.

## Mesoflora

A mesofloral assemblage was recovered from fossiliferous levels LV3 and LV4 of the Bozeș Formation. The specimens are generally well-preserved; however, most exhibit varying degrees of abrasion and cracking. Seventeen distinct types of angiosperm seeds and fruits (Figure 4A–Q) were identified and recorded as separate taxa. Due to compression and mechanical weathering, precise measurements of seed dimensions were often difficult to take.

Nine types of small anatropous seeds were recognized within the mesofloral material. Four of these (Taxa 1–4, Figure 4A–D) exhibit ornamented surfaces composed of polygonal facets forming distinctive seed coats. These seeds are subrounded to elliptical in shape ranging from 2.2 to 2.7 mm in length and 1.6 to 2.4 mm in breadth. A narrow circumferential furrow is consistently present in these specimens. One oblate seed with a

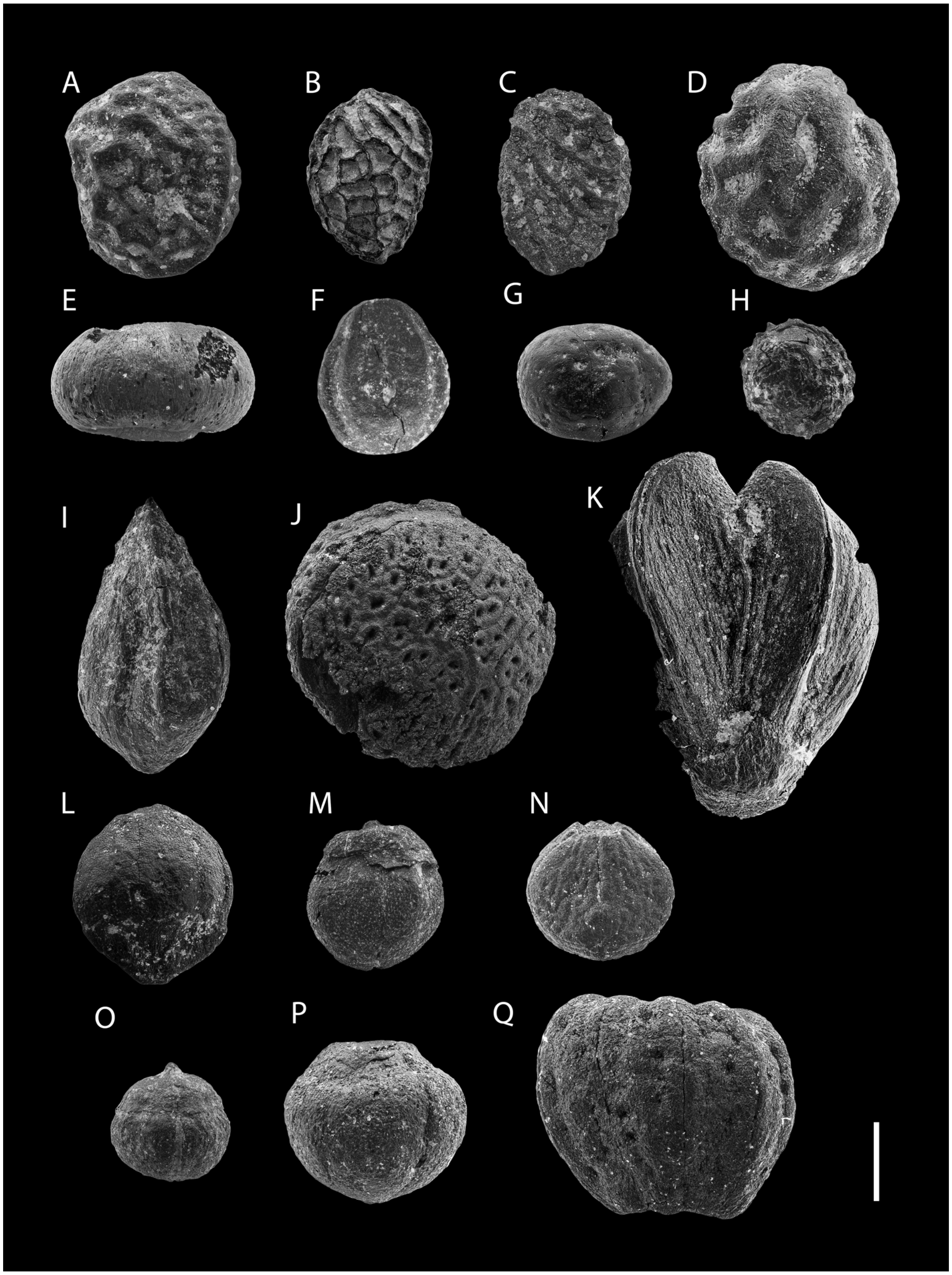

**FIGURE 4.** Specimens from the Petrești plant mesofossil assemblage. **A,** Taxon 1, sub-rounded seed with ornamented surface (NHMS 57478/LV4). **B,** Taxon 2, sub-rounded seed with ornamented surface (NHMS 57479/LV3). **C,** Taxon 3, sub-rounded seed with ornamented surface (NHMS 57467/LV4). **D,** Taxon 4, rounded seed with ornamented surface (NHMS 57464/LV4). **E,** Taxon 5, oblate seed (NHMS 57468/LV4). **F,** Taxon 6, elliptical seed (NHMS 57465/LV4). **G,** Taxon 7, rounded seed with smooth surface (NHMS 57481/LV3). **H,** Taxon 8, rounded seed (NHMS 57482/LV3). **I,** Taxon 9, rounded seed (NHMS 57477/LV4). **J,** Taxon 10, fruit assigned to Normapolles group (NHMS 57472/LV4). **K,** Taxon 11, fruit assigned to the Normapolles group (NHMS 57475/LV4). **L,** Taxon 12, pentacarpellate fruit with ornamented surface (NHMS 57463/LV4). **M,** Taxon 13, pentacarpellate fruit (NHMS 57471/LV4). **N,** Taxon 14, eight locules fruit (NHMS 57469/LV4). **O,** Taxon 15, fragmented spherical fruit (NHMS 57470/LV4). **P,** Taxon 16, four locules fruit (NHMS 57480/LV3). **Q,** Taxon 17, four locules fruit (NHMS 57474/LV4). Scale bar equals 1 mm.

shallow depression at each pole was identified as Taxon 5 (Figure 4E). It measures 0.7 mm in length and 1.2 mm in breadth, and its surface is covered with very fine linear striations connecting the two poles. Taxon 6 (Figure 4F) is represented by an elliptical seed with a surface pattern of fine concentric circles, lacking any discernible anatomical features. It measures 1.9 mm in length and 1.6 mm in breadth. Two additional rounded seeds with little to no surface ornamentation were documented as Taxa 7 and 8 (Figure 4G–H). Despite clear signs of weathering, both depressions and projections are evident on each grain. Taxon 7 measures 1.4 mm in length and 1.9 mm in breadth, while Taxon 8 is 1.4 mm in both dimensions. The last analyzed seed, designated as Taxon 9 (Figure 4I), has a distinct lenticular shape, lacks surface ornamentation, and measures 2.2 mm in length and 2 mm in breadth.

Two fruit specimens, designated as Taxon 10 and Taxon 11, exhibit morphological features characteristic of the Normapolles group (Figure 4J–K), including a distinct triangular shape and tricolpate apertures in polar view. Taxon 10 measures 6.3 mm in length and 3.6 mm in breadth, while Taxon 11 measures 1.9 mm in length and 2.2 mm in breadth. Similar to previously described specimens, these could not be assigned to specific lower-level taxa. The term “Normapolles” generally refers to fossil pollen grains from the Late Cretaceous to early Paleogene, characterized by a distinctive triangular amb and typically triporate structure (Pflug, 1953; Góczán et al., 1967; Tschudy, 1975; Polette and Batten, 2017). These forms have often been associated with members of the order Fagales.

In addition to the aforementioned seeds and fruits, the Petrești mesoflora includes six additional taxa of capsular fruits whit currently uncertain systematic affinities. These fruits exhibit varying numbers of capsules and are preserved at an early, indehiscent stage of maturity. No petals were observed in association with the fruits, and no style were preserved, likely due to abrasion. Taxon 12 (Figure 4L) is a pentacarpellate fruit with a rounded side composed of three locules and a flattened side with two locules. It measures 1.5 mm in both length and breadth. Although the surface is heavily abraded, the locules and their ornamentation remain discernible. Taxon 13 (Figure 4M) consists of four preserved locules, but its overall architecture suggests it is also pentacarpellate. This is the largest fruit specimen recorded, measuring approximately 4.4 mm in length and 3.2 mm in breadth. It lacks ornamentation, but the calyx is partially preserved. Taxon 14 (Figure 4N) is arguably the best-preserved specimen among the capsular fruits. It comprises six locules with an ornamented surface on one side and two flattened locules on the opposite side. The specimen measures 2.9 mm in length and 3.2 mm in breadth. Taxon 15 (Figure 4O) represents a fragment of a spherical fruit with well-preserved surface ornamentation. Although the specimen cracked during handling, it measures approximately 3.1 mm in diameter. Taxon 16 (Figure 4P) is a spherical fruit composed of four locules, measuring 1.4 mm in length and 1.5 mm in breadth. It shows no surface ornamentation, although the calyx is preserved. Taxon 17 (Figure 4Q) is strongly compressed and displays extensive fissuring. It measures 1.9 mm in length and 1.8 mm in breadth, a sub-spherical shape, and appears to consist of four locules. The calyx is partially preserved, and no ornamentation is visible.

The overall composition of the mesofloral assemblage recovered from the Bozeș Formation bears a general resemblance to other Late Cretaceous mesofloras from Europe. Similar to the Maastrichtian Budurone mesoflora of the Hațeg Basin, Romania (Lindfors et al., 2010), the specimens described herein may represent new, previously undescribed taxa, potentially reflecting the biogeographic isolation of the Petrești flora. Given the limited number of specimens available for each taxon, no formal systematic assignments are proposed at this time. Consequently, this study should be regarded as a preliminary report on the mesofloral content of the Bozeș Formation. The challenges in assigning these specimens to established genera or families highlight the need for further systematic investigation and comparative analysis.

## Macroflora

The macrofloral assemblage identified at Petrești is represented by a single taxon, collected from fossiliferous level LV3. The material belongs to the class *Polypodiopsida* and is tentatively assigned to cf. *Sphenopteris ungeri* Kvaček and Herman (in Herman and Kvaček, 2010) (Figure 5A–B).

The specimens consist of sterile, entire-margined, lanceolate pinnules with attenuate apices and decurrent bases. In one specimen, the pinnules appear to be basally fused (Figure 5B). The venation is pinnate, with a slender midvein extending towards the apex and numerous, thin second-

**FIGURE 5.** Leaf impressions from the Bozeș Formation cropping out near Petrești. **A–B,** apical pinnules of cf. *Sphenopteris ungeri* Kvaček and Herman 2010 (NHMS 57409/LV3, NHMS 57410/LV3). Scale bar equals 10 mm.

ary veins that branch dichotomously near the margin.

Although the material is fragmentary and poorly preserved, the morphological features closely resemble the apical pinnules of *Sphenopteris ungeri* described from the Late Cretaceous flora of Grünbach, Austria (Herman and Kvaček, 2007, 2010). This species was originally recorded in the Cretaceous flora of Austria under the name *Pecopteris striata* Presl in Sternberg (Unger, 1867). Cuticle fragments are present in the Petrești specimens; however, because of the poor state of preservation, cuticle extraction was not possible. Such preservation limitations are common for the plant macrofossils from the Petrești site.

*Sphenopteris ungeri* is frequently encountered in Late Cretaceous floras of Europe and is represented as a component of riparian vegetation, commonly occurring alongside *Ettingshausenia* (Herman and Kvaček, 2010).

## Amber

Sediment sieving yielded several amber fragments, all of which were recovered from fossiliferous levels LV3 and LV4. Most fragments are small, ranging from 1 to 3 mm in size, although a few larger specimens measure between 8 and 11 mm (see Figure 6). The amber exhibits an external coloration ranging from brown to yellow-brown, with a distinctly lighter interior that varies from white to light yellow or light brown. The outer surfaces are generally smooth, though some specimens display fine scratches and surface cracking. Morphologically, the amber fragments are predominantly cylindrical, rounded, or teardrop-shaped. The preservation of these delicate morphologies — especially in such fragments — suggests minimal transport or deposition within a calm aquatic environment near the site of resin exudation.

Cretaceous amber occurrences in Romania are poorly documented and limited to sporadic, often outdated reports. The earliest known reference originates from the unpublished manuscript of Paul Maria Joseph Partsch, who described in 1826 the amber from Săsciori, Transylvania (approximately 6 km south of Petrești) in his *Tagebücher seiner Reisen in Siebenbürgen* ("Diaries of his travels in Transylvania"). This account was later cited by Hauer and Stache (1863), bringing it into the formal scientific literature. Subsequent studies, including those by Zechmeister and Vrabely (1927), identified and described the amber from Alba County as a purported new mineral species, named Telegdit. Later mentions are brief and general, such as those by Protesco (1937) and Rabichon (1938), in broader reviews of Romanian amber deposits. The precise age of the Săsciori amber remains unresolved. Both Santonian and Campanian sedimentary units have been identified in the region (Marincaș, 1966, 1970; Tomescu, 1968), but the stratigraphic origin of the amber-bearing layers remains uncertain. Notably, the amber from Săsciori housed in the Brukenthal National Museum in Sibiu differs markedly from the Petrești material in terms of color, clarity, and fracture characteristics (NT, personal observation).

Codrea et al. (2012) briefly reported the presence of "yellowish amber-like resin" in the Rusca Montană Basin, potentially representing an occurrence of Maastrichtian amber.

Upper Cretaceous amber deposits are relatively uncommon in Europe. Nevertheless, several occurrences have been documented, including sites in Austria (Turonian–Santonian; Ősi et al., 2021), France (uppermost Albian–lowermost Cenomanian; Néraudeau et al., 2008; Adl et al., 2011), and Hungary (Santonian; Szabó, 1871; Ősi et al., 2012). The recent identification of amber from Petrești, dated to the Upper Campanian, expands this geographical and stratigraphic distribution and provides a valuable addition to the existing reports.

It is noteworthy that the amber from Petrești was recovered as rather a by-product of microvertebrate and micropaleontological sampling, and not through targeted collection efforts. Future investigations employing specialized recovery techniques, such as flotation in dense liquids, may facilitate the retrieval of a greater quantity of amber

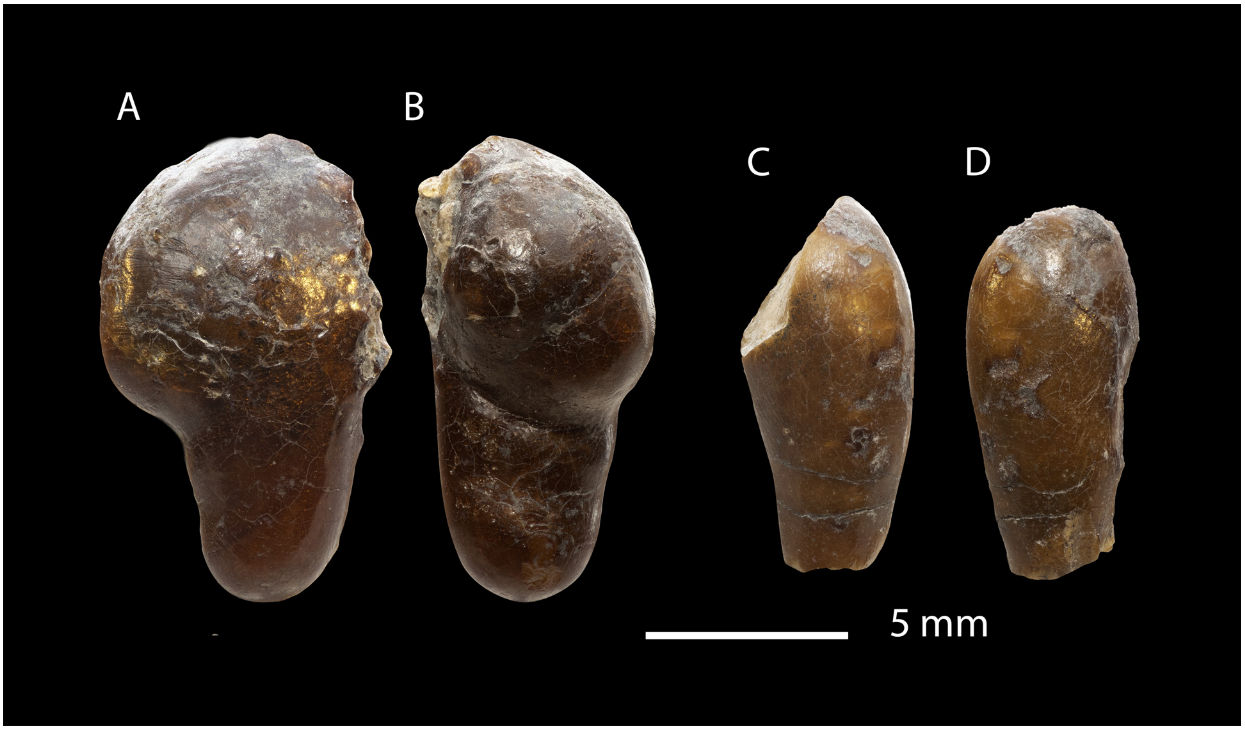

**FIGURE 6.** Amber specimens from Petrești. **A–B,** NHMS 57459/LV3. **C–D,** NHMS 57460/LV3.

specimens, thereby enabling comprehensive analyses.

## 2. Invertebrates

### Mollusks

**Cephalopods.** Three specimens of *Pachydiscus (Pachydiscus)* cf. *haldemsis* (Schlüter, 1867) (M) were recovered from LV5 (Figure 7). These specimens closely resemble *Pachydiscus (Pachydiscus)* cf. *haldemsis* in their compressed shell morphology and whorl section. However, *P. (P.)* cf. *haldemsis* is somewhat more evolute, exhibiting a U/D ratio = ~0.30 at 126 mm, compared to a U/D ratio of 0.25 at 237 mm reported in previous studies (Kennedy and Kaplan, 1997; Kaplan et al., 2005; Kennedy et al., 2007). The macroconch of *Pachydiscus (Pachydiscus) oldhami* (Sharpe, 1853) is also morphologically comparable, but differs by displaying a weaker and more crowded ribbing pattern. In *P. (P.) oldhami,* ornamentation diminishes in ontogeny, becoming largely absent on the late phragmocone stage, particularly on the inner flank (Kennedy and Summesberger, 1984; Kennedy, 1986a; Kennedy and Kaplan, 1997). A general comparison can also be drawn with the upper Campanian *Pachydiscus (Pachydiscus) colligatus* (Binkhorst, 1861) (see Kennedy, 1986a, 1986b, 1986c, 1986d; Martínez, 1997); however, the Petrești specimens are relatively more compressed and exhibit a narrow, rounded venter, in contrast to the broader rounded venter characteristic of *P. (P.) colligatus* (Kennedy, 1986a, 1986b, 1986c, 1986d). Given the incomplete, fragmentary, and somewhat crushed condition of the material, the specimens are provisionally assigned to *Pachydiscus (Pachydiscus)* cf. *haldemsis* (Schlüter, 1867) (M). This species has previously been reported from a wide geographic range, including Northern Ireland, Westphalia (Germany), the Gschliefgraben (Upper Austria), Poland, Sweden, Donbass (Ukraine), Kopet Dag Basin (Iran), Turkmenia, and Kastamonu (Turkey).

