Research Square

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Biostratigraphy and palaeoenvironments of the Upper Cretaceous fossil fish Konservat-Lagerstätten of Lebanon

Sibelle Maksoud
sibelle.maksoud@ul.edu.lb

Lebanese University
Tamara El Hossny
Natural History Museum of Geneva
Elias Samankassou
University of Geneva
Lionel Cavin
Natural History Museum of Geneva
Pierre Abi Saad
Memory of Time
Dany Azar
Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences
André Piuz
Natural History Museum of Geneva

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Abstract

Cenomanian deposits are well exposed in Lebanon and consist mainly of limestones that covers about 40% of the Lebanese territory. The sedimentary series is rich in fish fossils encountered in three different Cenomanian outcrops: Haqel, Hjoula and Nammoura. These sites are known for the exceptional preservation of their fossil content. However, over time, different authors proposed different ages and stratigraphic relationships.

Trying to fill this gap in knowledge, stratigraphic sections were measured, and samples taken from the three outcrops, considering thickness variations and facies changes in the *Konservat-Lagerstätten* interval. The micropalaeontological inventory focusing on benthic and planktonic foraminifera identified at family and generic level and when possible, specific level is provided. We identified benthic foraminifers (Biokovinidae, Charentiidae, Cuneolinidae, Dicyclinidae, Mayncinidae, Nezzazatidae, Orbitolinidae, Spiroplectaminidae, Gavellinellidae, Alveolinoidea, Hauerinidae, Spiroloculinidae and other Miliolidae). Among the planktonic foraminifers we identified Hedbergellidae (some with costulated test, Globigerinelloididae, Heterohelicidae and Rotaliporidae). Several calcispheres have been identified. Other biogenic components were identified, including rare dasycladalean algae, bryozoans, ostracods, echinoderms and bone debris.

Overall, the microfossils indicate a Middle Cenomanian age based on the presence of *Conicorbitolina conica* and *Favusella washitensis* present within the *Lagerstätten*. The macrofossil assemblages found within (echinoids and ammonites), above and/or below (ammonites) the *Lagerstätten* are surprisingly not in accordance with dating obtained by microfossils, and give a Late Cenomanian age.

The analysis of the relationship between the oxygen and carbon isotopes of the three outcrops is presented to follow and interpret the Ocean Anoxic Event 2.

The ichthyofauna list is compiled based on fieldwork by one of us (PAS) and literature. The fish assemblage is the most diverse in the Mesozoic in the world. The Haqel and Hjoula sites share approximately half of their species, while the Namoura site shares approximately 20% of its species with the other two localities. The comparison of the Lebanese fish faunas is discussed, as well as the origin of Haqel and Hjoula assemblages. We consider that the geographically restricted sites of Haqel and Hjoula correspond to submerged sinkholes with favorable living conditions in the water column, but anoxic conditions on the bottom that allow the preservation of carcasses, probably killed by algal blooms. The mixing in the same fossil beds of fish species that probably lived in different environments remains an open question.

INTRODUCTION

Lebanon has been famous for its fossil fish outcrops for centuries. Some authors believe that the first mention of these fossil deposits dates back to the antiquity as thought to be mentioned by Herodotus 2450 years ago (Davis, 1887; Lockyer, 1887). However, other authors could not confirm this as Herodotus' writings lacked any comments on fishes or fossils from this region (Gayet et al., 2003; Capasso, 2017). Thus, the first mention of such localities dates back to the fourth century, in the Armenian Chronicles of Eusebius of Caesarea, who noticed sea fishes on the highest mountain peaks in the quarries of Mount Lebanon, preserved in the rock layers till the present day, as evidence of the flood (Gayet et al., 2003; Capasso, 2017). The interest in these fossiliferous localities persisted during the Middle Ages, with the example of Sire Jean de Joinville, who wrote in the "Histoire de Saint Louis" about a present offered to King Louis IX while staying in Sayette (present day Sidon); the gift was a stone, when split in two, shows a fish on the inside (Petitot, 1824).

Centuries later, the Lebanese *Lagerstätten* became of a great importance among European scientists as of the early 19th century (Dalla Vecchia et al., 2001). Blainville (1818), Agassiz (1833-44), Botta (1833), Haeckel (1849), Pictet (1850), Pictet & Humbert (1866), Costa (1857), Fraas (1878), Dames (1886), Davis (1887), among many others from the latter century, all have made great contributions to the knopiwledge on the fossil content of the Lebanese deposits (Lockyer, 1887; Woodward, 1896).

Fossils recovered from these sites formed the base of many historical collections around the world, such as: the collection at the Museum of Natural History of Geneva, first studied by Pictet (1850), and later, after adding more fossils to the collection, studied by Pictet & Humbert (1866); Prof. Lewis who collected a great number of fossils including many new species, several of which are housed at the British Museum Natural History Department (nowadays, Natural History Museum), in part, based on which Davis wrote his memoir (Lockyer, 1887); Prof. Day who also collected several hundreds of fish fossils and crustacean from Haqel and Hjoula housed at the American University of Beirut, with some of these specimens studied by both Hay & Day (1903).

More recently, in the 20th and 21st centuries, these *Lagerstätten* remain famous worldwide for their rich and well-preserved fossil assemblage. They are significant in the palaeontological history, even more in palaeoichthyology; as Hückel (1970) even described several of these sites as "Fish Shales" localities. A review of the literature reveals the occurrence of 93, 72 and 40 species of "fish" (Chondrichthyes and Actinopterygii) in Haqel, Hjoula and Nammoura, respectively. New taxa are still being excavated and studied at a rate of one to five new taxa per year (Capasso, 2017).

The four major fossil outcrops are distributed in Cazas Jbail (Haqel and Hjoula) and Kesserwan (Nammoura and Sahel Alma). Haqel and Hjoula are thought to have very close ages, early to late Cenomanian (Gayet, 1980, 1988; Bannikov & Bacchia, 2000). Nammoura is considered to be of middle to late Cenomanian age (Dalla Vecchia & Venturini, 1999; Bannikov & Bacchia, 2000; Dalla Vecchia et al., 2002; Elgin & Frey, 2011). The youngest of these outcrops is Sahel Alma, regarded as having an age of late Senonian (Bannikov & Bacchia, 2000) or Santonian (Garassino, 1994; Elgin & Frey, 2011).

These four localities yield highly preserved varieties of invertebrates, plants and fishes (Hay, 1903; Woodward, 1942; Forey et al., 2003). Haqel and Hjoula are mostly famous for their fish content (Pictet, 1850; Pictet & Humbert, 1866; Hückel, 1970; Cappetta, 1980; Poyato-Ariza & Wenz, 2005; Capasso et al., 2010; Gayet et al., 2003; Taverne & Capasso, 2018; El Hossny et al., 2020). Nammoura is known as well for its marine invertebrates and fish content, but unlike the other localities, its terrestrial plant content is more abundant (Dalla Vecchia & Venturini, 1999; Elgin & Frey, 2011). As for Sahel Alma, the site is exhausted and no longer excavated (Capasso, 2017). Tetrapods are rather rare in all of the four localities: two pterosaur species, one found in Haqel (Dalla Vecchia et

al., 2001) and the other in Hjoula (Elgin & Frey, 2011). However, bird feathers and reptiles have been more frequently found in Nammoura (Bannikov & Bacchia, 2000; Rage & Escuillié, 2003; Tong et al., 2006).

Today, despite the great interest in these localities and the few investigations dealing with the stratigraphy and the formation of these deposits, as briefly mentioned above, there is still no consensus. Hence, the aim of the present paper, is to provide a first comprehensive study of three out of the four Lebanese Cretaceous sites Haqel, Hjoula and Nammoura, by integrating different approaches including biostratigraphical analyses, providing details on the micro palaeofauna found at each site, in addition to carbon and oxygen isotopes isotopic data. This will allow us to suggest an ages for the outcrops, a reconstruction of their palaeoenvironment and possible causes of death and preservation of the fauna during this well-known period.

Historical background on stratigraphy

Haqel and Hjoula

Botta (1833) subdivided the Lebanese Mesozoic stratigraphic sequence in three different "groups". He attributed the lower (Group 3) and the upper (Group 1) groups, composed of limestones, to the Upper Jurassic and Lower Cretaceous respectively. Between these groups he identified "Group 2" consisting of lignite-bearing green sandstones, but without providing any biostratigraphic data. In the middle part of his upper group, he mentioned the fossil fish layers of Haqel containing chert.

Pictet & Humbert (1866) assumed that the fish layers of Haqel are a "phase of the Cenomanian" (*op. cit.*: p. 239); and that these fish layers should be below the Hippurites beds (with *Hippurites lumbricalis*), i.e., below the Turonian strata, and above the "*Cardium hillanum"* strata. The two macrofossils mentioned were not illustrated by the authors.

According to Fraas (1878), the fish layers of Haqel represent localised facies and correspond to the "radiolite zone" which he attributed to the Turonian. Lewis (1878) mentioned the fish fossils of Hjoula that Diener (1886) supposed are similar to the one of Haqel layers. For the dating, Diener (1886) only followed the age attributed by Fraas (1878).

Douvillé (1910), who studied the rudists of the region, did not mention the fish outcrops but attributed the "limestones with radiolites" to the Cenomanian.

