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"LOCALITY 84", A NEW CRETACEOUS *KONSERVAT-LAGERSTÄTTE* IN THE JULIAN PREALPS (NE ITALY)

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Abstract. "Locality 84" is a new *Konservat-Lagerstätte* from the Friuli Carbonate Platform (NE Italy) preserving articulated fish skeletons and plant fossils. The fossil assemblage was collected in a carbonate olistolith of one of the megabeds characterising the upper Palaeocene-lower Eocene Grivò Flysch Formation in the Julian Prealps. Fish remains are dominant, but plant fossils form one third of the assemblage. The Late Cretaceous age of the "locality 84" olistolith is supported by the presence of the conifer *Frenelopsis* along with a plant fossil assemblage dominated by angiosperm leaves, by the rarity of acanthomorph teleosts represented by primitive forms and by the presence of pycnodontine pycnodontiforms. Further evidence (e.g., the affinity of some angiosperm leaves) suggests a Campanian-Maastrichtian age. The fossil assemblage differs from other similar fossil assemblages from the Cretaceous of the Friuli Carbonate Platform due to the extreme rarity of both shelled and non-shelled invertebrates, rarity of conifer shoots, a dominance of pycnodontiforms and basal non-acanthomorph teleosts (elopiforms, gonorhynchiforms, pachyrhizodontoids and putative albuliforms) in the ichthyofauna, with few acanthomorphs, no clupeomorphs, and no needlefish-like aulopiforms and chondrichthyans. The environment of deposition of the sediments containing the fossils may be a tidal flat or a restricted water body in the inner part of the Friuli Carbonate Platform but with a connection to the open sea.

Introduction

Ruggero Tonello (1928-2007) was born in Montenars (Udine Province, Friuli Venezia Giulia Autonomous Region, NE Italy) along the SW flank of the Julian Prealps. As a young man, he emigrated to work in the mines of New Caledonia and Congo. Around 1988, he started to search for and collect fossils, mainly in the environs of his hometown Montenars. Although we do not know what triggered his interest in fossils, it was likely influenced by his work as a miner, which accustomed him to dig in the rock. He was a very private person and rarely shared his passion for fossils. Furthermore,

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he was not aware of the details of the Italian legislation concerning fossils. On May 8th 1989, he discovered an outcrop yielding fish and plant fossils not far from his home along the western side of the Julian Prealps (Fig. 1). In his notes, he named this fossil-bearing locality “84” according to his practice of progressively numbering the places he explored for fossils. The outcrop was composed of dark “shaly” limestone and located in the woods near the road “Montenars-Plazzaris”. Tonello systematically extracted fossils in the “locality 84” from 1989 to 1992, but collected fossils occasionally until 1999. In 1995, he began collaborating with the Museo Friulano di Storia Naturale of Udine, donating some specimens that were deposited in the palaeontological collection of the museum, studied and published (Muscio 1997; Dalla Vecchia, Muscio & Tonello 2005). These included also a few specimens from “locality 84”, which were reported and figured in Dalla Vecchia (2008a). When Tonello died, his whole fossil collection (the dimensions of which were previously unknown) was given by his heirs to the Museo Friulano di Storia Naturale di Udine.

As shown in the geological section below, the Friuli Venezia Giulia Region of Italy and a portion of the neighboring Slovenia were part of the Friuli Carbonate Platform (the northern termination of the Adriatic Carbonate Platform, Vlahović et al. 2005) during Cretaceous and Eocene times. Several localities in this area yielded articulated fish remains and plants fossils like “locality 84”, such as other outcrops in the Montenars area (probably Cretaceous-Eocene in age, see below); the Lower Cretaceous Cornappo Torrent locality (Italy); the Lower and Upper Cretaceous olistoliths in the Vernasso locality of the Julian Prealps (Italy); the Upper Cretaceous Komen/Comeno, Tomaj and other minor localities of the Slovenian Karst; and the Upper Cretaceous Polazzo and Trebiciano localities of the Italian Karst (Fig. 1).

The goal of this paper is to preliminarily describe the fossil assemblage from “locality 84” as far as this is permitted by the state of preservation and preparation of the specimens, and to determine its taxonomic affinity and age. To achieve this, the fossil assemblage from “locality 84” has been compared with those from the localities of Friuli Venezia Giulia and Slovenia listed above.

Fig. 1 - Location of “locality 84” and the other sites in the Friuli Venezia Giulia Region (coloured area) and Slovenia mentioned in the text. Legend: 1, “locality 84”; 2, Cornappo Torrent; 3, Vernasso 1-3; 4, Polazzo; 5, Komen/Comeno; 6, Tomaj; 7, Trebiciano.

Institutional abbreviations – MCSNT, Museo Civico di Storia Naturale di Trieste; MFSN, Museo Friulano di Storia Naturale, Udine, Italy; MPC, Museo Paleontologico Cittadino di Monfalcone, Gruppo Speleologico A.d.F.

Materials, terminology and methods

Any information about the location and characteristics of “locality 84” and its fossils was obtained from the handwritten notes by the collector (available at the MFSN). In addition, all fossils from the locality had been labeled with “84” and most of them report also the date of collection. All fossils collected by R. Tonello at the “locality 84” are deposited at the MFSN in Udine. The collection consists of at least 651 samples (651 inventory numbers); 70 of them contain two or more specimens (macrorganisms), thus the minimum number of specimens is 721.

Samples are MFSN 3831; 15327; 25003-25007; 37635-37659; 37684-37687; 37737-37764; 38045-38140; 38214; 38644-38652; 38695-38717; 38742-38746; 38775-38781; 38814-38822; 38875-38894; 38896-38901; 38920-39002; 39222-39264; 39396-39405; 39407; 43575-43591; 43594-43629; 43631-43660; 43662-43721; 43723-43740; 43743-

43773; 43819; 45739; 50798; 50864-50871; 50873-50896; 50898-50910; 50912-50914; and 51967-88. MFSN 45179-180 (two pycnodontiform fishes) are considered to come from "locality 84" because were found associated with other samples from this locality. Three samples (MFSN 37688-37690) lack a locality number, but their lithology, fossil content and their association with MFSN 37687 (from "locality 84") suggest they also originate from "locality 84". MFSN 50751 (an acanthomorph fish) has a wrong locality number (117; a Norian site) but belongs to "locality 84" because it is the counterslab of MFSN 38898.

Eight samples are from "locality 84 west" (MFSN 38823; 39408; 43592-93; 43661; 43722; and 43741-43742); three are from "locality 84 south" (MFSN 38213, 38653, and 43630). Six samples (MFSN 43775, 50739-50742, and 50752-50753) are from "locality 'Cretus': above the road to Plazzaris, at the level of the locality 84 at the top of the hill". The relationships of these three localities ("locality 84 west", "locality 84 south", and "locality 'Cretus': above the road to Plazzaris, at the level of the locality 84 at the top of the hill") with "locality 84" are unclear. They may represent small outcrops of the same olistolith or belong to olistoliths from the same stratigraphic section as suggested by the fossils and the lithology of the samples (see below the discussion about the location of "locality 84" and its geological characteristics). The specimens from these localities are not used in the quantitative analyses.

Two rudist bivalves (MFSN 46403 and 46415) and a gastropod (MFSN 46275) listed as originating from "locality 84" in the MFSN inventory are preserved in a pale grey massive limestone that differs from that preserving the fish and plant fossils. These specimens likely come from a distinct olistolith and are not considered here.

Some specimens have been assigned two distinct inventory numbers, one for the slab and one for the counterslab. This happened because Tonello's collection was mixed up during transport from Tonello's house to the MFSN resulting in the slab and counterslab of the same specimen being packed and stored in different boxes and later inventoried under distinct numbers. Because of a mistake, two distinct specimens were inventoried under the number MFSN 38983, an elopiform and a gonorhynchiform fish.

All the specimens have been studied personally by the authors; two of them (FMDV and LS) have inventoried the material for the MFSN. Since no specimen has yet undergone preparation prior to this study, the systematic identification of the fish fossils should be considered as preliminary. Moreover, fossil fishes often opened along a sagittal plane when the rock containing them split into two mirror-image slabs leaving parts of the skeleton on each slab. This often hampers the identification of the skeletal elements. The fossils have been preliminarily identified to characterise the assemblage and to derive clues about its age by comparing it to other similar assemblages. Particular attention has been paid to the taxa with a biostratigraphic value (e.g., the Pycnodontiformes among fishes and *Frenelopsis* among plant fossils).

Unfortunately, we lack a detailed stratigraphic record for each specimen and their co-occurrences, as each specimen is preserved on a relatively small fragment of rock and the collector did not report the layers the specimens were found in, as it is common practice in systematic field work. However, the local geological conditions, the extent and nature of the outcrop, the lithology of the slabs containing the fossils and comparisons with similar occurrences in the Julian Prealps (Dalla Vecchia 2008a) suggest that the specimens likely originate from a single, relatively thin stratigraphic section, at best a few metres thick, represented by an olistolith of a megabed (see Geological setting and age). The rock from the outer part of the olistolith, exposed to weathering, exhibits a lighter colour compared to the rock from the inner part. Some parts of the olistolith and the fossils within them have also been affected by tectonics.

The coexistence of fish and plant fossils on a same slab in at least 44 samples (MFSN 37642; 37685; 38053; 38092; 38095; 38104; 38120; 38134-35; 38138; 38652; 38699; 38818; 38879; 38889; 38894; 38920; 38924; 38932; 38962-64; 38973; 38980; 38986; 38989; 38994-95; 39000; 43617; 43646; 43656; 43662; 43671-72; 43679; 43698; 43711; 43719; 43743; 50798; 50873; 50877; and 50914), suggests that they were associated during deposition, although it cannot be excluded that in the fossil-bearing stratigraphic section there existed distinct horizons of fish or plant remains exclusively.

For the definition of *Konservat-Lagerstätte* see Seilacher et al. (1985).

The reference for the classification and phylogenetic analysis of the pycnodontiforms is Poyato-Ariza (2020). In order to investigate the affinities of the taxon from “locality 84”, we performed a phylogenetic analysis by TNT 1.6 (Goloboff & Morales 2023) based on the data matrix in Poyato-Ariza (2020) adding the codings for the taxon from “locality 84”. We used a heuristic search method (Wagner trees) with 1000 starting replicates, saving one tree per replication, random taxon addition, three rounds of tree bisection and reconnection (TBR) swapping algorithm, and collapsing the trees after search. The random seed number was set to the default value. All characters are unordered and given equal weight. We obtained the Strict consensus tree and the 50% majority rule consensus tree with relative tree length, consistency index (CI) and retention index (RI).

Geographic position of “locality 84”

“Locality 84” is located in the territory of the municipality of Montenars (Fig. 1). Montenars is a dispersed municipality composed of several villages scattered in the mountains: San Giorgio, Sant’Elena, Santa Maria Maddalena, Lazzaretto, Isola (seat of the Municipality), Plazzaris, Flaipano, Cretto, etc.

According to R. Tonello’s notes, “locality 84” occurred on the right side of the road leading from the main nucleus of Montenars (S. Giorgio - Isola - S. Elena) to Plazzaris, in the hill named “Cretus” near the Faidumbli Brook, which are not reported in the map at scale 1:5,000 Sheet 049113 Montenars produced by the Autonomous Region Friuli Venezia Giulia and updated to 2004. According to Tonello’s notes, the locality is situated inside the woods and topographically higher on the flank of the Cretus hill with respect to the road. Based on the notes and the collaboration of Ruggero’s son, Rodolfo, who accompanied his father on his excursions, one of us (LS) identified the actual location of the outcrop. The coordinates of the outcrop are available on file at the MFSN. Today, the site is exhausted. Only the debris left by the quarrying activity of R. Tonello, mostly covered by vegetation, remains of the original outcrop of dark and thinly laminated limestone. Because of the olistolith nature of the site, it is rather unlikely that other specimens will be found there in the future or that further specimens were collected from the outcrop by other people.

Besides the four close localities mentioned above (“locality 84”, “84 west”, “84 south”, “locality ‘Cretus’: above the road to Plazzaris, at the level of the locality 84 at the top of the hill”), other eleven localities yielding fish and plant remains preserved in laminated limestone have been identified in the area based on Tonello’s notes and labels in the fossils: localities 21 and 21bis, 22, 122, 132, “Clapon” and “Clapon east, Plazzaris”, “Mt. Campeon, Plazzaris”, “near the Ciuc dai Giai”, and “along the mule track that leads from Flaipano to Pers” (Fig. 2). Two further localities have been reported by Romano Binutti (another fossil collector): “near the *roccolo* of Plazzaris” and “locality Rochul” (probably a same locality and possibly coinciding with one of Tonello’s localities). These localities occur in a ray of 2.5 kilometres from the “locality 84” (Fig. 2) and might represent, at least in some cases, the outcrop of olistoliths from the same stratigraphic horizon as “locality 84”. Unfortunately, the location of these outcrops is not as precisely established as that of “locality 84”. The fossils collected from those other localities are not described in this paper.

The vertebrate remains described by Dalla Vecchia, Muscio & Tonello (2005) were collected in a locality close to “locality 84”, but they were preserved in olistoliths that are distinct from that of “locality 84” (see the Geological setting and age section below).

Geological setting and age

The geology of the area where “locality 84” occurs is shown in the Geological Map of Italy at scale 1:50.000 - Sheet 049 Gemona del Friuli and discussed in its explanatory notes (Zanferrari et al. 2013). The only formation cropping out around “locality 84” is the upper Palaeocene-lower Eocene Grivò Flysch (Fig. 2). Mesozoic carbonates crop out to the north (Late Triassic and Jurassic in age) and to SE (Cretaceous in age). The Grivò Flysch is subdivided into three facies: a) well-bedded siliciclastic and hybrid turbidites with thicker carbonate turbidites; b) turbidites like in (a) but with carbonate megabeds interbedded, each tens to hundreds of metres thick, locally containing a basal olistostrome/megabreccia; and c) turbidites like in (a) but with layers of para-conglomerate rich in chert. Facies b occurs in the middle-lower part of the Grivò Flysch.

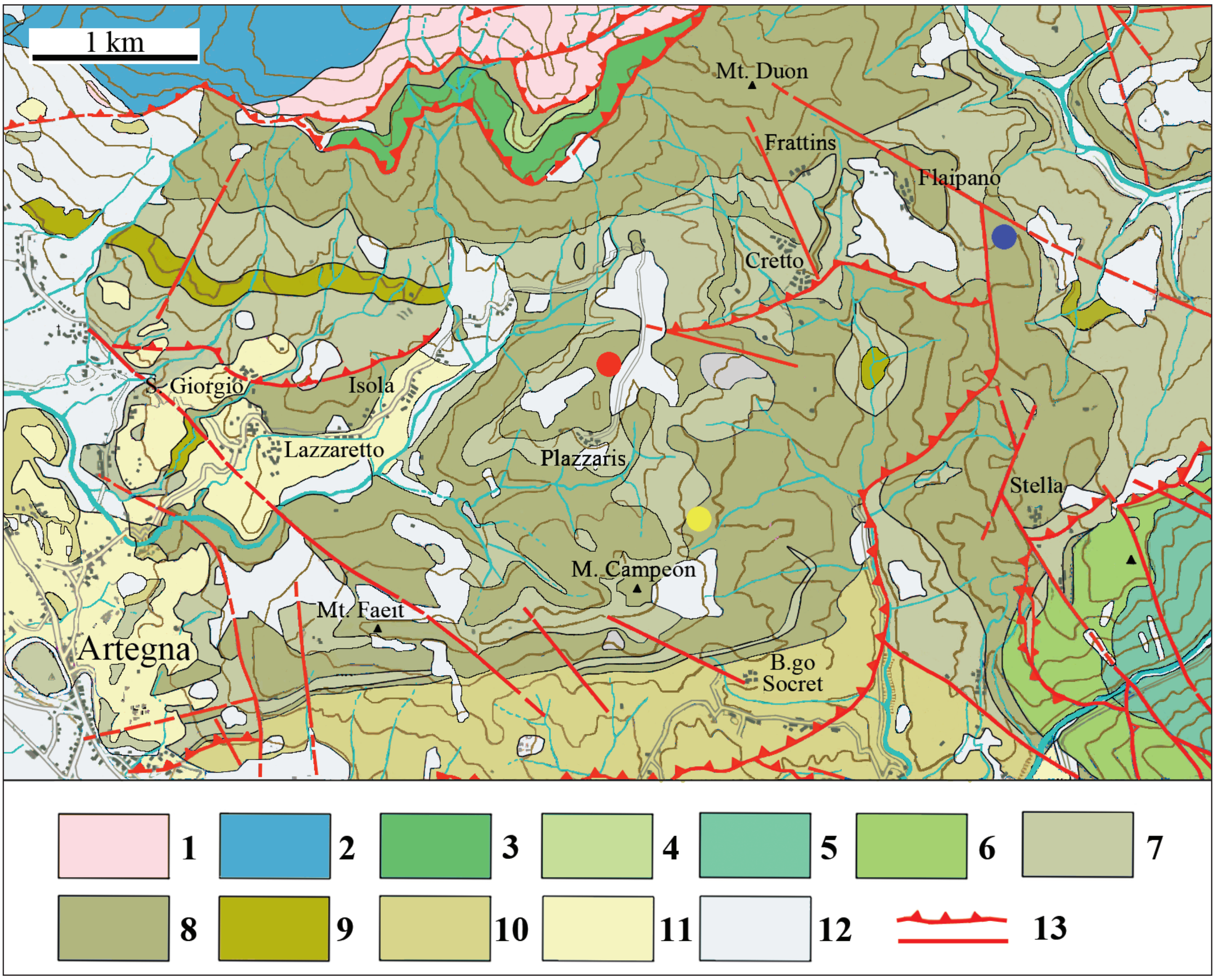

Fig. 2 - Location of "locality 84" in the territory of Montenars. Legend: 1, Dolomia Principale (Norian); 2, Jurassic limestone (mainly the Lower Jurassic Monte Zugna Formation); 3, Maiolica (upper Tithonian-Barremian); 4, Scaglia Variegata Alpina (Aptian-Cenomanian); 5, Cellina Limestone (Aptian-Cenomanian); 6, Monte Cavallo Limestone (Albian *p.p.* - upper Cenomanian); 7, Grivò Flysch, facies a (upper Selandian-Ypresian); 8, Grivò Flysch, facies b (Thanetian-Ypresian); 9, Grivò Flysch, facies c (Ypresian); 10, Savorgnano Marls and Sandstones (Ypresian); 11, moraines (Upper Pleistocene); 12, other Pleistocene-Recent deposits; 13, faults and thrusts. The red dot indicates "locality 84", the blue dot "locality 122", and the yellow dot "locality 21". Based on Zanferrari et al. (2013), modified.