For detailed descriptions, morphometric data, taxonomy, additional remarks, and supplementary imagery, refer to Supplementary materials, Section B.

**Gastropods.** A substantial assemblage of gastropods and bivalves was recovered from all five sampled stratigraphic levels. Gastropods dominate the mollusk fauna and encompass representatives from several higher taxonomic groups, including Seguenziida, Cycloneritida, Littorinimorpha, Sorbeoconcha, Neogastropoda, and Heterobranchia. Within Seguenziida, specimens belong to the family Chilodontaidae, represented by *Onkospira* sp. Figure 8A. The order Cycloneritida includes taxa from the families Neritidae — namely *Neritoptyx spinosa* (Pálfy, 1902) Figure 8B and *Neritoplica* sp. Figure 8C — and Deianiridae, represented by *Deianira bicarinata* (Zekeli, 1852) Figure 8D. Littorinimorpha is represented by Capulidae, possibly *Trichotropis* sp. Figure 8E, and Hydrobiidae, represented by *Parateinostoma* sp. Figure 8F. The most taxonomically diverse group is Sorbeoconcha, comprising multiple families: Ampullinidae *(Pseudamaura alkenyeriensis* [Pálfy, 1902]); Figure 8G, Cassiopidae *(Cassiope obvoluta* Schlotheim, 1820); Figure 8H), Procerithiidae (?*Rhabdocolpus* sp. and *Ageria* sp.; Figure 8I–J), Potamididae *Pirenella alvincziense* (Pálfy, 1902); Figure 8L), Pleuroceridae *(Pleurocera* sp.; Figure 8M), Turritellidae (?*Nairiella* sp.; Figure 8N), Hemisinidae *(Pyrgulifera boeckhi* Pálfy, 1902; Figure 8O), and Melanopsidae *(Melanopsis crastina* [Vidal, 1874] and *Campylostylus galloprovincialis* [Matheron, 1843]); Figure 8P–Q. Neogastropoda is represented by the family Volutidae, with specimens assigned to *Volutilithes* sp. Figure 8S. Additionally, two heterobranchs taxa were identified: one assigned to Acteonellidae *(Trochactaeon* sp.; Figure 8T), and another classified as Acteonoidea indet. (Figure 8U) due to poor preservation.

All gastropods recorded from LVs 1–3 are known from brackish or freshwater environments in other regions (Zekeli, 1852; Pálfy, 1902; Bandel and Riedel, 1994), whereas the gastropods from LVs 4–5 are fully marine. Genera such as *Volutilithes, Onkospira, Trochactaeon,* and *Nairiella* documented in these upper levels are widely distributed in Cretaceous marine sediments (e.g., Akopian, 1976; Sohl and Kollmann, 1985; Bakayeva, 2011). This contrast strongly indicates a pronounced T shift in water salinity occurring between LV4 and LV3.

The gastropod assemblage from LVs 1–3 shows strong compositional affinity with the Santonian gastropod fauna of the Ajka Formation in Hungary, which is interpreted as deposited in lacustrine-lagoonal to lagoonal-brackish water environments (Czabalay, 1983). Bandel and Riedel (1994) further characterized the Ajka assemblage as indicative of freshwater to brackish conditions. This paleoenvironmental interpretation is supported by analogous fauna from the Lower Cretaceous Weald Clay Formation (Radley, 1999; Radley and Allen, 2012).

The marine gastropod fauna from LVs 4–5 warrants more detailed investigation, particularly

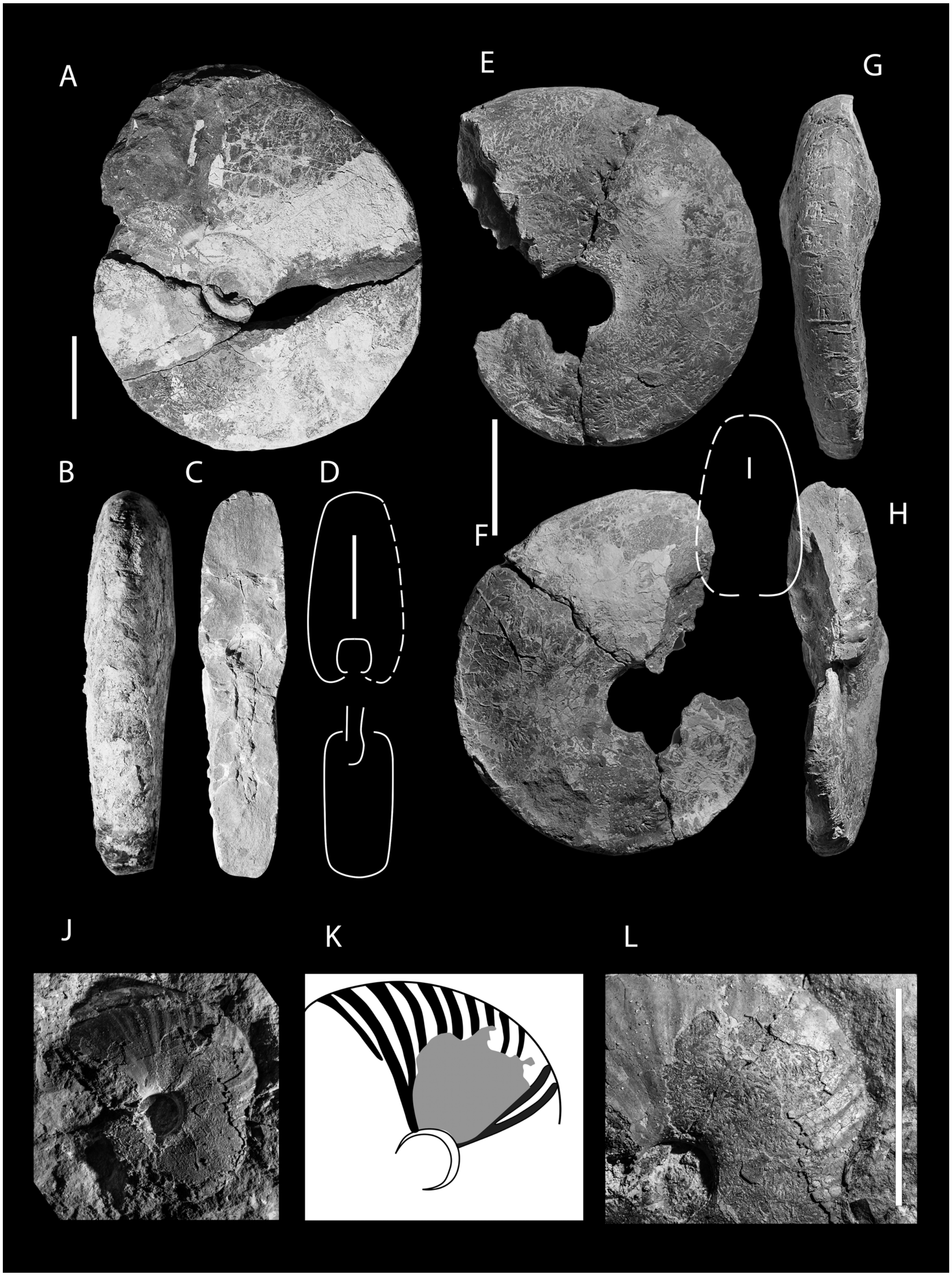

**FIGURE 7.** The ammonite *Pachydiscus* cf. *haldemsis* from Petrești. **A–D,** NHMS 57406/LV5 septate specimen in (A) lateral view, (B) ventral view, (C) apertural view, and (D) whorl section. **E–I,** NHMS 56556/LV5 septate specimen in (E) lateral view, (F) opposite lateral view, (G) ventral view, (H) apertural view, and (I) whorl section. **J–L,** NHMS 56581/LV5, juvenile specimen in (J) lateral view, (K) reconstructed ornamentation from (J), (L) close-up of (J), showing ornamentation. Scale bars equal 50 mm.

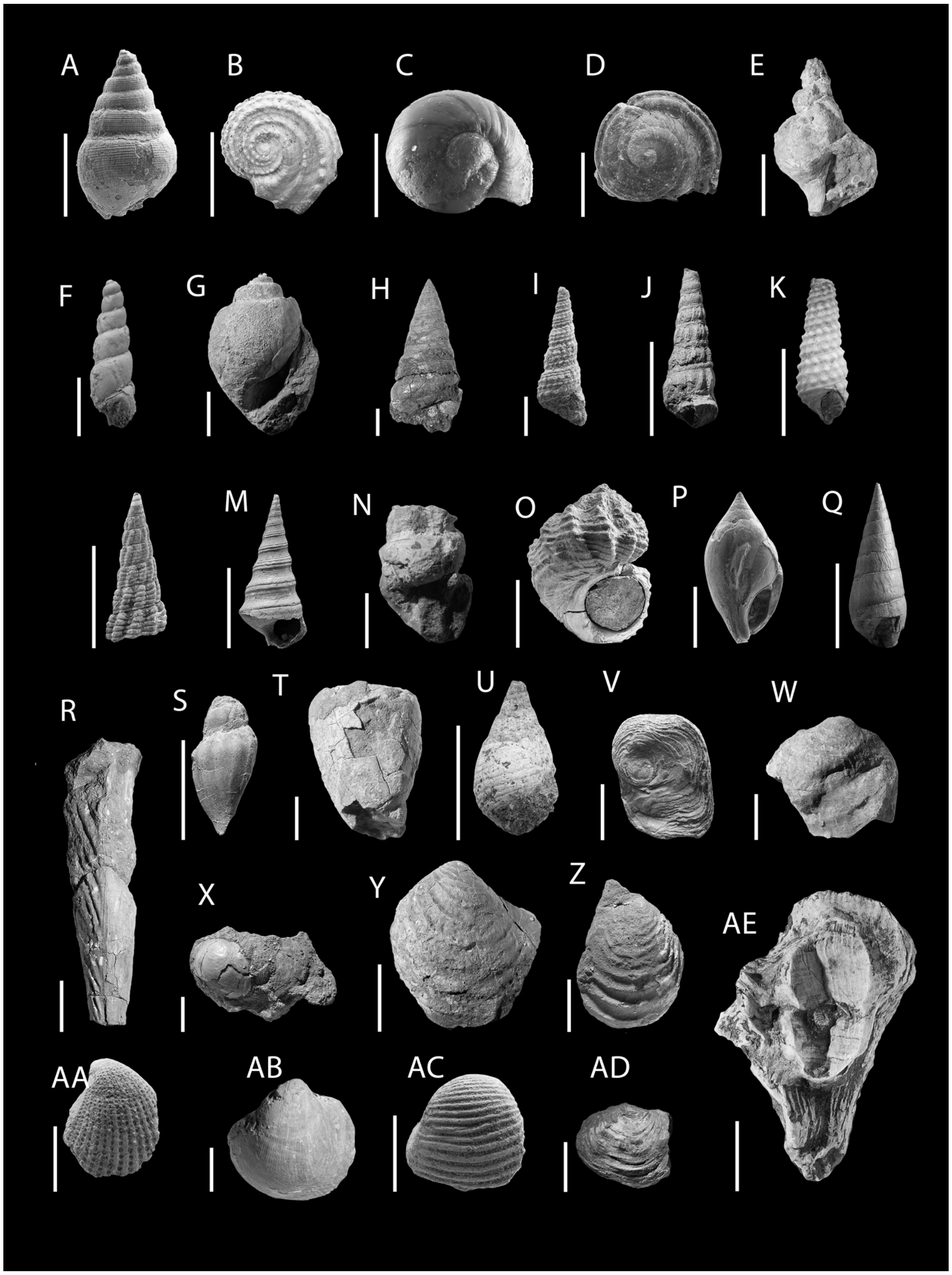

**FIGURE 8.** Gastropods and bivalves from Petrești. **A,** *Onkospira* sp. (NHMS 57098/LV1). **B,** *Neritopsis spinosa* (NHMS 56586/LV3). **C,** *Neritoplica* sp. (NHMS 56357/LV1). **D,** *Deianira bicarinate* (NHMS 56585/LV3). **E,** *Trichotropis* sp. (NHMS 56573/LV5). **F,** *Parateinostoma* sp. (NHMS 57355/LV1). **G,** *Pseudamaura alkenyeriensis* (NHMS 56554/LV5). **H,** *Cassiope obvoluta* (NHMS 57183/LV1). **I,** *Rhabdocolpus* sp. (NHMS 56770/LV4). **J,** *Ageria* sp. (NHMS 56569/LV5). **K,** *Pirenella* sp. (NHMS 57288/LV1). **L,** *Pirenella alvincziense* (NHMS 56587/LV1). **M,** *Pleurocera* sp. (NHMS 56588/LV1). **N,** ?*Nairiella* sp. (NHMS 56564/LV5). **O,** *Pyrgulifera boeckhi* (NHMS 57210/LV1). **P,** *Melanopsis crassatina* (HNMS 57142/LV2). **Q,** *Campylostylus galloprovincialis* (NHMS 57211/LV1). **R,** *Pinna* sp. (HNMS 56580/LV5). **S,** *Volutilithes* sp. indet. (NHMS /LV5). **T,** *Trochactaeon* sp. (NHMS 56571/LV5). **U,** Acteonoidea indet. (NHMS 57032/LV4). **V,** ?*Exogyra* sp. (NHMS 56758/LV4). **W,** *Pycnodonte* sp. (NHMS 56568/LV4). **X,** Anomiidae indet. (NHMS 56563/LV5). **Y,** ?*Platyceramus* sp. (NHMS 56575/LV5). **Z,** ?*Platyceramus* sp. (NHMS 56577/LV5). **AA,** *Venericardia* sp. (56577 NHMS/LV4). **AB,** *Granocardium* sp. (NHMS 56555/LV5). **AC,** ?*Corbula* sp. (NHMS 57031/LV4). **AD,** *Panopea* sp. (NHMS 56578/LV5). **AE,** *Sauvagesia* sp. (NHMS 56552/LV5). Scale bars = 1 mm (C, F, and I); 3 mm (K, P, U, AA, and AC); 5 mm (A, B, D, L, M, and V); 10 mm (H, N, O, Q, T, and W); 20 mm (E, G, J, S, X, Z, AB, AD, and AE); 30 mm (R); and 50 mm (Y).

focusing on smaller-sized faunal elements. Nevertheless, the occurrence of *Trochactaeon* sp. suggests affinities with warm, shallow-water Tethyan faunas (Sohl and Kollmann, 1985).

**Bivalves.** The bivalve assemblage is almost entirely confined to the lower part of the investigated section, specifically LVs 4–5. The greatest diversity is observed in the lowermost level (LV5), which yields at least seven species. This assemblage includes inoceramid bivalves (?*Platyceramus* sp.; Figure 8Y), the pinnid *Pinna* sp. (Figure 8R), an indetermined anomiid (Figure 8X), the gryphaeid oyster *Pycnodonte* sp. (Figure 8W), a cardiid, *Granocardium* sp. (Figure 8AB); the hiatellid *Panopea* sp. (Figure 8AD), and a radiolitoid rudist, *Sauvagesia* sp. (Figure 8AE). In the overlying LV4, species richness is notably reduced, with only three taxa recorded: a gryphaeid oyster (tentatively *Exogyra* sp.; Figure 8V), a cardiid (cf. *Venericardia* sp.; Figure 8AA), and a corbulid (possibly *Corbula* sp.; Figure 8AC).

## Echinoids and Asteroids

Echinoderms are represented by only three specimens within the investigated section. Two echinoid specimens, both poorly preserved and preserved solely as internal molds with minor remnants of the original tests, were recovered from LV5. Specimen NHMS 57412-LV5 displays a broad, flattened test with long, relatively narrow ambulacra (Figure 9A). In contrast, specimen NHMS 57411-LV5 is more globular in shape, with comparatively broader ambulacrum than in the other specimen (Figure 9B). These morphological distinctions suggest that the two individuals may represent two different species. Based on their overall test morphology, both specimens may be attributed to the family Hemiasteridae (J. Gallemí, personal comm., 14 January 2024). Asteroidea are represented in the Petrești deposits by two associated ossicles recovered from LV5 (specimen NHMS 57462). This specimen is poorly preserved, likely due to mechanical abrasion (Figure 9C–E).

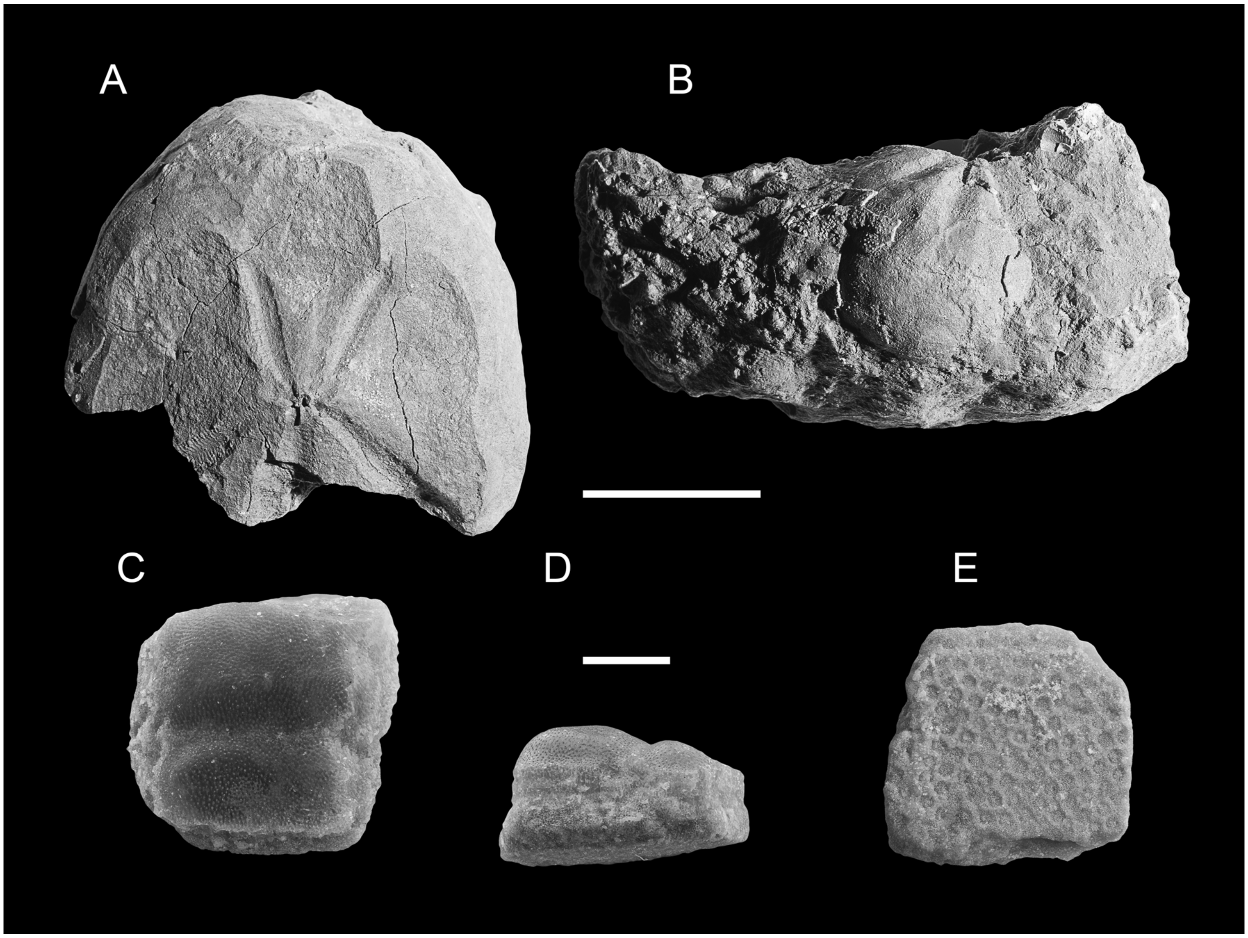

**FIGURE 9.** Echinoids and asteroids from Petrești. **A,** Hemiasteridae indet. (NHMS 57412/LV5). **B,** Hemiasteridae indet. (NHMS 57411/LV5). **C–E**, Asteroidea indet. (NHMS 57462/LV5). Scale bars equal 20 mm (A, B); 1 mm (C–E).