Zumoffen (1926) described the fish fossil layers of Haqel as follow: "les calcaires à poissons occupant le fond d'une gorge étroite… toute la surface couverte d'une grande quantité d'éboulis… de plaques, de dalles et de schistes qui sont dans un désordre indescriptible, et qui rendent l'étude stratigraphique très difficile sinon impossible" [the fish limestones are in the bottom of a narrow gorge... the whole surface covered with a large amount of scree... plates, slabs and schists which are in an indescribable disorder, this makes the stratigraphic study very difficult or impossible]. He therefore adopted the stratigraphy of Humbert (*In* Pictet & Humbert 1866) and placed the fish fossil beds of Haqel in the Cenomanian. For Hjoula, he considered that "le gisement de Djoula (Hjoula) n'est qu'une continuation ou l'extension de celui de Hackel (Haqel), les caractères pétrographiques et paléontologiques semblent le prouver" [the outcrop of Hjoula is a continuity or an extension of the Haqel outcrop as proven by the petrographic and palaeontologic characters].

From a stratigraphic point of view, Zumoffen (1926) located these fossil fish layers directly below the *Nerinae requieni* bed which marks the lower limit of the Turonian. This stratigraphic assumption was not accepted by Dubertret & Vautrin (1937). The latter questioned this limit and considered that *Nerinea requieni* is a synonym of *Nerinae pseudonobilis* Choffat which cannot be used as a stratigraphical marker. They assumed that it can be found in the typical Cenomanian as well as in the Turonian *Hippurites* beds in Lebanon (*op. cit.*: p. 64).

Dubertret (1955, 1963) referred to the Cenomanian as C4 on his geological maps. He described the fossil fish-bearing layers of Hjoula and Haqel as following "Hadjoula et Hakel, se situent sensiblement au même niveau stratigraphique, en plein Cénomanien ; la roche est un calcaire en plaquettes, dur, parfois silicifié" [Hjoula and Haqel are almost at the same level, within the Cenomanian; the rock consists of laminated limestone, hard and sometimes silicified].

Patterson (1967) described the Haqel section as follow: "fish beds are at least 20 m. thick and their base has not been seen: above they pass into flaggy, unfossiliferous limestones" (*op. cit.*: p. 70). He did not provide a stratigraphic interpretation for the fish-bearing deposits. He did not study the stratigraphy of the Hjoula outcrop in the village: "the building, cultivation and the inhabitants prevented me" (*op. cit.*: p. 70). However, he used fish fossils for correlation and dating, attributing Haqel and Hjoula to the mid-Cenomanian and adding that a "more precise stratigraphical work" is needed (*op. cit.*: p. 73).

Hückel (1970) subdivided the Cenomanian sequence into seven units. He attributed the fish fossil layers of Hjoula to his "Cenoman IVd" subunit and the Haqel fish fossil layers to his "Cenoman Va" subunit. Despite the extensive work on these sites, his subdivision of the two fish-bearing outcrops, with same microfossil content (*op. cit.*: p. 117), into two different subunits was based on silica (SiO_2) abundance he adopted form Roger (1946). In addition, Hückel (1970) dated these two subunits as a "later part of the early Cenomanian" (*op. cit.* p. 9) again using another author's data: both *Acanthoceras mantelli* (Sowerby, 1814) and *Orbitolina concava concava* (synonym of *Orbitolina* (*Orbitolina*) *concava* (Lamarck, 1816)) were identified by Zumoffen (1926) but never been illustrated; were used as biostratigraphic markers for this age assignment.

Saint-Marc (1969, 1974) has done an enormous amount of work on the micropalaeontology of the Late Cretaceous in Lebanon. However, he did not measure his own sections and sampled from sequences in Haqel and Hjoula. He only stated (1974, p.45) that "très morcelée par des accidents tectoniques, cette région demande une étude très serrée pour déterminer la position stratigraphique des gisements" [so much affected by tectonic accidents, this region needs a study to define the stratigraphy of these outcrops]. The age he attributed to these outcrops was deduced from the presence of a single macrofossil, namely the ammonite *Acanthoceras mantelli* (Sowerby, 1814), mentioned by Zumoffen (1926) and subsequently by Hückel (1970). This ammonite, not illustrated as

stated above, is nowadays considered a synonym of *Mantelliceras mantelli* (Sowerby, 1817) and viewed as doubtful by Whippich & Lehmann 2004 (see below). We assume that this could be the only conclusion Saint-Marc made without considering the microfossils.

Hemleben (1977) followed Hückel's subdivisions of the Cenomanian sequence and was able to date the Cenoman subunits IVd and Va which correspond to Hjoula and Haqel deposits respectively. He inferred a late Cenomanian age for both deposits from planktonic foraminifera. However, most of foraminifers from the assemblages he mentioned were not illustrated, *i.e.*, *Praeglobotruncana stephani* (Gandolfi, 1942), *Rotalipora cushmani* (Morrow, 1934) and *Rotalipora greenhornensis* (Morrow, 1934). He showed only one section attributed to "*Rotalipora*" in his Fig. 1 (p. 241). This equatorial section is not diagnostic and do not allow a specific determination.

Walley (1997) merely introduced the name of Sannine Formation for the unit C4 defined by Dubertret (1955, 1963).

Wippich & Lehmann (2004) considered the occurrence of the ammonite *Acanthoceras mantelli* (Sowerby, 1814) (found by Zumoffen (1926)) from lateral facies supposed to be equivalent to Haqel *Lagerstätte*), *i.e.*, *Mantelliceras mantelli* (Sowerby, 1817) to be doubtful. They assume it has been used by several authors to date the fish layers but could correspond to several taxa of the family Acanthoceratidae de Grossouvre, 1894. In turn, they described and illustrated the ammonite *Allocrioceras* cf. *annulatum* (Shumard, 1860) found in Hjoula *Lagerstätten* levels (not found in Haqel as mentioned in Whippich & Lehmann 2004; Lehmann pers. comm. 2023) and attributed these sequences to the late Cenomanian. Unfortunately, Wippich & Lehmann (2004) did not provide a geological section showing the level's occurrence of this ammonite. Following P. Abi Saad, the ammonites (*Allocrioceras* cf. *annulatum*) come from about 50 cm above the uppermost chert level and are also found within the fish *Lagerstätte* in Hjoula.

Lehmann et al. 2024 precise the age constrains of the Hjoula *Lagerstätte* based on new founds of well-preserved ammonites. They give a Late Cenomanian age but unfortunately the authors do no give a precise field section showing where their ammonite come from (see § biostratigraphy).

For the Nammoura outcrop, Dalla Vecchia et al. (2002) provided a detailed stratigraphy with palaeontological content and dating. They divided the section into 8 units. The *Lagerstätte* correspond to their "unit 3", subdivided into four subunits (a-d). Following the authors, the subunits a-b lack microfossils, whereas subunit "b" has chert concretion and subunit "d" consists of wackestones/packstones with calcispheres, bivalves and crinoid fragments. In "unit 4", above the Nammoura *Lagerstätte*, the authors mentioned the presence of (undetermined) rudists with two fossil markers, namely *Conicorbitolina* cf. *conica* and *Pseudedomia drorimensis*, both of which were illustrated (2002, p. 64, Text-Fig. 14A-B). Dalla Vecchia et al. (2002) attributed an age of middle Cenomanian for the Nammoura *Lagerstätte*.

The stratigraphical position of the Haqel and Hjoula outcrops has changed over time and with the index fossils used (Table A). The latter, namely macrofossils (*i.e.*, ammonites) and microfossils (*i.e.*, orbitolinids) were used or mentioned by authors but not systematically illustrated or revised to fit the actual stratigraphic range. In the following, we present the macro- and microfossil assemblages of the measured sections to constrain the stratigraphical position of these outcrops studied. In additional, the microfacies and fossil assemblages are used to infer the depositional environment and the conditions that favoured the exceptional preservation of fossils in the units considered as *Lagerstätte*.

Table 1
Name and age attribution for Haqel and Hjoula outcrops through time.

Author	Botta (1833)	Pictet & Humbert (1866)	Fraas (1878)	Diener (1886)	Zumoffen (1929)	Hückel (1970)	Saint-Marc (1974)	Dubertret (1963)	Walley (1997)	W Le (2
Description	Poissons fossiles de Hakel (p. 150) [fish layers of Haqel]	Fishes of Hackel (p. 239)	Die Schiefer von Hakel (p.86) [fish layers of Haqel]	Scheifer von Hackel (p. 29) [layers of Haqel] = Schiefer von Hazhûla (p. 38) [layers of Hjoula]	Gisements à poisons à Hackel (p. 118) et a Djoula (p. [fish fossil layers in Haqel and Hjoula]	Die fischschiefer von Hâqel and Hjoûla [The fish layers of Haqel and Hjoula]	Gisements de poissons de Haqel et Hjoula (p. 47) [Haqel and Hjoula outcrops]	Couches à poissons de Hadjoula et Hakel [Hajoula and Haqel fish beds]	Haqel and Hajifia *Lagerstätten* = Sannine Formation (p. 11)	Hj
Dating	Early Cretaceous	Cenomanian	Turonian	Turonian	Cenomanian	Early Cenomanian	Early Cenomanian	Cenomanian C4	Cenomanian	La Ce
Marker	Facies attribution	"*Hippurites lumbricalis*", "*Cardium hillanum*	"Radiolite zone"	Adopted from Fraas (1878)	*Nerinae requieni*	"*Acanthoceras mantelli*", "*Orbitolina concava concava*"	Adopted from Hückel (1970) and Zumoffen (1926)	Facies	Adopted from Dubertret (1963)	*A* cf *a*

MATERIAL AND METHODS

The three localities studied Haqel, Hjoula and Nammoura are all private quarries located in the Mouhafazet (Governorate) Mount Lebanon, Central Lebanon. Haqel and Hjoula are in the Caza (district) of Byblos, nearly forty kilometres North-East of Beirut: GPS coordinates are respectively 34°09'53"N, 35°45'27"E and 34°08'01"N, 35°44'36"E (Fig. 1). However, Nammoura is in Kesserouane Caza, twenty-five kilometres NE of Beirut: GPS coordinates 34°3'21"N, 35°41'13"E (Fig. 2). The stratigraphic sections were measured with a Jacob Stuff. Hundred petrographic thin sections of limestones from the three localities were

manufactured. One thin section set is stored at the Department of Earth Sciences, University of Geneva (Switzerland), and duplicates are stored at the Natural History Museum of the Lebanese University, Faculty of Science II, Fanar El-Matn (Lebanon). The main microfossils were systematically identified and photographed under a Leica DM2500 stereomicroscope.