The Grivò Flysch was deposited in the late Campanian-middle Eocene Friuli Basin (Julian Basin of Tunis & Venturini 1992; Venturini et al. 2023), an WNW-ESE elongated depression which was rimmed to N by the incipient southern Alps, to NE by the uprising Julian Alps and to SW and S by the Friuli Carbonate Platform (Ogata et al. 2014: fig. 3C; FCP). The Friuli Basin was a deep-water foredeep basin located in front of the advancing Dinaric thrust system and migrating to SW with it. The area of Montenars represents the preserved northern extremity of the basin. At least 23 megabeds of facies b (up to 260 m thick; Ogata et al. 2014), which are graded and composed of a megabreccia at the base and a megaturbidite at the top, crop out along the Italian side of the Julian Prealps (Tunis & Venturini 1992; Pini & Ponton 2023). The megabreccia is often composed of metric-decametric olistoliths of carbonate platform limestone that is mostly Cretaceous in age, but olistoliths made of Cretaceous basinal limestone and shallow water Palaeocene limestone also occur (Zanferrari et al. 2013; Ogata et al. 2014; Venturini et al. 2023). The megabeds represent the mass transport deposit of catastrophic submarine landslides into the deep-water Friuli Basin, which originated from the collapse and retreat of the faulted NE margin of the FCP and were triggered by seismic shocks and other factors (Ogata et al. 2014).

During the Cretaceous, the FCP was surrounded by the Slovenian, Carnian and Belluno Basins and was the northernmost part of the large Adriatic Carbonate Platform which was isolated in the Western Tethys between the Afro-Arabian and Eurasian continents (see Philip et al. 2000a, b).

Carbonate olistoliths in the Grivò Flysch often preserve shallow water invertebrate associations of Cretaceous age (e.g. Tommasi 1891; Dalla Vecchia et al. 2004; Venturini et al. 2023). The 264-m-thick megabed n. 11 in the Italcementi Quarry of Vernasso (San Pietro al Natisone municipality, Udine Province) presents at its base huge limestone olistoliths of Cretaceous age (the largest block has an estimated volume of 70,000 m^3) that have been known to yield fish and plant fossils since the 19th century (see below).

Therefore, the dark laminated limestone yielding fish and plant remains at “locality 84” belonged to a limestone olistolith of a megabed within the Grivò Flysch, with a plausible Cretaceous-Palaeocene age. According to Venturini et al. (2023), the fossil-bearing megabeds in the Montenars territory are the youngest within the Grivò Flysch (younger than megabed 11). The olistoliths of the Grivò Flysch megabeds are segments of the stratigraphic section of the NE portion of the FCP (Venturini et al. 2023). The fossil assemblage from “locality 84” provides information about organisms and environments that existed in a time to be established within the Cretaceous-Palaeocene interval in the FCP. That part of the platform is today mostly buried under the thick post-middle Eocene clastic succession; portions crop out in the nearby Mt. Bernadia (Julian Prealps), along the southern margin of the Carnian Prealps, in the Judrio valley (Julian Prealps), in the Mt. Sabotino and along the Isonzo valley, and in the Karst.

- FISH
  - Actinopterygii
    - Pycnodontiformes
      - Pycnodontidae
        - Pycnodontinae
    - Teleostei
      - Elopiformes
      - ?Albuliformes
      - Gonorhynchiformes
        - Chanidae
      - Crossognathiformes
        - Pachyrhizodontoidei
          - Pachyrhizodontidae
      - Acanthomorpha
        - Beryciformes
        - ?Percomorphacea
- PLANTS
  - Angiospermae
    - *Dicotylophyllum proteoides*
    - *Dicotylophyllum* sp. 1
    - *Dicotylophyllum* sp. 2
    - *Dicotylophyllum* sp. 3
    - *Plantaginopsis* sp.
    - *Aenigmatophyllum* cf. *gothani*
    - *Aenigmatophyllum* sp.
    - ? *Papillaephyllum*
    - ?*Barykovia*
  - Gymnospermae
    - Coniferophyta
      - *Frenelopsis* sp. 1
      - *Frenelopsis* sp. 2
      - ?*Frenelopsis*
      - *Widdringtonites* sp.
      - *Pagiophyllum* sp. 1
      - *Pagiophyllum* sp. 2
      - *Brachyphyllum* sp.
    - Ginkgophyta
      - *Eretmophyllum obtusum*
      - ?*Phoenicopsis*
    - Pteridospermatophyta
      - *Pachypteris* sp.

Tab. 1 - Fish and plant taxa identified in the fossil assemblage from “locality 84”.

The fossil assemblage: general observations

“Locality 84” yielded the most abundant and diverse fossil assemblage among those discovered by R. Tonello within the fossil-bearing limestone olistoliths of the megabeds in the Montenars territory.

The fossil assemblage is almost entirely composed of ray-finned fishes, leaves and small fragments of plant fossils (Tab. 1). Notably, the assemblage lacks chondrichthyan fish remains (e.g., isolated teeth), tetrapod remains, and common aquatic invertebrates (molluscs, crustaceans, echinoderms, etc.). The absence of chondrichthyans, tetrapods, and common aquatic invertebrates in the sample is not a collecting bias (i.e., Tonello did not prefer to collect some kind of fossils rather than others). Tonello’s written notes and the personal observation of one of us (FMDV) confirm that Tonello collected every fossil remain he found.

Actinopterygii

Bony fish are represented by 438 specimens (61% of the total sample). They are small to medium-sized, total length ranging from 35 mm to about 450 mm (MFSN 38920 is 390 mm long without skull). Most of the specimens are more or less well-articulated skeletons (Figs. 3-7), but detached and isolated skeletal portions (e.g., caudal portions; MFSN 38821, 38960, and 43710) also occur. In many cases, the eyeballs were probably kerogenised (see Osés et al. 2017) and are preserved as a black spot. Eyeballs preservation, the skeletal articulation and the often undisturbed scale cover suggest a rapid burial of the carcasses and/or an environment of deposition with conditions (e.g, anoxy) that slowed down decomposition before burial (Osés et al. 2017). The dark colour of the rock and the undisturbed thin lamination also suggest anoxic conditions in the sediment deposition environment.

We focused mainly on the specimens and selected characters that may allow establishing the taxonomic composition, affinity and age of the fossil fish assemblage. In order to have an overall view of the characteristics of the ichthyofauna, the assemblage has been subdivided into three main groups: pycnodontiforms, non-acanthomorph teleosts, and acanthomorphs. Therefore, this analysis is provisional; a more detailed taxonomic assessment of the fossil ichthyofauna from "locality 84" is in progress and hopefully will be published in the future.

Eight to 12 specimens are coprolites that were plausibly produced by fish because of their small size and shape.

- Pycnodontiformes

Pycnodontiformes (Fig. 3) are represented by 143 specimens which are 20% of the total assemblage and 33% of the fish assemblage. Pycnodontiformes are a group of basal neopterygians ranging in age from the Late Triassic to the early Eocene (Poyato-Ariza & Wenz 2002; Poyato-Ariza 2015, 2020). They are characterized by many autapomorphies, some of which are easy to identify also in partially and poorly preserved specimens (the "pycnodont look" of Poyato-Ariza 2015): laterally compressed, high to rounded body shape; teeth on vomer and prearticular arranged in rows; ribs alate; contour scales differentiated into dorsal ridge and ventral keel scales (Poyato-Ariza & Wenz 2002). The pycnodontiforms are the only fossils from "locality 84" to have been reported and figured in literature to date (Dalla Vecchia 2008a: 224, fig. 218).

Pycnodontinae. All pycnodontiforms from "locality 84" belong to a single taxon. Standard length ranges 40-195 mm and the total length ~53-238 mm. Their maximum body height/standard length ratio is ca. 0.53 (e.g., MFSN 25004; Fig. 3A) and the general body shape is hence intermediate between discoid and fusiform (Poyato-Ariza 2020: 452). The dorsal apex is positioned at the point of insertion of the dorsal fin and the dorsal prominence is absent. The ventral apex is absent. The mouth gape is sub-horizontal. There is no prognathism and the snout is elongated and pointed. There are two premaxillary teeth that are very flattened and fully incisiform. Vomerine teeth have an oval outline and are arranged in three regular rows (Fig. 3D). The main vomerine tooth row consists of 8-9 teeth, with no teeth alternation. The lower jaw bears two dentary teeth which are much flattened and fully incisiform as the premaxillary teeth. The prearticular teeth are also arranged in three regular tooth rows; the main row presents 8-9 teeth. The crowns are extremely elongated with their long axis perpendicular to the row axis. Vomerine and prearticular crowns present crenulations and grooves. The caudal fin has a double emarginated morphology (see specimens MFSN 25003 and 25005; Fig. 3B-C). The flank scales are incompletely ossified, forming elongated scale ribs in a clathrate pattern. The scales cover only the abdominal region, are arranged in parallel dorsoventral rows, and ornamented with tubercles. There are no scutellum-like contour scales. A bifid scale roofs the cloaca dorsally and the anterior cloacal scales are not modified. The dorsal and anal fins are strip-like. The caudal pedicle is clearly differentiated.

According to the phylogenetic analysis (strict consensus tree; SI, Fig. 1A), "locality 84" pycnodontiform results to be a pycnodontine pycnodontid, although the tree is poorly resolved. It results to be the sister taxon of the Pycnodontini (i.e., *Pycnodus* + *Oropycnodus*) and more derived than *Polazzodus* and *Tergestinia* in four of the six equally parsimonious trees (as shown by the 50% majority rule tree; SI, Fig. 1B); it is the sister taxon of *Tergestinia* + *Sylvienodus* + *Polazzodus* in the other two.

The taxon from "locality 84" shares the two autapomorphies of the Pycnodontinae according to the diagnosis of the Subfamily by Poyato-Ariza (2020: 470): dermal skull posteriorly shortened so

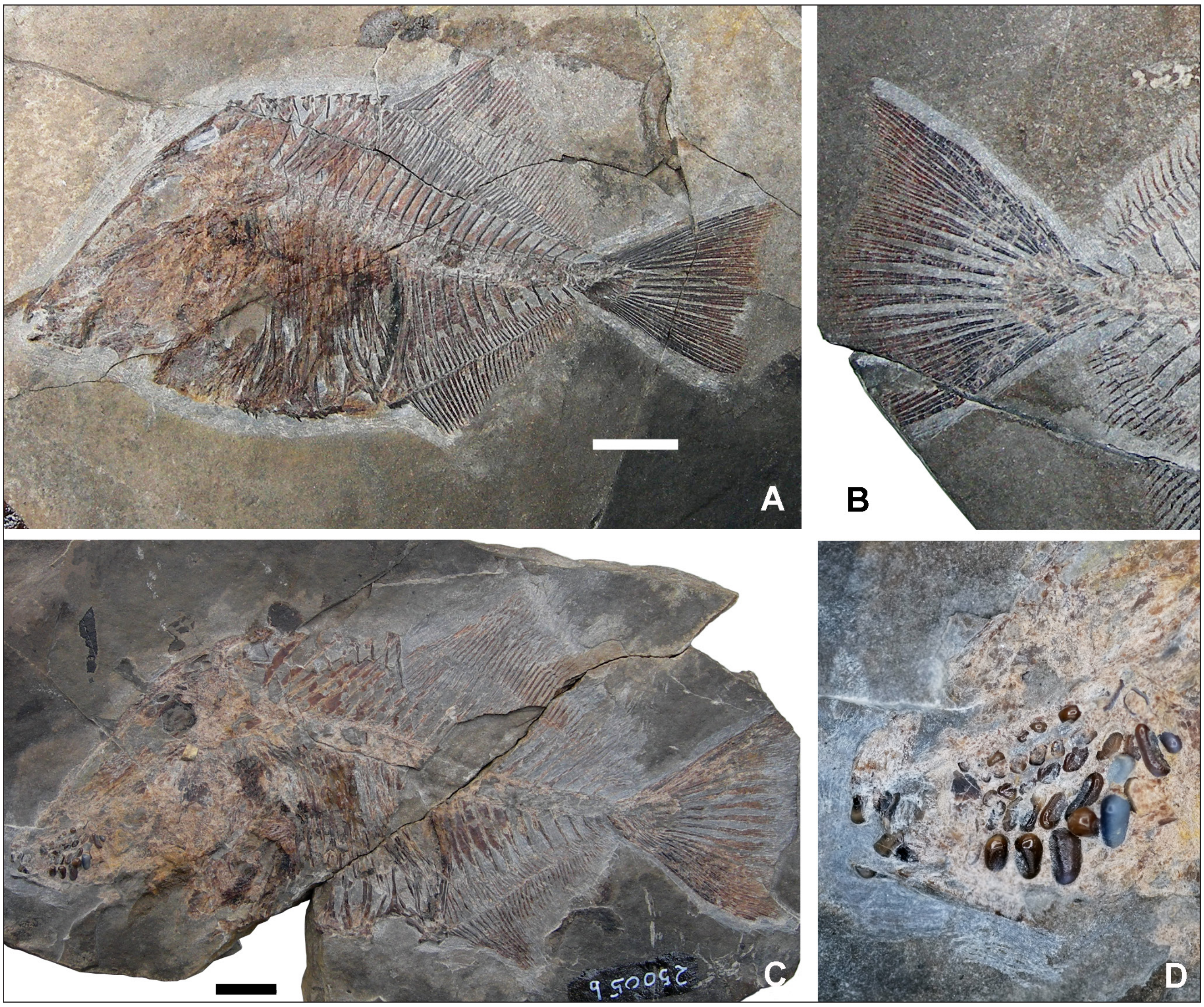

Fig. 3 - Pycnodontinae. A) MFSN 25004; B) caudal fin of MFSN 25003; C) MFSN 25005; and D) dentition of MFSN 25005. The scale bars equal 10 mm.

that the supraoccipital bone is posteriorly exposed in lateral view as a thin blade along the posterior border of the skull roof; and presence of two posterior expansions in the cleithrum that frame dorsally and ventrally a high notch for the insertion of the pectoral fin. It shares also a combination of characters that is unique of this clade: flank scales reduced to an osseous bar in a clathrate pattern of squamation; preopercular bone reduced in height, as high as the exposed, ornamented portion of dermohyomandibular bone or lower; ornamented portion of the dermohyomandibula expanded accordingly in height; and presence of a bifid scale roofing the cloaca dorsally. The morphology of the dorsal ridge scales (hammer-shaped and anteriorly pointed) and the count of the spines of the ventral keel scales of the taxon from "locality 84" are unique, as are its tooth morphology and counts. The naming of the new taxon will be the object of a future publication

- Non-acanthomorph teleosts

They are the most common fishes in the sample. Four orders have been preliminarily identified within non-Acanthomorpha teleosts: elopiforms, gonorhynchiforms, crossognathiforms, and possibly albuliforms (Tab. 1).