## Corals

Although relatively rare, a few specimens belonging to the families Cunnolitidae and Phyllosmiliidae were identified in LV5. Six individuals of the genus *Cunnolites* Alloiteau, 1952, ranging in diameter from 25 to 55 mm, were successfully recovered (Figure 10A–D). These specimens are well preserved, exhibiting no evidence of basal attachment structures or overgrowth margins. While several subgenera and species of *Cunnolites* have been described (e.g., El-Asa'ad, 1990; Gameil et al., 2018), other authors have emphasized the taxonomic challenges posed by the high degree of morphological variability within the genus (Baron-Szabo, 1998, 1999), which complicates species-level identification.

In addition to *Cunnolites*, two conical coral specimens were recovered from the same level, measuring 40 and 69 mm in height, respectively, and exhibiting an elliptical apical outline (Figure 10E–H). These specimens have been assigned to the genus *Aulosmilia* Alloiteau, 1952, based on morphological features (H. Löser, personal comm., 20 February 2024).

## Insects

In addition to plant and reptile remains, the terrestrial biotic elements of the Petrești fossil assemblage also include certain fossil morphotypes interpreted as insect ichnofossils.

Ovoid-shaped microfossils with prominent longitudinal ridges were recovered in association with mesofloral material. These structures range in length from 1.8 to 2.8 mm, and in width from 1.6 and 1.9 mm. The ridges covering their surface are triangular in cross-section, and conspicuous projections are present at both the apical and basal ends of the specimens (Figure 11A–B). Initially, microfossils of this morphology were attributed to the angiosperm seed species *Spirellea kvacekii* (Knobloch) Knobloch and Mai, 1983 (Knobloch and Mai, 1983, 1986). However, Heřmanová et al. (2013) argued that the terminal projections and absence of a micropyle scar are diagnostic of insect eggs. Consequently, this morphotype was

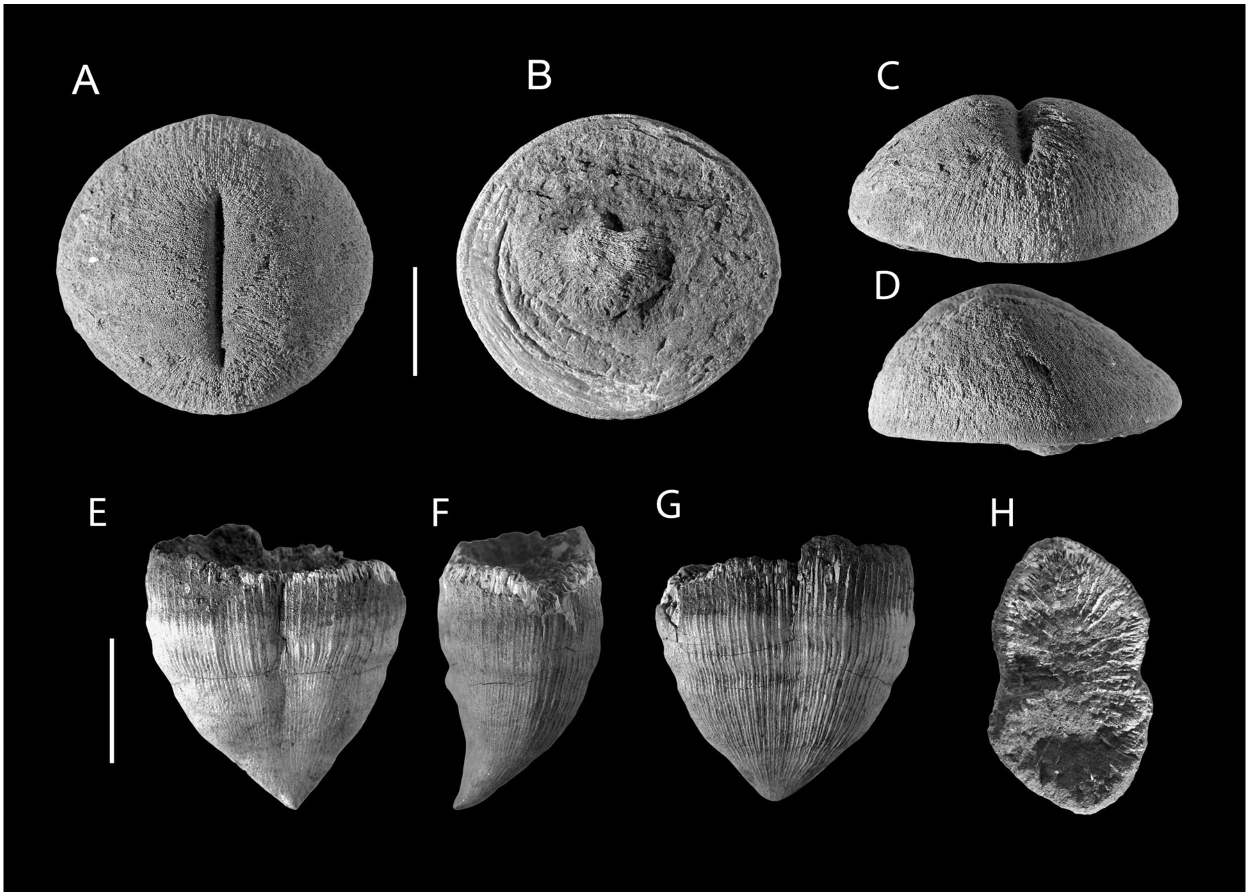

**FIGURE 10.** Corals from Petrești. **A–D,** *Cunnolites* sp. (NHMS 56561/LV5). **E–H,** *Aulosmilia* sp. (NHMS 56572/LV5). Scale bars equal 20 mm.

reassigned to *Knoblochia cretacea* Heřmanová et al., 2013, an ichnotaxon related to insects. While the insect origin of *K. cretacea* is now widely accepted, its precise systematic placement remains uncertain. Similar remains have previously been reported from the Maastrichtian continental deposits of the Haţeg Basin (Bodor et al., 2014).

Another morphotype identified in the Petreşti assemblage consists of elongated granules with a hexagonal cross-section, approximately 1.8 mm in length and 1.0 mm in width (Figure 11C). These microfossils have been identified as termite coprolites based on their strong morphological similarity to the fecal pellets of extant termites. They have been widely documented across global sites ranging from the Lower Cretaceous to the Pleistocene, typically attributed to Isoptera and described under the ichnospecies *Microcarpolithes hexagonalis* Vangerow 1954 (Colin et al., 2011; Heřmanová et al., 2021) or more generally as termite coprolites (Ősi et al., 2021). Fragments of *M. hexagonalis* are particularly abundant in the Petreşti deposits, especially within levels LV4 and LV3. This ichnotaxon has also been reported in large numbers from the Maastrichtian deposits of the Haţeg and Rusca Montană basins in Romania, as well as from the Santonian deposits of Iharkút, Hungary (Vasile et al., 2013).

## 3. Vertebrates

### Fish

Although relatively scarce, fish remains are present throughout all analyzed stratigraphic levels at the site. A total of 38 identifiable specimens — including teeth, otoliths, and scales — were recovered. Part of the material was assigned to the Class Chondrichthyes (cartilaginous fishes), representing both the Division Selachii, Order Lamniformes (aff. Lamniformes indet.; Figure 12A–C) and the Division Batomorphii, Family Rhinobatidae *(Paratrygonorrhina amblysoda* Kriwet et al., 2007; Figure 12D–H). In addition to chondrichthyans, representatives of the Class Actinopterygii (ray-finned fishes) were also identified. These include the orders Lepisosteiformes *(Atractosteus* sp.; Figure 12I–N, and *Lepisosteus* sp.; Figure S2 in the Supplementary materials), Aulopiformes (*Enchodus petrosus* Cope, 1874; Figure 12O–Q), Elopiformes (*Paralbula casei* Estes, 1969; Figure 12R–T), and Actinopterygii indet. (Figure 12U–W). Additionally, a new genus and species of basal percomorph fish is described from this locality by Trif and Schwarzhans as *Paraplesiopoma transylvanica* n.

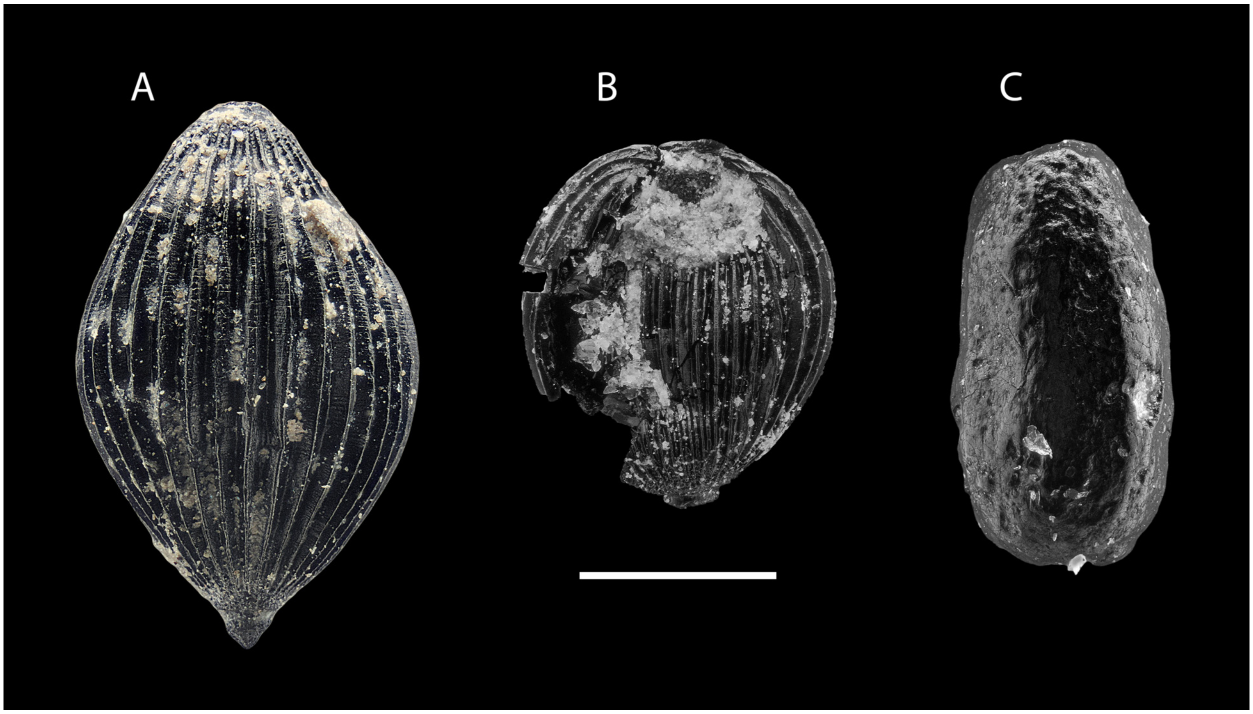

**FIGURE 11.** Insect ichnofossils representing eggs and coprolites from the Petrești mesofossil assemblage. **A–B,** *Knoblochia cretacea*, insect eggs, (A) NHMS 57483/LV3, (B) (NHMS 57473/LV4). **C,** *Microcarpolithes hexagonalis*, termite coprolite (NHMS 57476/LV4). Scale bar equals 1 mm.

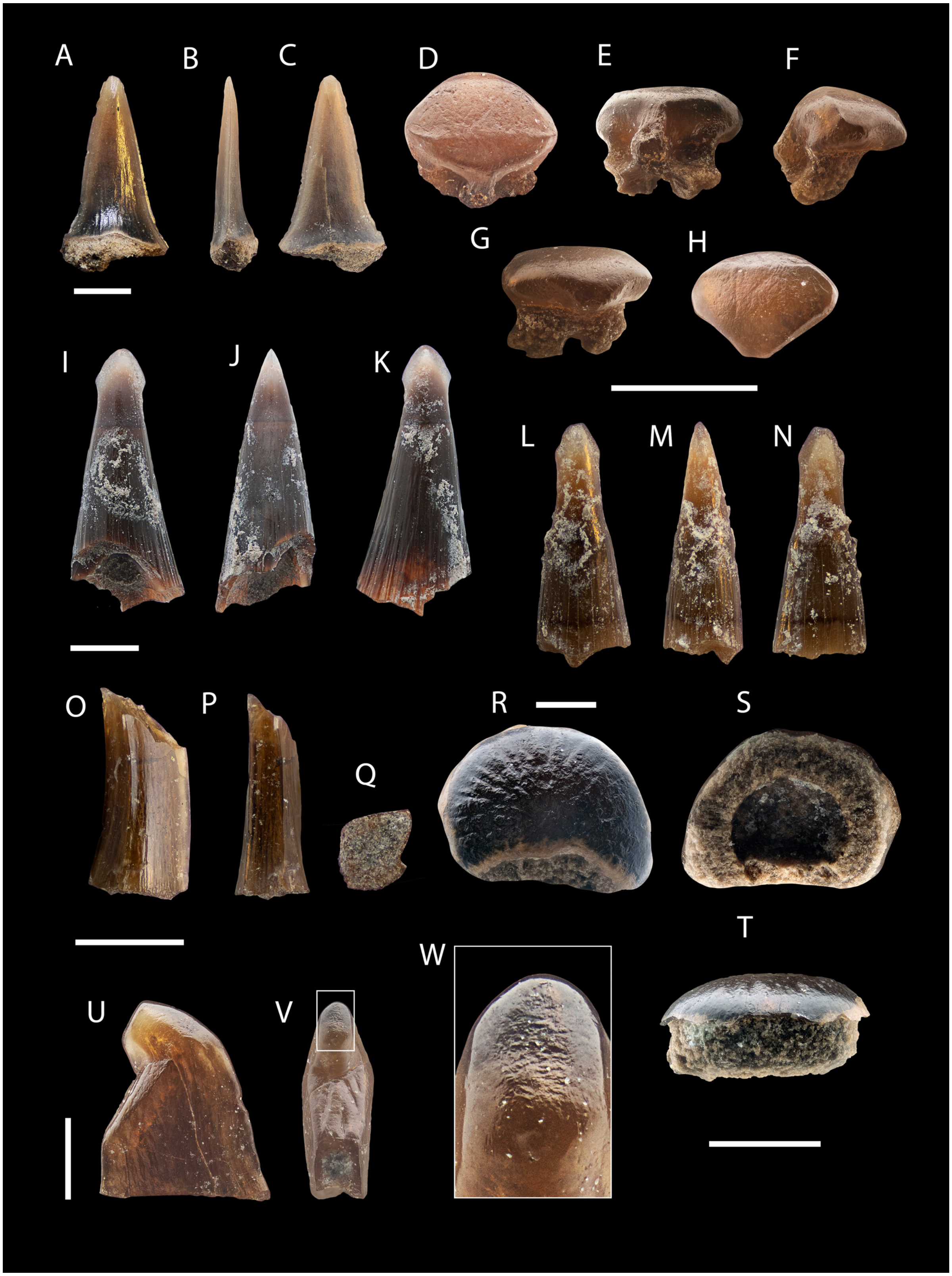

**FIGURE 12.** Fish teeth from Petrești. **A–C,** Lamniformes indet. (NHMS 57427/LV5). **D–H,** *Paratrygonorrhina amblysoda* Kriwet et al., 2007 (NHMS57422/LV4). **I–K** and **L–N,** *Atractosteus* sp. (NHMS 57439/LV3 and NHMS 57440/LV3). **O–Q,** *Enchodus* cf. *petrosus* (NHMS 57426/LV4). **R–T,** *Paralbula casei* (NHMS 57421/LV4). **U–W,** Actinopterygii indet. (NHMS 57419/LV4). Scale bars = 0.5 mm (I–K, L–N, and U–V); 1 mm (A–C, D–H, O–Q, and R–T).

gen. et n. sp., representing Percomorpha incertae sedis (see description below).

## SYSTEMATIC PALEONTOLOGY

Infraclass TELEOSTEI Müller, 1846
Subsection ACANTHOMORPHA Rosen, 1973
Division ACANTHOPTERYGII Artedi, 1738
Subdivision PERCOMORPHA Hay, 1903
Basal PERCOMORPHA incertae sedis
Genus *PARAPLESIOPOMA* n. gen. Trif and Schwarzhans
Figure 13

**zoobank.org/54D1553C-7595-438C-9DBD-3645CC04CB7C**

**Type species.** *Paraplesiopoma transylvanica* n. sp. Trif and Schwarzhans

**Remarks.** The otolith terminology follows Koken (1884).

**Etymology.** The genus name, *Paraplesiopoma,* refers to its morphological resemblance to the Late Cretaceous otolith-based genus *Plesiopoma* Schwarzhans, 2010.

**Diagnosis.** Fossil otolith-based genus tentatively associated with basal Percomorpha. Otoliths small (maximum not exceeding 3.5 mm in length), elongate oval in shape with rounded posterior tip and projecting, rounded rostrum. Otolith length to height ratio (OL/OH) 1.40–1.75, height to thickness ratio (OH/OT) 2.2–2.7. Antirostrum and excisura minute. Inner face distinctly convex. Sulcus long, clearly divided into ostium and cauda. Ratio cauda length (CaL) to ostium length (OsL) 1.40–1.55; ratio ostium height (OsH) to cauda height (CaH) 1.5–2.2. Ostium open anterior-dorsally, ventrally expanded, and with clearly defined ostial colliculum; cauda slightly flexed along entire course; no ventral furrow.

**Comparison.** *Paraplesipoma* exhibits an otolith morphology reminiscent of several percomorph, particularly eupercarian, taxa distinguished by a broad, short ostium and a slender, slightly curved cauda. This configuration, referred to as “heterosulcoid” by Schwarzhans (1978) is widespread among numerous unrelated teleost clades. However, *Paraplesiopoma* lacks additional diagnostic features that would allow for a more precise taxonomic placement beyond basal Percomorpha. Its generalized oval shape and absence of a ventral furrow are considered plesiomorphic, paralleling conditions observed in more basal teleost groups such as Elopiformes, Albuliformes, and Aulopiformes (see Schwarzhans, 2018 for comparative data). For instance, Elopiformes otoliths tend to be slenderer with a less pronounced ventral expansion of the ostium; Albuliform otoliths typically display a diagonally positioned sulcus (e.g., in Pterothrissidae) or a sharply curved caudal tip (e.g., in Albulidae). In Aulopiformes such as Paraulopidae, the dorsal margin of the ostium is characteristically expanded both upward and backward. It cannot be excluded, however, that in a phylogenetic sense *Paraplesiopoma* is of sub-percomorph affinities.