Geochemical analyses were performed to measure Carbon and Oxygen isotope ratios on all the collected samples.

LITHOFACIES DESCRIPTION AND MICROFACIES

Haqel section (Figs. 3-5)

The section presented here starts in the lowest outcropping layers in the riverbed and ends at the top of the Fish layer below a gap of outcrop (scree) leading to limestones with stylolites.

a) Blue grey limestones

The blue grey limestones are 4.6 m thick and occur in the basal part of the section. Laminated cherts are present in the last 30 cm. Limestones are composed of wackestones with calcispheres and allochthonous (present only in some thin laminae i.e. most probably displaced from shallower environments) benthic foraminifera (*i.e.*, orbitolinids, textularids, miliolids, cuneolinids, hauerinids), small planktonic foraminifera (hedbergellids) and echinoderm fragments. The main macrofossils encountered *in situ* are ophiurids, shrimps, small fishes and coprolites.

b) Light-yellow limestone

The massive limestone is 17 me thick, it appears light-yellow on fresh surfaces. Chert nodules or centimetric lenses are common within the first four meters and are more laminated in the following levels (Fig. 4D-E). At 17 meters from the base of the section a thick bed of 1.5 m displays slumps and load cast structures (Figs. 5A, B). The top of this unit contains chert lenses.

Limestones are composed of packstones with calcispheres, planktonic foraminifers (*i.e.*, hedbergellids, favusellids) and autochthonous benthic foraminifera (*i.e.*, Gavellinellidae, *Spiroplectammina* sp.). The macrofossils at the top are very diverse and listed below (see paragraph: Microfossils assemblages).

c) Massive grey limestones

The 9 m thick massive grey limestones are massive and display multiple stylolites in first three meters (Fig. 5C). The limestone is composed of wackestones with allochthonous (in laminae, see above) benthic foraminifera (alveolinoids, miliolids, textularids and nezzazatids). No macrofossils were observed.

Hjoula section (Figs. 6-9)

This section is made up from the assembling of three different places which are difficult to correlate precisely (? tectonics, gaps, screes, etc.). We estimate the thickness as about 13 meters. It was hard to follow the layers successions because of the random excavation made by the owner, which prevent the access to most of the layers (Fig. 9C). Two main facies were identified, separated by an unconformity.

a) Blue grey limestones (Fig. 8A)

The 2 m thick blue grey limestones are composed of wackestones with rudists (Fig. 7A), bivalves (Fig.7A), autochthonous benthic foraminifera (alveolinoids, miliolids, nezzazatids, textularids) and echinoderms.

b) Light-yellow and grey limestones (Fig. 8C)

The 11 m thick limestones are partly laminated and includes chert nodules at the base. They are composed of packstones with calcispheres and planktonic foraminifera (*i.e.*, hedbergellids, favusellids).

Nammoura section (Fig. 10)

Light-yellow to grey limestones

This section is 30 meters thick and consists of partly laminated limestones displaying some chert nodules. Limestones are composed of fine-grained mudstones. Only very rare rotaliids and hedbergellids were identified, along with some rare calcispheres.

Microfossils assemblage

It is worth noting that the beautiful benthic foraminifers well known from the Cenomanian shelf (see e.g. Saint-Marc 1974) are absent from the samples collected in these series except eventually in the laminae that appear only in some very rare levels (e.g. samples TH7, TH22) and are probably due to small turbidites or tempestites bringing these shells from the shelf down to the small basins where the sections are studied.

Haqel section

Unit a) Allochthonous (in laminae, see above) benthic Foraminifera: Orbitolinidae (Fig. 11C), *Biconcava* (?), Gavelinellidae, *Spiroplectammina* sp., *Spiroloculina* sp. (Figs. 12M-N), "Nummuloculinas" (Fig. 12O), *Istriloculina* sp. (Fig. 12 Q), *Pyrgo* sp. (Fig. 12R), *Quinqueloculina* sp., *Moncharmontia apenninica* (De castro, 1966), *Moncharmontia compressa* (De castro, 1966), *Neodubrovnikella* ?*turonica* (Said & Kenawy, 1957), *Novalesia* sp., *Nezzazata* gr.

gyra-conica, *Nezzazata simplex* Omara, 1956, *Nezzazatinella* sp., Rotaliidae; planktonic Foraminifera: *Favusella washitensis* (Carsey, 1926) (Fig. 14B-C), *Whiteinella* sp. (Fig. 14A), *Rotalipora* sp.; other rests: Ostracoda, Bryozoa and echinoderms.

Unit b) Calcispheres: *Pithonella ovalis* (Kaufmann, 1865) (Fig. 13A), *Pithonella sphaerica (*Kaufmann, 1865) (Fig. 13B), *Stomiosphaera sp.* (Figs. 13C, I)*; autochthonous benthic Foraminifera:* Gavellinellidae, *Spiroplectammina* sp.; planktonic Foraminifera: *Favusella washitensis*, *Muricohedbergella planispira* (Tappan, 1940) (Figs. 14G-H), *Muricohedbergella delrioensis* (Carsey, 1926) (Fig. 14I), *Laeviella ?* (Fig. 14D, F), *Whiteinella* cf. *baltica* Douglas and Rankin, 1969 (Fig. 14E) and *o*ther rests: Ostracoda, echinoderms and bones debris.

Unit c) Calcisphere: *Pithonella sphaerica (*Kaufmann, 1865); allochthonous (in laminae, see above) benthic Foraminifera: ?Orbitolinidae, *Biconcava* (?), *Cuneolina* sp. (Fig. 12A-B), *Nezzazatinella* sp. (Fig. 12C), *Nezzazata simplex* Omara, 1956 (Fig. 12F), *Novalesia ?*, *Spiroplectammina* sp. (Fig. 12E), *Sellialveolina* sp., *Istriloculina* sp., *Quinqueloculina* sp., *Spiroloculina* sp., "Nummuloculinas"*, Moncharmontia apenninica* (De castro, 1966), *Neodubrovnikella* ?*turonica* (Said & Kenawy, 1957) (Fig. 12D), *Nezzazata* gr. *gyra-conica* and; planktonic Foraminifera: Heterohelicidae.

Hjoula section

Unit a) Autochthonous benthic Foraminifera: *Simplalveolina simplex* (Reichel, 1936) (Figs. 11 A-B), *Sellialveolina* sp., *Biconcava* (?) (Fig. 11D), *Dicyclina* sp. (Fig. 11F), *Istriloculina* sp., *Merlingina* (?) (Fig. 11E), *Spiroloculina* sp., *Neodubrovnikella* ?*turonica* (Fig. 11G), *Nezzazatinella* sp., *Spiroplectammina* sp. and Cuneolindae.

Unit b) Calcispheres: *Pithonella trejoi* (Figs.13D, F-G), *Pithonella perlonga* (Fig. 13H), *Pithonella sphaerica (*Kaufmann, 1865), *Stomiosphaera sp. (Fig. 13E, J-K); allochthonous (in laminae, see above) benthic Foraminifera: Gavelinellidae, Spiroplectammina* sp. (Figs. 12I-J), "Nummuloculinas" (Fig. 12P); *allochthonous* green algae (organo-genus): *Terquemella* sp. (Figs. 12K-L); planktonic Foraminifera: Globigerinelloididae (Fig. 14D), *Favusella washitensis* (Figs. 15E, I), *Muricohedbergella delrioensis*, *Muricohedbergella planispira* (Pl. 15B-C), *Praeglobotruncana* cf. *delrioensis* (Plummer, 1931) (Fig. 15K), ?*Praeglobotruncana* sp.), Rotaliporidae (*Thalmanninella* cf. *appenninica* (Renz, 1936) (Figs. 15F-H)), *Whiteinella* sp. (Fig. 15J) and other rests: bones debris.

Macrofossils assemblage

Haqel section

The macrofauna list was provided by P.A.S. (one of us and the owner of the quarry) (Table 2):

Unit a): ray-finned fish, shrimps*,* brittle stars and squids.

Unit b): *Gaudryella*.

Unit c): Ray-finned fishes: *Aipichthys*, *Anguillavus*, *Apateopholis*, *Armigatus*, *Charitopsis*, *Diplomystus*, *Eubiodectes*, *Eurypholis*, *Gaudryella*, *Halec*, *Sardinioides (Leptosomus)*, *Nematonodtus*, *Osmeroides*, *Pararaja*, *Petalopteryx*, *Pseudoberyx*, *Primigatus*, *Enchodus*, pycnodonts, *Trewavasia*, "flying fishes", small teleosteans; Chondrichthyes: *Chimera*, *Cyclobatis major*, *Cyclobatis oligodactylus, Cyclobatis* sp., *Rhinobatos hakelensis*, *Rhinobatos maronita*, *Rhinobatos whitfieldi*, *Rhinobatos* sp.*, Rhombopterygia,* sharks; Sauropterygians: ichthyosaurs; "Invertebrates": *Palinurus*, *Pseudastacus*, shrimps, crabs, squids, crinoids and brittle stars.

Unit d) no macrofossils were found.

Units a and b have not been sufficiently excavated. This likely explains the poor record of macrofossil remains.

One of us D.A. found *Mantelliceras mantelli* (Sowerby, 1817), the present synonym of *Acanthoceras mantelli sensu* Hückel (1970) at Haqel (Fig. 16) 15 meters below the fossil fish *Konservat-Lagerstätte* level.