Elopiformes. Most of the non-acanthomorph teleosts from "locality 84" assemblage are elopiforms (at least 46 specimens: MFSN 38092; 38708-09; 38743; 38780; 38814; 38818-19; 38876-

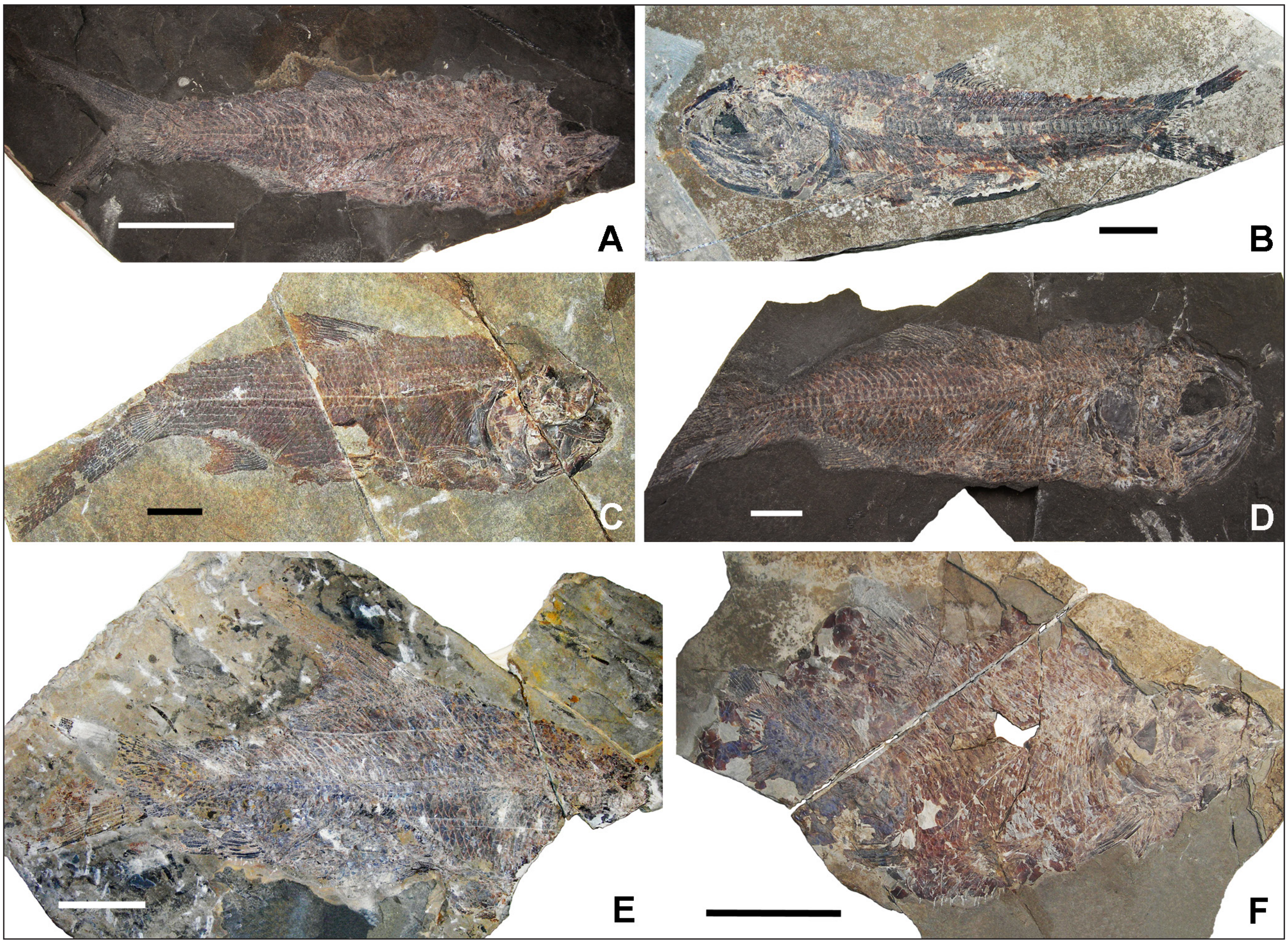

Fig. 4 - Elopomorpha. A-D) Elopiformes (MFSN 43686; MFSN 38972; MFSN 38973; MFSN 38949); and E-F) putative Albuliformes (MFSN 38920 and MFSN 38991). The scale bars equal 50 mm in A and E-F, 10 mm in B-D.

77; 38879-80; 38886-89; 38892- 93; 38896; 38902; 38922-23; 38937; 38941; 38942/38983-43; 38945-46; 38948-49; 38957; 38959; 38961/43691; 38970; 38972-75; 38977; 38979; 38987-88; 43642; 43654; 43656/43681; 43684; 43686; 43753; and 43764-65; Fig. 4A-D). They appear to belong to a single species with standard length ranging 87-200 mm (the longest specimen is MFSN 43686, Fig. 4A). The body of these fishes has a relatively slender outline. The head is large compared to the body size, with a very large orbit and elongated, curved and almost edentulous jaw bones with very small villiform teeth arranged in patches, as it is common within the elopiforms (see Forey 1973 and Forey et al. 1996). There are pectoral and pelvic splints, i.e. thin bony flanges associated with the edge of the outermost fin ray, an elopiform feature (Forey 1973; Forey et al. 1996; Alves et al. 2020; see SI, Fig. 2-3). The pectoral splint is a character diagnostic of the basal elopomorphs (Forey 1973; Forey et al. 1996; Filleul & Lavoué 2001). The vertebral column consists of 55-56 vertebral centra which are higher than long and with weak ornamentation on the side. The dorsal fin inserts around the body mid length; the pelvic fin is located just anteriorly to the level of the dorsal fin; the anal fin inserts at the level of the posterior end of the dorsal fin (Fig. 4A-D). The squamation consists of small and ovate cycloid scales of rather regular size which are slightly higher than long and ornamented with numerous concentric circuli. Elopiformes is a clade of marine and brackish elopomorphs that comprises two living genera, *Elops* (ladyfish) and *Megalops* (tarpons) (Nelson et al. 2016) as well as 24 Mesozoic and seven Cenozoic extinct species (Alves et al. 2020).

Albuliformes. The fossil fish assemblage includes only two putative albuliform specimens (MFSN 38920 and 38991), both comparatively deep-bodied and large-sized being ca. 370 and 198 mm in standard length and ca. 450 -ca. 224 mm in

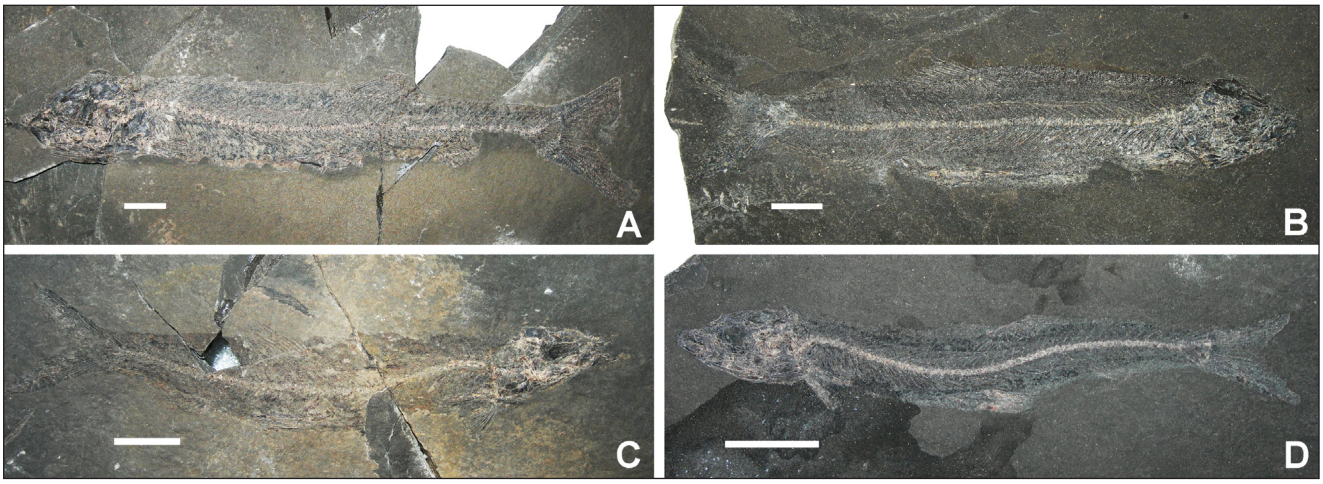

Fig. 5 - Gonorhynchiformes, Chanidae. A) MFSN 38940; B) MFSN 38944; C) MFSN 38965; and D) MFSN 39396. The scale bars equal 10 mm.

total length, respectively. MFSN 38920 (Fig. 4E) is perfectly articulated but headless. MFSN 38991 (Fig. 4F) has a relatively long and deep head with a short snout. Its orbit is large and occupied by the black spot of organic matter representing the remains of the eyeball. They both have highly falcate dorsal and anal fins, a long anal fin base, and elongated fourth dorsal and anal fin rays (SI, Figs 4 and 5A). The longest fin rays are more than six times longer than the posteriormost fin rays (MFSN 38920). There is a pectoral fin splint (MFSN 38991; SI, Fig. 6). The body is covered with cycloid scales of moderately large size with numerous horizontal radii (SI, Fig. 5). The scales are tightly imbricated so that the exposed portion is about twice as high as long (SI, Fig. 5C). MFSN 38920 is tentatively referred to the same taxon as MFSN 38991, because it has the same squamation pattern and a similar overall morphology. The general body shape, squamation pattern and fins shape of these specimens resemble those of the albuliform *Brannerion* from the Aptian-Albian of Brazil (see Blum 1991; Forey & Maisey 2010; Mayrink et al. 2010). They are provisionally referred to as indeterminate albuliforms because of the incomplete preservation of the head and pending further preparation. Albuliformes is another clade within the Elopomorpha. It is an extant and fossil marine group with low diversity which appeared during the Early Cretaceous (Mayrinck et al. 2010).

Gonorhynchiformes. The gonorhynchiforms represent a second major component of the assemblage (at least 27 specimens: MFSN 38717; 38744/38878; 38745; 38882; 38890-91; 38940; 38944; 38957; 38965, 38975-76; 38980-81; 38982-84; 38988-89; 38997; 39396; 43651; 43654; 43680; 43690; and 43693-94; Fig. 5). All referred specimens appear to belong to a single species with a long and slender body and a triangular head relatively elongated anteroposteriorly. Standard length ranges 65-127 mm and total length 74-145 mm. There are some differences in relative body depth between individuals (cf. Fig. 5B and D) possibly due to sexual dimorphism (Guadarrama & Cantalice 2025). The orbital region does not exhibit any indication of the presence of orbitosphenoid and basisphenoid and in the axial skeleton there are three sets of intermuscular bones (SI, Fig. 7) as in other gonorhynchiforms (Fink & Fink 1981, 1996; Grande & Poyato-Ariza 1999; Amaral et al. 2013). The dorsal fin inserts at the body mid-length, whereas the pelvic fin inserts just at the same level of the dorsal fin. There are about 50 vertebral centra. The following combination of characters allows referring these specimens to the Chanidae: frontals large at the postorbital and orbital levels, with an acute anterior border; premaxilla large, very broad, concave-convex and with long oral process; maxilla swollen posteriorly to a bulbous outline, with a curved posterior border; quadrate anteriorly displaced, with correspondingly elongated posteroventral process of the quadrate, interoperculum and anteroventral limb of the preoperculum; quadrate-mandibular articulation displaced anteriorly to the level of the orbit; limbs of the preoperculum at straight angle and preopercular expansion present; operculum expanded, occupying about one third of the total head length (SI, Figs. 7-8; Poyato-Ariza &

Fig. 6 - Crossognathiformes, Pachyrhizodontidae, MFSN 38921. The scale bars is centimetric.

Martìn-Abad 2016; Guadarrama & Kantalice 2025). The Gonorhynchiformes have seven extant genera and fossil gonorhynchiforms are known from the Early Cretaceous (Berriasian) to the Early Miocene (Fara et al. 2009; Poyato-Ariza et al. 2010; Guadarrama & Kantalice 2025). The Chanidae have a single living species (*Chanos chanos*) and a Berriasian-Burdigalian fossil record (13 genera and 17 species; Guadarrama & Kantalice 2025).

Crossognathiformes. MFSN 38921 (Fig. 6) is a nearly complete specimens with a standard length of ca. 240 mm. Its skull is crushed and poorly preserved, showing the dorsolateral side. The jaws are elongated and recurved upward towards the anterior end, bearing medium-sized and wide-spaced teeth. Tooth count for each jaw is not clear, because the jaw bones are only partially preserved and teeth are displaced. Wide and flat bones interpreted as fused and expanded infraorbitals are present around the posterior and the ventral margins of the orbit. There are three sets of intermuscular bones (SI, Fig. 9). The caudal-fin rays are hypurostegic, especially in the upper lobe, with the bases of the principal rays crossing obliquely over the entire upper hypural series (SI, Fig. 10). The caudal skeleton exhibits six hypurals, two epurals, and two uroneurals (Fig. SI, Fig. 10). The first and second hypurals are fused together on more than half of their length. The first uroneural reaches the third preural centrum. The parhypural is fused with the first preural centrum. There is the parhypurapophysis. The specimen belongs to the Pachyrhizodontidae based on the expanded and fused infraorbitals, the first and second hypurals fused together for almost their entire length, the first uroneural reaching at least the second preural centrum, the parhypural fused with the first preural centrum and strong hypurostegy (Forey 1977; Cavin 2001). Also MFSN 38820 might be a pachyrhizodontid exhibiting the presence of the parahyurapophysis (Cavin 2001). The morphology of the caudal skeleton and the upward recurved jaws are not reminiscent of any known pachyrhizodontid, but three sets of intermuscular bones are reported only in the Cenomanian-Turonian *Elopopsis* (Forey 1977). Thus, the specimen is here referred to an indeterminated pachyrhizodontid. Crossognathiformes is an order of extinct fish erected by Taverne (1989) to contain the crossognathids and the pachyrhizodontoids. Pachyrhizodontidae is a typical Late Jurassic-Cretaceous clade with only a single species from the Cenozoic (early Eocene) (Cavin 2001; Arratia & Tischlinger 2010).

- Acanthomorpha

The Acanthomorpha, or spiny-rayed fishes, are the largest group of living teleost fishes. They have been historically recognized based on the presence of true fin spines in the dorsal and anal fins (Rosen 1973; Johnson & Patterson 1993); the presence of a haemaxanal complex (Blot 1969); the thoracic position of the pelvic girdle (Taverne 2011); and pelvic fin rays numbering seven (Otero & Gayet 1996). Only 16 specimens (MFSN 38058; 38077; 38098; 38778; 38954; 38992; 38898/50751;

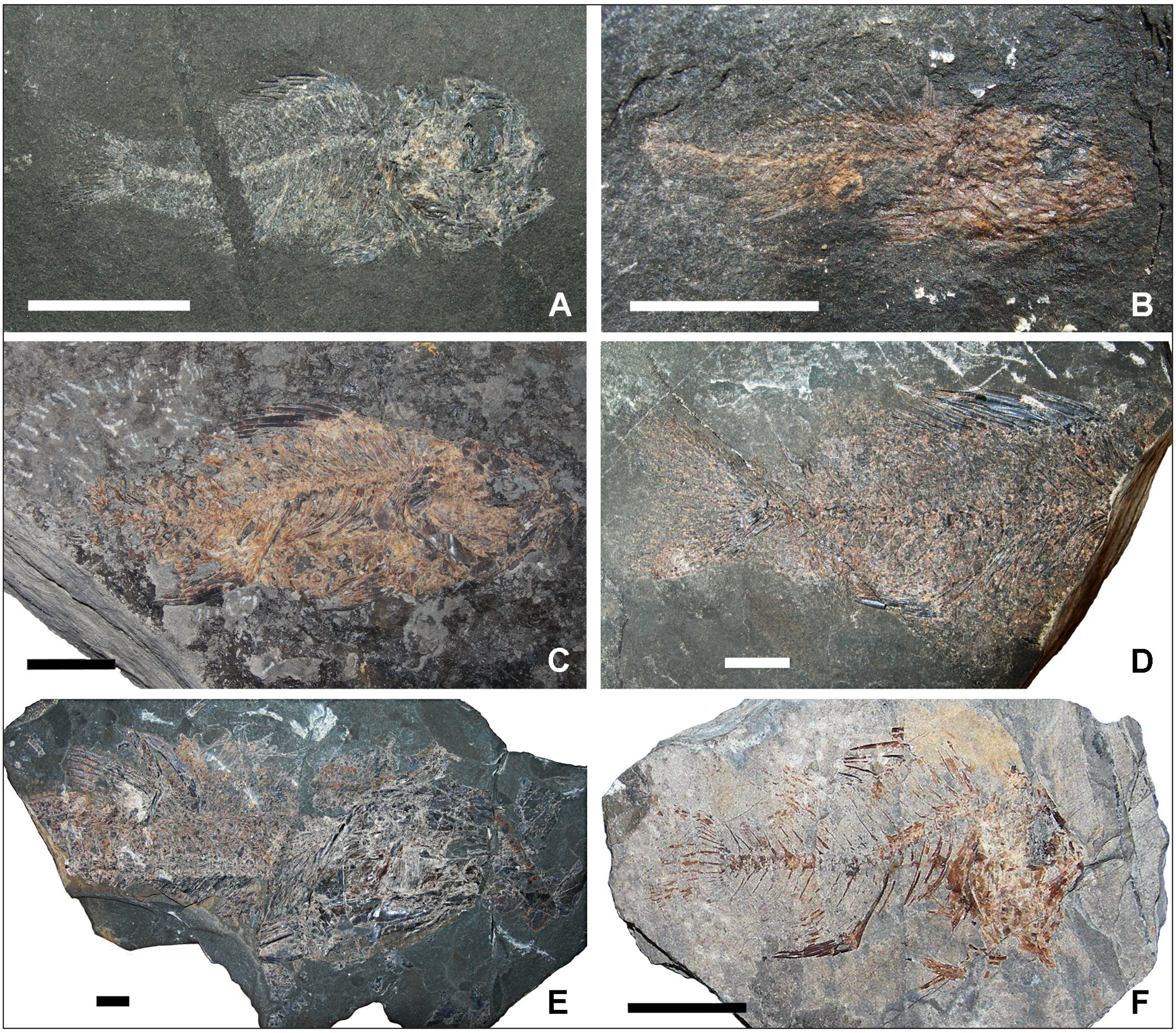

Fig. 7 - Acanthomorpha. A) Indeterminate Beryciformes, MFSN 38994; B) ?Percomorphacea, MFSN 50751; C) ?Percomorphacea, MFSN 43751; D) indeterminate acanthomorph, MFSN 38098; E) indeterminate acanthomorph, MFSN 43697; and F) indeterminate acanthomorph, MFSN 38992. The scale bars equal 10 mm.