As previously noted, *Paraplesiopoma* closely resembles otoliths of the fossil basal percomorph otolith-based genus *Plesiopoma* Schwarzhans, 2010 known from several species from Coniacian to early Paleocene (Schwarzhans, 2010, 2012). *Plesiopoma* was initially placed within the family Acropomatidae, but has more recently been reinterpreted as Percomorpha incertae sedis (Schwarzhans et al., 2024). The two genera are differentiated by the presence of a ventral furrow in *Plesiopoma* — a derived percomorph character, and by its ostium and cauda being of nearly equal length.

**Species.** The type species is *Paraplesiopoma transylvanica* sp. nov. from the Campanian of Romania. Additional species include *P. bagassiana* (Nolf, 2003), originally described as “genus Acropomatidarum *bagassianus”,* and *P. santoniana* (Nolf, 2003), originally described as “genus Haemulidarum *santonianus”,* both from the Santonian of Spain.

*Paraplesiopoma transylvanica* n. sp.
Trif and Schwarzhans
Figure 13

**zoobank.org/D9BC31EB-7B86-423E-A65E-ABC4A3BA9A62**

**Type locality.** Petrești, Alba County, Romania.

**Stratum typicum.** Level 4 (see Figures 2 and 3A).

**Age.** Campanian.

**Etymology.** Named after the Transylvanian Basin.

**Holotype.** NHMS 57413/LV4 (Figure 13A–D).

**Paratypes.** Specimens NHMS 57414 (Figure 13E), 57415 (Figure 13F–G), 57416 (Figure 13H), and 54718 (Figure 13I–J), all originating from the same stratigraphic level and locality as the holotype.

**Diagnosis.** OL:OH = 1.55–1.65; OH:OT = 2.4–2.7. Maximal observed length ca 3.3 mm. Dorsal and ventral rims regularly curved without angles. Ostium distinctly shorter and wider than cauda, slightly upward directed, mainly ventrally expanded; CaL:OsL = 1.4–1.5; OsH:CaH = 1.5–1.8.

**Description.** Otoliths are small, elongate-oval, and moderately thick, with maximum observed length reaching 3.3 mm (holotype: 2.75 mm long). The

**FIGURE 13.** A new fish taxon from Petrești. **A–D,** *Paraplesiopoma transylvanica* n. gen. et n. sp., holotype (NHMS 57413/LV4). **E,** paratype (NHMS 57414/LV4). **F–G**, paratype (NHMS 57415/LV4). **H,** paratype (NHMS 57416/LV4). **I–J,** paratype (NHMS 54718/LV4). Scale bar equals 1 mm.

dorsal rim is regularly curved, slightly and irregularly undulating. The ventral rim is regularly curved, smooth or with fine crenulation, particularly in small specimens (Figure 13I–J); in the larger specimens the crenulation is less intense and primarily along preventral rim (Figure 13H). The anterior tip displays a massive, moderately pointed to rounded rostrum that is positioned slightly above the otolith axis; the rostrum length is about 15–20% of OL. The antirostrum and excisura are minute. The posterior rim is rounded, positioned slightly inferior to the level of the rostrum.

The inner face is distinctly convex with a supramedially positioned, long, somewhat deepened sulcus. The ostium is anteriorly opening to the predorsal rim, its relatively flat dorsal margin is about half the length of the deeply expanded ventral margin; the ostium is slightly upward inclined at

7–10°, which is best visible along the straight central part of the ventral margin of the ostium. The cauda is longer than the ostium and distinctly narrower, slightly flexed along the entire course and reaches close to the posterior rim of the otolith. CaL:OsL = 1.4–1.5; OsH:CaH = 1.5–1.8. The dorsal depression is long, narrow, ventrally bound by a distinct crista superior towards the sulcus, and its dorsal margin is gradual, indistinct. There is no ventral furrow discernible. The outer face is flat to convex, relatively smooth except for the presence of occasional short radial furrows along its ventral rim.

**Discussion.** *Paraplesiopoma transylvanica* is the only otolith-based species identified in the transitional brackish deposits of Petrești. Its occurrence suggests adaptation to such marginal environment. In contrast, the stratigraphically slightly older Santonian congeners, *P. santoniana* and *P. bagassiana* are known from fully marine deposits (Nolf, 2003). *Paraplesiopoma santoniana* differs from *P. transylvanica* in the more pointed posterior tip of the otolith and the slightly downward inclined cauda (versus straight and slightly flexed). *Paraplesiopoma bagassiana* is more compact than *P. transylvanica* (OL:OH = 1.4–1.6 vs 1.55–1.65) and thicker (OH:OT = 2.2 vs 2.4–2.7). *Paraplesiopoma transylvanica* differs from both its congeners in the dorsal margin of the ostium being less expanded, which is reflected in a lower OsH:CaH ratio (1.5–1.8 measured from drawings in Nolf, 2003 versus 1.9–2.3 in the Petrești specimens), and in the ostium being slightly upward inclined (versus horizontal in the new species).

A comprehensive reconstruction of the ichthyofauna at Petreşti remains challenging due to the low species richness. Nonetheless, comparative evidence offers insights into paleoecological conditions. *Paratrygonorrhina amblysoda* (level LV4), previously recorded only in the Spanish and French Pyrenees, is interpreted as a nektobenthic ray associated with marginal littoral environments (Gheerbrant et al., 1997; Kriwet et al., 2007). Similarly, *Paralbula casei* (LV4 and LV5) and *Enchodus* cf. *petrosus* (LV4) are known from shallow marine and coastal plain environments, often linked to fluvially influenced estuarine or deltaic systems (Becker et al., 2010; Schubert et al., 2017). The indeterminate aff. Lamniformes indet. material from LV4 is too fragmentary for ecological inference.

The presence of the gars *(Atractosteus* sp. and *Lepisosteus* sp.) in levels LV1, LV2, and LV3 may indicate a stronger continental influence. At least one of these genera is already documented in Maastrichtian continental deposits from Romania (e.g., Csiki et al., 2008; Solomon et al., 2022b).

For additional taxonomic details, measurements, discussions, and supporting figures, refer to Supplementary materials, Section C.

## Herpetofauna

The herpetofaunal assemblage recovered from various stratigraphic levels is relatively limited in both diversity and abundance. The identified material includes two urostyles, several incomplete jaw elements, a fragment of a vertebral neural arch, and a number of isolated teeth. These remains were assigned to representatives of amphibians (Anura), and reptiles (Squamata and Crocodylomorpha). The amphibian remains were attributed to the anuran clade Alytidae (?Alytidae indet., specimen NHMS 57446, levelLV1), represented by a urostyle characterized by distinctly bipartite cotyles and well-developed transverse processes (Figure 14A–F). Additional anuran remains — comprising a urostyle, a partial dentary, and a vertebral fragment — are referred to Anura indet. (Figure 14G–O).

The reptilian material includes both squamates and crocodylomorphs. A partially preserved lower jaw was attributed to Scleroglossa indet., potentially representing a scincoid taxon (Figure 14P–R). The crocodylomorph remains are represented by a possible ziphosuchian, tentatively identified as cf. *Doratodon* sp. (Figure 14S–W), and an isolated tooth is attributed to cf. Allodaposuchidae indet. (Figure 14X–Z). Additionally, the presence of non-avian theropod dinosaurs is inferred based on the occurrence of eggshell fragments (Figure 15A–F), although no osteological remains were identified.

The amphibian material provides evidence for the presence of at least two distinct anuran taxa: ?Alytidae and Anura indet. Alytidae is an anuran clade with many primitive features that includes a group of species associated with aquatic habitats *(Discoglossus* and *Latonia)* and another stoutly built group with semi-fossorial habits *(Alytes).* Their natural habitats are temperate forests, Mediterranean-type shrubby vegetation, rivers, freshwater marshes, freshwater springs, and rocky areas (Sanchiz, 1998; Dubois, 2005; Blackburn and Wake, 2011; Beukema et al., 2013).

The reptilian assemblage includes both lizard and crocodylomorph remains. The lizard material is represented by a specimen assigned to Scleroglossa indet., potentially within the clade Scincoidea. The crocodylomorphs appear to comprise

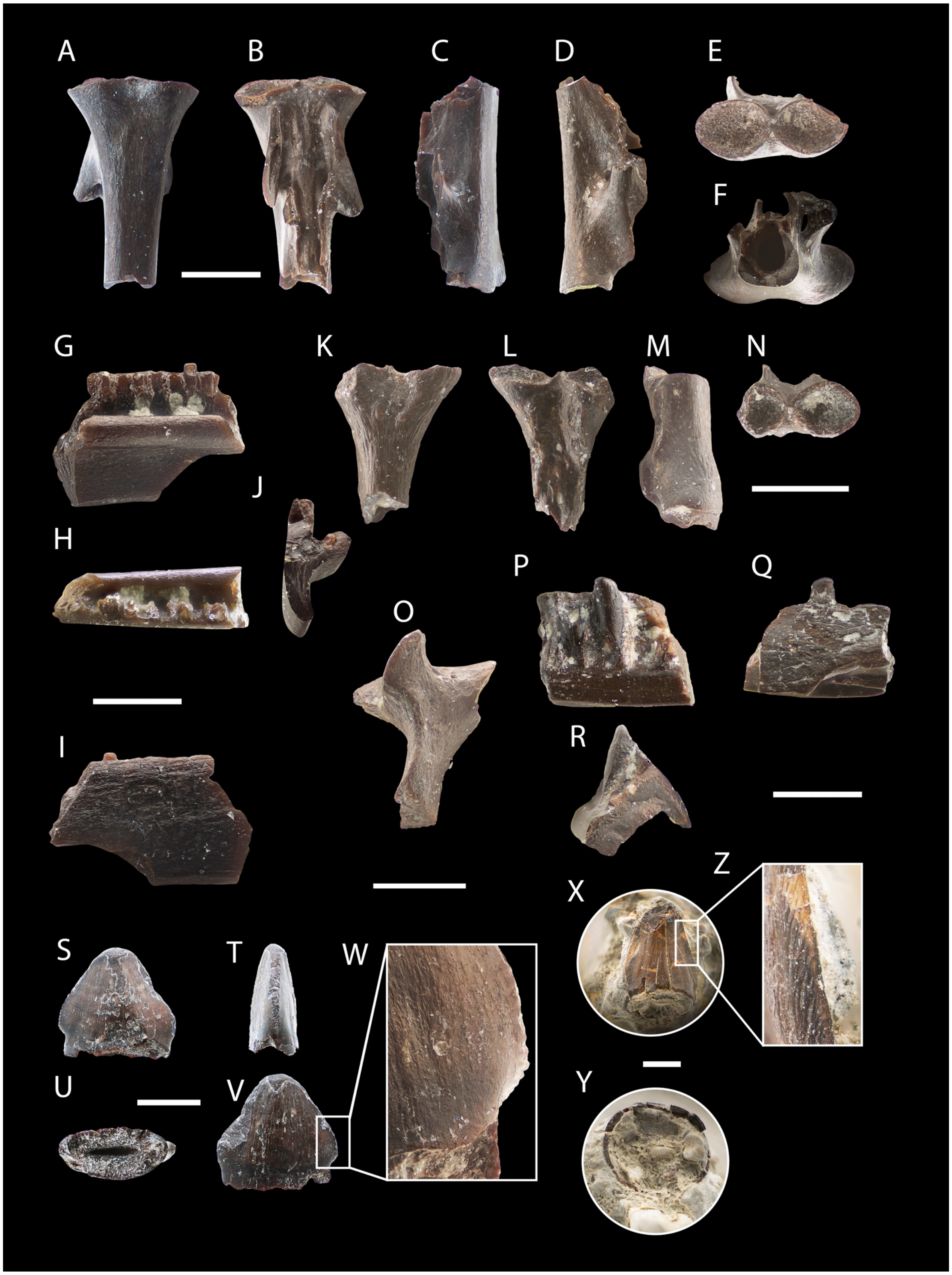

**FIGURE 14.** Amphibians and reptiles from Petrești. **A–F,** ?Alytidae indet., urostyle, (NHMS 57446/LV1) in (A) dorsal, (B) ventral, (C) left lateral, (D) right lateral, (E) anterior, and (F) posterior views. **G–O**, Anura indet., left dentary (NHMS 57447/LV3) in (G) medial, (H) dorsal, (I) lateral, and (J) posterior views; urostyle (NHMS 57448/LV1) in (K) dorsal, (I) ventral, (M) lateral, and (N) anterior views; and neural arch of vertebra (NHMS 57449/LV1) in (O) lateral view. **P–R,** Scleroglossa indet., left dentary (NHMS 57450/LV1) in (P) medial, (Q) lateral, and (R) anterior views. **S–W,** cf. *Doratodon* sp. tooth (NHMS 57451/LV3) in (S) labial, (T) distal (or mesial), (U) basal, and (V) lingual views with (W) detail of basal serration. **X–Z,** cf. Allodaposuchidae indet., (NHMS 57452/LV1) in (X) lingual and (Y) basal views, with (Z) detail of cutting edge. Scale bar = 0.5 mm (G–I); 1 mm (A–F, K–N, O, and P–R); and 2 mm (S–V, X–Y).

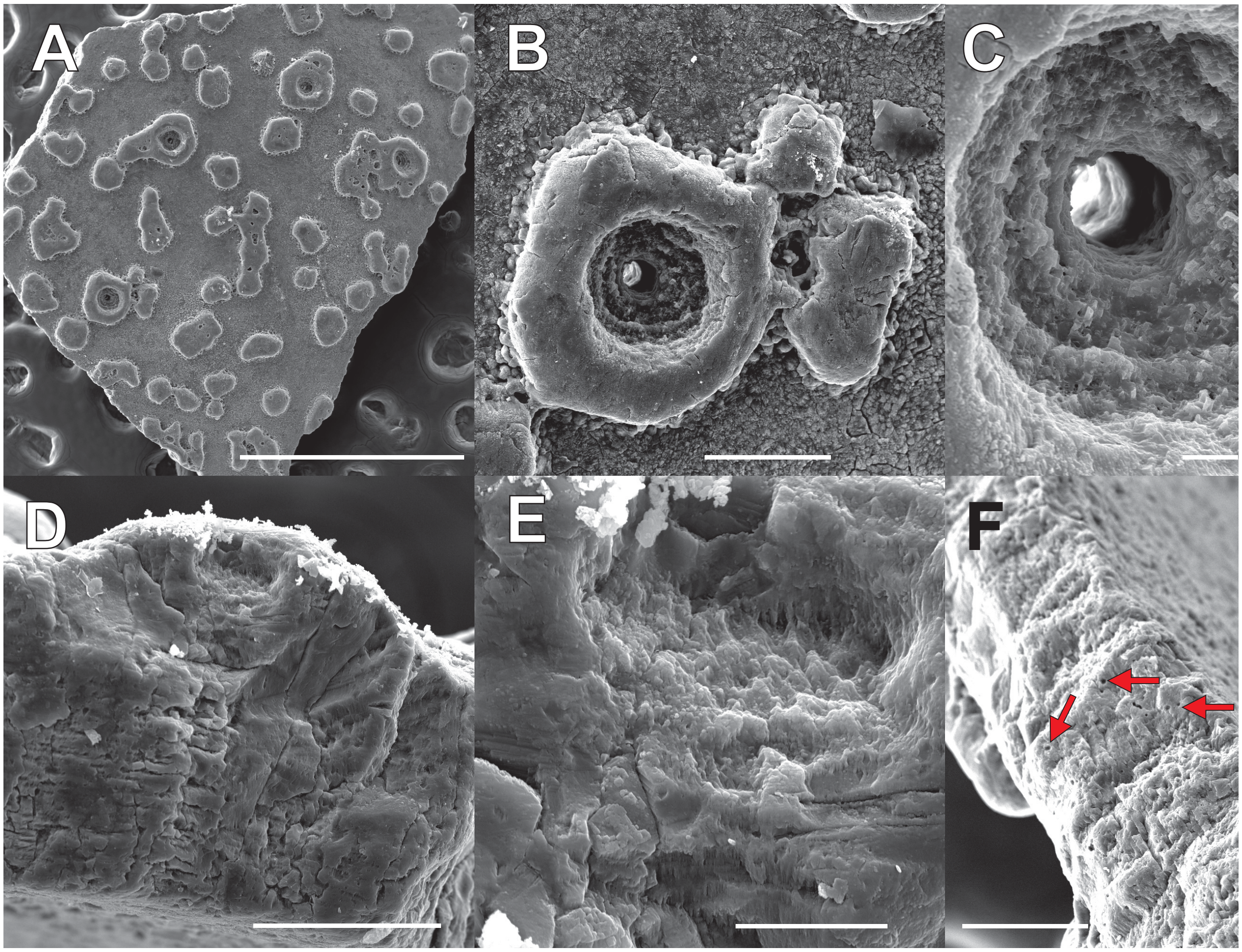

**FIGURE 15.** Eggshells from Petrești. **A–C,** NHMS 57456/LV1; (A) external morphology of eggshells displaying irregular tubercles and gas exchange pores; (B) closeup of a group of tubercles; (C) a close-up view of one of the gas exchange pores that extends through the entire thickness of the shell. **D–F,** NHMS 57457/LV2; (D) longitudinal section of a pore; (E) detail of the upper section of the pore; (F) the radial section of the eggshell displaying the tabular structure; the arrows indicate minute perforations. Scale bars equal 20µm (E); 50µm (C); 100µm (B, D, and F); and 1 mm (A).

two taxa. Based on the typical tooth morphology (labiolingually flat, ziphodonty), a *Doratodon*-like crocodylomorph can be identified (note, however, that caution is needed — identification of ziphosuchians and atoposaurids below family level, based on a single isolated tooth, might be doubtful, because several distinct tooth morphotypes can be present in a single individual. Moreover, besides the zipchosuchian *Doratodon*, at least two taxa of atoposaurids are present in the Transylvanian landmass (e.g., Venczel and Codrea, 2019). The second tooth is rather generalized in morphology. The crenulation of the second tooth together with the general morphology resemble a tooth from the posterior region of the jaw of a semi-aquatic eusuchian, being comparable with members of Allodaposuchidae. Thus, it is tentatively assigned to cf. Allodaposuchidae indet. In this group, the enamel surface usually bears some apicobasal coarse ridges (e.g., Narváez et al., 2020; note, however, that it can be smooth in some cases, this is a variable character). Allodaposuchidae is a clade of basal eusuchians known from the Late Cretaceous (Campanian and Maastrichtian) of Europe, being an endemic group of the European archipelago (Narváez et al., 2015, 2016, 2020; Blanco and Brochu, 2017) and even the type material of *Allodaposuchus precedens* is previously reported from Romania (the lower Maastrichtian of Vălioara) (Nopcsa, 1928; Narváez et al., 2020).

*Doratodon* is an enigmatic extinct crocodyliform that inhabited the western Tethyan archipelago during the Late Cretaceous, corresponding to present-day Romania, Hungary, southern France, and Spain. Members of this genus were relatively small-bodied, characterized by ziphodont dentition and inferred to have had a terrestrial lifestyle with adaptations consistent with active predation (Martin et al., 2006, 2010; Martin, 2007; Vasile, 2008; Vasile and Csiki, 2011; Rabi and Sebők, 2015).