Hjoula section

The macrofossil list was provided by one of us P.A.S. who worked in the 80s for ten years in this quarry (Table 2):

Unit a): *in situ*

Unit b): Ray-finned fishes: *Aipichthys*, *Anguillavus*, *Armigatus*, *Apateopholis*, *Coccodus*, *Diplomystus*, *Enchelion*, *Eubiodectes*, *Eurypholis*, *Gaudryella*, *Halec*, *Hajulia*, *Holocentrus*, *Nematonotus*, *Palaeobalistum*, *Pateroperca*, *Phylactocephalus*, *Prionolepis*, *Pseudoberyx*, pycnodonts, *Pycnosteroides*, *Rhyncodercetis*, *Sedenhorstia*, *Stichocentrus*, large teleosteans, "flying fish"; Chondrichthyes: *Cyclobatis*, *Rhinobatos*, *Rhombopterygia*, sharks, sawfish; Coelacanths; "Invertebrates": shrimps, , limulids, *Nautilus*, cuttlefishes, crinoids, worms.

Table 2: List of fish fossils from Haqel (HK), Hjoula (HJ) and Nammoura (NA)

TAXA			HK	HJ	NA
Chondrichthyes					
Elasmobranchii	Cretoxyrhinidae	*Plicatolamna semiplicata* (Agassiz, 1843)	X	X	
	Hemiscylliidae	*Mesitia emiliae* Kramberger, 1885	X		
	Parascylliidae	*Pararhincodon lehmani* Cappetta, 1980a	X		
	Scyliorhinidae	*Scyliorhinus bloti* Cappetta, 1980a	X		
		Scyliorhinus arambourgi Cappetta, 1980a		X	
	Anacoracidae	*Squalicorax falcatus* (Agassiz, 1843)			X
	Pseudocoracidae	*Pseudocorax kindlimanni* Jambura et al., 2021	X		
	Sclerorhynchidae	*Libanopristis hiram* (Hay, 1903)		X	
		Micropristis solomoni (Hay, 1903)		X	
	Squatinidae	*Squatina cranei* Woodward, 1888		X	
	Ptychodontidae	*Ptychodus decurens* Agassiz, 1839		X	
	Rhinobatidae	*Rhinobatos grandis* (Davis, 1887)	X		
		Rhinobatos hakelensis Cappetta, 1980a	X		
		Rhinobatos maronita (Pictet & Humbert, 1866)	X		
		Rhinobatos whitfieldi (Hay, 1903)		X	
	Rhinobatidae	*Rhombopterygia rajoides* Cappetta, 1980b		X	
	Rajidae	*Pararaja expansa* (Davis, 1887)		X	
	Cyclobatidae	*Cyclobatis major Davis, 1887*	X	X	
		Cyclobatis oligodactylus Egerton, 1844	X	X	X
		Cyclobatis tuberculatus Cappetta, 1980b	X		
Sarcopterygii					
	Latimeriidae	*Macropomoides orientalis* Woodward, 1942	X	X	
Actinopterygii					
Ionoscopiformes		*Spathiurus dorsalis* Davis, 1887	X		
	Aphanepygidae	*Aphanepygus dorsalis* (Davis, 1887)	X		
		Petalopteryx syriacus Pictet, 1850	X		
Pycnodontiformes		Pycnodont sp.			X
	Nursalliidae	*Nursallia goedeli* (Heckel, 1856)	X	X	X
		Proscinetes sp.			X
	Palaeobalistidae	*?Palaeobalistum libanicum* Kramberger, 1895	X		
	Coccodontidae	*Coccodus armatus* Pictet, 1850	X		
		Coccodus lindstroemi Davis, 1890†	X		
		Coccodus insignis Hay, 1903		X	
		Paracoccodus woodwardi Taverne & Capasso, 2014b	X		X
		Corusichthys megacephalus Taverne & Capasso, 2014b	X		
		Hensodon spinosus (Hennig, 1907)	X		
	Trewavasiidae	*Trewavasia carinatus* (Davis, 1887)	X		
	Pycnodontidae	*Rhinopycnodus gabriellae* Taverne & Capasso, 2013b	X		
		*Acrorhinichthys poyato*i Taverne & Capasso, 2015a	X		X
		Libanopycnodus wenzi Taverne & Capasso, 2018			X
		Sigmapycnodus giganteus Taverne & Capasso, 2018	X		
		Flagellipinna rhomboides Cawley & Kriwet 2019	X		

		Akromystax tilmachiton Poyato-Ariza & Wenz, 2005	X		
		Haqelpycnodus picteti Taverne & Capasso, 2018	X		
		Nursallia tethysensis Capasso et al., 2009			X
	Gladiopycnodontidae	*Gladiopycnodus karami* Taverne & Capasso, 2013a	X		
		Gladiopycnodus byrnei Marrama et al., 2016		X	
		Monocerichthys scheuchzeri Taverne & Capasso, 2013a	X		
		Rostropycnodus gayeti Taverne & Capasso, 2013a	X		
		Joinvillichthys lindstroemi Taverne & Capasso, 2014a	X		
		Joinvillichthys kriweti Taverne & Capasso, 2014a	X	X	
		Pankowskichthys libanicus Taverne & Capasso, 2014a	X	X	
		Hayolperichthys pectospinus Taverne & Capasso, 2015b	X		
		Ducrotayichthys cornutus Taverne & Capasso, 2015b	X		
		Tricerichthys wenzi Taverne & Capasso, 2015b	X		
		Stenoprotome hamata Hay, 1903	X		
		Ichthyoceros spinosus Gayet, 1984	X		
	Gabrayelichthyidae	*Gabrayelichthys uyenoi* Nursall & Capasso, 2004	X	X	
		Gabrayelichthys vexillarius Nursall & Capasso, 2004	X		
		Maraldichthys verticalis Nursall & Capasso, 2004	X		
Teleostei	incertae sedis	*Prognathoglossum kalassyi* Taverne & Capasso, 2012			X
		Capassopiscis pankowskii Taverne, 2022	X		
		Petersichthys libanicus Taverne, 2021	X		
		Palaeopantodon vandersypeni Taverne, 2021	X		
Ichthyodectiformes		*Eubiodectes libanicus* (Pictet & Humbert, 1866)	X	X	X
Aspidorhynchiformes		*Belonostomus* sp. 1			X
		Belonostomus sp. 2			X
Elopomorpha	Elopidae	*Davichthys gardnieri* Forey, 1973a	X		
		Ctenodentelops striatus Forey et al., 2003			X
	Megalopidae	*Sedenhorstia libanica* (Woodward, 1901)	X		
		Sedenhorstia dayi (Hay, 1903)		X	
		Sedenhorstia orientalis Goody, 1969a		X	
	Pterothrissidae	*Hajula multidens* Woodward, 1942	X	X	
	Albulidae	*Lebonichthys lewisi* (Davis, 1887)	X		
		Lebonichthys namouresis Forey et al., 2003			X
Anguilliformes		*Anguillavus bathshebae* Hay, 1903	X	X	
		Anguillavus quadripinnis Hay, 1903		X	
		Abisaadia hakelensis (Davis, 1887)	X		
		Urenchelys germanus Hay, 1903		X	
		Enchelion montium Hay, 1903	X		
		Luenchelys minimus Belouze et al., 2003			X
Tselfatiiformes		*Protobrama avus* Woodward, 1942		X	
		Protobrama woodwardi Taverne & Gayet, 2004		X	
		Eusebichthys byblosi Taverne & Gayet, 2004	X		
		Abisaadichthys libanicus Taverne & Gayet, 2004		X	
		Rhamphoichthys taxidiotis El Hossny et al., 2023	X		

		Tselfatia formosa Arambourg, 1943			
Clupeomorpha	incertae sedis	*Ornategulum sardiniodes* (Pictet, 1850)	X	X	
	Parclupeidae	*Armigatus brevissimus* (de Blainville, 1818)	X	X	
		Armigatus namourensis Forey et al., 2003			X
		Armigatus alticorpus Forey et al., 2003			X
		Diplomystus birdi Woodward, 1901	X	X	
		Triplomystus noorae Forey et al., 2003			X
		Triplomystus oligoscutatus Forey et al., 2003			X
		Sorbonichthys elusivo Bannikov & Bacchia, 2000			X
		Scutatoclupea bacchiai Bannikov, 2015			X
	Clupeiformes	*Scombroclupea macrophthalma* (Heckel, 1849)	X	X	X
		Scombroclupea diminuta Forey et al., 2003			X
Gonorhynchiformes	Gonorhynchidae	*Charitopsis spinosus* Gayet, 1993b	X		
		Charitosomus hakelensis (Davis, 1887)	X		
Euteleostei	incertae sedis	*Pseudoberyx syriacus* Pictet & Humbert, 1866	X	X	
		Pseudoberyx bottae Pictet & Humbert, 1866	X	X	
		Pseudoberyx grandis Davis, 1887	X		
		Gaudryella gaudryi (Pictet & Humbert, 1866)	X	X	X
		Gharbouria libanica Gayet, 1988a			X
		Ginsburgia operta Patterson, 1970	X	X	
		Lebrunichthys nammourensis Taverne & Capasso, 2020a			X
		Stanhopeichthys libanicus Taverne & Capasso, 2020b		X	
		Ypsiloichthys sibelleae El Hossny & Cavin, 2023	X		
Aulopiformes	Chirothricidae	*Exocoetoides minor* Davis, 1887		X	X
		Telepholis tenuis (Davis, 1887)	X	X	
	Ichthyotringidae	*Ichthyotringa delicata* (Hay, 1903)	X	X	
	Apatepopholidae	*Apateopholis laniatus* (Davis, 1887)	X		X
	Dercetidae	*Rhynchodercetis hakelensis* (Pictet & Humbert, 1866)	X		
		Rhynchodercetis serpentinus (Hay, 1903)		X	
		Rhynchodercetis gracilis Chalifa, 1989a			X
		Rhyncodercetis yovanovitchi Arambourg, 1954			X
	Prionolepidae	*Prionolepis cataphractus* (Pictet & Humbert, 1866)	X	X	
	Enchodontidae	*Enchodus marchesetti* (Kramberger, 1895)	X	X	
		Enchodus mecoanalis Forey et al., 2003			X
		Spinascutichthys pankowskiae Murray et al., 2022			X
	Eurypholidae	*Eurypholis boissieri* Pictet, 1850	X	X	X
		Saurorhamphus giorgiae Bannikov & Bacchia, 2005			X
	Halecidae	*Phylactocephalus microlepis* Davis, 1887	X	X	
		Hemisaurida hakelensis Goody, 1969b	X		
		Serrilepis prymnostrigos Forey et al., 2003		.	X
		Serrilepis minor Forey et al., 2003			X
	Aulopodidae	*Nematonotus bottae* (Pictet & Humbert, 1866)	X		X
		Nematonotus longispinus (Davis, 1887)		X	
Myctophiformes	Sardinioididae	*Sardinioides minimus* (Agassiz, 1839)	X	X	