38994/43671; 43615; 43640, 43718, 43751; 43697; and 50891-93; Fig. 7) can be referred to the Acanthomorpha for the presence of at least one of the aforementioned features. They represent 3.6% of the fish sample.

The oldest skeletal record of the acanthomorphs is from the upper Albian-Cenomanian of Mexico (Murray 2016) and the Cenomanian of Lebanon (Hadjoula, Hakel and Namoura sites; Forey et al. 2003; Gayet et al. 2012); they remained a minority component of the ichthyofaunas up to the early Eocene (Chen et al. 2014).

Most of the specimens (MFSN 38058; 38077; 38098; 38778; 38954; 38992; 43615; 43640, 43718; 43697; and 50891-93; Fig. 7D-F) are referred to indeterminate acanthomorphs because of their incomplete and/or poor state of preservation. These indeterminate acanthomorphs are different to each other for size and body shape and belong to at least two distinct species. The other specimens in the sample belong to the clades Beryciformes and possibly Percomorphacea.

Beryciformes. They are represented by a single, small sized specimen (MFSN 38994/43671; Fig. 7A) whose standard length is ca. 27 mm. The head is deep and short, with a short snout; the dorsal profile of the skull is rounded with low to absent supraoccipital crest. The body is moderately deep.

There are 27 vertebral centra, 13 abdominal and 12 caudal. The dorsal fin consists of eight spines and at least nine soft rays. The pelvic fins are thoracic with a spine and six soft rays (SI, Fig. 11A). The anal fin bears three spines and six soft rays. The haemaxanal complex inserts at the level of the fourteenth vertebral centrum and there are at least seven pterygiophores. The dorsal-fin spines exhibit a chain-link articulation (SI, Fig. 11B), which is a characteristic shared by beryciforms and percomorphaceans (Johnson & Patterson 1993). However, the count of soft rays in the pelvic fin of the Percomorphacea is five or less (Johnson & Patterson 1993; Wiley & Johnson 2010; SI, Fig. 10). The oldest Beryciformes are Cenomanian in age and are represented by nine genera from the Lebanese sites (Forey et al. 2003; Gayet et al. 2012). Beryciformes is a relatively primitive order within the Acanthomorpha; it was common during the Late Cretaceous and is represented today by 30 genera and 161 species (Nelson et al. 2016).

Percomorphacea. MFSN 38898/50751 and 43751 are two putative percomorphaceans. MFSN 38898/50751 (Fig. 7B) is small (standard length is ca. 26 mm), preserved in part and counterpart, and lacks the caudal rays. Its head is longer than deep and almost triangular with a pointed snout. The dorsal fin presents ten spines and ten soft rays. The anal fin includes three spines and seven soft rays. The vertebral count is 23-24. MFSN 43751 (Fig. 7C) is nearly complete and articulated but the caudal rays are poorly preserved. It has a moderately deep and relatively fusiform body and a triangular head that is slightly longer than high. The vertebral column consists of 29-30 vertebral centra. The discontinuous dorsal fin inserts around mid length, the anal fin insertion is just posterior to the level of the posterior end of the dorsal fin. The pelvic fins are thoracic. The dorsal fin rays consist of eight spines and about eight soft rays; the anal fin rays have three-four spine and ca. eight soft rays; and the pelvic fin has a single spine and five soft rays (SI, Fig. 12). Scales are small and ctenoid. Meristic counts, overall body shape (deeper head and shorter snout of MFSN 43751 respect to MFSN 38898/50751, larger size of MFSN 43751) and the fin shape differ between the two specimens suggesting they belong to distinct genera. Percomorphaceans are identified by a combination of skeletal features (Johnson & Patterson 1993; Wiley & Johnson 2010) the most evident of which in our specimens are the thoracic pelvic fins with fewer than six soft rays. Percomorphacea is the most diversified of all living ray-finned fish clades (Nelson et al. 2016). They spread and differentiated between the Danian and the Lutetian (Guinot & Cavin 2016), but were already present since the onset of the Late Cretaceous (Cenomanian), with multiple species known from the Campanian-Maastrichtian (Arratia et al. 2004; Friedman et al. 2023).

Terrestrial plants

The plant fossils are abundant within the fossil assemblage, comprising 237 samples (33% of the total). The remains are small and fragmented, consisting mainly of small and isolated leaves (4-80 mm long), axes (50-180 mm long) and conifer shoot fragments (25-40 mm long). In some cases, plant remains are associated on the same rock slab (2-10 remains). The fossils are preserved as compressions with a thin coal layer and venation details are rarely visible making an assignment at species level difficult. However, the morphological characters allow a tentative assignment to higher taxa (Tab. 1). Plant remains are here presented in order of abundance.

- Angiosperms

Most plant fragments (at least 130 isolated leaves and two putative shoot fragments) belong to the angiosperms. Most of the leaves are assigned to the genus *Dicotylophyllum* (Figs. 8-10). This genus is commonly used for dispersed dicotyledonous leaves of unknown affinity, typically due to poor preservation of the plant remains. These leaves reach up to 80 mm in length, though most have a lamina that is only 20-35 mm long. Their margin is entire although preservational artifacts can sometimes give the illusion of an incised margin. Leaves of the *Dicotylophyllum*-type are generally assigned to angiosperms based on their overall leaf shape, the distinctive petiole attached to the lamina with a decurrent base and, where visible, the typical angiosperm-type venation pattern. The absence of secondary veins (or even the midvein in *Dicotylophyllum* sp. 1) does not permit to assign these specimens to any family within the angiosperms. Four *Dicotylophyllum* morphotypes are distinguished in the floral assemblage under investigation.

Eleven leaves (MFSN 37647, 37655-56, 37659, 37743-744, 38081, 39238, 43587, 43591,

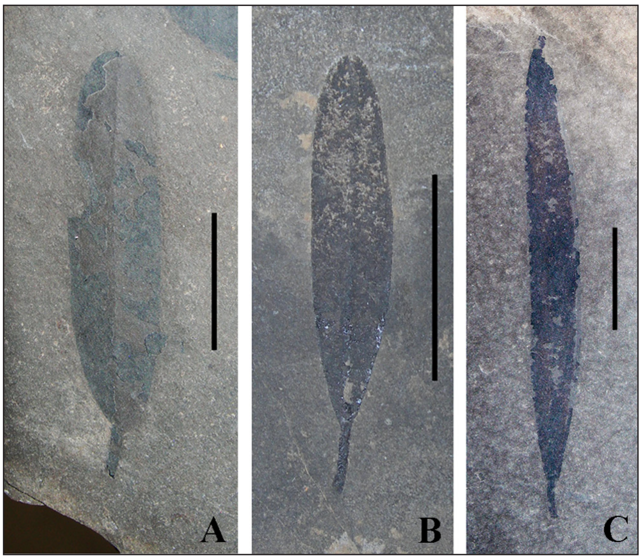

Fig. 8 - *Dicotylophyllum proteoides*. A) MFSN 37655; B) MFSN 43587; and C) MFSN 37744. The scale bars equal 10 mm.

and 43669) are assigned to *Dicotylophyllum proteoides* (Unger) Herman et Kvacek, 2010 characterized by long lanceolate leaves with a rounded apex and a decurrent basis (Fig. 8). In some leaves (e.g., MFSN 37655; Fig. 8A), marginal feeding traces of the DT 81 type *sensu* Labandeira et al. (2007) are observed. *Dicotylophyllum proteoides* occurs in the lower Campanian flora of the Grunbach Formation of Austria (Herman & Kvaček 2010). *D.* cf. *proteoides* is reported from the upper Campanian-Maastrichtian of Poland (Halamsky 2013). This taxon resembles the specimen from the Lower Cretaceous of the Profeti locality (Caserta Province, S Italy) referred by Bartiromo (2007: fig. 65/1) to *Dicotylophyllum*. Also the specimens from the lower Campanian of Tomaj (Fig. 1) referred to *Eucalyptus* sp. by Dobruskina et al. (1999: pl. 12, figs 4 and 6-7) resemble closely in shape and midrib our specimens of *D. proteoides*.

Dicotylophyllum sp. 1 (MFSN 37639-40; 37652; 37657; 37740; 37747; 37751; 37757; 37760-61; 37763; 37765; and 37768; Fig. 9A-D) is characterized by obovate (leaf lamina length to width ratio 1.5-1.8; Fig. 9A-B) to moderately elongated (leaf lamina length to width ratio 2.4-2.7; Fig. 9C-D) leaves. The leaves have a broad rounded apex and a decurrent base. The length of the petiole varies in relation to leaf length being longer in more elongated specimens. The leaves reach up to 20 mm in total length. Despite the distinct petiole, the specimens lack a clear midvein. This taxon resembles the specimens from the Lower Cretaceous of Pietraroja (Benevento Province, S Italy) described as *Dicotylophyllum* by Bartiromo (2007: fig. 65/2-3). It resembles also the leaf figured in Dalla Vecchia & Tentor (2004: fig. 44A) from the Santonian of Polazzo (Fig. 1).

The leaves of *Dicotylophyllum* sp. 2 (MFSN 37638; 37641-47; 37656; 37737-42; 37748-50; 37752-56; 37758-59; 37762; 37764; 38082; 38122; 38124; 38134; 38214; 38900-901; 39232; 39235; 39237; 39239-41; 43575-77; 43580-81; 43583; 43585-86; 43588-89; 43592; 43662; 43664; 43666-67; 43670; 43738; and 51983-84; Fig. 9E-N) are the most common in the plant fossil assemblage. They are more or less elongated (leaf lamina length to width ratio 2-4.5) with a rounded apex and a distinct midvein that generally extends to the apex. The lamina is 16 to 31 mm long, the petiole is generally short. Some leaves are slightly asymmetric along an ideal line connecting the petiole with the apex (MFSN 43580, 43670; Fig. 9G), and the petiole is asymmetrically placed (MFSN 39232, 43662, and 43580; Fig. 9E). In rare instances, leaves are attached to an axis showing their arrangement on it (MFSN 39240-41 and 38081; Fig. 9N). Some of the leaves (e.g., MFSN 43667, Fig. 9K) feature marginal feeding traces of the DT 81 type *sensu* Labandeira et al. (2007). *Dicotylophyllum* sp. 2 resembles closely *Daphnites goeppertii* Ettingshausen, 1867 from the Cenomanian of Niederschoena (Saxony, Germany) based on the general leaf shape, though our specimens lack distinct secondary veins. It also resembles the not better-defined angiosperm leaves from the middle-upper Aptian of Profeti (Caserta Province, S Italy) figured by Bartiromo et al. (2009: pl. 5, figs 3-8); "Angiosperm 1" from the upper Aptian of Cusano Mutri (Benevento Province, S Italy) figured by Bartiromo (2009: fig 70); the simple and petiolate angiosperm leaves with entire margin and a single primary vein from the uppermost Cenomanian of Monte Colle (Verona province, N Italy) figured by Gomez et al. (2015: fig. 10); *Phyllites proteaceus* from the Campanian of Vernasso (Fig. 1) as figured by Bozzi (1891: pl. 106, fig. 6-7); and the leaves from the lower Campanian of Tomaj (Fig. 1) referred to *Magnoliaephyllum* sp. by Dobruskina et al. (1999: pl. 12, figs 1-3).

Dicotylophyllum sp. 3 leaves are narrow, lanceolate to almost linear with a pointed apex, and are relatively abundant in the sample (MFSN 37648; 37650-51; 37654; 37657; 37745-46; 37763; 38079;

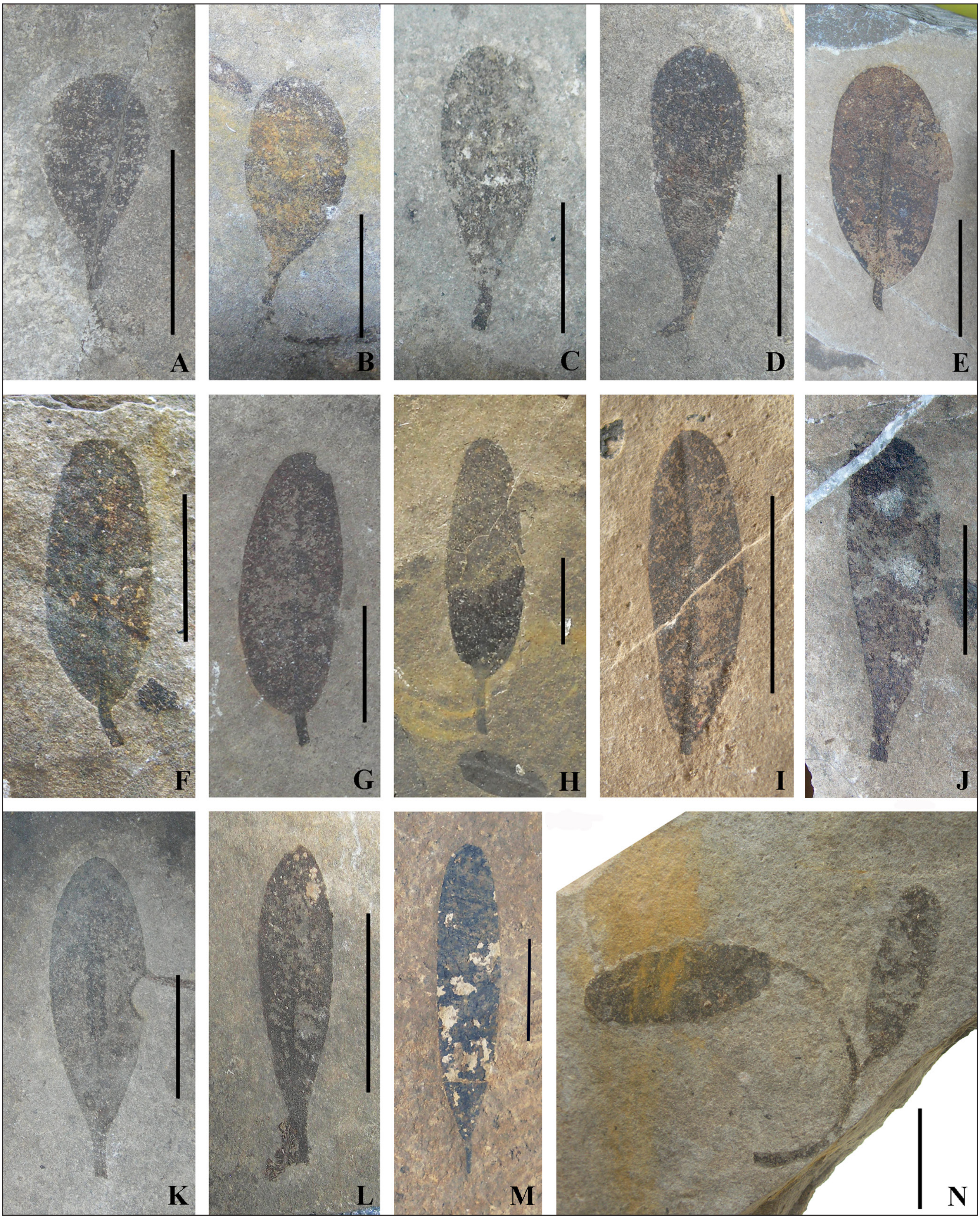

Fig. 9 - *Dicotylophyllum*. A) *D.* sp. 1, MFSN 37757; B) *D.* sp. 1, MFSN 43665; C) *D.* sp. 1, MFSN 43668; D) *D.* sp. 1, MFSN 37751; E) *D.* sp. 2, MFSN 39232; F) *D.* sp. 2, MFSN 37750; G) *D.* sp. 2, MFSN 43670; H) *D.* sp. 2, MFSN 38900; I) *D.* sp. 2, MFSN 37752; J) *D.* sp. 2, MFSN 37641; K) *D.* sp. 2, MFSN 43667; L) *D.* sp. 2, MFSN 37741; M) *D.* sp. 2, MFSN 38901; and N) *D.* sp. 2, MFSN 39241. The scale bars equal 10 mm.