Modern crocodiles are typically confined to tropical and subtropical regions, largely due to their limited reproductive success in colder climates (Alderton, 1991). As such, fossil representative of Crocodyliformes serve as valuable proxies for reconstructing paleoclimatic and paleoecological conditions (Berg, 1965; Markwick, 1998). Analyses of extant crocodilian distribution suggest that temperature is a critical factor governing their global range, with the minimum average annual temperature for current species being approximately 14.2°C (Markwick, 1998). It is important to emphasize, however, that this threshold applies to crown-group crocodilians. The ecological tolerances and niche requirements of the more diverse Mesozoic crocodylomorphs were likely broader, and may have differed substantially from those of modern forms (see the discussion in Mannion et al. (2015) regarding long-term biodiversity decline). Carvalho et al. (2010) documented spatial and temporal patterns in the distribution of terrestrial Crocodyliformes throughout the Cretaceous, noting an expansion of medium- to large-bodied taxa during the Late Cretaceous. These taxa were often active terrestrial predators, and their distribution appears to have been significantly influenced by paleotemperature. Notably, large non-marine radiations of notosuchians and eusuchians are well documented during this interval (e.g., Carvalho et al., 2010; Bronzati et al., 2015). However, a decline in crocodyliforms biodiversity is observed from the Campanian to the Maastrichtian in both Europe and North America, which may reflect a long-term global cooling trend during the Late Cretaceous (Mannion et al., 2015). Nevertheless, de Celis et al. (2018) proposed that additional biotic and abiotic factors — beyond paleotemperature alone — may have significantly influenced crocodyliform macroevolution during the Mesozoic, suggesting a more complex evolutionary narrative than previously recognized.

For comprehensive descriptions, morphometric data, taxonomic revisions, and supplementary visual material, refer to Supplementary materials, Section D.

## Eggshells

A limited number of eggshell fragments exhibiting comparable morphological characteristics were recovered from the LV1 and LV2 levels (specimens NHMS 57456–57458). The external surface of these fragments is sculptured, displaying moderately spaced tubercles with irregular — occasionally subcircular — outlines (Figure 15A), imparting a nodular texture to the shell surface. Most tubercles exhibit a relatively smooth surface; however, some display minute pitting, and a subset — typically the larger tubercles — are perforated by funnel-shaped channels (Figure 15B–E). The diameter of these perforations ranges from 2.2 to 4.1 µm. The thickness of the eggshells, measured in the intertubercular regions, ranges from 173 to 247 µm. A distinctive feature observable in radial sections of all three specimens is the presence of tabular structures oriented parallel to the eggshell surface (Figure 15F). The functional or structural significance of these features remains uncertain at this stage (Figure 15F). Notably, no vertical zoning, layering, or columnar structures are evident within the examined samples.

**Remarks.** Eggshells exhibiting similar morphological characteristics have previously been reported as “geckonoid eggshell fragment” or “geckoid eggshell fragments” from the Maastrichtian deposits of the Hațeg and Rusca Montană basins (Vasile and Csiki, 2011; Csiki-Sava et al., 2016). Other thin-shelled eggs from the Hațeg Basin, sometimes referred to as the “thin egg type” (Codrea et al., 2002), have also been interpreted as having gekkotan affinities and were assigned to the geckoid morphotype sensu Garcia (2000), based on the morphological classification proposed therein. Additionally, Maastrichtian eggshells from the Transylvanian Basin (Oarda de Jos locality) were tentatively identified as ?*Pseudogeckoolithus* (Codrea et al., 2010a). However, due to the lack of detailed descriptions and illustrative documentation, it remains uncertain whether these latter two reports pertain to the same morphotype.

Recent investigations by Choi et al. (2020) on similar eggshells from Upper Cretaceous deposits of Europe have revealed distinct crystallographic features, particularly in the orientation of calcite grain axes. These microstructural criteria have proven to be useful in differentiating fossil and extant eggshells that share a superficially similar outer nodular ornamentation. Based on these crystallographic analyses, Choi et al. (2020) concluded that the so-called “geckoid” eggshells from the European Upper Cretaceous are more accurately attributed to maniraptoran theropods, and are assignable to the oogenus *Pseudogeckoolithus*. At present, two, and possibly three, oospecies within this genus are recognized from the Upper Cretaceous deposits of Romania (Choi et al., 2020). Given that crystallographic analysis was not conducted in the present study, and considering the limited number of specimens and insufficient data to assess variability in surface ornamentation, we tentatively assign our eggshell material to *Pseudogeckoolithus* sp.

For a concise summary of the taxonomic composition and stratigraphic distribution of fossils across the five levels of the Petrești section refer to Table 1.

## PALEOENVIRONMENTAL PERSPECTIVES

Based on the fossil assemblages recovered from this transitional sequence, three distinct latest Cretaceous paleoenvironments can be inferred, each reconstructed to varying degrees of detail: marine, brackish-estuarine, and continental. A gradual increase in continental influence is evident from the lowermost level (LV5) to the uppermost level (LV1) (see Figure 3).

Two of these paleoenvironments — the marine and brackish-estuarine settings — are illustrated in Figure 16A–B.

The marine paleoenvironment (Figure 16A) is interpreted as a shallow coastal setting characterized by a mixed assemblage of marine taxa, indicative of relatively stable salinity conditions. The presence of stenohaline organisms such as ammonites (e.g., *Pachydiscus*), echinoids, and asteroids supports this interpretation. However, the accompanying ichthyofauna — including *Paratrygonornina, Paralbula,* and *Echodus* — suggests fluvial influence, consistent with a nearshore environment subject to terrestrial input. The presence of plant debris and amber further corroborates this interpretation. This marine assemblage is best represented at stratigraphic level LV5. The subsequent level, LV4, likely marks the onset of environmental transition.

Sedimentation rates at LV5 appear to have been relatively high. Evidence supporting this interpretation includes the occurrence and preservation of the solitary coral *Cunnolites*, a cosmopolitan genus typically associated with tropical to warm-temperate environments. *Cunnolites* is commonly found in non-reefal settings, favoring sandy to sandy-silty substrates — conditions inferred for the Petreşti section. Notably, the absence of basal pedestals, macroboring traces, and overgrowth features on our *Cunnolites* specimens implies rapid sedimentation, as such features typically form under conditions of slower deposition that permit vertical coral growth and substrate colonization (Sanders and Baron-Szabo, 2005, 2008). In addition, the relatively small size of our specimens (maximum diameter of 55 mm) compared to the known maximum size for the taxon (~400 mm) suggests abbreviated lifespans, likely attributable to the stress of high-sedimentation rates (Sanders and Baron-Szabo, 2005).

The progressive reduction in bivalve diversity observed upward through the Petreşti section is interpreted as a response to increasingly marginal marine conditions. Fully marine assemblages appear to be restricted to the lowermost beds, particularly those exposed at level LV5. In contrast, levels LV4, LV3, and LV1 yield assemblages dominated by more tolerant taxa, such as corbulid bivalves. The presence of corbulids in these strata may indicate low sedimentation rates and episodic influence from low-salinity waters, as members of this group are known to tolerate brackish conditions better than most other marine bivalves (Lewy and Samtleben, 1979). The bivalve assemblage is notably depauperate in epifaunal taxa, with the absence of typically common forms such as arcoids, pectinids, and mytilids. Additionally, several infaunal groups frequently encountered in coeval marine deposits — such as crassatellids and veneroids — are also absent or rare. The recorded diversity among infaunal bivalves may reflect a combination of low sedimentation rates and suboptimal conditions within the substrate, possibly including fluctuating salinity, low oxygen levels, or unstable sedimentary regimes.

The occurrence of *Sauvagesia* sp. within this assemblage is considered allochthonous. The valves are broken, compressed, and show signs of erosion, suggesting post-mortem transport from a different depositional setting. It is likely that these specimens were introduced into the Petreşti environment by wave or current action (L. Săsăran, pers. comm., 06 December 2024).

The occurrence of corbulid bivalves in LV4 at Petrești may indicate periodic influence from low-salinity waters — conditions that corbulids are known to tolerate more effectively than most other marine bivalves (Lewy and Samtleben, 1979). The recorded low diversity among infaunal bivalves may also reflect reduced sedimentation rates and potentially unfavorable substrate conditions.

The brackish, estuarine paleoenvironment reconstructed for portions of the Petrești section

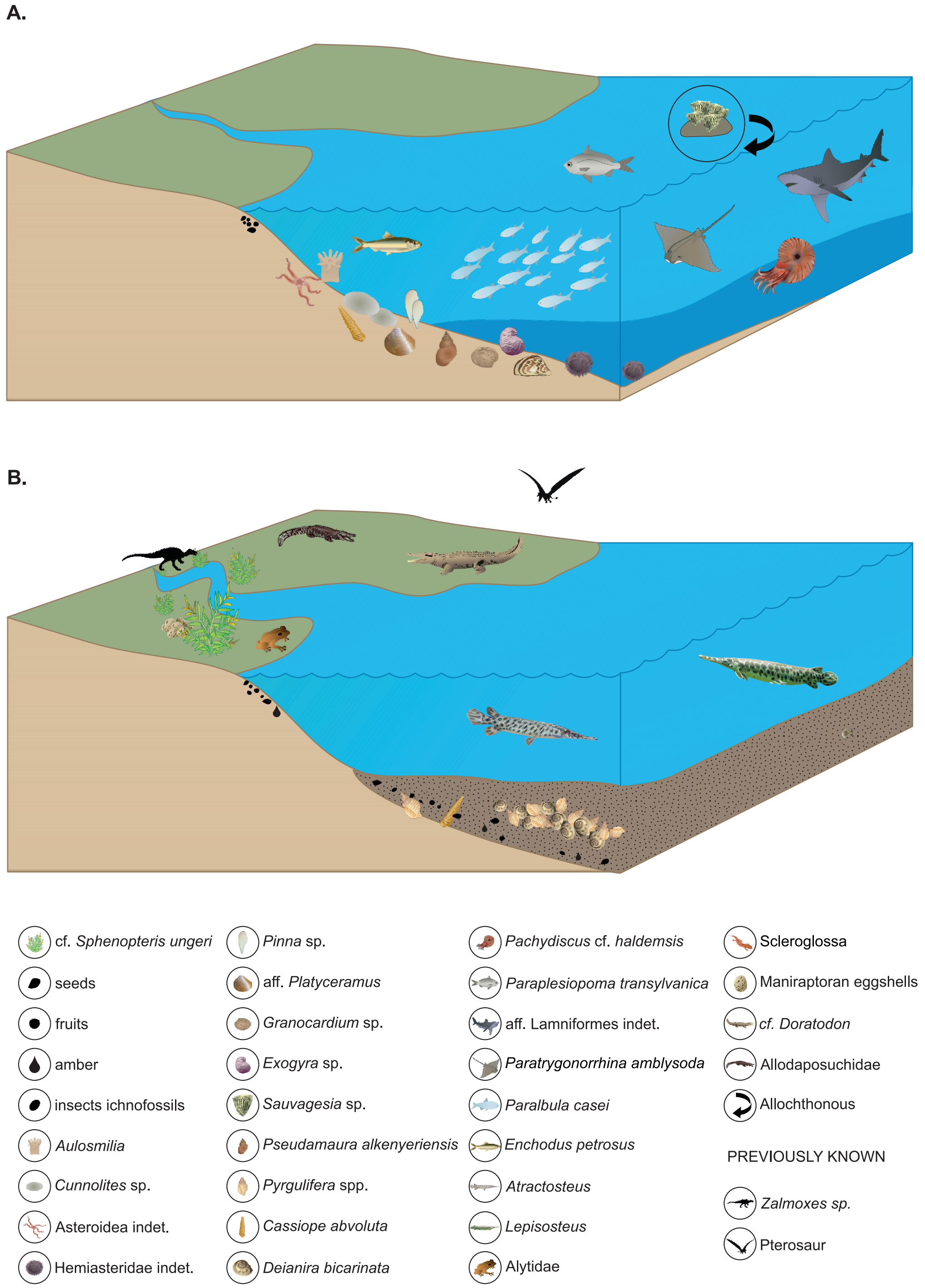

**FIGURE 16.** Reconstructions of the paleoenvironmental settings represented in the studied Petrești section, based on the fossil assemblages identified. **A,** marine (corresponding to LV5 and LV4) *(Aulosmilia, Cunnolites,* Asteroidea, Hemiasteridae, *Pinna*, ?*Platyceramus*, *Granocardium,* ?*Exogyra, Pachydiscus,* aff. Lamniformes, *Paratrygonornina, Paralbula, Echodus,* and *Paraplesiopoma*), with reduced continental influence *(Pyrgulifera, Cassiope,* amber, seeds, and fruits). **B,** estuarine with increased continental influence (corresponding to LV3, LV2, and LV1) *(Sphenopteris, Atractosteus, Lepisosteus,* Scleroglossa, ?Alytidae, cf. *Doratodon*, Allodaposuchidae, maniraptoran theropods, *Zalmoxes*, Pterosauria, seeds, fruits, amber, and insects). Part of the symbols used was provided by the Media Library of the Integration and Application Network, University of Maryland Center for Environmental Science (CC BY-SA 4.0). *Sauvagesia* is represented in the medallion, as it is most probably allochthonous and originating from a different environment.

(Figure 16A) is characterized by the complete absence of ammonites and corals, indicating a departure from fully marine conditions. The gastropod assemblage exhibits a marked shift in taxonomic composition, with *Pyrgulifera* and *Campylostylus* often forming dense accumulations of shells. The bivalve component is notably absent in these facies. The localized concentration of mollusk remains suggests episodic high-energy depositional event, likely associated with increased freshwater influx and river discharge, which may have transported and concentrated shells during periods of enhanced hydrodynamic activity.

An increasing terrestrial influence up the section is also reflected in the ichthyofaunal assemblage. In the upper stratigraphic levels (LV3–LV1, Lepisosteiformes — particularly *Atractosteus* and *Lepisosteus* — replace the fish taxa that dominate the lower, marine levels (e.g., *Echodus, Paralbula,* and the chondrichthyan taxa). This faunal turnover coincides with a marked increase in the abundance of plant debris and amber, particularly in levels LV3 through LV1, supporting the interpretation of a brackish to estuarine depositional environment for these strata.

The nature of the continental paleoenvironment at Petreşti remains relatively poorly constrained, as it is currently inferred from sparse and predominantly allochthonous remains. The occurrence of the fern *Sphenopteris ungeri* suggests the presence of riparian vegetation, a hypothesis further supported by the associated reptilian assemblage, which includes crocodyliforms. Additional evidence of terrestrial conditions is provided by fragmentary remains of frogs and lizards, although the finds are limited and do not yet allow for a detailed ecological reconstruction. The floral assemblage, primarily composed of seeds and fruits, is characterized by relatively low taxonomic diversity when compared to other Cretaceous floras (e.g., Knobloch and Mai, 1986). However, it is broadly comparable in richness to the Maastrichtian mesoflora of the Haţeg Basin (Lindfors et al., 2010). Expanded sampling and systematic analysis of plant material would be necessary to obtain a more comprehensive picture of mesofloral diversity and composition. Previous discoveries from the region (e.g., Vremir 2010; Vremir et al., 2015) provide additional support for the presence of a diverse terrestrial ecosystem during the latest Cretaceous, despite the taphonomic and sampling limitations currently affecting the Petreşti record.

To support the interpretative framework for the ecological transition from marine to brackish environments, a basic statistical analysis was conducted, incorporating cluster analysis and the construction of a species distribution chart (for the data used refer to Supplementary materials, Section E and F).

Cluster analysis based on Jaccard similarity index and employing the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) was performed to assess the relationships among stratigraphic sampling levels, using presence/absence data of recorded taxa. Given the potential of calcareous nannoplankton to obscure genuine taxonomic and ecological patterns — particularly within dynamic marine–estuarine transitional zones — analyses were carried out on two separate datasets to distinguish their potential influence.

The initial analysis, encompassing the complete assemblage of taxa identified at the Petrești site, yielded a main cluster with a basal similarity of 0.21. Within this cluster, a distinct subcluster was formed by level LV4 (similarity: 0.26), while a second subcluster included levels LV1, LV2, and LV3, which exhibited pairwise similarities ranging from 0.36 to 0.39 (Figure 17A).

Although a superficial interpretation of these clustering results might suggest a relatively high degree of faunal similarity — and, by implication, a homogeneous ecological composition across the sampled levels — this interpretation is likely misleading. The apparent homogeneity is primarily attributed to the inclusion of calcareous nannoplankton in the dataset. In marine–estuarine transitional environments, the distribution pattern of nannoplankton may not accurately reflect local ecological gradients. These organisms, being susceptible to advective transport due to water mass mixing, can be episodically introduced into brackish or even freshwater-influenced settings. As a result, their presence may mask ecologically meaningful signals associated with more environmentally sensitive taxa.

The second dataset, which excludes calcareous nannoplankton taxa, produced a clustering pattern that diverges significantly from that obtained in the initial analysis. Although the overall topology of the resulting dendrogram may appear similar to that of the complete dataset, the distinctions revealed are considered to offer deeper insights into the underlying ecological and biological dynamics.