		Sardinioides attenuatus Woodward, 1901	X	X	
		Sardinioides pontivagus (Hay, 1903)	X	X	
		Acrognathus dodgei Hay, 1903	X	X	
	Ctenothrissidae	*Ctenothrissa vexillifer* (Pictet, 1850)	X		
		Ctenothrissa protodorsalis Gaudant, 1978a	X		
		Ctenothrissa signifer Hay, 1903		X	
		Heterothrissa signeuxae Gaudant, 1978a		X	
	Pattersonichthyidae	*Pateroperca libanica* Woodward, 1942		X	
		Pateroperca robusta Gaudant, 1978e		X	
		Pattersonichthys delicatus Goody, 1969b		X	
		Phoenicolepis arcuatus Gaudant, 1978a		X	
		Humilichthys orientalis Gaudant, 1978a		X	
Acanthomorpha	incertae sedis	*Gigapteryx tethyestris* Forey et al., 2003			X
	Polymixiidae	*Berycopsis pulcher* Bannikov & Bacchia, 2005		X	
	Blochiidae	*?Cylindracanthus libanicus* (Woodward, 1942)	X	X	
	Pharmichthyidae	*Pharmacichthys venenifer* Woodward, 1942	X		
		Pharmacichthys numismalis Gayet, 1980b	X		
	Aipichthyidae	*Aipichthys minor* (Pictet, 1850)	X	X	
		Aipichthys velifer Woodward, 1901	X		
		Aipichthys oblongus Gayet, 1980b	X		
	Pycnosteroididae	*Pycnosteroides levispinosus* (Hay, 1903)		X	
Beryciformes	incertae sedis	*Plesioberyx maximus* Gayet, 1980b	X		
		Plesioberyx discoides Gayet, 1980b	X		
		Cryptoberyx minimus Gaudant, 1978c		X	
	Holocentroidei	*Stichocentrus liratus* Patterson, 1967b		X	
		Stichocentrus elegans Gaudant, 1969		X	
		Stichocentrus spinulosus Gayet, 1980b		X	
		Paracentrus lebanonensis Forey et al., 2003			X
		Caproberyx pharsus Patterson, 1967b	X		
	Trachichthyoidei	*Stichopteryx lewisi* (Davis, 1887)	X	X	
		Lissoberyx dayi (Woodward, 1942)		X	
		Lissoberyx arambourgi Gaudant, 1969		X	
	Trachichthyoidei	*Lissoberyx denticulatus* Gayet, 1980b		X	
		Microcapros libanicus Gayet, 1980c		X	
		Libanoberyx spinosus Gayet, 1980b		X	
		Hgulichthys spinus Otero et al., 1995		X	
Tetraodontiformes		*Plectocretacicus clarae* Sorbini, 1979	X		

INTERPRETATION

Biostratigraphy

Benthic Foraminifera

Haqel: *Orbitolina (Conicorbitolina) conica* (D'Archiac, 1837) (sample TH7, Fig. 11C) and *Sellialveolina* sp. (TH7 and TH22) occur directly at the base of the *Lagerstätten* in Haqel. *Orbitolina (Conicorbitolina) conica* (D'Archiac, 1837) is Early to Middle Cenomanian (Cherchi & Schroeder, 2004) and *Sellialveolina* sp. are known in Lebanon from the Early to the Late Cenomanian (St-Marc 1974 found *S. vialii* from Early to Middle Cenomanian and *S. drorimensis* from Early to

Late Cenomanian). Rare sections attributed to *Moncharmontia appenninica* (Fig. (and its var. *compressa*) are found in Haqel (Th3; Th22). The first occurrence of this species is known as Middle Cenomanian (Schlagintweit & Moghadam 2021).

Hjoula: The presence of (one) section of *Nummofallotia apula* at the top of Hjoula section (Th31, Fig. xxx) indicates the Middle Cenomanian or younger (FO during the Middle Cenomanian following Schroeder & Neumann 1985). The presence of *Simplalveolina simplex* (Hjoula, Samples number DA7 (=TH23) and DA2 (=TH23), Figs. 11, A-B) indicates an Early to Late Cenomanian age (Schroeder & Neumann 1985).

Nammoura: the *Lagerstätten* located in the Unit 3 of Dalla Vecchia et al. (2002) does not contain stratigraphic fossil, while their Unit 4 contains *S. drorimensis* (Early to Late Cenomanian), *O.* (*C.*) *conica* (Early to Middle Cenomanian) *P.* gr. c*retacea* (Middle to Late Cenomanian); *S. laurinensis* (Middle to basal Late Cenomanian) giving a Middle Cenomanian age for this Unit. Based on benthic Foraminifers, the Nammoura *Lagerstätten* may then be Middle Cenomanian or older (Early Cenomanian?). Dalla Vecchia et al., 2002 mention Nammoura "could be coeval with Hjoula and Haqel sites or even older" contrarily to their previous statement (Dalla-Vecchia & Venturini 1999).

Planktonic Foraminifera

Costullate hedbergellids are present along both sections Haqel and Hjoula. They are attributed to both *Paracostellagerina libyca* (*Hedbergella costellata* St Marc 1973) and *Favusella washitensis*.

P. libyca is proposed as Albian P. appenninica Zone to Early Cenomanian T. globotruncanoides Zone (Mikrotax.org 2024) but Saint-Marc 1973 reported the presence (type level) of *H. costellata* in the Middle Cenomanian of Ech Chouaïfât-Deir Qoubil (Lebanon).

Favusella washitensis (Figs. 14B-C; Figs. 15E-I) is proposed as Albian T. rohri zone to Early Cenomanian T. globotruncanoides zone (Mikrotax.org 2024) but Carter & Hart 1977 as well as Kennedy 1969 reported the presence of *F. washitensis* during the Middle Cenomanian (just below the Orbirhynchia mantelliana Band which is at the upper limit of the Middle Cenomanian Turrilites costatus Zone) in England. Quality sections of *Favusella washitensis* with inflated chambers, strongly depressed sutures and 3-4 rapidly enlarging chambers in the last whorl are characteristic e.g. at the top of Hjoula section sample Th30 in Figure 6.

Among the rare rotaliporids some (rather rare) sections found in Hjoula can be attributed to *Thalmanninella* cf. *appenninica* (Figs. 15F-H) (F.O. in Albian T. appenninica Zone) which has a last occurrence in the middle part of the *R. cushmani* zone (L.O. in the Middle Cenomanian A. rhotomagense ammonite Zone).

We did not recognize the *Praeglobotruncana stephani*, *Rotalipora cushmani* and *R. greenhornenis* mentioned (not illustrated) by Hemleben (1977). We should mention that he surprisingly did not note the presence of the characteristic costulate sections of *F. washitensis*.

Nannofossils

The samples collected by Lehmann et al. (2024) show a moderate to poor preservation of the nannofossils with a low diversity. Most observed taxa are long ranging and Cenomanian markers are absent. The presence of "two singles" *Corollithion kennedyi* support the Cenomanian age.

Ostracods: Hemleben (1977) mentions *Cythereis oertlii* Bishoff, a species proposed to be common to very abundant from the lower Albian to the lowermost Cenomanian (Bishoff, 1963) but also in younger Cretaceous levels by more recent authors (e.g. El Nady et al. 2008).

Ammonites

Zumoffen (1926, p. 121) reports the index ammonite *Acanthoceras mantelli* (*Mantelliceras matelli*) SE of the *Lagerstätten* Hackel, a little higher on the slope. It may be the same he mentioned p.118 in marly limestones with *Eoradiolites lyratus* Conrad and lamellibranch casts, located below compact massive limestones deposited in thick beds with abundant silex. This ammonite is located by Hückel 1970 within the strata located just above the *Lagerstätten*. This record, followed by many subsequent authors, is however considered as doubtful by Whippich and Lehmann 2004 as the specimen has never been figured or described.

Whippich & Lehmann 2004 reported the presence of *Allocrioceras* cf. *annulatum* in both Haqel and Hjoula. According to the authors (who followed Kennedy 1988) *A. annulatum* is characteristic of the Metoicoceras geslinianum ammonite Zone of the Late Cenomanian. The specimens are reported from "Cenomanian lithographic limestones of the Lebanon" from both Haqel and Hjoula; however, Lehmann (comm. pers. 2023) corrected the presence of *A.* cf. *annulatum* in Hjoula only – not in Haqel. No precision is given on the exact stratigraphic position of the ammonites, although they are supposed to come from the *Lagerstätten* layers.