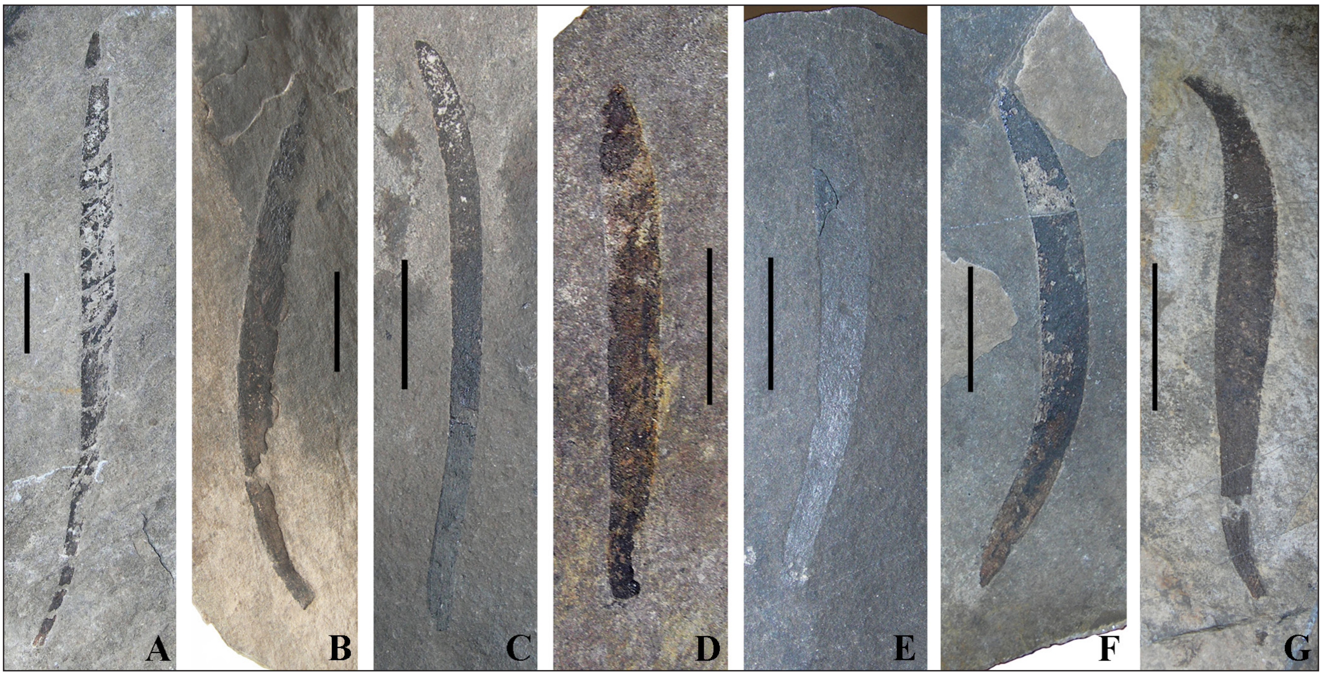

Fig. 10 - *Dicotylophyllum* sp. 3. A) MFSN 43600; B) MFSN 37746; C) MFSN 43589; D) MFSN 39253; E) MFSN 43599; F) MFSN 43604; and G) MFSN 39254. The scale bars equal 10 mm.

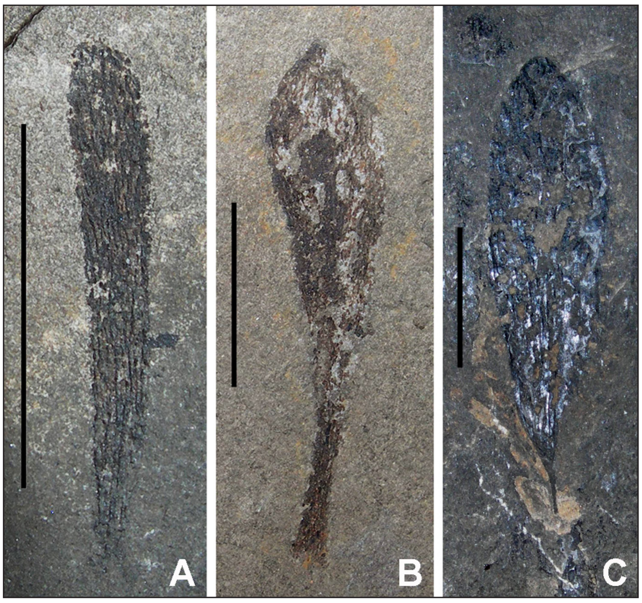

Fig. 11 - *Plantaginopsis* sp. A) MFSN 37760; B) MFSN 37653; and C) MFSN 43584. The scale bars equal 10 mm.

38138; 38140; 38889; 38894; 38980; 39253-54; 43589; 43599-600; 43604; and 43734-37; Fig. 10). They are similar in morphology and differ only in size. The margin is entire, no distinct venation is visible. They are up to 80 mm long and often found associated (i.e. two or more isolated leaves on the same slab; e.g. MFSN 37745 and 38140) or associated to the leaves of *Dicotylophyllum* sp. 1 and *D.* sp. 2 (e.g. MFSN 37657 and 43589). Currently, all elongated, linear leaves with a broad base (no petiole) are grouped within this taxon, although it is possible that not all specimens belong to the same natural genus and species. The leaves resemble those of certain conifer taxa such as *Podozamites* or *Elatocladus*, but they lack distinct parallel veins and are much longer and linear.

Plantaginopsis is a genus that encompasses narrowly elliptical to linear leaves that narrow gradually to a clasping base lacking a petiole. Similar leaves are present also in the plant fossil assemblage from “locality 84” (MFSN 37653 37760; 43576; 43584; and 51985; Fig. 11). These specimens not only share the general shape of the genus, but also preserve the characteristic more or less parallel venation (Fig. 11). MFSN 37653 (Fig. 11B) resemble also “Angiosperma 3” from the lower Aptian of Cusano Mutri (Benevento province, S Italy) figured by Bartiromo (2007: fig. 72).

Eleven leaf fragments are characterized by almost falciform segments with a symmetrical and restricted base (MFSN 38781; 38899; 39227; 39245-47; 39249-50; 43596-97; and 51987; Fig. 12A-G). The leaf apex is bluntly acute with a terminal pinna (e.g., MFSN 39249; Fig. 12A). The apex of each segment is acute, terminating bluntly, the proxi-

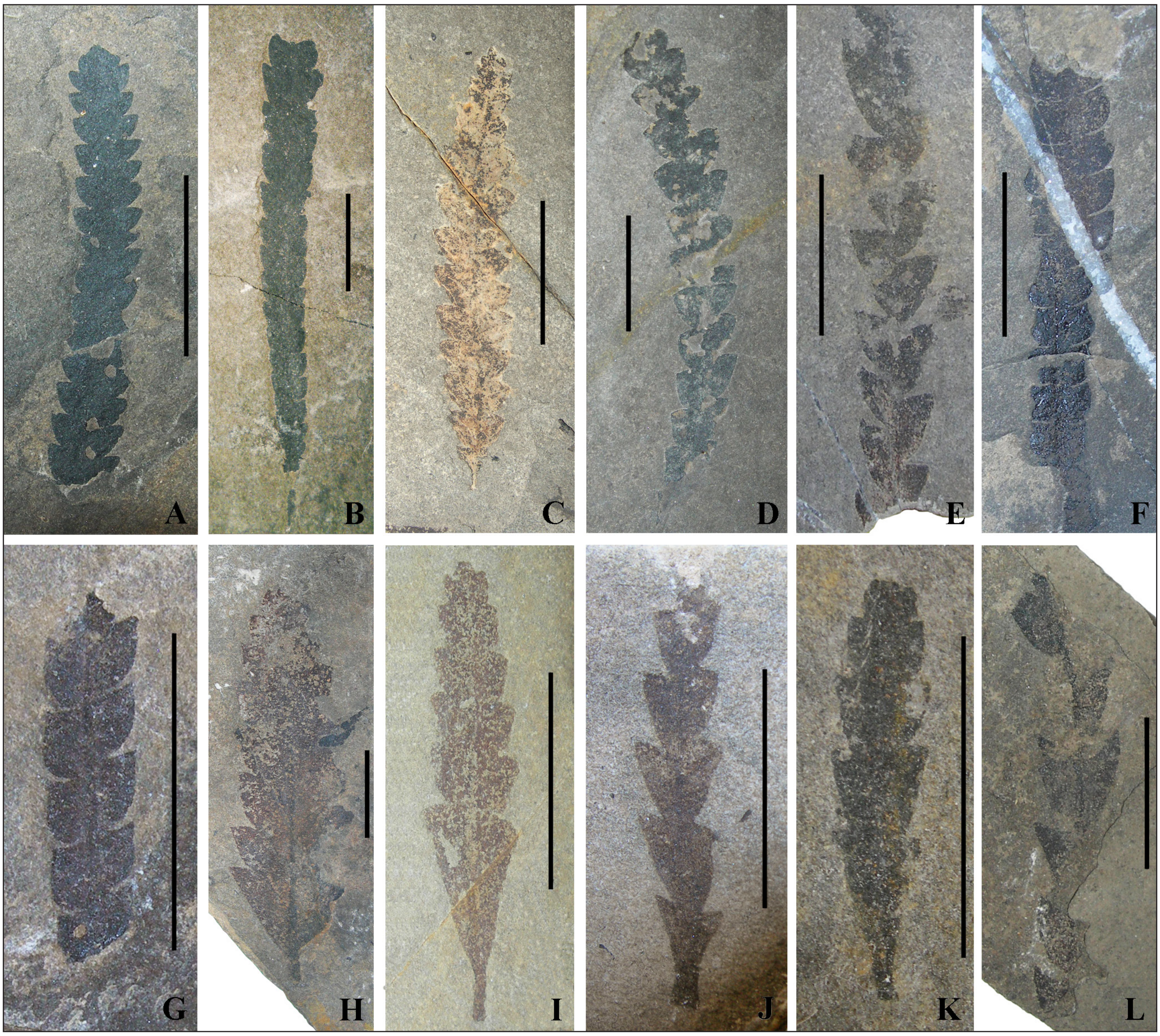

Fig. 12 - *Aenigmatophyllum* and *Papillaephyllum.* A) *Aenigmatophyllum* cf. *gothani,* MFSN 39249; B) *A.* cf. *gothani*, MFSN 38781; C) *A.* cf. *gothani,* MFSN 39227; D) *A.* cf. *gothani*, MFSN 39246; E) *A.* cf. *gothani*, MFSN 39247; F) *A.* cf. *gothani*, MFSN 43597; G*) A.* cf. *gothani*, MFSN 51987; H) *Aenigmatophyllum* sp., MFSN 39223; I) *Aenigmatophyllum* sp., MFSN 39224; J) *Aenigmatophyllum* sp., MFSN 51988; K) *Aenigmatophyllum* sp., MFSN 39231; and L) ?*Papillaephyllum*, MFSN 38085. The scale bars equal 10 mm.

mal flanks of the segments are convex, the distal ones are straight to (e.g., MFSN 39249 and 39247; Fig. 12A and E). Each segment is attached with the entire base to the rachis; only one midvein can be distinguished, no further venation pattern can be observed. Apically and basally the segments reduce in size. The leaves have sometimes a slightly leathery appearance with a thick, coaly material. These leaf fragments resemble very closely *Aenigmatophyllum gothani* (Krestew) Hartung et Gothan, 1939 from the Upper Cretaceous of Bulgaria (Hartung & Gothan 1939) and the Turonian of Romania (Givulescu 1982). They also show some resemblance to *Quercophyllum*, particularly *Quercophyllum tenuinerve* Fontaine, 1889 from the Lower Cretaceous of USA, due to the thick leaf substance, smaller basal segments and poorly defined venation.

Four leaves (MFSN 39223-24, 39231, and 51988; Fig. 12H-K) are tentatively assigned to the genus *Aenigmatophyllum*, though not assigned to any species. This taxon includes narrowly elliptical, serrate leaf "pinnae" fragments with a symmetrical, restricted base (e.g., MFSN 39224; Fig. 12I). The leaf apex is bluntly acute, with a terminal pinna

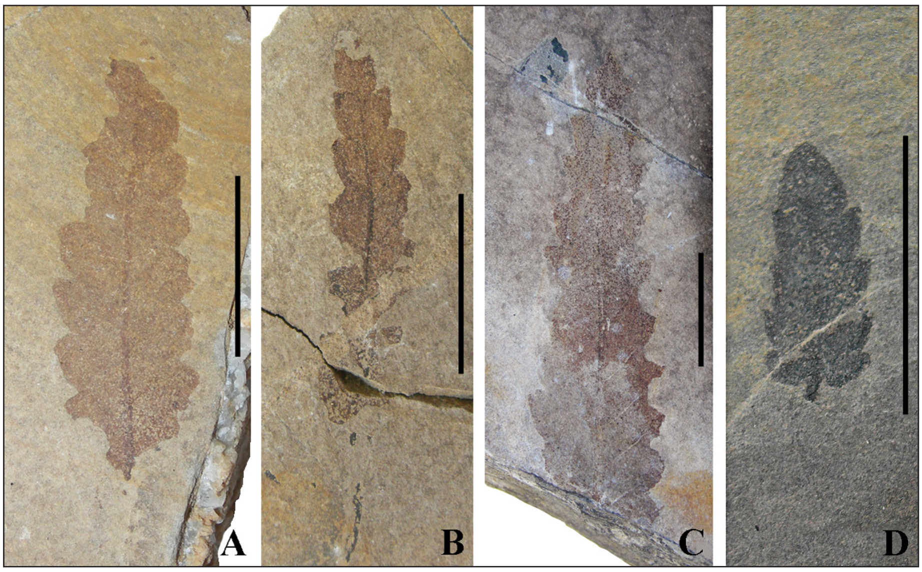

Fig. 13 - Putative *Barykovia* sp. A) MFSN 39225; B) MFSN 39229; C) MFSN 39228; and D) MFSN 39263. The scale bars equal 10 mm.

(Fig. 12I). The segments are attached with the entire base, arranged almost oppositely to the rachis. Both midvein and secondary veins are indistinct.

One specimen (MFSN 38085; Fig. 12L) represents a simple, narrowly serrate leaf with deeply incised teeth. The distal flank of each tooth is cavate, whereas the proximal flank of the tooth is straight to convex. Unfortunately, the teeth are not well distinct. The segment resembles *Papillaephyllum labutae* Čepičková et Kvaček, 2023 from the Cenomanian of the Czech Republic in overall morphology but differs because of the missing papillae and the more deeply incised lamina. Since there is so far only one specimen, we tentatively assign it to the genus *Papillaephyllum* without any species assignment.

Five leaf fragments with an oblong to narrow elliptical, symmetric shape (MFSN 39225; 39228-29; 39263; and 43578; Fig. 13) could belong to *Barykovia* sp. The leaf base and apex are, unfortunately, not preserved except in specimen MFSN 39263, which appears to represent a small or juvenile leaf fragment. The leaf margin is dentate to serrate, with teeth that are more or less regularly spaced and triangular to rounded triangular in shape. The venation is irregular pinnate, with a straight, distinct midvein. Secondary veins arise oppositely at an angle of approximately 40-50°. Quaternary veins are not preserved. One secondary vein enters each lobe/dentate expansion of the leaf lamina (Fig. 13A-B) that terminates with a pointed apex (Fig. 13C-D). These specimens closely resemble *Barykovia kamchatica* Moiseeva, 2012 from the Campanian of the eastern Siberia (Moiseeva 2012; Moiseeva & Sokolova, 2014, fig. 4a-d), but the lack of the base and apex precludes an assignment at species level.

In addition, two shoot fragments could belong to angiosperms, but are too badly preserved for a determination at genus/species level. Angiosperm shoot fragment type 1 (MFSN 43595; Fig. 14A) has a long petiole that divides apically dichotomously. Each bifurcating axis bears a series of sub-triangular leaves/segments, which appear to increase in size towards the apex. Putative angiosperm shoot fragment type 2 (MFSN 43601; Fig. 14B-C) has a long axis with distally small, pinnae-like segments arising alternately from the axis. The distal leaves (Fig. 14C) are inserted alternately to the rachis. Due to the poor preservation and the absence of a discernible venation, no taxonomic assignment is made, and it cannot be excluded that the specimen belongs rather to the fern or seed ferns.

- Coniferophyta

Conifers are much less abundant than angiosperms, represented by only 19-22 specimens, but they include several taxa. Among these are at least two morphotypes of the cheirolepidiacean *Frenelopsis*. Unfortunately, shoot fragments do not yield cuticles, preventing an assignment at species level. *Frenelopsis* sp. 1 (MFSN 37658; 38087; 39259; 43592; and 43594; Fig. 15A-C) is characterized by articulated shoot fragments consisting of long sheaths with internodes exceeding 20 mm in length and 3 mm in width. These shoots lack grooves or sutures between adjacent leaves and terminating in a whorl of two (or 3) leaves (e.g., MFSN 37658; Fig. 15A).