In this refined analysis, levels LV1, LV2, and LV3 form a coherent cluster, characterized by relatively high Jaccard similarity indices, ranging from 0.33 to 0.40 (Figure 17B). This pattern indicates

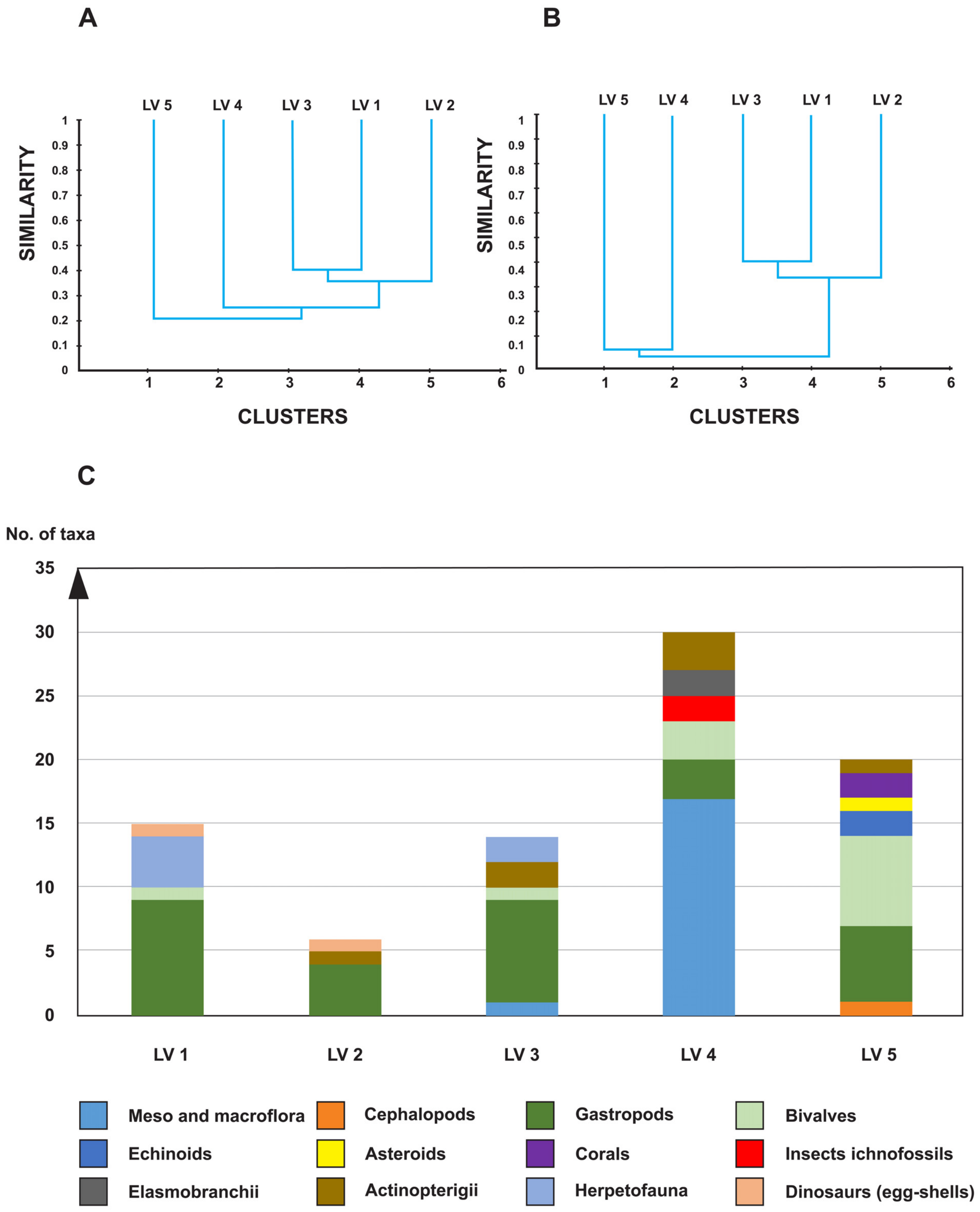

**FIGURE 17.** Statistical analyses. **A,** cluster analysis based on the complete taxonomic dataset from Petrești. **B,** cluster analysis based on the dataset excluding calcareous nannoplankton taxa. **C,** distribution chart depicting the stratigraphic occurrence and abundance of the identified taxa.

considerable taxonomic overlap and implies relatively stable environmental conditions across these stratigraphic intervals. By contrast, levels LV4 and LV5 diverge much earlier in the dendrogram, at substantially lower similarity values (Jaccard index >0.1), reflecting a faunal composition markedly different from that of the LV1–LV3 cluster. Although LV4 and LV5 form a weakly defined subgroup, the low degree of similarity suggests limited taxonomic overlap, with their apparent association largely driven by the shared presence of a single species.

The hierarchical structure of the dendrogram suggests a two-step faunal turnover: first, a compositional shift between LV5 to LV4, followed by a more pronounced transition between LV4 and the LV1–LV3 cluster. The tight clustering of levels LV1–LV3 is interpreted as indicative of a phase of relative palaeoecological stability, in the uppermost part of the Bozeș Formation.

Integration of the cluster analysis results with the taxonomic distribution patterns, as depicted in the species distribution chart (Figure 17C), supports the interpretation that the grouping of levels LV1–LV3 is primarily driven by the consistent occurrence of gastropod and bivalve taxa. In contrast, the assemblages of LV4 and LV5 exhibit greater taxonomic heterogeneity, incorporating mesofloral remains, cephalopods, asteroids, corals, echinoids, and fish. This broader faunal diversity likely accounts for the distinct separation of LV4 and LV5 in the cluster analysis, and is interpreted as reflective of more variable and potentially transitional environmental conditions at these stratigraphic levels.

## CONCLUSIONS

This study provides critical insights into the paleoenvironmental and paleobiological evolution of the upper Campanian Bozeş Formation at Petreşti, within the southern Transylvanian Basin. The main conclusions are as follows:

1. A major paleoenvironmental shift from marine to brackish conditions has been precisely documented and correlated with the stratigraphic horizon LV4. While the transition had been recognized in prior research, our study provides a more detailed documentation and confirms its stratigraphic position through a well-characterized fossil assemblage.
2. The study presents important new paleontological data that refine and expand the known faunal and floral composition of the upper estuarine deposits of the Campanian Bozeș Formation at Petrești, located in the southern Transylvanian Basin.
3. The environmental transition is interpreted as gradual, progressing from a marine to an estuarine setting with increasing continental influence. There is no evidence supporting an abrupt or catastrophic shift.
4. A revised taxonomic reassessment of the ammonite assemblage has led to the reclassification of specimens previously assigned to *Pachydiscus neubergicus* and *P. colligatus* which are now referred to as *Pachydiscus* cf. *haldemsis*, based on newly collected and better-preserved material.
5. The diversity of gastropods and bivalves, formerly limited to a few genera such as *Cerithium, Pyrgulifera,* and *Barbotella*, has been substantially revised, with at least 30 taxa now recognized. This expanded diversity underscores the need for continued systematic investigation in the region.
6. This study documents, for the first time within the Bozeş Formation, the occurrence of echinoids, asteroids, plant seeds, fruits, amber, and the first recorded impressions of plants associated with the brackish transition. Additional significant discoveries include insect eggs and coprolites preserved alongside amber.
7. The identification of vertebrate remains — including fishes, anurans, scleroglossan lizards, crocodyliforms, and maniraptoran theropods — further augments the vertebrate diversity previously known from the formation. Notably, the Anura and Scleroglossa specimens represent the oldest known Cretaceous occurrences of these clades in Romania.
8. A new percomorph bony fish taxon, *Paraplesiopoma transylvanica* n. gen. n. sp., is described herein.
9. From a paleoenvironmental standpoint, a marked compositional shift is evident between LVs 4–5 and LVs 1–3. The fossil assemblage in LV4 and LV5, dominated by marine invertebrates and vertebrates (including ammonites, gastropods, bivalves, starfish, echinoids, and fish), is indicative of normal salinity conditions, whereas the assemblage in LVs 1-3 reflects a transition toward brackish and continental influence. This is evidenced by

a reduction in bivalve diversity (from over seven to three species) and the appearance of terrestrial indicators such as seeds, fruits, amber, and fragments of carbonized wood, although these occur in relatively low abundance.

10. Several avenues for future research are proposed, including more detailed investigations of meso- and macrofloral assemblages, comprehensive analyses of amber, and refined taxonomic work on gastropod and bivalve assemblages.
11. Collectively, this study significantly advances our understanding of the late Campanian biodiversity in marginal marine environments, highlighting the ecological dynamics at the marine–terrestrial interface during the Late Cretaceous in the Transylvanian Basin.

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## SUPPLEMENTARY MATERIALS

# A diverse Campanian biota from the Bozeș Formation (Petrești, Romania): Insights into the paleontology and paleoecology of a transitional sequence

**Nicolae Trif, Roxana Pirnea, Andrej Čerňanský, Werner Schwarzhans, Ramona Bălc, Sreepat Jain, Andrzej Kaim, Sofia Bakayeva, Krzysztof Hryniewicz**

The Supplementary materials contain additional information that due to its excessive length and details is not included in the main text for reasons of clarity and brevity. This information primarily encompasses taxonomic discussions and detailed descriptions of the significant occurrences. References to the Supplementary materials from the main text follow the format "refer to Supplementary materials, Section XX". Conversely, references to figures in the main text, when cited within the Supplementary materials, are worded as "Figure XX (in the main text)".

## A. Calcareous nannoplankton

The illustrated calcareous nannoplankton assemblage includes several biostratigraphically diagnostic species indicative of a Campanian age for the studied section. The presence of these taxa provides a robust basis for stratigraphic correlation and supports the chronostratigraphic framework applied to this interval (see Figure S1).

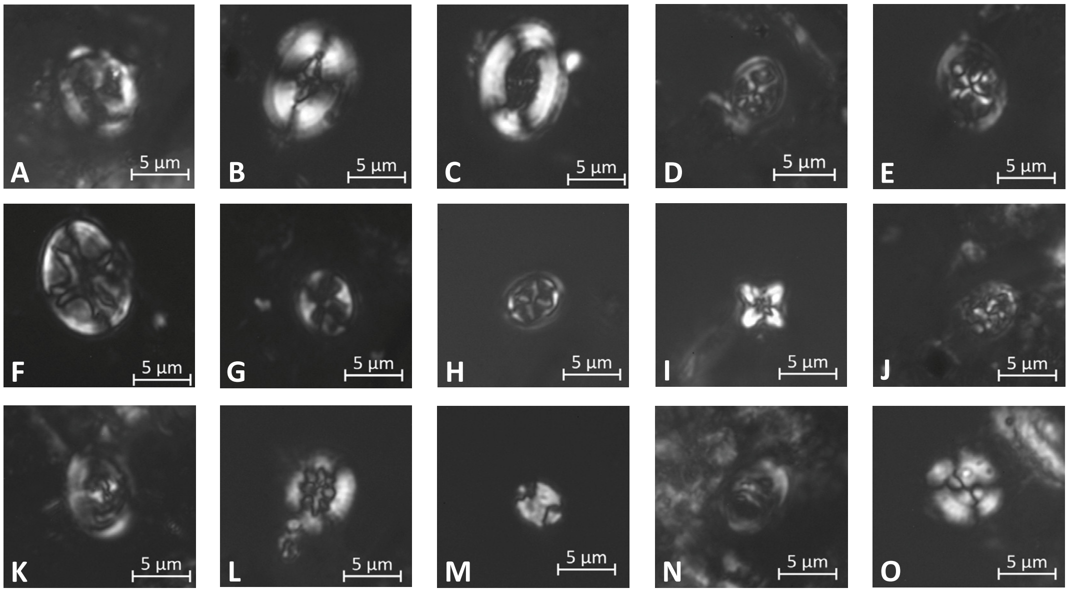


**FIGURE S1.** Selected calcareous nannoplankton fossils identified in the uppermost part of the Bozeș Formation at Petrești. **A,** *Arkhangelskiella cymbiformis* (Vekshina, 1959) (LV5). **B,** *Broinsonia parca constricta* (Hattner et al., 1980) (LV5). **C,** *Broinsonia parca parca* ((Stradner, 1963) Bukry, 1969) (LV5). **D,** *Chiastozygus amphipons* ((Bramlette and Martini, 1964) Gartner, 1968) (LV1). **E,** *Chiastozygus bifarius* (Bukry, 1969) (LV5). **F,** *Eiffellithus eximius* ((Stover, 1966) Perch-Nielsen, 1968) (LV2). **G,** *Eiffellithus gorkae* (Reinhardt, 1965) (LV5). **H,** *Helicolithus trabeculatus* ((Górka, 1957) Verbeek, 1977) (LV4). **I,** *Micula staurophora* ((Gardet, 1955) Stradner, 1963) (LV1). **J,** *Prediscosphaera cretacea* (Arkhangelsky, 1912) Gartner, 1968 (LV1). **K,** *Reinhardtites anthophorus* (Deflandre, 1959) Perch-Nielsen, 1968 (LV2). **L,** *Retecapsa crenulata* (Bramlette & Martini, 1964) Grün in Grün and Allemann, 1975 (LV1). **M,** *Russellia laswellii* (Risatti, 1973) (LV5). **N,** *Tranolithus orionatus* ((Reinhardt, 1966a) Reinhardt, 1966b) (LV1). **O,** *Watznaueria barnesiae* (Black in Black and Barnes, 1959) Perch-Nielsen, 1968 (LV1).

**TABLE S1.** Calcareous nannofossils raw data (number of specimens in ~700 fields of view).

| Species | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|
| *Amphizygus brooksii* | 0 | 2 | 1 | 1 | 0 |
| *Amphizygus minimus* | 0 | 1 | 0 | 1 | 0 |
| *Arkhangelskiella cymbiformis* | 1 | 0 | 1 | 0 | 2 |
| *Biscutum constans* | 1 | 0 | 0 | 0 | 0 |
| *Broinsonia parca constricta* | 0 | 0 | 0 | 1 | 2 |
| *Broinsonia parca parca* | 0 | 0 | 0 | 0 | 1 |
| *Calculites ovalis* | 0 | 1 | 0 | 0 | 0 |
| *Chiastozygus amphipons* | 0 | 1 | 2 | 1 | 3 |
| *Chiastozygus bifarius* | 0 | 0 | 0 | 2 | 1 |
| *Chiastozygus litterarius* | 0 | 1 | 0 | 0 | 0 |
| *Cretarhabdus striatus* | 0 | 0 | 0 | 0 | 1 |
| *Cribrosphaerella ehrenbergii* | 0 | 6 | 1 | 6 | 7 |
| *Cylindralithus coronatus* | 0 | 0 | 0 | 0 | 2 |
| *Eiffellithus eximius* | 3 | 7 | 5 | 9 | 11 |
| *Eiffellithus gorkae* | 0 | 0 | 0 | 0 | 1 |
| *Eiffellithus turriseiffelii* | 0 | 1 | 0 | 1 | 0 |
| *Eprolithus floralis* | 0 | 0 | 0 | 0 | 1 |
| *Gartnerago segmentatum* | 0 | 0 | 0 | 1 | 0 |
| *Helicolithus trabeculatus* | 0 | 1 | 0 | 1 | 1 |
| *Lithastrinus grillii* | 0 | 0 | 0 | 0 | 0 |
| *Loxolithus armilla* | 0 | 0 | 1 | 3 | 0 |
| *Lucianorhabdus maleformis* | 0 | 1 | 0 | 2 | 2 |
| *Manivitella pemmatoidea* | 0 | 0 | 0 | 1 | 1 |
| *Micula staurophora* | 1 | 3 | 2 | 3 | 3 |
| *Placozygus fibuliformis* | 0 | 0 | 0 | 1 | 0 |
| *Prediscosphaera cretacea* | 1 | 4 | 4 | 2 | 11 |
| *Reinhardtites anthophorus* | 1 | 5 | 0 | 0 | 1 |
| *Retecapsa crenulata* | 1 | 6 | 5 | 7 | 14 |
| *Rhagodiscus achlyostaurion* | 0 | 2 | 0 | 0 | 0 |
| *Russellia laswellii* | 0 | 0 | 0 | 0 | 1 |
| *Staurolithites sp.* | 0 | 1 | 0 | 0 | 0 |
| *Tranolithus orionatus* | 1 | 6 | 2 | 2 | 3 |
| *Watznaueria barnesiae* | 10 | 39 | 33 | 19 | 73 |
| *Watznaueria quadriradiata* | 0 | 0 | 1 | 0 | 0 |
| *Zeugrhabdostus bicrescenticus* | 0 | 0 | 1 | 0 | 1 |
| *Zeugrhabdotus diplogrammus* | 0 | 1 | 2 | 0 | 0 |
| **Total** | **20** | **89** | **62** | **64** | **143** |
| **Relative abundance** | **0.02** | **0.13** | **0.09** | **0.09** | **0.21** |

## B. Ammonites

Order AMMONOIDEA von Zittel, 1884
Suborder AMMONITINA Hyatt, 1889
Superfamily DESMOCERATOIDEA von Zittel, 1895

### Family PACHYDISCIDAE Spath, 1922
### Genus *PACHYDISCUS* von Zittel, 1884
### Subgenus *PACHYDISCUS (PACHYDISCUS)* Zittel, 1884

1884 *Pachydiscus*, Zittel, p. 466

1900 *Parapachydiscus*, Hyatt, p. 570

1955 *Pseudomenuites*, Matsumoto, p. 169

1958 *Joaquinites*, Anderson, p. 218

**Type species.** The lectotype of *Ammonites haldemsis* (Schlüter, 1867, p. 19), by subsequent designation of Kennedy and Summesberger (1984, p. 158).

### *Pachydiscus (Pachydiscus)* cf. *haldemsis*
### (Schlüter 1867) (M)
Figure 7A–L (in the main text)

**Dimensions.** See Table S2.

**Description.** In the present study, 2 specimens (Figure 7A–D and Figure 7E–H in the main text) are considered macroconchs, whereas the third (smaller) fragmentary specimen (Figure 7J–L in the main text) is considered as juvenile.

**Specimen no. NHMS 57406/LV5 (Figure 7A–D in the main text).** Shell large ($D_{max}$ = 237 mm), compressed (T/H = 0.51), evolute (U/D = 0.25), and with a shallow umbilicus. The maximum estimated shell diameter is 375 mm, assuming a body chamber of 3/4 of a whorl. Primary ribs are not visible due to the worn nature of the specimen. However, at the end of the middle whorl (at the exposed fragment at around 200 mm shell diameter), few, distant and moderately strong, feebly concave primary ribs with thin intercalatories are noted. The umbilical wall is feebly convex, the umbilical shoulder is broadly rounded, and the whorl section is compressed and oval. The whorl section is somewhat squarish in the inner whorl. The flanks are flattened and very feebly convergent, the ventrolateral shoulders broadly rounded, and the venter is very feebly convex. The flanks are corroded, and no ornament is noted on the outer whorl.

Specimen no. NHMS 56581/LV5 is a juvenile (Figure 7J–L in the main text). The other two septate specimens (Figure 7A–E and Figure 7F–H in the main text) are incomplete, fragmentary, and somewhat crushed. The larger one is 164 mm (Figure 7A–D in the main text) and the smaller one is 101 mm in shell diameter (Figure 7E–F in the main text). Coiling is moderately involute (U/D = 0.19–0.20). The umbilicus is moderately deep with subvertical walls, undercut, and with no umbilical shoulder distinguishable from the flanks. The outer flank is slightly convex, converging to narrow rounded ventrolateral shoulders and venter. However, due to compression, the venter is slightly deformed (Figure7B, D in the main text). The smaller specimen shows (Figure 7E–F in the main text) broad, prorsiradiate ribs, concave on the outer flank with the gradual weakening of the ornamentation. The primaries divide into two prorsiradiate secondaries with an intervening single intercalatory (Figure 7E–F in the main text). The sutures are typical for the genus — deeply and intricately incised (see Figure 7E in the main text).

**Geographic distribution.** Germany, Austria, Poland, Sweden, Ukraine and Iran; Turkey.

**TABLE S2.** Dimensions of the measured ammonites.

| Specimen inventory number | Dimensions | D | H | T | U | T/H | U/D | Figure 7 (in the main text) |
|---|---|---|---|---|---|---|---|---|

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| NHMS 57406/LV5 | $D_{max}$ | 237 | 97 | 49 | 59 | 0.51 | 0.25 | Figure 7A–D |
| | $D_{Phragmocone}$ | 214 | 106 | 44 | 34 | 0.42 | 0.16 | |
| NHMS 56556/LV5 | $D_{Phragmocone}$ | 164.3 | 79 | ~46.2 | 29.8 | 0.58 | 0.18 | Figure 7E–H |
| | $D_{Phragmocone}$ | 101 | 86.9 | — | 16.7 | — | 0.17 | |

**Notes:** $D_{max}$ = shell measured at maximum diameter; $D_{Phragmocone}$ = shell measured at phragmocone; H = height of whorl; T = thickness of whorl; U = umbilicus; T/H = ratio of whorl thickness and whorl height; U/D = ratio of umbilicus and shell diameter.