Lehmann et al. (2024) reported that ammonites only occur in Hjoula. They report the presence of well-preserved ammonites determined as: *Eucalycoceras rowei* which characterize the lower Late Cenomanian Calycoceras (P.) guerangeri Zone; *Eucalycoceras* cf. *pentagonum* from the lower Late Cenomanian Calycoceras (Proeucalycoceras) guerangeri Zone; *Euomphaloceras varicostatum* known from the Late Cenomanian of India, only known in levels possibly equivalent to the Metoicoceras geslinianum Zone in the middle Late Cenomanian; *Forbesiceras* aff. *baylissi* mainly known form the Early Cenomanian Mantelliceras dixoni Zone, but that also occur in the Middle Cenomanian; no Late Cenomanian records yet but since the genus is known in the Late Cenomanian and several species show a rather long stratigraphic range, the occurrence of the species *baylissi* in the Late Cenomanian is convincing following the authors. Lehmann et al. (2024) also identify the ammonites of Alessandrello et al. 2016 as *Neolobites* (?) sp. and consider this identification

confirm the Late Cenomanian age (Neolobites vibrayeanus / Calycoceras guerangeri Zone) for the “sublithographic limestones” *sensu* Lehmann et al. (2024), i.e., the fish beds.

Biostratigraphic discussion and conclusion:

The benthic Foraminifera give a Middle Cenomanian age; the planktonic Foraminifera give an Albian to Middle Cenomanian age, and the Ammonites give a Late Cenomanian age.

Some benthic foraminifera occur in laminae (e.g. sample TH7, TH22 in Haqel) and are probably reworked from shallower sediments in small/distal turbidites. However, the laminae do not show any pebble containing (or not) the benthic foraminifera; the shells do not show any sign of wear and could then be considered as contemporaneous with the surrounding sediment.

From the data mentioned above, the age given by microfossils is then Middle Cenomanian with the huge advantage being that we know exactly from which level they come within the lithographic limestones of the *Lagerstätten* (Figs. 3, 6).

The rare well preserved ammonites’ specimens used for biostratigraphy in the Lebanese *Lagerstätten* have the unfortunate disadvantage of never being precisely located in the field. The age they provide is different from the one obtained with microfossils.

The precise age of Haqel and Hjoula *Lagerstätten* although known as Cenomanian since decades does not seem to be totally solved yet. Confrontation of the biostratigraphic data between ammonite and foraminifera makes the age question remains open as well as the possible contemporaneousness of the *Lagerstätten*.

It may be solved in the future by further detailed field work and precisely located new ammonite findings; although (as mentioned by St Marc (1974)), significant tectonic in the area definitely makes correlation between outcrops difficult. Indeed, contiguous outcropping levels may be of rather different ages as we can note regarding e.g. the maps and diagrams of the *Lagerstätten* made by Hückel (1970).

Chemiostratigraphy

Geochemical analyses were performed to measure Carbon and Oxygen isotope ratios on all the collected samples for the sections Haqel and Hjoula (Figs. 3, 6). The Anoxic levels are missed in sampling or the C/T boundary was not reached.

Elemental mapping

Field emission scanning electron microscope (FESEM) images and Energy Dispersive Spectroscopy (EDS) quantification were acquired using a TESCAN MAIA3 GMU with energy dispersive X-ray (EDX) spectroscopy (OXFORD ULTIM MAX 170). The sample was uncoated and EDS analyses with Large Area Mapping (LAM) technique was completed using an accelerating voltage of 20 keV at a working distance of 5 mm for acquisition rate ~30000 cps/s. The EDS elements in this study were collected at 20 keV with ~100000 counts/s and ~30% dead time.

We made elemental mapping using a MAIA3 Triglav TESCAN SEM and we distinguished in Haqel section a passage from a layer rich with Mg to another deprived of this element.

Correlations

The two sites Haqel and Hjoula are distant by 3.7 km.

Along our Haqel section, there is no clear macroscopic unconformity visible along the encompassed series on the field. The area is highly affected by tectonic accidents and correlations between the different outcrop is difficult. Hückel (1970) made the most comprehensive field work of the area. The *Lagerstätten* consist of packstones with calcispheres and planktonic foraminifers. Laminae containing benthic foraminifers (*e.g.,* Alveolinoidea or Orbitlolinidae) are sometimes observed along the section.

A lower unconformity is observed in Hjoula marked by the change in facies from lumachellic bed with rudists (Figs. 8A-B) shells, alveolinoids and orbitolinids to a fine laminated bed.

The facies (light-yellow limestones), microfacies (packstones) and the microfossil assemblage of calcispheres, benthic and planktonic foraminifers are similar in both *Lagerstätten*. All these data summed up allow a rough stratigraphic correlation.

The topmost part of the Hjoula section is not exposed (due to screes and random excavation of the topmost layers (Fig. 9C)).

Our Nammoura section would be directly correlated with the “units 2 and 3” of Dalla Vecchia et al. (2002) because we found only some rare calcispheres with rare *Muricohedbergella* sp. in our samples.

The micropalaeontological data (this work) as well as the new ammonite data (Lehmann et al. (2014)) do not allow to give a more precise correlation than the one previously proposed e.g. by Hückel (1970) based on field data (lithostratigraphy, sedimentology). As a reminder, Hückel proposed Hjoula *Lagerstätte* being slightly older (Cenoman IVd) than Haqel *Lagerstätte* (Cenoman Va). New well-located ammonites combined with detailed field work (lithostratigraphy, sedimentology, tectonic) may then be the only key to a more precise correlation between the *Lagerstätten*.

DEPOSITIONAL ENVIRONMENT

A review

Pictet and Humbert (1866) suggested that Haqel deposition was formed aside the land due to the presence of an insect (a wingless Orthoptera, *op. cit.*: p. 240).

In 1938, van Straelen considered that the Haqel deposition “ne sont point des formations bathyales… ils appartiennent à la zone néritique, voire littorale, et rappellent les dépôts se formant dans les baies qui découpent les massifs récifaux… ils sont des récifs à radiolites et à Hippurites qui passent latéralement aux calcaires grenus en bacs minces” [are not a bathyal formation… but a neritic or even littoral zone. They remind the depositions formed in the bay and that encompasses the reefal environments… they represent reefs with radiolites and Hippurites passing laterally to grainy limestones in thin beds].

Roger (1946) considered that all the palaeobiologic data could not be separated from the palaeogeographic data. He subdivided faunal assemblages of Haqel and Hjoula to four different groups: necton with Selacians; planktonic with branchiopods, *Antedon* and globigerinids; bathypelagic with *Istieus*, *Dercetis*, Myctophidae and benthic with *Limulus*, *Sculda*, worms and *Pseudosculda*. He described the palaeoenvironment as several hundred of meters deep (with the occurrence of crustacean and globigerinids). He considered that the fish beds were laid on a deoxygenated bottom in channels between shallow reefs (with rudists) away from the coast.

Patterson (1967) provided a preliminary observation on the palaeoenvironment. He suggested that the fish beds were deposited in a submarine canyon (a trap for fishes and invertebrates) with a deoxygenated bottom and a supply of fine sediments. He interpreted the death of this high number of fishes as “mass mortalities caused by toxins released in " waterbloom " conditions, and that the high percentage of silica in the rocks (21% at Hakel, not detrital but colloidal, Roger, 1946: p. 77) results from the solution of diatom frustules”.

Hückel (1970), suggested that the fish beds of Haqel and Hjoula were deposited in small tectonic basins (some hundreds of meters wide and up to 270m deep) in a “subsequent stagnant stage… they may have been re-deposited by occasional small-scale suspension currents. Locally they interfinger with the beds of the surrounding sea floor” (*op. cit.* p. 9).

In 1977, Hemleben represented a general depositional scheme to Haqel and Hjoula deposits. He suggested that they correspond to tectonic troughs at the border between shelf and basin filled with allochthonous and pelagic sediments. For Hemleben (1977) the fossil preservation was favored by an oxygen deficiency and a rapid sedimentation. He explained the massive mortality of the fauna by the upwellings causing red tides in this marginal shelf environment.

Walley (1997) claimed that these layers have been deposited in low oxygen environments, and the biotas possibly represent localised zones of chemoautotrophic communities based around deep water methane seeps.

Dalla Vecchia et al. (2002) focused their work on the Nammoura outcrop. They suggested a small non-tectonic marine basin environment bordered by clinoform with a normal fauna death deposition. However, they adopted the hypothesis of Hemleben (1977) for Haqel and Hjoula *Lagerstätten*. They considered these two depositions were formed in tectonic basins but with different macrofaunal composition.

Our interpretation

Our palaeoenvironmental interpretation is based on the microfacies and fossil assemblage, which is composed of abundant micro and macrofauna. In the studied sections, the occurrence of Orbitolinids and Alveolinoids in very thin laminae (Fig. 8C) indicate they are redeposited in sediments interpreted as distal turbidites (or tempestites). The thin bedded (?) muddy limestone (wackestones) of the *Lagerstätten* and the mud-dwelling *Istriloculina* (Arnaud-Vanneau and Slitter, 1995; Omaña & Alencáster, 2009) suggest a quiet water environment (decantation) surrounding the *Lagerstätten* of Haqel and Hjoula. In our opinion, the presence of marine fauna i.e., fishes, sharks, shrimps, ammonites… as well as terrestrial fauna i.e., pterosaurs (Dalla Vecchia, 2001; Kellner et al., 2019) and numerous non-dislocated insects (Maksoud & Azar, 2021) in Hjoula outcrop indicate the presence of an emerged land (island(s)) closer than the several hundreds of kilometres proposed for the coastline by previous authors. The complete preservation of marine and terrestrial animals marks a smooth deposition of the layers.