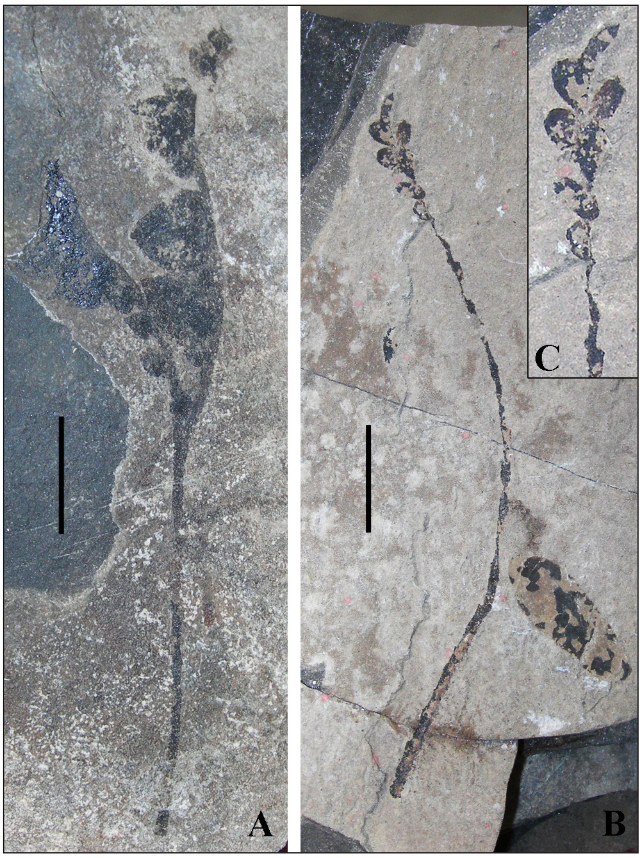

Fig. 14 - Shoot fragments possibly belonging to the angiosperms. A) MFSN 43595; B) MFSN 43601; and C) detail of B. The scale bars equal 10 mm.

The free leaf tip is about 1 mm long. *Frenelopsis* sp. 2 (MFSN 39252/43602; Fig. 15D) is represented by a shoot fragment with much shorter internodes, approximately 2.5 mm long and 2 mm wide, and shows three leaves arising from alternating whorls. The leaves are less than 1 mm long. There are some putative shoot fragments that are 30-40 mm long and 2-3 mm wide, linear without distinct leaf bases (MFSN 37685; 38107; 38139; 38896; 38989; 39260; and 43592; Fig. 15E). The general shape of the structures and the articulate nature suggest that they belong also to the genus *Frenelopsis*.

Frenelopsis has been reported from many Cretaceous localities in Italy (e.g., Gomez et al. 2002; Dalla Vecchia & Tentor 2004; Bartiromo 2007; Bartiromo et al. 2009, 2012; Giusberti et al. 2016) and in the rest of Europe, Sudan, Tajikistan, Malaysia, Japan, USA and Brazil (Marmi et al. 2023).

Some irregularly branching conifer shoots (MFSN 39408 and 43661 both from "locality 84" ovest; Fig. 15F-G) with very small leaves (1.5-2 x 0.5-1 mm) are attributed to the genus *Widdringtonites*. The leaves are subtriangular in shape with a slightly rounded apex (e.g., MFSN 39408) and a decurrent base. They are appressed, sessile and imbricate slightly. Apically the shoots branch several times forming groups of terminal shoots that are slightly narrower than the penultimate shoots, arising from the axis at an angle of 20-25°. A roundish structure, approximately 4-4.5 mm in diameter, occurs close to one of the penultimate shoots. The slightly irregular shape and the short stalk suggest this could be a cone, supporting the assignment to the family Cupressaceae. Similar material has been described from the Turonian-Coniacian of northeastern Russia as Cupressaceae gen. et sp. indet. cf. *Widdringtonites* sp. (Herman & Sokolova 2016).

Short, unbranched conifer shoot fragments with leaves that are much longer than wide (MFSN 39251, 39261, and 43740) are assigned to the genus *Pagiophyllum*. We distinguish two taxa. *Pagiophyllum* sp. 1 (MFSN 39251 and 43740; Fig. 15H) has up to 7 mm long and 1 mm wide leaves that imbricate substantially along the axes. The leaves are falcate in lateral view, with acute apices that slightly curve towards the axis. The leaves resemble *Geinitzia* in general leaf arrangement and shape, but differ due to the less falcate and imbricate leaves. MFSN 39251 closely resemble "*Pagiophyllum* sp. nov." as figured by Dobruskina et al. (1999, pls 4-6) from the lower Campanian of Tomaj (Fig. 1). *Pagiophyllum* sp. 2 is a badly preserved shoot fragment (MFSN 39261; Fig. 15I) with only a few attached leaves. The leaves are up to 5 mm long and 0.5 mm wide, arising at an angle of about 45° and are linear with a pointed apex. The straight leaf shape suggests that it may belong to a different species, but the fragmentary nature and poor preservation prevent a more detailed assignment. Additionally, the missing cuticles preclude assignment of either taxa to any cuticle-based genus and species.

A poorly preserved dispersed leaf (MFSN 51986; Fig. 15J) is tentatively referred to the genus *Brachyphyllum* based on the broad outline and the wide attachment area of the leaf to the shoot. The leaf is subtriangular with a slightly pointed apex, 9 mm long and 5 mm wide. Unfortunately, this is the only specimen found so far in the "locality 84", but it differs noticeably in shape and size from all other conifer remains found in the plant fossil assemblage. Similar leaves are more common in the locality 122 (MFSN 43789; 43792; 43799; and

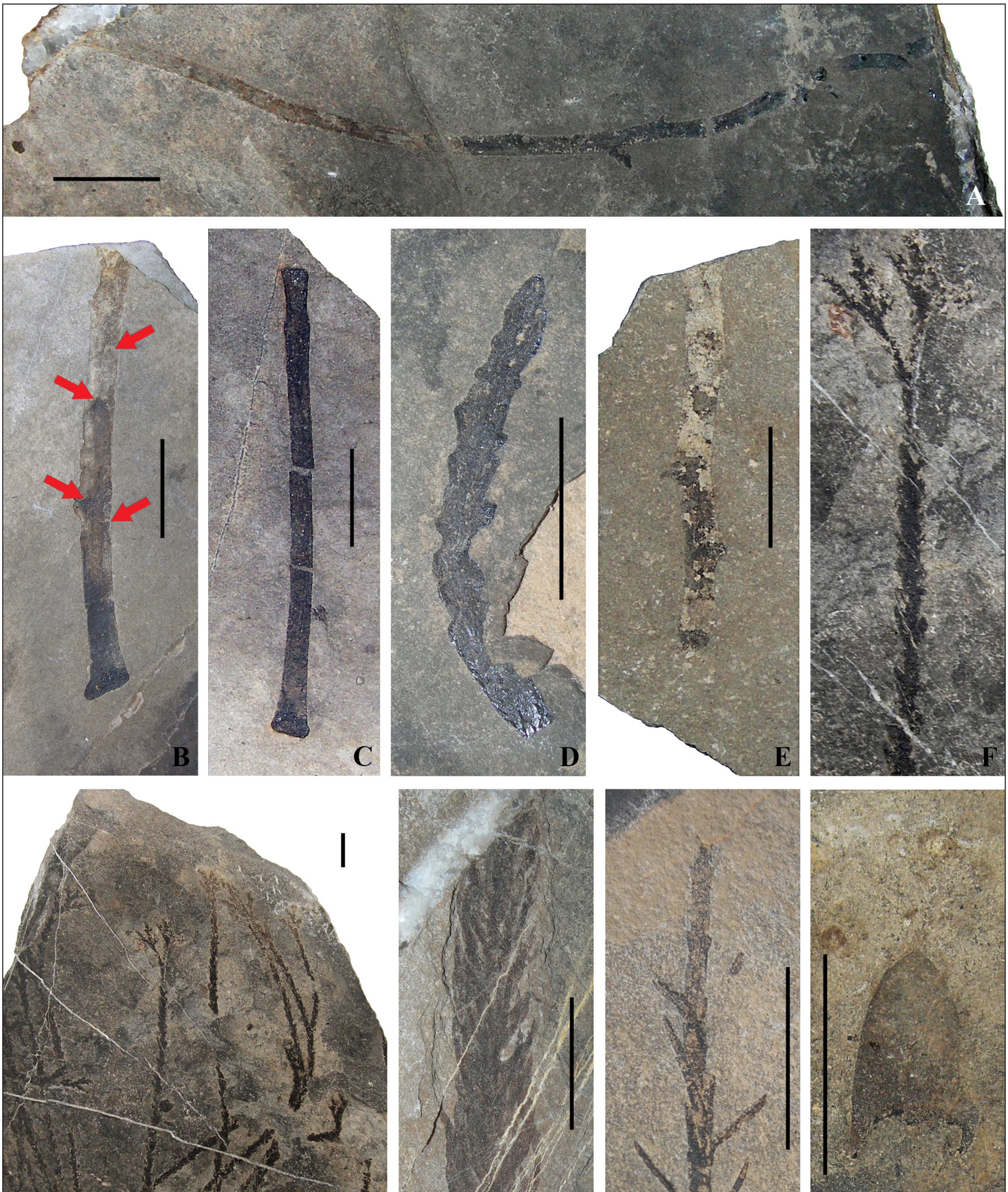

Fig. 15 - Conifers. A) *Frenelopsis* sp. 1, MFSN 38087; B) *Frenelopsis* sp. 1, MFSN 37658 (arrows point to the leaves); C) *Frenelopsis* sp. 1, MFSN 39259; D) *Frenelopsis* sp. 2, MFSN 43602; E) ?*Frenelopsis*, MFSN 38896; F) *Widdringtonites* sp., detail of MFSN 39408b; G) *Widdringtonites* sp., MFSN 39408b; H) *Pagiophyllum* sp. 1, MFSN 39251; I) *Pagiophyllum* sp. 2, MFSN 39261; and J) *Brachyphyllum* sp. leaf, MFSN 51986. The scale bars equal 10 mm.

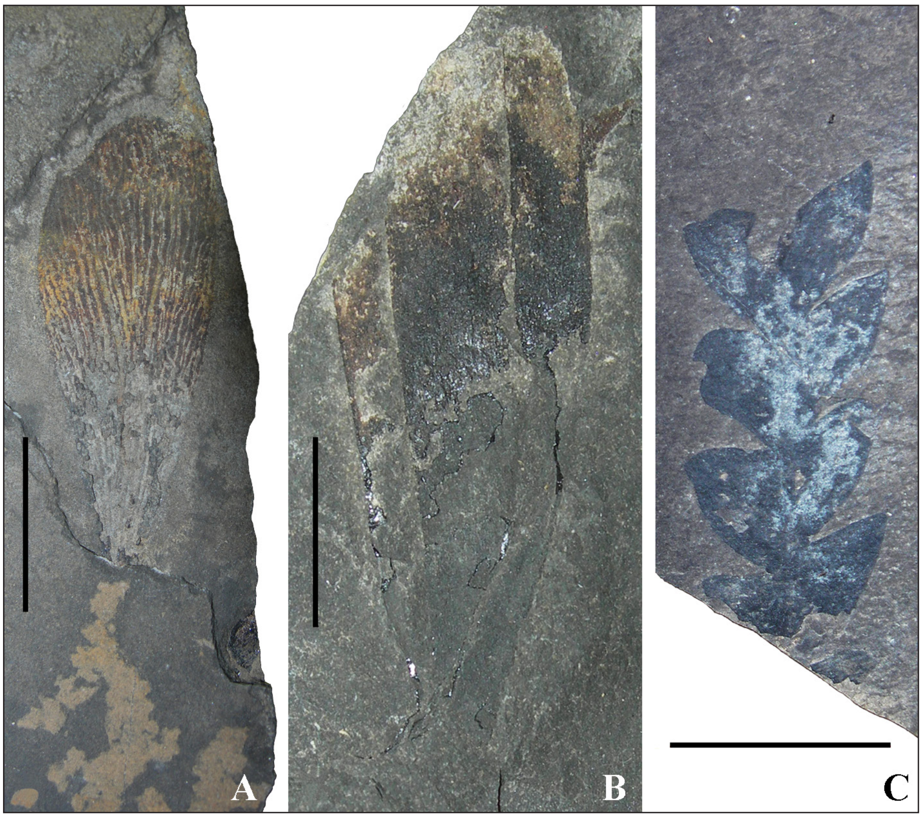

Fig. 16 - Ginkgophytes and seed fern. A) *Eretmophyllum obtusum*, MFSN 39262; B)?*Phoenicopsis*, MFSN 43593; and C) *Pachypteris* sp., MFSN 39248. The scale bars equal 10 mm.

43800) and closely resembles the leaves from Vernasso 1 (Fig. 1) referred to *Araucaria macrophylla* by Bozzi (1891) and those from Tomaj (Fig. 1) referred to *Araucarites*? by Dobruskina et al. (1999: pl. 11, figs. 1-6). However, MFSN 51986 is 1/3 the length of the leaves of *Araucaria macrophylla* from Vernasso, and about half the length of those from Tomaj and "locality 122".

- Ginkgophyta

The ginkgophytes are represented by two distinct leaf morphotypes. The first morphotype is a simple, entire-margined, oblanceolate, and partly asymmetrical leaf (MFSN 39262; Fig. 16A). The petiole is absent but the leaf increases slightly from the narrow cuneate base leaf lamina to the rounded apex. The veins are parallel, subparallel, branching dichotomously and do not reach the top of the apex instead terminating in the converging apex margins. Leaf shape and venation pattern correspond to *Eretmophyllum obtusum* (Velenovský) Kvacek, 1999 from the Cenomanian of Bohemia.

The second morphotype (MFSN 43593; Fig. 16B) resembles a leaf bundle of *Phoenicopsis*. It shows four linear leaves that arise from the same base suggesting that they belong to the same shoot fragment. The segments are of similar width with an obtuse apex and parallel veins. Some smaller isolated leaves (MFSN 37649-50; 37654; 38079; and 38120) resemble isolated leaves of *Phoenicopsis*, although they do not preserve parallel veins. *Phoenicopsis* is found in the Cretaceous of the Northern Hemisphere (Nosova et al. 2020). Unfortunately, no cuticle is preserved, preventing a confident assignment to this genus.

- Pteridospermatophyta

One fragment (MFSN 39248; Fig. 16C) may belong to the seed ferns. It is characterized by subtriangular segments attached to the rachis. Each pinna is subtriangular in shape with a slightly pointed to rounded apex. The leaf texture is very thick, suggesting that cuticle may be present. The pinnae exhibit extensive plant-animal interactions, including marginal feeding traces of the DT 81 type *sensu* Labandeira et al. (2007). The veins are not clearly distinguishable. The thick, leathery texture and the shape of the segments support a seed fern affinity. Kerner (1895) figured leaf fragments with pinnae of similar shape as *Pachypteris dalmatica* Kerner, 1895 or *Pachypteris ovata* Brongniart, 1828 from the Turonian of the Hvar/Lesina Island (Croatia). The small dimension of the fragment does not permit us to assign the specimen confidentially to any species.

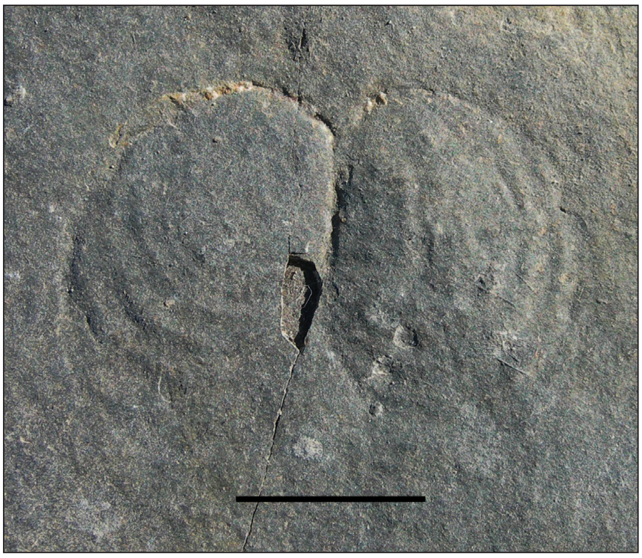

Fig. 17 - The only invertebrate (MFSN 43507), a bivalve. The scale bars equal 10 mm.

MFSN 43610, on the other hand, is a roundish structure of about 12 mm diameter that can be assigned to the typical genus for dispersed seeds, *Carpolithes* sp. The specimen is not found in anatomical connection with any vegetative fragment of a plant, making an assignment at major plant group difficult.

In summary, the plant fossil assemblage is dominated by angiosperms, with less abundant representation from other plant groups, including conifer shoots, putative ginkgophyte and seed fern remains. Lycophytes, horsetails, ferns and cycadophytes are so far missing in the plant fossil assemblage.

Invertebrates

Only one specimen (MFSN 43507) belongs to the invertebrates. It is the impression of an articulated but open bivalve shell sculptured with external commarginal ribs and fine radial striae (Fig. 17). It may be referred to an inoceramid bivalve (cf. Schneider et al. 2013: fig. 4).

DISCUSSION

Comparison with other fossil fish-bearing sites of the Julian Prealps and Karst

In the Julian Prealps and Karst, portions of the Friuli Basin and the FCP crop out. The fossil assemblage from "locality 84" is compared here with similar assemblages preserved within different horizons of the Cretaceous FCP sequence.