## C. Fish

Class CHONDRICHTHYES Huxley, 1880
Subclass EUSELACHII Hay, 1902
Infraclass ELASMOBRANCHII Bonaparte, 1838
Division SELACHII Cope, 1871
Superorder GALEOMORPHII Compagno, 1973
Order LAMNIFORMES Berg, 1958
Lamniformes indet.
Figure 12A–C (in the main text)

**Material.** One tooth (NHMS 57427/LV5).

**Description.** The tooth is very small, measuring 3.3 mm in height. Only the main cusp is preserved with no lateral cusplets and only a very small part of the root. The lingual side of the cusp is very slightly convex and it has weak, irregular striations on its lower half. The labial side is flat and smooth. The contact with the root is almost straight labially, with a small chevron bump on the lingual side. A sharp cutting edge is preserved but it is chipped.

**Remarks.** The fragmentary stage and the relatively common shape of the crown make us cautious in allocating the tooth even at the order level. The few observable characters could broadly indicate the order Lamniformes. Several genera have this type of symmetrical crown for teeth in central positions, as well as striations on the lingual face.

Division BATOMORPHII Cappetta, 1980
Order RAJIFORMES Berg, 1940
Suborder RHINOBATOIDEI Fowler, 1941
Family RHINOBATIDAE Müller and Henle, 1838
Genus *PARATRYGONORRHINA*
Kriwet, Soler-Gijón, López-Martínez, 2007
*Paratrygonorrhina amblysoda*
Kriwet, Soler-Gijón, López-Martínez, 2007
Figure 12D–H (in the main text)

**Material.** One tooth (NHMS 57422/LV4).

**Description.** The crown of the tooth is slightly broader than long and it is almost rhombic in occlusal view. The occlusal surface is almost flat and smooth but a small transversal crest is visible. In apical view the labial margin is rounded and convex while the lingual margin is more angular, almost forming a triangle. In profile view the lingual side is very abrupt but not quite vertical with a central uvula and two lateral ones. The central uvula is quite short, barely descending below the level of the crown in lateral view. This central uvula is covered by longitudinal irregular striations. The lateral uvulae are very short and very little visible. Some very short striations are visible on the distal and mesial ends. Also, the labial part of the crown strongly overhangs the root in profile view. The root, although not completely preserved, has two lobes. Its height seems to be equal to the height of the crown. The root is displaced lingually. Unfortunately, the presence some adhering sediment particles does not allow observing the central part of the root, to see if it hides one or more central foramina.

**Remarks.** Although the analyzed tooth is not in the best state of preservation, it corresponds quite well to the diagnosis of the type specimens of *P. amblysoda*. Therefore, we confidently assign this tooth to that species.

The genus *Paratrygonorrhina* and its only known species, *P. amblysoda*, were described for the first time from the upper Campanian of the Orcau 2 locality, in the Tremp-Gaus Basin (lower part of the Tremp Formation), Northern Spain (Kriwet et al., 2007). Besides its locality of origin, the authors consider that several specimens previously described under the name of *Rhinobatos* sp. can actually be assigned to this species. Some of these specimens come from the same formation (Soler-Gijón and López-Martínez, 1995, 1998) but others come from the uppermost Cretaceous of Petites Pyrenees (Haute-Garonne and Ariege, France) and the Maastrictian "Marnes d'Auzas" Formation (from the same region) (Gheerbrant et al., 1997, Pl. 1, figure 3a–c). We are therefore dealing with a very rare species, which originates from formations which, as in our case, were formed on the edges of continental areas during the late Campanian–Maastrichtian time period.

Class ACTINOPTERYGII Klein, 1885
Order LEPISOSTEIFORMES Hay, 1929
Family LEPISOSTEIDAE Cuvier, 1825

Leaving little doubts regarding their allocation at the family level, Lepisosteidae teeth are rather easily recognizable by their sharp, conical shape and the presence of strong folds at their base. However, their more precise allocation to one of the two Upper Cretaceous genera is much more difficult. Indeed, for a while the difference between *Lepisosteus* and *Atractosteus* were not even recognized by Grande (1980) although later, in his monumental work on Lepisosteidae, he changed his previous opinion and recognized the genera *Atractosteus* and *Lepisosteus* as valid (Grande, 2010). However, this recognition had no direct impact on the methods of identifying isolated elements such as teeth or scales. In fact, Grande did not differentiate the two genera based on the morphology of their teeth, such a difference being noticed later by paleontologists trying to identify potential distinctive characters based on his very detailed descriptions and illustrations. One of the observed differentiating characters was the spear-like shape of the tip of the fangs of *Atractosteus*, a shape that is not found in any species of *Lepisosteus*. However, a closer look shows that although the difference mentioned above is perfectly valid, *Atractosteus* also has a series of secondary teeth where this character is not present. To solve this problem, an analysis — using images obtained with the electron microscope — of the ganoine ornamentation present on lepisosteid scales or hemitrichs recovered from the same sediment as the teeth was proposed as being useful. Since both teeth morphologies are present in the studied outcrop, we performed such an investigation, following a significant number of other authors who used the same method in order to differentiate between the two genera (see Gayet and Meunier, 2001; Gayet et al., 2002; Blanco et al., 2017; Szabó and Ősi, 2017; Ősi et al., 2021).

Genus *ATRACTOSTEUS* Rafinesque, 1820
*Atractosteus* sp.
Figure 12I–N (in the main text)

**Material.** Two teeth (NHMS 57439/LV3, NHMS 57442/LV3).

**Description.** Conical, pointed teeth, circular or slightly elliptical in cross-section. The acrodine cap has a spear-like shape. The base of the tooth is covered by strong and deep folds.

Genus *Lepisosteus* Lacepède 1803
*Lepisosteus* sp.
Figure S2A–F (in the Supplementary materials)

**Material.** Two hemitrichs (NHMS 57484/LV2, 57485/LV2) and one scale (NHMS 57486/LV3).

**Description.** The hemintrichs are very small elements of the fin ray skeleton of the fish. These elements exhibit an elongated morphology with a slightly arched transverse section. Their surface is covered by several elongated, ovoid regions of ganoin, arranged parallel to the longitudinal axis. The scale is about 4 mm long, tear shaped, and has a black and shiny surface.

**Remarks.** The presence of both Lepisosteidae genera in the same deposits is not uncommon. The same situation was found for example in Upper Cretaceous deposits of Spain (Blanco et al., 2017) or Alabama (USA) (Ikejiri et al., 2013). Remains of Lepisosteidae are often found in the Upper Cretaceous (Maastrichtian) continental deposits of Romania. On several occasions, they were left identified only at the family level (Codrea et al., 2013; Solomon et al., 2022) although sometimes they were referred either to *Atractosteus* or to *Lepisosteus* (Csiki et al., 2008), with the sharp, pointed teeth assigned to the genus *Lepisosteus* and the lanceolate ones to the genus *Atractosteus*. To confirm the presence of the genus *Lepisosteus*, however, in our opinion tubercle density analysis should be performed on associated scales or other fish remains that preserve ganoin. This call is also valid for other locations around the world where one or the other of these genera have been reported.

Order AULOPIFORMES Rosen, 1973
Family ENCHODONTIDAE Woodward, 1901
Genus *ENCHODUS* Agassiz, 1835
*Enchodus petrosus* Cope, 1874
Figure 12O–Q (in the main text)

**Material.** Three teeth (NHMS 57425/LV4, NHMS 57426 /LV4, and NHMS 57428/LV4).

**Description.** Asymmetric teeth with a straight to slightly concave lingual face and a convex labial face. The anterior cutting edge it is positioned rather anteromedially and is sharp and straight. The posterior part of the tooth has posterolateral carinae with parallel cutting edges, forming an unmistakable asymmetric cross-section (see Figure 12 in the main text). Some striations can be observed at the base of one of the specimens, but for the other specimens is unclear whether such striations were never present or just the teeth are very eroded.

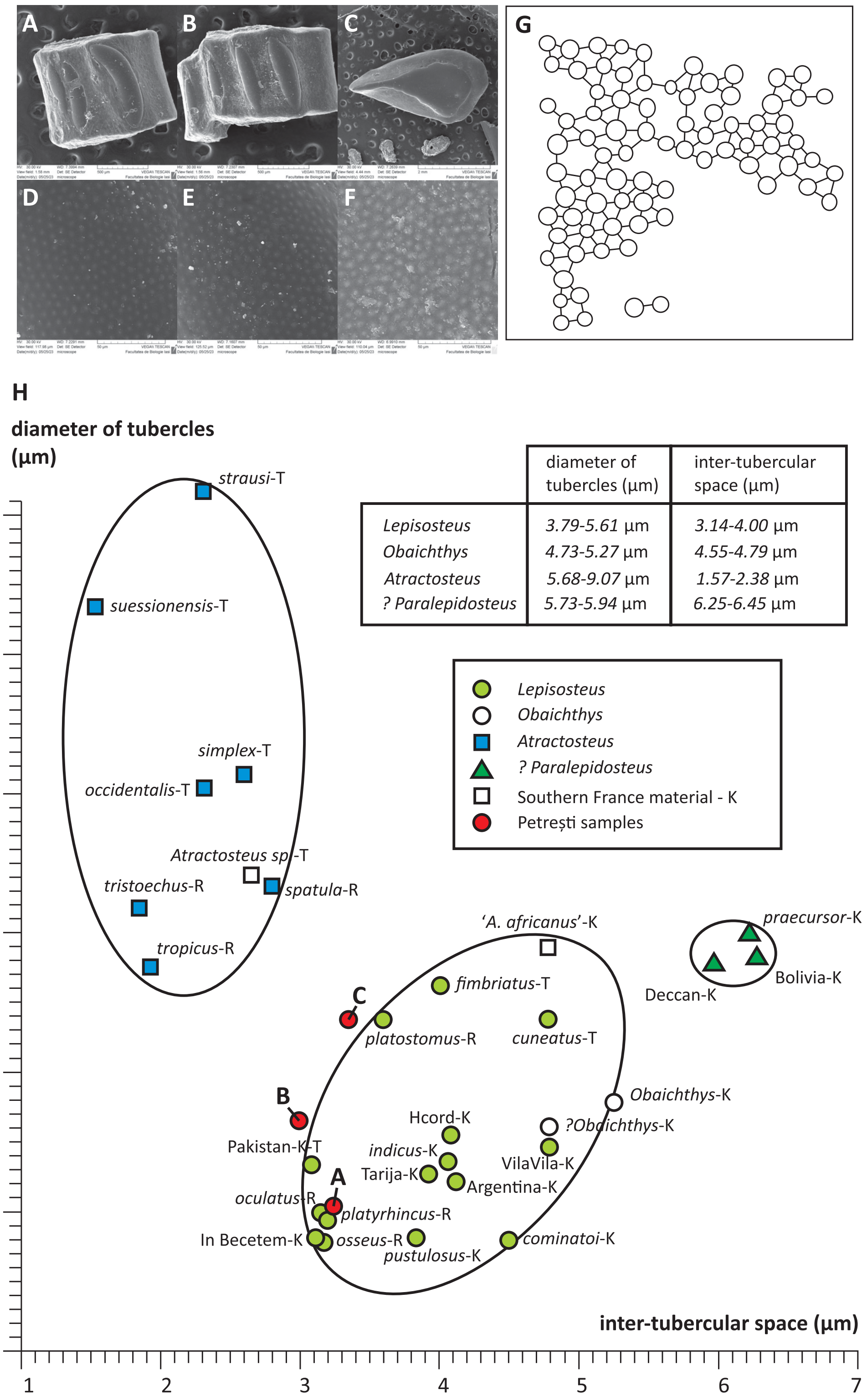
**Remarks.** The isolated teeth of the different *Enchodus* species can be distinguished based on their shape (straight or sinusoidal), the presence of one or several (up to three) posterior or rather posterolateral cutting edges, cross-section (symmetrical, asymmetrical, degree of roundness), and the presence or absence of a postapical barb. Since the teeth from our sample do not preserve the apex, only their general shape and cross-section, as well as the number of cutting edges will be considered.

A tooth with an asymmetric cross section, very similar to that of our Petrești teeth is illustrated by Becker et al. (2010, figure 6i) under the name *E. petrosus*. This cross section is very different from that seen in other *Enchodus* species. For example, both *E. ferox* Leidy, 1855 and *E. gladiolus* (Cope, 1872) have a tooth cross section with both labial and lingual faces strongly convex, and only one posterior cutting edge. The species *E. dirus* Leidy, 1857 also has symmetrical teeth in cross-section, with only a single anterior cutting edge (Goody, 1976, p. 105). Considering the similarities with *E. petrosus* and the differences from the other three species of *Enchodus*, we assign the teeth from Petresti to the species *E. petrosus.*

The species *E. petrosus* has been extensively documented from the Upper Cretaceous of North America, with a range from Coniacian to Maastrictian (Goody, 1976; Becker et al., 2010). Notably, its presence has also been reported in Europe, in the Campanian Rybushka Formation of Russia (Ebersole et al., 2022).

In Romania, the only previous mention of the Enchodontidae family comes from the Cenomanian of Dobrogea where it was reported as Enchodontidae indet. (Trif and Codrea, 2022b).

Order ELOPIFORMES Sauvage, 1875
Family PHYLLODONTIDAE Sauvage, 1875
Genus *PARALBULA* Blake, 1940
*Paralbula casei* Estes, 1969
Figure 12R–T (in the main text)



| | diameter of tubercles (µm) | inter-tubercular space (µm) |
|---|---|---|
| *Lepisosteus* | *3.79-5.61* µm | *3.14-4.00* µm |
| *Obaichthys* | *4.73-5.27* µm | *4.55-4.79* µm |
| *Atractosteus* | *5.68-9.07* µm | *1.57-2.38* µm |
| *? Paralepidosteus* | *5.73-5.94* µm | *6.25-6.45* µm |

**FIGURE S2.** Measurements of the ornamentation of fish hemintrichs and scales and assignment of the Petrești lepisosteid samples. **A–F,** close-ups of the ganoine surfaces of specimens NHMS 57484/LV2, 57485/LV2, and 57486/LV2. **G,** example of measurements of tubercle diameters and the inter-tubercular distances on ganoine on NHMS 57484. **H,** assignment of the Petrești samples to *Lepisosteus* cross-referenced with previous studies (Gayet and Meunier, 2001; Gayet et al., 2002; Blanco et al., 2017; Szabó and Ősi, 2017; Ősi et al., 2021).

**Material.** Five teeth (NHMS 57421/LV4, NHMS 57423/LV4, NHMS 57424/LV4, NHMS 57434/LV5, and NHMS 57438/LV5).

**Description.** The teeth are very small with a maximum diameter of 1.8 mm. In occlusal view their contour ranges from circular to subcircular. The profile is hemispherical. The crown's enamel is thin and it has a rather strong radial rugosity radiating from center of the tooth towards the margins. The base is also circular with a central cavity.

**Remarks.** Several species of *Paralbula* have a similar ornamentation on their teeth, and distribution data indicate that their stratigraphical range could overlap (Estes, 1969; Schein et al., 2011; Ebersole et al., 2019). In his work on phyllodont fishes and their relationships, Estes (1969) underlines in his diagnosis of *P. casei* that the species has "crowns coarsely-sculptured in partially radiate or irregular pattern" and that this species differs from *P. marylandica* Blake, 1940 in having well-developed surface sculpture and a very thin enamel-like layer. The stratigraphic range of *P. marylandica* also seemed to exclude it from being confounded with *P. casei* that was reported usually only from the Eocene. Recent data indicate that *P. marylandica* might be also present in the uppermost Cretaceous–lowermost Paleocene basal Hornerstown Formation (USA) (Schein et al., 2011). However, a more thorough investigation of this material is still needed, including detailed description and better illustrations than those available in the poster presented by Schein et al. (2011). The species *P. stromeri* (Weiler, 1929) has a smooth crown that lacks ornamentation (Estes, 1969), while in *P. salvani* (Arambourg, 1952) the surface is weakly rugose or irregular ("surface légèrement chagrinée ou irrégulière", Arambourg, 1952, p. 254). Furthermore, both *P. stromeri* and *P. salvani* also seem to be restricted to the Paleocene. Accordingly, we conclude that our specimens belong to *P. casei.*

*Paralbula casei* is a common species in the Upper Cretaceous but it was also reported from the Ypresian (Eocene) of London Clay Formation in Bognor Regis, Sussex (UK) (Estes, 1969) and from the lower-to-middle Eocene (Ypresian to Bartonian) of Claiborne Group in Alabama, USA (Ebersole et al., 2019).

In the Upper Cretaceous, *P. casei* has been reported from the Campanian uppermost Blufftown Formation, Georgia (USA) (Case and Schwimmer, 1988), the middle Campanian of the Aguja Formation in West Texas (USA) (Schubert et al., 2017), the upper Campanian of Demopolis Formation, Mississippi (USA) (Manning and Dockery, 1992), and the Campanian of Dinosaur Park Formation, Alberta, (Canada) (Beavan and Russel, 1999), but also from the Maastrichtian Fox Hill Formation, South Dakota (USA) (Becker et al., 2009). In Europe, *P. casei* occurs in the middle?–upper Cenomanian of the La Cabaña Formation (Spain) (Vullo et al., 2009), and most recently was also described from the Campanian Rybushka Formation (Russia) (Ebersole et al., 2022).

### Actinopterygii indet.,
Figure 12U–W (in the main text)

**Material.** One tooth (NHMS 57430/LV1).

**Description.** The tooth is 1.2 mm high, 0.4 mm thick, and 1 mm in its widest part. Nonetheless, its base is broken and thus the complete height of the tooth remains unknown. The hook of the tooth makes an angle of 127° with its base. The tip of the hook is flat and covered with an irregular rugosity. The chewing surface is marked by four deep striations.

**Remarks.** The general shape suggests that this specimen is a pharyngeal tooth of unknown affinity. Pharyngeal teeth were encountered previously in the Upper Cretaceous (Maastrichtian) of Romania (Trif and Codrea, 2022a, figure 4A–E). The morphotype described by us in this work is, however, different from the Maastrichtian form.

## D. Herpetofauna

Class AMPHIBIA, Gray 1825
Order ANURA Rafinesque, 1815
Family ALYTIDAE Fitzinger, 1843
?Alytidae indet.
Figure 14A–F (in the main text)

**Material.** One urostyle, NHMS 57446/LV1.

**Description.** The proximal (anterior) portion of a urostyle is available in the material. The urostyle gradually widens anteriorly (in dorsal and ventral views). At its anterior end, it is characterized by two distinct, elliptical and slightly depressed anterior cotyles (fossa condyloidea), with median notches on the dorsal and ventral sides. These cotyles have a short median contact and form a bicondylar articulation with the sacral vertebra. Two broken, but well-developed postsacral transverse processes are directed posterolaterally. In the posterior region, there is also one pair of posteriorly open spinal nerve foramina. The dorsal crest is damaged. The ventral region of the bone is smooth.