Haqel *Lagerstätte* corresponds to the same deposition environment as Hjoula. In addition to the marine fauna (fishes, shrimps, etc.), both outcrops have yield pterosaurs; and insects (Azar et al., 2024) but rare fossils of plants were recorded in Haqel. Worth noting that it could be possible to find them in the future and Hjoula which could be a bit more away from the emerged land based on the presence of fossil insects.

Calcispheres and Gavelinellidae are known from low oxygen and high nutrient sediments (Omaña et al., 2014; 2019). This could be the main reason behind the death and the exceptional preservation of the fauna in Haqel and Hjoula outcrops.

Considering the planktonic foraminifers, we note the frequent small sized morphotypes (hedbergellids and rare globigerinelloids) observed all over the sections of Haqel and Hjoula in association with ornamented *Hedbergellid* (*Paracostellagerina lybica*) and Favusellid (*Favusella washitensis)*. Both groups Hedbergellids and Globigerinelloids, indicate usually a shallow epicontinental sea or a marginal sea (Eicher & Worstell, 1970; Leckie, 1987). Also, we found *Favusella washitensis* in several levels in both sections Haqel and Hjoula; this species is particularly characteristic of warm shallow water environments i.e., such as marginal seas or carbonate platforms (Barr, 1972; Koutsoukos et al., 1989; Longoria & Gamper, 1977; Saint-Marc, 1973).

We also found some (very) rare Heterohelicids characteristic of epicontinental sea fauna (Leckie, 1987) in Haqel.

The rare occurrence of the keeled genera i.e., *Thalmanninella* and *Praeglobotruncana* which are, in general, deeper dwelling planktonic foraminifera (Hart & Bailey, 1979; Leckie, 1989) indicate a moderate depth. Carinate forms were more often (less rarely) encountered in Hjoula.

The dominance of epicontinental species suggests that the depth around these basins should not exceed 100 meters (Hart & Bailey, 1979).

Our Nammoura field section (Fig. 10) can be easily correlated with the field section of Dalla Vecchia et al. (2002) (i.e., unit 3). We adopt the environmental interpretation of the authors: The geometry of their section shows the *Lagerstätten* began to form in a small a marine basin bordered by a clinoform that was not deeper than 50 meters.

Fossil fish assemblages

Systematic excavations carried out for decades by one of us (P.A.S) and his team in the sites of Haqel and Hjoula have provided a wealth of information on the stratigraphic distribution of fish taxa, as well as their abundance and their type of conservation (Table 2). The data is particularly instructive in the Haqel site, where they have been collected for 30 years in the 5.5 meters thick unit c section (Fig. 3). Twenty-six beds were defined in this unit during the excavation. The abundance of fossil fish is highest in the lower part of the unit, from bed 26 to bed 18. These beds contain a slightly fewer calcispheres than the upper part of the unit. The three lowest levels (26-24, Figs. 17A-D) are very rich in ray-finned and cartilaginous fishes, and *Pseudastacus* decapods. In bed 26, the density of certain taxa is very high in some areas, and field estimates show that it can reach 15 specimens per square meter for the fish *Eurypholis* and 10 specimens per square meter for the crustacean *Pseudastacus*. Bed 24 (Fig. 17D) is characterized by its lithology and is the only one in this rich lower part of the unit to contain favuselids. Bed 23, characterized by the presence of chert nodules and ostracods, does however contain some fossil fish, such as pycnodonts, and the only ammonite found in the section. The two upper beds (22 and 21) are very rich in cartilaginous and ray-finned fish. Bed 22 is subdivided into three distinct layers. The lowest layer produces the greatest diversity of fish, the middle layer contains crinoids, and the top layer contains mainly small fish, *Sardinioides* (“*Leptosomus*”) and *Petalopteryx*. Bed 21 contains large specimens of pycnodonts and *Enchodus*, numerous *Cyclobatis* rays, squids preserved with tentacles, and specimens of most other known fish taxa at the locality. Bed 20 is a thin layer of chert nodules and Bed 19 is rich in most cartilaginous and ray-finned fish species (Figs. 17E-F). In an excavation area, the number of *Cyclobatis*, *Rhinobatos* and *Palinurus* lobster reached 1 per square meter, and 0.3 for the shark. Bed 18 above is particularly rich in *Gaudryella*, as well as other taxa such as *Petalopteryx*, *Apateopholis*, *Trewavasia*, *Rhinobatos* guitarfish, and sharks (Figs. 17G-H). Bed 17 is a 1.5 meter thick layer without vertebrate remains, but with textularids in its middle depth, and some echinoderms and an increase in calcispheres in its upper part. The presence of cross-stratifications indicates that this layer was deposited in a channel.

Above this level, the deposits of unit c are characterized by the presence of hedbergells and favuselids, absent in the lower part of unit, and by a lower density of fossil fish except for certain layers. The lowest bed (16) is particularly rich in *Cyclobatis*, the thin layer 15 is rich in *Armigatus* (about 15 per square meter), cartilaginous fish but few *Eurypholis*. The area between beds 15 and 14 is very rich in *Nematonotus*, and bed 14 is characterized by a high density of small fish and small crabs, both reaching a density of about 20 per square meter. Following a layer with chert nodules (layer 13), two layers contain many decapods. The lowest (bank 12) gives mainly shrimps and the highest (bank 11) contains mainly small crabs, with a density reaching 100 per square meter, as well as some fish. Above this "crab layer", are two thick (0.3 m) and dense layers (beds 10 and 8) without fossil fish separated by a thin layer (3 cm) containing about 0.5 *Cyclobatis* per square meter. Bed 7 contains few fish, mostly disarticulated and not always preserved flat, which can cross several layers inside the bed. It also yielded the only ichthyosaur remains found in this quarry (reference). Bed 6 is the highest bed with some disarticulated fish, covered by five beds with no large fossil fish but only rare small fish and shrimp. The upper two layers are characterized by an increase in calcispheres, textularids, nezzazatids, cuneolinids and miliolids.

DISCUSSION

Palaeoenvironment

During the Cenomanian, Lebanon and the whole Arabian Peninsula were part of the African platform in the northern part of the Gondwana super-continent (Philip et al., 1993). In Cenozoic times, opening of the Red Sea separated the Arabian Peninsula from Africa. Like the mid-Cenomanian Nammoura outcrop, Haqel and Hjoula fish layers were deposited during the Middle or Late Cenomanian, in small, shallow basins with a low water flow (Dalla Vecchia and Chiappe, 2002; Dalla Vecchia et al., 2002). Thus, mild oscillations of the relative sea level produced an exceptional “sandwich of shallow water carbonate facies (often rudist bearing) alternating with finely-bedded or laminated mudstones” as described by Ferry et al. (2007). Such palaeoenvironment together with the morphology of the small collapse basins (Hückel 1970) and the dysoxic / anoxic conditions probably caused by phytoplankton blooms (Patterson 1967, Hückel 1970, Hemleben 1977) provide suitable conditions for the excellent preservation of the rich fauna consisting of: fishes (Forey et al., 2003), reptiles (Dalla Vecchia et al., 2001), crustaceans (Garassino, 2000), annelids (Bracchi & Alessandrello, 2005), cephalopods (Wippich & Lehmann, 2004; Fuchs, 2006), etc.

In many samples (e.g. Th11, Th38), the size of the fragmentated shells is remarkably calibrated / sorted (e.g. “chewed” by fishes and/or arranger by bottom currents). Laminae appear very clearly in many samples. The proportion of mud in the samples varies over time. A sample (Th30) shows a non-dismantled echinoderm (ophiurid), suggesting a calm bottom (maybe due to the absence of currents and/or absence of predators).

The rich benthic foraminifera assemblage of the Cenomanian platforms in Lebanon mentioned by Saint-Marc (1974), is absent from the samples taken from the studied sections. It only appears in very rare cases (Th7, Th22) in laminae, perhaps linked to small underwater avalanches dragging this material from the platform down to the small basins where the sections were made. The sampled beds could be considered as exceptional layers from the Lebanese Cenomanian.

Fish assemblages

Variations between the Lebanese Cenomanian fish assemblages (Fig. 18)

Forey et al. (2003) provided a comparison between several Cenomanian fish assemblages from various Tethys localities and the English Chalk, with particular emphasis on the three Lebanese assemblages Nammoura, Haqel and Hjoula. We compare here the figures obtained by Forey et al. (2003) with data updated in the present study. The new compilation is not only based on discoveries made in the quarry dug by one of us (P.A.S.), but based on a review of the literature. (Fig. 17) shows the number of species in each assemblage and the number of shared species calculated as in Forey et al. (2003), i.e., the total number of shared species divided by the total number of species at the least rich locality expressed in %, for the two studies separated by two decades. The number of described species has increased significantly, 20% for Haqel, 24% for Hjoula and 33% for Nammoura, but the percentage of species shared between the assemblages is quite similar, only a 2% difference between Nammoura and the two other assemblages, and a slightly greater decrease between Haqel and Hjoula, from 54 to 44% of shared species.

Over the past two decades, new taxa have been particularly numerous in the pycnodonts, with 26 new species, including some in the Pycnodontidae (Taverne & Capasso, 2013a, 2015a, 2018, Cawley & Kriwet, 2017, 2019, Poyato-Ariza & Wenz, 2005) but especially in the highly derived Coccodontidae (Taverne & Capasso, 2014a), Gladiopycnodontidae (Taverne & Capasso, 2013b, 2014b, 2015b) and Gebrayelichthyidae (Nursall & Capasso, 2004). The unique morphology of the last three families, endemic to Lebanese Cenomanian sites, is an enigma to understand their biology. These bizarre pycnodonts are very rare and have been found mainly at Haqel (Capasso, 2024), but we cannot decide at this stage whether this is due to real differences caused by different environmental conditions or whether it is due to collection bias.