Other localities in the megabeds of the Montenars territory. "Locality 84" has yielded the most abundant and diverse fossil assemblage among those discovered by R. Tonello in the limestone olistoliths of the Grivò Flysch megabeds in the Montenars area (Fig. 2). Due to the age of the megabeds and olistoliths, the fossil assemblages from these localities are likely Cretaceous in age, though a Palaeocene-early Eocene age cannot be discarded (Dalla Vecchia 2008a). The most important locality after "locality 84" is "locality 122" located close to the Flaipano hamlet, about 2.5 km ENE from "locality 84" (Fig. 2). However, Tonello's notes are somewhat unclear, making its exact position difficult to trace. "Locality 122" yielded 94 samples (MFSN 43779-43818, 50748-50750, 50771-50794, and 50845-50863) comprising 67 terrestrial plant remains (71% of the samples), 20 bivalves (21% of the samples), and only three slabs with fish remains (four distinct specimens including an isolated scale and no pycnodontiform; 4% of the assemblage). Unlike "locality 84", where fish fossils are abundant, terrestrial plant fossils dominate in "locality 122", whereas fish are rare. The simple petiolate leaves with entire margin and distinct midvein (e.g. MFSN 43780; 43783; 43785-86; 43791; 43795; 43812; and 43814) resemble *Dicotylophyllum proteoides* and *Dicotylophyllum* species 1 and 2 from "locality 84". *Frenelopsis* is also present (MFSN 43794; 43803; 43805; and 50748). The assemblage includes four single leaves (MFSN 43789; 43792; 43799; and 43800) similar to that from "locality 84" we have referred to *Brachyphyllum*. Additionally, a possible seed or fruit has been found (MFSN 43801). Plant and fish remain are preserved in black laminated limestone, whereas the bivalves, which seem to belong to a single taxon, occur in black massive limestone, possibly from a different olistolith or a distinct interval within the same olistolith.

"Locality 21" is also important, but its precise location is uncertain due to the vague nature of Tonello's notes (the position in Fig. 2 is tentative). This locality yielded 63 samples (MFSN 38718; 38747-48; 38782; 38813; 38902-904; 39406; 50724; 50799-810; 50872; 50911; 50915-932; and 50725-50730), including 45 fish remains (71% of the specimens), 15 fragmentary terrestrial plant fossils (24%), and one invertebrate (a bivalve). Fossils are preserved in a black and irregularly laminated limestone. Fishes are neither well-preserved nor diversified and are sometimes concentrated in a way suggesting a mass death event. Only one pycnodontiform has been identified. Additionally, a large coprolite (MFSN 50728, 60 mm long) was recovered from this locality. A detailed comparison with "locality 84" will be possible only after the preparation of the specimens.

Vernasso Quarry olistoliths. Fish and plant fossils from the olistoliths of the Grivò Flysch megabeds of the Julian Prealps had already been reported in the literature, notably those found in the olistoliths within the megabed n. 11 of the abandoned Italcementi Quarry near Vernasso, already mentioned above. This locality is situated about 35 km SW of "locality 84" on the flank of the Mt. dei Bovi near the Natisone River (Fig. 1). Megabed n. 11 in the Italcementi Quarry section contains immense olistoliths (ranging from 10 to 100 m in size) in its basal megabreccia. These olistoliths are composed of shallow water carbonates and have been providing fossils at least since the first half of the 19th century.

Three kinds of olistoliths that yielded fish and plant fossils can be distinguished in the megabed n. 11, representing distinct stratigraphic levels. These olistoliths, composed of rather different carbonate lithologies, are labelled here Vernasso 1-3. Vernasso 1 consists of boulders of massive black calcilutite (white when weathered) containing terrestrial plant remains (Bozzi 1888, 1891), marine molluscs (Tommasi 1891) and rare fish remains (Dalla Vecchia 2008a). Hundreds of samples from these boulders are stored in several museums across northern Italy. The fossil assemblage was initially dated to the early Senonian (Tommasi 1891) and later to the Coniacian-Santonian (Gomez et al. 2002), but recent calcareous nannofossil analysis has revised the age to the Campanian (Roghi et al. 2023). Fish are represented by a few specimens of dercetid aulopiforms (*Dercetis* and *Benthesikyme*; Bassani 1895; Canestrelli 1915) and a couple of teeth of the shark *Squalicorax* (Dalla Vecchia 2003; FMDV pers. obs.). Dercetids, characteristically elongate, long-jawed marine fishes, are known from the Cenomanian to the Palaeocene of Europe, Middle East, North Africa, Mexico and South America (Forey et al. 2003; Blanco & Alvarado-Ortega 2006; Khalloufi et al. 2010; Gayet et al. 2012; Belmonte 2014; Taverne & Goolaerts 2015). Neither dercetids nor sharks are present in "locality 84" fossil assemblage. More abundant and diverse are the plant fossils (over 400 specimens; Giusberti et al. 2017). Unlike "locality 84", the plant assemblage is dominated by conifers, including *Araucaria macrophylla* Bozzi, 1891 (Araucariaceae), *Cunninghamites elegans* (Corda) Endlicher, 1847 (Cupressaceae), *Cyparissidium gracile* Heer, 1874 (?Cupressaceae), *Geinitzia* (= *Sequoia*) *ambigua* (Heer, 1874) and *G.* (= *Sequoia*) *concinna* (Heer, 1874) (?Taxodiaceae), and *Frenelopsis koenigii* (von der Marck, 1863) (Cheirolepidiaceae). Leaves of *Araucaria macrophylla* resemble the leaf from "locality 84" that we have referred to *Brachyphyllum*. Amber has been found associated with Araucariaceae, Cupressaceae and, possibly, Cheirolepidiaceae (Giusberti et al. 2017). Angiosperm leaves (*Arundo groenlandica* Heer, 1874; *Myrica vernassiensis* Bozzi, 1891; *Phyllites proteaceus* Bozzi, 1891; *P. platanoides* Bozzi, 1891; and *Rhus antigua* Bozzi, 1891; Bozzi 1891) are also present, but are rarer than conifers. *Phyllites proteaceus* (see Bozzi 1891: 378, pl. 16, fig. 6-7) resembles *Dicotylophyllum* sp. 2 that is common in "locality 84", whereas *Myrica vernassiensis* (see Bozzi 1891, pl. 16, fig. 5) shows some resemblance with the specimens assigned putatively to *Barykovia* in "locality 84" (Fig. 14).

The Vernasso 2 olistoliths consist of grey to whitish (but black if not oxidized), thinly-bedded and laminated, porcellanaceous limestone. These boulders predominantly preserve small ellimmichthyform clupeomorphs (Dalla Vecchia 2008a: figs. 207-208), 1.5-6 cm long. They are currently under investigation (Amalfitano et al. 2023). Additionally, a juvenile specimen of the amiiform *Amiopsis* cf. *prisca* Kner, 1863 was reported by Amalfitano et al. (2022). Isolated scales of relatively large fishes (Dalla Vecchia 2008a: fig. 209) and fish coprolites (Dalla Vecchia 2008a: fig. 210) are also present. Invertebrates from these olistoliths include small gastropods and bivalves, decapod crustaceans (*Penaeus vernassensis* Garassino et Teruzzi, 1995 and an unnamed caridean shrimp; Garassino & Teruzzi 1995), and rare ophiuroids (FMDV, pers. obs.). Terrestrial plants are absent. These olistoliths have been dated to the late Hauterivian-early Barremian (Muscio & Venturini 1990) based on the presence of the benthic foraminifer *Orbitolinopsis capuensis* (De Castro, 1964).

Vernasso 3 olistoliths consist of grey-greenish, massive and weakly dolomitised limestone with an accumulation of fish carcasses up to 1 cm thick where the body outline of the single individuals is rarely identifiable (Dalla Vecchia 2008a: figs 211-213). Most carcasses belong to pycnodontiformes based on the morphology of the often undisturbed tooth batteries (Dalla Vecchia 2008a: fig. 214). The genera *Proscinetes, Anomaeodus* and *"Palaeobalistum"* have been preliminarily identified based on these tooth batteries (Muscio & Venturini 1990), though a detailed study of the specimens is still pending. This accumulation may represent a pycnodontiform mass death. The amiiform *Amiopsis* cf. *prisca* is also present (Dalla Vecchia 2008a; Amalfitano et al. 2022) like in Vernasso 2 olistoliths. This olistolith has been dated to the late Hauterivian-early Barremian too (Muscio & Venturini 1990).

The fossil assemblage of "locality 84" is remarkably different from those of the upper Hauterivian-lower Barremian Vernasso 2 and 3 olistoliths, but partly resembles the Campanian Vernasso1 fossil assemblage. Both share small angiosperm leaves (*Phyllites protaceous* vs. *Dicotylophyllum* sp. 2), shoots of *Frenelopsis*, and the subtriangular, broad conifer leaves with a wide attachment area that we refer to *Brachyphyllum*. Despite these similarities*, Phyllites protaceous* is quite rare in the Vernasso 1 assemblage, which is dominated by conifers.

The megabeds in the Montenars area are younger than the Vernasso megabed n. 11 (Venturini et al. 2023), suggesting that the section containing the fossils of the "locality 84" might have been originated in a more inner position of the carbonate platform because of the south-westward migration of the collapsing platform margin. The difference in position within the carbonate platform may account for the faunal and floral differences between the two associations.

The Cornappo Torrent Konservat-Lagerstätte. The Cornappo Torrent site (Dalla Vecchia 2008a) is located in the Julian Prealps near the town of Torlano (Nimis municipality, Udine Province), only six km SE of "locality 84" (Fig. 1). This small fossil-bearing outcrop occurs in the banks of the torrent flowing along the SE flank of the Mt. Bernadia Massif. The Mesozoic portion of the massif and the corresponding mountains on the left side of the Cornappo Valley are considered a fragment of the NE margin of the FCP (Venturini et al. 2023). Fossils occur in the Kimmeridgian-Albian Cellina Limestone (Zanferrari et al. 2013) and are Barremian in age (Dalla Vecchia 2008a). The ca. 8 m-thick fossil-bearing section consists in black, well-bedded and thinly laminated limestone (Dalla Vecchia 2008a). Over 2550 samples from this locality are housed in the MFSN collections. At least 52% of the specimens are fish, 14% plants and 21% invertebrates. Coprolites are relatively common. The ichthyofauna has only been cursorily described (Dalla Vecchia 2008a). Unlike "locality 84" but similar to Vernasso 2, the ichthyofauna is dominated by small basal clupeomorphs (Dalla Vecchia 2008a: fig. 225) representing 79% of the fish assemblage. Larger fish are represented by pycnodontiforms (Dalla Vecchia 2008a, fig. 226; 2.2% of the fish assemblage) and the amiiform *Amiopsis prisca* (see Dalla Vecchia et al. 2008), the latter also reported from Vernasso 2 and 3. Amiiforms account for 4% of the fish assemblage but 75% of the specimens are isolated scales. The relatively rarer pycnodontiforms are larger (total length 23-30 cm), comparatively shorter-snouted, and have a heavier ventral scales covering relatively to those from "locality 84"; at least MFSN 27036 and MFSN 25001 have also a different dentition. The absence of acanthomorphs in the T. Cornappo assemblage and the presence of basal neopterygians, such as the macrosemiid *Notagogus* and the aspidorhynchids, are consistent with the site's Early Cretaceous age.

Unlike "locality 84", invertebrates are relatively common, although rarer than fish. Crustaceans are by far the most common (69%) invertebrates. They include the decapod crustaceans *Penaeus cornappensis* Garassino, 1997, *Tonellocaris brevirostrata* Garassino, 1997, a galatheid anomuran, and a homolid brachyuran (Garassino 1997). Some bedding surfaces are rich in small valves that may belong to conchostracan crustaceans (Dalla Vecchia 2008a). Other invertebrates are, in order of abundance, gastropods (including nerineoids), bivalves, crinoids and probable jellyfish impressions (FMDV, pers. obs.).

Unlike "locality 84", the plant remains are nearly exclusively small conifer twigs (*Brachyphyllum?*, *Cupressinocladus* sp.; Dalla Vecchia 2008a), with a possible cycadeoid leaf and a possible horsetail axis. A few slabs also show concentrations of calcareous algae on the bedding surfaces (FMDV, pers. obs.).

The Komen/Comeno Konservat-Lagerstätte. The historical locality of Komen/Comeno (e.g., D'Erasmo 1946; Medizza & Sorbini 1980; Calligaris 1992; Cavin et al. 2000; Jurkovšek & Kolar-Jurkovšek 2007; Palci et al. 2008) consists of several fossil-bearing outcrops located near the homonymous town in the Slovenian Karst close to the Italian-Slovenian border (Fig. 1). Fossils occur within the ca. 100 m thick Komen Limestone of the Povir/Monrupino Formation, dated biostratigraphically to the middle-late Cenomanian (Palci et al. 2008). The lithology is a dark grey-black, thin-bedded limestone with nodules and layers of chert intercalated with thinly laminated stromatolites. The Komen Limestone originated into an intraplatform basin separated by a tidal flat from the close emergent part of the carbonate platform (Palci et al. 2008).

The most abundant fossils are fish fossils (437 of the 481 specimens listed by Palci et al. 2008; 91%); 380 fish specimens are determined to the genus level. Vertebrates include also 12 reptiles (semi-aquatic marine squamates). Plant remains are represented by conifer shoots (24 specimens; 5% of the assemblage). The rare invertebrates are rudist bivalves, ammonites, crustaceans, and echinoderms. This museum-based fossils assemblage may be collection-biased toward larger, better-preserved specimens and vertebrates, as suggested by Palci et al. (2008). However, it provides an idea of the fossil assemblage, especially for fish (Cavin et al. 2000; Palci et al. 2008). It is unclear whether the taxa listed by Palci et al. (2008) and also reported below are based on the original determination of the specimens (from specimen labels) or on a recent systematic revision of the collections. The inclusion of Jurassic taxa (e.g., *Leptolepis*) and outdated generic names (*Leptotrachelus*) suggests the use of older sources. The most abundant fish are clupavid teleosts (*Clupavus*; 36% of the fish sample), ichthyodectid teleosts (*Chirocentrites*, *Thrissops*, and *Carsothrissops*, 15%) and pycnodontiforms (*Coelodus*; 8.7%). The amiiform *Amiopsis* is represented by two specimens. Clupeomorphs include *Clupavus*, *Diplomystus,* and *Scombroclupea*, which form 41% of the fish assemblage, whereas Myctophids (*Leptosomus* and *Dactylopogon*) are only 2.5%. Other non-acanthomorph teleosts (73 specimens, 17% of the sample) are, in decreasing order of abundance, the aulopiform *Saurorhamphus* (14 specimens), the aspidorhynchid *Belenostomus* (12), the crossognathiform *Elopopsis* (9), the aulopiform '*Leptotrachelus*' and the aulopiform *Enchodus* (7), the clupeocephalan *incertae sedis Pseudoberyx* (5), the aulopiform *Halec* (5), the salmoniform *Gaudryella* (5), the aulopiform *Hemisaurida* (4) and *Volcichthys* (3), the aulopiform *Nematonotus* (1) and the gonorhynchiform *Parachanos* (1). Altogether, the non-acanthomorph teleosts form 75% of the fish assemblage (13% of the fishes are not determined to the genus level). Acanthomorphs are represented by the berycid *Beryx* and *Lobopterus*, the aipichthyid *Aipichthys*, the protriacanthid *Protriacanthus*, and the trachichthyid *Hoplopteryx*; they form only 1.4% of the fish assemblage. Although the ichthyofauna is similarly dominated by non-acanthomorph teleosts, the taxonomic composition of the Komen/Comeno assemblage differs significantly from that of "locality 84". Additionally, the plant fossil assemblage at Komen/Comeno consists only of conifers (see also Dobruskina et al. 1999) unlike the more diverse flora at "locality 84".

Other Konservat-Lagerstätten *of the Slovenian Karst.* The carbonate platform sequence of the Slovenian portion of the Karst (Trieste-Komen Plateau) that crops out between the towns of Komen and Tomaj (Fig. 1) contains additional fish and plant-bearing horizons at higher stratigraphic levels compared to the Komen/Comeno *Konservat-Lagerstätte* (Dobruskina et al. 1999; Cavin et al. 2000). Although these localities have yielded a low number of specimens, at least three are worth of considering here.

The upper Cenomanian-Turonian 'Komen pelagic limestone' (a horizon within the Repen Formation) represents the drowning of the platform during the Oceanic Anoxic Event 2 and contains pelagic organisms (calcispheres, pithonellas and ammonites) and no plant remains (Cavin et al. 2000). Near Tomačevica, it yielded the aulopiform *Enchodus* and a tooth of the durophagous shark *Ptychodus* (Cavin et al. 2000). Abundance of pelagic organisms and absence of terrestrial plants clearly reflect a depositional environment different from that of "locality 84".