**Remarks.** The urostyle described here is characterized by the presence of distinctly bipartite cotyles and of transverse processes. Such features can be observed in several anuran taxa such as alytids, gobiatids, pelodytids, palaeobatrachids, leptodactylids, and bufonids (Špinar, 1972; Duellman and Trueb, 1986; Roček and Nessov, 1993; Sanchiz, 1998). Leptodactylids and bufonids have only vestigial transverse processes (Duellman and Trueb, 1986), unlike the well-developed processes of the urostyle from Bozeș Formation. A combination between a single pair of postsacral transverse processes, bicondylar sacro-urostylar articulation and a poorly developed neural crest on the urostyle suggests referral of the urostyle to Alytidae (Roček, 1994, 2013; Bailon, 1999). Unfortunately, the dorsal crest is damaged and thus its exact shape is unknown. Accordingly, the preserved morphology of the urostyle indicates that the specimens may belong to pelodytids, gobiatids or alytids. We allocate it tentatively to Alytidae, but caution is needed. In any case, this element does not allow an allocation to a generic or specific level. The Alytidae is a clade of frogs with many primitive features which consists of extant genera such as *Alytes, Discoglossus,* and *Latonia*. Historically, this group has been referred to as Discoglossidae, but the older name Alytidae has priority (e.g., Sanchiz, 1998; Dubois, 2005; Blackburn and Wake, 2011). This clade is well known from the Cretaceous of Romania (Venczel et al., 2016).

Anura indet.
Figure 14G–O (in the main text)

**Material.** Left dentary, NHMS 57447/LV3 (Figure 14G–J); urostyle, NHMS 57448/LV1 (Figure 14K–N); and fragment of a neural arch, NHMS 57449/LV1 (Figure 14O).

**Description.** Jaw. Only a fragment of a left dentary is preserved (Figure 4G–J). It is lightly built. The dental crest supports eight tooth positions (one tooth still has the neck preserved that reaches beyond the dental crest). The subdental shelf is thin and horizontal. It is well expanded medially, and its medial margin is rounded in cross-section and bent dorsally. The lateral surface is smooth, slightly weathered. The dentary protrudes ventrally to form a vertical wall. The distal section of this wall is slightly bent medially. Thus, the element is slightly convex laterally.

**Dentition.** The tooth implantation is pleurodont. At the tooth base, huge resorption pits are present. All tooth crowns are missing, possibly indicating the presence of pedicellate teeth in which the tooth crown and base (both composed of dentine) are separated by a layer of uncalcified dentine.

**Vertebra.** Only a small fragment of a left neural arch is preserved. It bears an anterodorsally wide root portion of the transverse process and prezygapohysis. The preserved portion of the process is roughly elliptical in a sagittal section, being anteroposteriorly compressed.

**Urostyle.** Only a proximal portion of a urostyle is preserved. It markedly widens anteriorly, being ended by two more-or-less oval distinct cotyles. These cotyles are not in median contact, however, instead a short gap is present between them. Two broken, but well-developed postsacral transverse processes are present. The ventral region of the element is not entirely smooth; it possesses a pair of bizarre, knob-like processes (or rugosities).

**Remarks.** The dentary most likely belonged to Alytidae (a group, to which the dentary might fit morphologically and which is documented here based on other elements). However, pedicellate teeth can be found in many amphibians (Davit-Béal et al., 2007), and the poor preservation of the specimen do not allow a reliable more specific identification.

The processes (or rugosities) on the ventral surface of the urostyle are atypical and thus can be diagnostic at some level. Unfortunately, the ventral morphology of the urostyle is poorly documented in the literature and thus this specimen is allocated here only to Anura indet. Although the transverse processes are present, several small differences between the urostyle described here and the urostyle referred to ?Alytidae described above exist, e.g., (1) presence of bizarre knob-like ventral processes, (2) the shape of the cotyles — oval vs. more elliptical (depressed); (3) median contact of the cotyles — absent vs. present; and (4) proximal region in dorsal (and ventral) view is markedly widened vs. moderately widened. These differences might indicate the presence of at least two frog taxa at the locality.

Class REPTILIA Laurenti, 1768
Clade DIAPSIDA Osborn, 1903
Clade LEPIDOSAUROMORPHA Benton, 1983
Superorder LEPIDOSAURIA Haeckel, 1866
Order SQUAMATA Oppel 1811
Scleroglossa Estes, de Queiroz and Gauthier 1988

Scleroglossa indet.
Figure 14P–Q (in the main text)

**Material.** A left dentary, NHMS 57450/LV1.

**Description.** Only a small fragment of the left dentary is preserved. It preserves three tooth positions; however, only one tooth is still attached to the bone. The tooth crown is heavily worn and its base has a large resorption pit. The dentition is pleurodont. The dental crest is distinctly high, reaching more than twice a height of the robust subdental shelf. The dental sulcus (sulcus dentalis) is absent, at least in the preserved portion. The ventral region of the dentary with the Meckelian canal is broken off and missing. The lateral side of the bone is weathered.

**Remarks.** Unfortunately, the poor preservation does not allow more precise determination of this specimen. The combination of the limited features that can be observed (e.g., pleurodont dentition, absence of the dental sulcus, and tooth replacement pattern) might likely indicate a scincoid rather than other lizards (e.g., Yadav et al., 2023 and references therein). From Maastrichtian deposits of Haţeg Basin, taxa such as the paramacellodid *Becklesius (B. nopcsai* and *B.* cf. *hoffstetteri)* and the polyglyphanodont *Bicuspidon hatzegiensis* have been documented (Folie and Codrea, 2005).

Clade CROCODYLOMORPHA Walker, 1970
Clade CROCODYLIFORMES Hay, 1930
Clade MESOEUCROCODYLIA Whetstone and Whybrow, 1983
Clade NOTOSUCHIA Gasparini, 1971 (sensu Pol et al., 2014)
Clade ZIPHOSUCHIA Ortega et al., 2000
Genus cf. *DORATODON* Seeley, 1881
Figure 14S–W (in the main text)

**Material.** One isolated tooth, NHMS 57451/LV3.

**Description.** Only one isolated small tooth (3.5 mm high, and 3.6 mm wide) is available in the material in which the crown together with the base of the root is preserved. The tooth crown is slightly stepped from the root and a constriction is present here. The crown is roughly triangular in shape, longer than high, giving it a low lanceolate morphology. It is markedly laterally compressed, having a lenticular cross-section. The labial side appears to be more or less oval, being slightly more convex than the lingual side. Both have a slightly bulged central region. The cutting edges are mostly damaged, but serration (ziphodonty) is clearly preserved in some places (mainly visible on the edge of the crown close to the tooth root). The denticles are rectangular in lingual view, gradually increasing their size apically (the more distal portion is, however, damaged). Surface ornamentation is fine, although its exact naure is partly concealed by the longitudinal cracks in the enamel. In the region where the enamel surface is exposed, the striation is formed by numerous very fine and tiny, discontinuous ridges that are aligned apicobasally (parallel or sub-parallel) rather than anastomized. However, the wrinkled appearance of the enamel surface is very weak here, being of low relief, especially on the lingual side. The ridges fade out as they draw close to the cutting edges (carinae); those located closer to the cutting edges are directed slightly towards these edges.

**Remarks.** Isolated crocodyliform teeth from the Haţeg Basin, such as the one described here, were sometimes described as *Doratodon* (Grigorescu et al., 1999), or as *Sabresuchus* (previously as *Theriosuchus) sympiestodon* (Martin et al., 2010, 2014). Rabi and Sebők (2015) stated (and figured) the presence of basal constriction in the teeth of *Doratodon*. The zyphodonty (in contrast, teeth of *Sabresuchus* are pseudoziphodont, see, e.g., Martin et al., 2014) and the constriction is present in the tooth described here, thus the allocation to *Doratodon*-like taxon is reasonable. However, this type of teeth also resembles those of *Aprosuchus ghirai* (see Venczel and Codrea, 2019).

Clade EUSUCHIA Huxley, 1875
Clade ALLODAPOSUCHIDAE Narváez et al., 2015
Figure 14X–Z (in the main text)

**Material.** One isolated tooth, NHMS 57452/LV1.

**Description.** The isolated tooth is preserved still in the rocky matrix, so only its lingual side and its base in cross-section is exposed. It is small (3.1 mm high and 2.1 mm wide) and conical, gradually narrowing towards the apical region, but the tip is damaged. The tooth has a rounded base, but starts to be more labio-lingually compressed in the apical region; here, the tooth is also slightly lingually curved. The tooth crown is roughly triangular and its margins protrude in the form of cutting edges (carinae), forming subtle concavities. The cutting edges are well developed, sharp, with no serrations observed. Besides the longitudinal cracks present in the enamel, the lingual surface is clearly ornamented with fine, but well-visible longitudinal striations. In the central region of the crown, these are parallel or sub-parallel, aligned more-or-less apicobasally, whereas those located close to the mesial/distal edges are slightly diverted towards these edges.

**Remarks.** The conical tooth with a rounded base is typical for Allodaposuchidae crocodylomorphs. It differs from the tooth described above by its conical shape rather than being labiolongually flat and absence of denticles (not ziphodont type). That indicates the occurrence of at least two taxa at the locality.

## E. Statistical analysis data source

**TABLE S3.** Source table used for the statistical analyses.

| No. | Taxon | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|---|
| 1 | *Amphizygus brooksii* | 0 | 1 | 1 | 1 | 0 |
| 2 | *Amphizygus minimus* | 0 | 1 | 0 | 1 | 0 |
| 3 | *Arkhangelskiella cymbiformis* | 1 | 0 | 1 | 0 | 1 |
| 4 | *Biscutum constans* | 1 | 0 | 0 | 0 | 0 |

| No. | Taxon | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|---|
| 5 | *Broinsonia parca constricta* | 0 | 0 | 0 | 1 | 1 |
| 6 | *Broinsonia parca parca* | 0 | 0 | 0 | 0 | 1 |
| 7 | *Calculites ovalis* | 0 | 1 | 0 | 0 | 0 |
| 8 | *Chiastozygus amphipons* | 0 | 1 | 1 | 1 | 1 |
| 9 | *Chiastozygus bifarius* | 0 | 0 | 0 | 1 | 1 |
| 10 | *Chiastozygus litterarius* | 0 | 1 | 0 | 0 | 0 |
| 11 | *Cretarhabdus striatus* | 0 | 0 | 0 | 0 | 1 |
| 12 | *Cribrosphaerella ehrenbergii* | 0 | 1 | 1 | 1 | 1 |
| 13 | *Cylindralithus coronatus* | 0 | 0 | 0 | 0 | 1 |
| 14 | *Eiffellithus eximius* | 1 | 1 | 1 | 1 | 1 |
| 15 | *Eiffellithus gorkae* | 0 | 0 | 0 | 0 | 1 |
| 16 | *Eiffellithus turriseiffelii* | 0 | 1 | 0 | 1 | 0 |
| 17 | *Eprolithus floralis* | 0 | 0 | 0 | 0 | 1 |
| 18 | *Gartnerago segmentatum* | 0 | 0 | 0 | 1 | 0 |
| 19 | *Helicolithus trabeculatus* | 0 | 1 | 0 | 1 | 1 |
| 20 | *Lithastrinus grillii* | 0 | 0 | 1 | 0 | 0 |
| 21 | *Loxolithus armilla* | 0 | 0 | 1 | 1 | 0 |
| 22 | *Lucianorhabdus maleformis* | 0 | 1 | 0 | 1 | 1 |
| 23 | *Manivitella pemmatoidea* | 0 | 0 | 0 | 1 | 1 |
| 24 | *Micula staurophora* | 1 | 1 | 1 | 1 | 1 |
| 25 | *Placozygus fibuliformis* | 0 | 0 | 0 | 1 | 0 |
| 26 | *Prediscosphaera cretacea* | 1 | 1 | 1 | 1 | 1 |
| 27 | *Reinhardtites anthophorus* | 1 | 1 | 0 | 0 | 1 |
| 28 | *Retecapsa crenulata* | 1 | 1 | 1 | 1 | 1 |
| 29 | *Rhagodiscus achlyostaurion* | 0 | 1 | 0 | 0 | 0 |
| 30 | *Russellia laswellii* | 0 | 0 | 0 | 0 | 1 |
| 31 | *Staurolithites sp.* | 0 | 1 | 0 | 0 | 0 |
| 32 | *Tranolithus orionatus* | 1 | 1 | 1 | 1 | 1 |
| 33 | *Watznaueria barnesiae* | 1 | 1 | 1 | 1 | 1 |
| 34 | *Watznaueria quadriradiata* | 0 | 0 | 1 | 0 | 0 |
| 35 | *Zeugrhabdostus bicrescenticus* | 0 | 0 | 1 | 0 | 1 |
| 36 | *Zeugrhabdotus diplogrammus* | 0 | 1 | 1 | 0 | 0 |
| 37 | Taxon 1 | 0 | 0 | 0 | 0 | 0 |
| 38 | Taxon 2 | 0 | 0 | 0 | 0 | 0 |
| 39 | Taxon 3 | 0 | 0 | 0 | 0 | 0 |
| 40 | Taxon 4 | 0 | 0 | 0 | 0 | 0 |
| 41 | Taxon 5 | 0 | 0 | 0 | 0 | 0 |
| 42 | Taxon 6 | 0 | 0 | 0 | 0 | 0 |
| 43 | Taxon 7 | 0 | 0 | 0 | 0 | 0 |
| 44 | Taxon 8 | 0 | 0 | 0 | 0 | 0 |
| 45 | Taxon 9 | 0 | 0 | 0 | 0 | 0 |

| No. | Taxon | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|---|
| 46 | Taxon 10 | 0 | 0 | 0 | 0 | 0 |
| 47 | Taxon 11 | 0 | 0 | 0 | 0 | 0 |
| 48 | Taxon 12 | 0 | 0 | 0 | 0 | 0 |
| 49 | Taxon 13 | 0 | 0 | 0 | 0 | 0 |
| 50 | Taxon 14 | 0 | 0 | 0 | 0 | 0 |
| 51 | Taxon 15 | 0 | 0 | 0 | 0 | 0 |
| 52 | Taxon 16 | 0 | 0 | 0 | 0 | 0 |
| 53 | Taxon 17 | 0 | 0 | 0 | 0 | 0 |
| 54 | cf. *Sphenopteris ungeri* | 0 | 0 | 0 | 0 | 0 |
| 55 | *Pachydiscus* cf. *haldemsis* | 0 | 0 | 0 | 0 | 1 |
| 56 | *Pirenella alvincziense* | 1 | 0 | 1 | 0 | 0 |
| 57 | *Pleurocera* sp. | 1 | 1 | 1 | 0 | 0 |
| 58 | *Pyrgulifera boeckhi* | 1 | 1 | 1 | 0 | 0 |
| 59 | *Campylostylus galloprovincialis* | 1 | 1 | 1 | 0 | 0 |
| 60 | *Neritoplica* sp. | 1 | 0 | 0 | 0 | 0 |
| 61 | *Parateinostoma* sp. | 1 | 0 | 0 | 0 | 0 |
| 62 | *Pirenella* sp. | 1 | 0 | 1 | 0 | 0 |
| 63 | *Cassiope obvoluta* | 1 | 0 | 0 | 0 | 0 |
| 64 | *Onkospira* sp. | 0 | 0 | 0 | 1 | 0 |
| 65 | *Melanopsis crastina* | 1 | 1 | 1 | 0 | 0 |
| 66 | ?*Rhabdocolpus* sp. | 0 | 0 | 0 | 1 | 0 |
| 67 | Acteonoidea indet. | 0 | 0 | 0 | 0 | 1 |
| 68 | *Pseudamaura alkenyeriensis* | 0 | 0 | 0 | 0 | 1 |
| 69 | *Trichotropis* sp. | 0 | 0 | 0 | 0 | 1 |
| 70 | *Ageria* sp. | 0 | 0 | 0 | 0 | 1 |
| 71 | Voluthidae indet. | 0 | 0 | 0 | 0 | 1 |
| 72 | *Acteonella renauxana* | 0 | 0 | 0 | 0 | 1 |
| 73 | ?*Nairiella* sp. | 0 | 0 | 0 | 0 | 1 |
| 74 | *Neritopsis spinosa* | 0 | 0 | 1 | 0 | 0 |
| 75 | *Deianira bicarinata* | 0 | 0 | 1 | 0 | 0 |
| 76 | *Venericardia* sp. | 0 | 0 | 0 | 1 | 0 |
| 77 | *?Corbula* sp. | 1 | 0 | 1 | 1 | 0 |
| 78 | *?Exogyra* sp. | 0 | 0 | 0 | 1 | 0 |
| 79 | ?*Platyceramus* sp. | 0 | 0 | 0 | 0 | 1 |
| 80 | *Granocardium* sp. | 0 | 0 | 0 | 0 | 1 |
| 81 | *Panopea* sp. | 0 | 0 | 0 | 0 | 1 |
| 82 | *Pycnodonte* sp. | 0 | 0 | 0 | 0 | 1 |
| 83 | *Pinna* sp. | 0 | 0 | 0 | 0 | 1 |
| 84 | Anomiidae indet. | 0 | 0 | 0 | 0 | 1 |
| 85 | Hemiasteridae indet. 1 | 0 | 0 | 0 | 0 | 1 |
| 86 | Hemiasteridae indet. 2 | 0 | 0 | 0 | 0 | 1 |

| No. | Taxon | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|---|
| 87 | Asteroidea indet. | 0 | 0 | 0 | 0 | 1 |
| 88 | *Cunnolites* sp. | 0 | 0 | 0 | 0 | 1 |
| 89 | *Aulosmilia* sp. | 0 | 0 | 0 | 0 | 1 |
| 90 | aff. Lamniformes indet. | 0 | 0 | 0 | 1 | 0 |
| 91 | *Paratrygonorrhina amblysoda* | 0 | 0 | 0 | 1 | 0 |
| 92 | *Atractosteus* sp. | 0 | 0 | 1 | 0 | 0 |
| 93 | *Lepisosteus* sp. | 0 | 1 | 1 | 0 | 0 |
| 94 | Paralbula casei | 0 | 0 | 0 | 1 | 1 |
| 95 | *Enchodus* cf. *petrosus* | 0 | 0 | 0 | 1 | 0 |
| 96 | *Paraplesiopoma transylvanica* | 0 | 0 | 0 | 1 | 0 |
| 97 | ?Alytidae indet. | 1 | 0 | 0 | 0 | 0 |
| 98 | Anura indet. | 1 | 0 | 1 | 0 | 0 |
| 99 | Scleroglossa indet. | 1 | 0 | 0 | 0 | 0 |
| 100 | cf. *Doratodon* sp. | 0 | 0 | 1 | 0 | 0 |
| 101 | Allodaposuchidae indet. | 1 | 0 | 0 | 0 | 0 |
| 102 | Maniraptoran theropods | 1 | 1 | 0 | 0 | 0 |

## F. Distribution chart data source

**TABLE S4.** Source table for the distribution chart.

| Groups | LV1 | LV2 | LV3 | LV4 | LV5 |
|---|---|---|---|---|---|
| Meso and macroflora | 0 | 0 | 1 | 17 | 0 |
| Cephalopods | 0 | 0 | 0 | 0 | 1 |
| Gastropods | 9 | 4 | 8 | 3 | 6 |
| Bivalves | 1 | 0 | 1 | 3 | 7 |
| Echinoids | 0 | 0 | 0 | 0 | 2 |
| Asteroids | 0 | 0 | 0 | 0 | 1 |
| Corals | 0 | 0 | 0 | 0 | 2 |
| Insects ichnofossils | 0 | 0 | 0 | 2 | 0 |
| Elasmobranchii | 0 | 0 | 0 | 2 | 0 |
| Actinopterigii | 0 | 1 | 2 | 3 | 1 |
| Herpetofauna | 4 | 0 | 2 | 0 | 0 |
| Dinosaurs | 1 | 1 | 0 | 0 | 0 |

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