The Tomaj Limestone of the Lipica Formation is probably early Campanian in age because it lies above the *Keramosphaerina tergestina* (Stache, 1889) horizon corresponding to the Santonian-Campanian boundary (Steuber et al. 2005; Cestari 2002; Venturini 2005) and below the uppermost part of the Lipica Formation containing the early Campanian foraminifer *Calveziconus lecalvezae* Caus et Cornella, 1982. The Tomaj assemblage possibly shares with that from Vernasso 1 the presence of placenticeratid ammonites (Venturini et al. 2023). Six places close to Tomaj village yielded fish and plant fossils; a fossil feather has also been found (Buffetaut et al. 2002). Presence of pelagic micro- and macrofossils (ammonites and saccocomid crinoids) and chert testify to a comparatively deep environment and connections with the open sea, also because the locality was probably close to the carbonate platform margin. The ichthyofauna includes a possible rhinobatid chondrichthyan, an indeterminate pycnodontiform, possibly the ichthyodectiform *Chirocentrites microdon* Heckel, 1849, indeterminate ichthyodectids, eight specimens of *Enchodus*, two specimens of the aulopiform *Rhynchodercetis*, and three acanthopterygians including a specimen of the trachichthyid *Hoplopteryx stachei* (Gorjanović-Kramberger, 1895). A mass death of small non-acanthopterygian euteleosteans has also been found (Cavin et al. 2000). The fossil macroflora is dominated by conifers (42 specimens; Dobruskina et al. 1999) belonging to *Brachyphyllum*, *Pagiophyllum*, a new unnamed conifer genus (it appears to be segmented like *Frenelopsis* and it may be such; see Dobruskina et al. 1999, pls. 7-10), large and isolated conifer scales referred to *Araucarites*?, and a cone. The taxon mentioned as "*Pagiophyllum* sp. nov." by Dobruskina et al. (1999, pls. 4-6) resembles *Pagiophyllum* sp. 1 of "locality 84". Scales referred to *Araucarites*? resemble the leaves of *Araucaria macrophylla* from Vernasso 1 and the smaller leaf from "locality 84" that we have referred to *Brachyphyllum*. Angiosperms are represented by only nine isolated leaves, whereas indeterminate ferns and horsetails occur with a single specimen each. Angiosperms have been referred to *Magnoliaephyllum*, *Sassafras* and *Eucalyptus* (Dobruskina et al. 1999: pl. 12, figs 1-10), although the referral to extant genera for Cretaceous fossils should be avoided (see Coiffard et al. 2012). *Eucalyptus* leaves resemble those of *Dicotylophyllum proteoides* and those of *Magnoliaephyllum* are similar to *D*. species 2 from the "locality 84".

Finally, Dobruskina et al. (1999) reported a single *Pagiophyllum* specimen from the upper Campanian-Maastrichtian Liburnian Formation of Divača-Sežana.

The Polazzo Konservat-Lagerstätte. Polazzo (Fogliano-Redipuglia municipality, Gorizia Province, NE Italy) is a town located on the SW side of the Italian portion of the Karst (Fig. 1). The locality is actually composed of two distinct sites, A and B, located about 750 m apart, both Santonian in age, which have been object of systematic excavation (Dalla Vecchia & Tentor 2004). The section of site A was about two metres thick, whereas that of site B was only 1.20 m in thickness (Dalla Vecchia & Tentor 2004). The site A yielded 774 specimens, whereas site B yielded 1027 specimens up to 2003 (Dalla Vecchia & Tentor 2004) plus at least further 191 specimens from 2004 to 2014 (FMDV, pers. obs.). Specimens are deposited at the MPC. Fishes are the most common fossils in both sites, reaching at least 80% of the specimens in site B (Dalla Vecchia & Tentor 2004). The aulopiform *Rhynchodercetis* and the pycnodontiformes form 9% and 8.5% of the site B ichthyofauna, respectively. The pycnodontine *Polazzodus coronatus* Poyato-Ariza, 2010 occurs in both site A and B; Poyato-Ariza 2010). *Polazzodus gridellii* (d'Erasmo, 1952) was probably found close to site A (Poyato-Ariza 2020). Small sized acanthomorphs are also present (Dalla Vecchia & Tentor 2004: figs. 66-69) forming 2.3% of the fish remains collected in site B. All those acanthomorphs were provisionally referred to the "Beryciformes" by Dalla Vecchia & Tentor (2004), because two specimens from site A had been referred to the Family Holocentridae by Guidotti (1983), which he had included in the Beryciformes (it actually belongs to the Holocentriformes). Some specimens from site A have been tentatively referred in literature to the aulopiform *Enchodus* and the gonorhynchiform *Parachanos* (Nardon 1990; Dalla Vecchia & Tentor 2004: figs. 56 and 64-65). One specimen from site A belongs to an anguilliform (Dalla Vecchia & Tentor 2004: fig. 55). However, most specimens are small-sized (2-10 cm long) and undetermined non-acanthomorph teleosts that are waiting for a study, some of which have been tentatively referred to the Cypriniformes (Dalla Vecchia & Tentor 2004: figs. 57-59). Unlike the "locality 84", the Polazzo sites yielded tetrapod fossils: site A yielded disarticulated chelonian bones and two crocodyliform teeth (Dalla Vecchia & Tentor 2004), site B the tooth of a notosuchian crocodyliform (Dalla Vecchia & Cau 2011).

Plant remains are rarer than fish. About 200 plant fossils have been collected, nearly all from site A. Site B yielded only a few conifer shoots and indeterminate remains (less than 3% of the whole assemblage from that site). Plants from site A share with "locality 84" the presence of *Frenelopsis* (Dalla Vecchia & Tentor 2004: figs. 38-40). However, unlike "locality 84" 75% of the plant fossils is represented by conifers (*Frenelopsis, Brachyphyllum*, *Cunninghamites* sp., *Pagiophyllum*, cf. *Sphenolepis*; Dalla Vecchia & Tentor 2004: figs 41-43) and *Frenelopsis* represents 45% of the conifers. A few small, simple petiolate leaves with entire margin and no veins have been referred by Dalla Vecchia & Tentor (2004: fig. 44A-B) to the Ginkgoales; in "locality 84", similar specimens have been referred to *Dicotylophyllum* sp. 1. Only two specimens have been identified as angiosperm leaves (Dalla Vecchia & Tentor 2004: fig. 44C-D). The two sites A and B originated in tidal flat and shallow lagoonal depositionary settings (Dalla Vecchia & Tentor 2004).

The Trebiciano Konservat-Lagerstätte. Trebiciano locality (near Trebiciano/Trebče, Trieste municipality, Trieste Province; Fig. 1) is a lens of dark and thinly laminated limestone within the carbonate platform sequence of the Karst. It is most probably latest Cretaceous in age (late Campanian-Maastrichtian) because of its stratigraphic position within the Liburnian Formation (Dalla Vecchia 2008b) and the presence of the foraminifer *Murciella* (Venturini et al. 2008), although an early Palaeocene age had been initially suggested (e.g., Bannikov & Sorbini 2000). The fossil assemblage is fish-dominated with about 200 specimens stored at the MCSNT according to Bannikov & Sorbini (2000), and 98 specimens deposited at the MPC at least 85% of which are fish. These specimens have been only partly and mostly cursorily studied. Pycnodontiforms are represented by at least nine (according to Taverne et al. 2019) small-sized specimens (total length 2.34-4.33 cm) referred to the pycnodontine *Tergestinia sorbinii* Capasso, 2000 (Capasso 2000; Taverne et al. 2019). However, Capasso (2000: 263-264) mentioned the presence of 21 pycnodontiform specimens from Trebiciano in the collection at the MCSNT, belonging to at least four distinct taxa. The other fish taxa are also small sized and unique to this site. The most common fish (36 specimens; Bannikov & Sorbini 2000) is the purported gonorhynchiform *Landinia dolcei* Bannikov et Sorbini, 2000. The acanthomorph *Bacchiaichthys zucchiae* Bannikov et Sorbini, 2000 (15 specimens; Bannikov & Sorbini 2000) has been reported as "an intermediate form between batrachoidiforms and trachinoid perciforms" (Bannikov & Sorbini 2000: 16). The paracanthopterygian acanthomorph *Trebiciania roseni* Sorbini et Bannikov, 1996 is represented by ten specimens (Sorbini & Bannikov 1996). The ophidiiform percomorph *Pastorious methenyi* Carnevale et Johnson, 2015 (the oldest ophidiiform known to date) is based on a single specimen (Carnevale & Johnson 2015). Eighteen clupeomorph specimens have been referred to *"Diplomystus" trebicianensis* Bannikov et Sorbini, 2000 by Bannikov & Sorbini (2000). Two specimens have been reported as "holosteans" by Bannikov & Sorbini (2000: 15) because they are "covered with very thick scales"; they are the "basal neopterygians" mentioned by Carnevale & Johnson (2015: 772). This ichthyofauna is rather unlike that from "locality 84", showing a comparatively higher percentage of acanthomorphs, a minor percentage of pycnodontiforms, the presence of clupeomorphs, and peculiar taxa like *Landinia dolcei*.

Crustacean decapods (15 specimens, nine of which referred to the benthic Erymidae, four to penaeidean shrimps, and one possible to a caridean shrimp) have been described by Garassino & Ferrari (1992), who mention also the presence of gastropods in the sample. The rare remains of small crocodyliforms (FMDV, pers. obs.) have never been described. The site yielded also plant fossils (Taverne et al. 2019), but they are uncommon (one of us, FMDF, saw a just a conifer shoot during the 1997 field works in the site). The presence of charophytes in some horizons of the section suggests a fresh water or brackish environment or at least a mixed marine-fresh water setting (Dalla Vecchia et al. 2005).

Only a ramified conifer twig and very small, still unstudied teleost fishes (mostly belonging to a single species; FMDV pers. obs.) have been found in the Villaggio del Pescatore site (Duino Aurisina Municipality, Italy), which yielded abundant dinosaur remains (Dalla Vecchia 2008b), is also within the Liburnian Formation and is located in the southern margin of the Karst, 21 km NW of the Trebiciano locality.

Age of "locality 84" assemblage

Initially, the study of nannofossils in a sample from "locality 84" revealed a nearly monotypic association of *Cyclicargolithus floridanus* (Roth et Hay in Hay et al., 1967) suggesting a minimum early Eocene age. However, this unusual monotypic association is probably the result of a contamination of the sample (E. Fornaciari, pers., comm.). Other samples did not reveal any significative presence of foraminifers, nannoplancton or charophytes.

The presence of the cheirolepidiacean conifer *Frenelopsis* in the plant fossil assemblage supports its Cretaceous age because this widespread genus has a Berriasian-Maastrichtian range (Gomez et al. 2014; Marmi et al. 2023). Although pycnodontiforms occur also in the Palaeocene of France (*Oropycnodus ponsorti* Poyato-Ariza et Wenz, 2002) and lower Eocene of NE Italy (Bolca, Verona province; *Abdobalistum thyrsus* Poyato-Ariza et Wenz, 2002, *Nursallia veronae* Blot, 1987, *Palaeobalistum orbiculatum* Blainville, 1818 and *Pycnodus apodus* [Volta, 1809]) (Poyato-Ariza & Wenz 2002), their abundance is also in agreement with the Cretaceous age of the locality as well as the rarity of the acanthomorph teleosts (Chen et al. 2014) and their belonging to relatively basal groups. The presence of the acanthomorphs restricts the maximum dating to the Albian-Cenomanian (Chen et al. 2014). The pycnodontine pycnodontiforms have a Late Cretaceous-early Eocene range (Poyato-Ariza 2020). A Late Cretaceous age (Fig. 18) is also supported by the marked differences with the Hauterivian-Barremian fossil assemblages of the Cornappo Torrent and Vernasso 2-3, the partial resemblances with Comeno/Komen (late Cenomanian) and Polazzo (Santonian) ichthyofaunas due to the rarity of acanthomorphs, and the Vernasso 1 and Tomaj localities (Campanian) for the presence of angiosperm leaves. Rudists found in the olistoliths of the megabeds near Plazzaris (hence the same megabed of "locality 84" or stratigraphically close ones) have an upper Cenomanian-Maastrichtian stratigraphic range (Venturini et al. 2023). A Campanian-Maastrichtian age (Fig. 18) is suggested by the possible presence of the Percomorphacea in the ichthyofauna and the abundance of angiosperm leaves within the plant assemblage (Coiffard et al. 2012). The affinity with some Campanian-Maastrichtian angiosperm taxa from Central Europe and Asia also indicates a latest Cretaceous age. However, the plant fossil assemblage is puzzlingly dissimilar to those of the latest Cretaceous *Konservat-Lagerstätten* of the FCP, which are conifer-dominated.

Conclusions

The fossil assemblage from "locality 84" is Late Cretaceous in age, possibly Campanian-Maastrichtian, and it is unlike all other assemblages from the Cretaceous of the FCP preserving articulated fish skeletons and plant fossils. It is characterised by the absence of invertebrates, both shelled (molluscs and echinoderms) and non-shelled (crustaceans). The flora is dominated by small angiosperm leaves and includes rarer conifers, ginkgophytes and seed ferns, whereas the other assemblages from the FCP are conifer-dominated, like also are those from other Upper Cretaceous Italian localities yielding plant fossils like Magliano Vetere (Salerno Province, S Italy, Middle Cenomanian; Bartiromo et al. 2019), Quero (Belluno Province, NE Italy; Bonarelli Level, Cenomanian/Turonian boundary; Gomez et al. 2015), Carcoselle (Treviso Province, NE Italy, Bonarelli Level; Pigozzo 2002; Giusberti et al. 2016), 'Monte Colle' (Verona Province, NE Italy; Bonarelli Level; Gomez et al. 2015); Surbo (Lecce Province, S Italy; upper Turonian-Campanian; Meleleo et al. 1984; De Pirro et al. 2023); and Monte Acuto (Foggia Province, S Italy; upper Santonian;

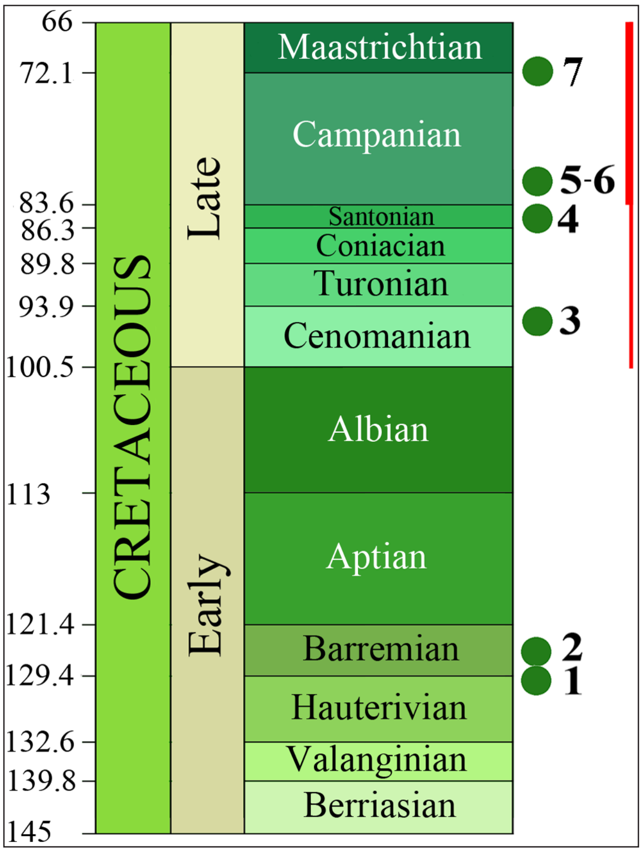

Fig. 18 - Geochronological range of "locality 84" (Late Cretaceous, probably Campanian-Maastrichtian; red line) and dating of the other similar fossil-bearing localities of the Friuli Venezia Giulia Region and Slovenia (green dots) mentioned in the paper (see Fig. 1 for locations). The numbers on the left side refer to the age in millions of years. Legend: 1, Vernasso 2 and 3; 2, Cornappo Torrent; 3, Komen/Comeno; 4, Polazzo; 5, Vernasso 1; 6, Tomaj; 7, Trebiciano/Trebče.

Gomez et al. 2008). Only the small upper Cenomanian-lower Turonian plant fossil assemblage from the basinal Gavarno Formation of the Sommaschio Brook (Bergamo Province, N Italy) seems to present a relative abundance of angiosperm leaves ("Proteaceae") in respect to the conifer fossils (Venzo 1951: 234-236). Unfortunately, those fossils have never been described in detail and fully figured.

The ichthyofauna is also peculiar being dominated by pycnodontiforms and basal non-acanthomorph teleosts (elopiforms, gonorhynchiforms, crossognathiforms, and possibly albuliforms), whereas acanthomorphs (including Beryciformes and possibly Percomorphacea) are rare. Clupeomorphs and needlefish-like aulopiforms as *Dercetis* and *Rhynchodercetis*, which are common in marine ichthyofaunas from the Upper Cretaceous of the Tethyan carbonate platforms (Forey et al. 2003; Gayet et al. 2012; Belmonte 2014) or adjacent basins (Khalloufi et al. 2010), are absent. Chondrichthyans are lacking. This ichthyofauna is suggestive of a shallow marine or brackish environment. The absence of marine invertebrates, chondrichthyans, aquatic reptiles and the abundance of terrestrial plant fossils suggest a tidal flat or a restricted water body (lagoon or brackish coastal lake) in an inner platform setting far from open sea influence as possible depositionary environment. However, the presence of fast-swimming teleosts like the pachyrhizodontids suggests some connection to the open sea.

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