Other new taxa include several tselfatiiformes (Taverne & Gayet, 2004, 2005), a group of ray-finned fish currently under study by one of us (T.E.H.), and several taxa referring to the Pantodontidae (Taverne & Capasso, 2012, Taverne, 2021, 2022), although we consider their identification still uncertain. The latter have not been included in the Fig. 18 (environment- fish).

Fieldwork conducted by one of us (P.A.S.) provided qualitative data on compositional variations within each assemblage, bed by bed, but these qualitative data do not allow for the characterization of clear trends from quantitative data. However, general differences are observed between the faunal composition of the Haqel and Hjoula sites. Pycnodonts, and particularly Coccodontoidea, are more diverse at Haqel than at Hjoula (Table 2). This is also the case for holosteans, gonorynchids, and elopomorphs. In contrast, myctophiforms and beryciforms appear to be more diverse at Hjoula than at Haqel. If these differences are not solely due to collection bias, they would indicate a higher proportion of benthic genera at Haqel and a higher proportion of demersal-pelagic genera at Hjoula.

Trophic network and mode of life (Fig. 19)

Although differences exist between the taxonomic compositions of the ray-finned fishes from Haqel and Hjoula sites, the assemblages are broadly similar, and it is difficult at this stage to decide whether the variations are caused by real environmental differences (the ages of the two localities are very close) or by sampling or recording biases. Therefore, we discuss the food web structure of the two merged assemblages. Except in special cases, the diet of ray-finned fishes is often not very specific, and the positioning of a species or genus in a food web must be considered approximate. Here, we position the genera in the food web based on jaw characters and general morphology, and by comparing them with analogous or closely related extant species whose diets are known. This general reconstruction of the food web is preliminary, and the proposed hypotheses need to be tested in the future by quantitative and modeling methods. We primarily used Fishbase.org and Friedman et al. (2020), respectively for the identification of diet and living environments (i.e., benthic, dermersal, pelagic) of extant counterparts of the extinct taxa.

Most pycnodonts are characterized by crushing dentition adapted to a durophagous diet. Their bodies are generally deep and flat, making them ecologically analogous to extant triggerfish (Balistidae) or filefish (Monacanthidae). Although the latter are often related to coral reefs, this is not always the case for pycnodonts, as in Lebanese sites for example. These fish could feed on benthic invertebrates, crabs, shrimps, crinoids or perhaps rudists present in the lateral facies. Capasso (2019) suggested that at least one genus, Acrorhinichthys, could feed on small teleosts. The typical morphotype of Bauplan pycnodonts belonging to the families Pycnodontidae and Nursallidae, described mainly from Haqel, represents about one-third of the genera. Based on a series of new discoveries made mainly in the last two decades, Taverne & Capasso (2013b), Marramà et al. (2016) and Capasso (2024) have demonstrated that two-thirds of the pycnodont genera from Haqel and Hjoula belong to taxa with unique morphologies during the long history of this clade, which are restricted to this time and space (i.e. the Cenomanian of Lebanon). This explosion of morphological space occupied by pycnodonts concerns a single clade, the Coccodonoidea, represented mainly by species found in Lebanese sites. Within this clade, coccodontids and trewavasiids have a morphology reminiscent of the Bauplan of the generalist pycnodonts, although some show signs of protection against predators, including spines and horns and a hypertrophied pectoral girdle (Marramà et al., 2016). The common *Coccodus* shows a kind of dorsoventral flattening indicating a possible benthic lifestyle. Gladiopycnodontids and gebrayelichthyids show a more derived morphology: the former have dorsal spines, cephalic and nuchal horns, and an enlarged pectoral girdle, while the latter have a unique, extremely deep and short silhouette. The morphological features present in both families, namely a rigid armored trunk and a rostrum are reminiscent of those of the Syngnathiformes. We suggest that these fish were suction feeders, mainly on small planktonic crustaceans, similar to Syngnathiformes, although we have no evidence that they were able to do pivot feeding like seahorses and pipefish (Longo et al., 2018).

Other planktivores from Haqel and Hjoula are clupeiforms and probably some basal euteleosts (*Gaudryella*, *Ginsburgia*). Like most extant clupeiforms, they were probably schooling ram filter feeders, as indicated by their general body morphology reminiscent of their extant counterparts, their high relative abundance within the assemblage, and their preservation often forming monospecific accumulations caused by mass mortality, notably for *Armigatus* and *Scombroclupea*. (Forey et al., 2003). Ionoscopiforms and aphanepygids are holosteans with ganoid scales, a shallow body, a non-protrusing mouth, and poorly developed fins that probably correspond to a benthodemersal lifestyle and an invertivorous-detritivorous diet. We also include gonorynchids in this group. Extant elopomorphs feed mainly on small fish, crustaceans, and mollusks (elopiforms, anguilliforms), and this was probably also true for their Cenomanian counterparts due to the general similarity of their body plan. Extant myctophiforms, beryciforms, and basal acanthomorphs are mainly pelagic-

demersal and feed on small fish and invertebrates. The morphology of Cretaceous representatives of these groups is close to that of extant species, and we consider them to have a similar diet and environment. We have added the undetermined euteleosts *Ypsiloichthys* and *Pseudoberyx* to this group. Most tselfatiiforms have a morphology similar to extant veliferids, and we suggest that they were also pelagic fish feeding on zooplankton and small invertebrates. An exception among tselfatiiforms is *Rhamphoichthys*, whose morphology indicates a fast pelagic piscivorous fish (El Hossny et al., 2023). *Eubiodectes*, an ichthyodectiform, as well as all aulopiformes, exhibit body and jaws morphologies typical of piscivorous predators. Only among aulopiformes, chirothricids may have fed partly on invertebrates.

It is worth mentioning that several diverse clades at the Hagel and Hjoula sites are now more abundant in deep waters (beryciformes, aulopiformes) (Xu et al., 2025), much deeper than the estimated depth of Cretaceous assemblages. This situation is best explained by the fact that several groups of marine ray-finned fishes first diversified in relatively shallow environments before migrating to deeper environments, probably driven out by the presence of new competitors.

In summary, the food webs that we can reconstruct from fish diets are not specific to an unique environment, but correspond to a fairly wide range of environments. Schools of pelagic planktivores (clupeiformes, small euteleosts) lived in open environment, not deep below the sea level. Meanwhile, beryciformes, myctophiformes, basal acanthopterygians, and euteleosts probably thrived in the dermersal zone and fed on a wide variety of invertebrates and small fishes. Closer to the bottom probably lived anguilliformes, and perhaps gonorynchids and halecomorphs, which could be detritivores. Coccodontoids lived near the bottom, feeding on plankton and other tiny items, while other pycnodonts fed on shelly or soft invertebrates. Other piscivorous fishes belonged mainly to the aulopiformes, with varied body morphology. The rare ichthyodectiform *Eubiodectes* was also piscivorous. The ecology and diet of all fish presented here are preliminary and based on superficial qualitative observations. These hypotheses will then need to be verified by morphometric analysis.

The position of the Cenomanian Lebanese fish assemblages worldwide

Taken together, the three Cenomanian Lebanese fish assemblages collected 141 ray-finned fish species, compared to slightly more than half the number of species in the famous Late Jurassic Solnhofen Archipelago, Germany (74 species according to our compilation), although the German site localities cover a longer time period (Late Kimmeridgian to Early Tithonian) and a wider geographical range, or the Middle Triassic locality of Monte San Giorgio that straddles the Italian-Swiss border and also contains 74 species (Romano et al., 2014). Indeed, the three Cenomanian Lebanese fish assemblages together represent the most specious ray-finned fish assemblage of the Mesozoic, and one of the most specious “fish” assemblages of the Phanerozoic. Probably the most specious assemblage of “fishes” is that of Monte Bolca, from the Eocene of Italy, with about 250 described species (Carnevale & Pietsch, 2009). The Cenomanian is a period with a very high diversification rate of ray-finned fishes (Guinot & Cavin, 2016), which is positively correlated with sea temperature throughout the Late Mesozoic (Guinot & Cavin, 2020). The high peak of actinopterygian diversity in the Cenomanian is associated with a high rate of biological diversification, but also with the presence of numerous fish localities around the Tethys (Slovenia, Croatia, Lebanon, West Bank, Egypt, Algeria, Morocco, Mexico) and in the Boreal Basin (UK, France).

Origin of the fish accumulations

The very high taxic diversity and good preservation of fossil fish from the two sites of Hakel and Hjoula make them unique in the Mesozoic. This situation implies that the conditions of accumulation and preservation of these assemblages have been exceptional, otherwise similar fossiliferous deposits would be more frequent. The abundant calciphaerulids, visible in thin sections of Lagerstätten sediments, are considered evidence of algal blooms. For decades, it was generally accepted that Lebanese Lagerstätten were caused by plankton blooms (e.g., Patterson 1967, Hemleben 1976, 1977) near the edge of the continental shelf (e.g., Hemleben 1977), in deep canyons (e.g., Roger 1946, Patterson 1967), or in small local basins (e.g., Hückel, 1970). However, contemporary sediments lateral to the Lagerstätten are equally rich in calciphaerulids, but do not contain the remarkable fauna found at Hakel and Hjoula. This also applies to the incredible amount of calcisphaerulid-rich sediments (contemporary or not) elsewhere on Earth, which are generally not particularly rich in macrofossils. Although we do not exclude poisoning as the origin of the mass mortality, we suggest that the topographic conditions of the sites were the main reason for the concentration of fossils. Rather than Canyon (Patterson, 1967), Hückel (1970) suggested that the Hakel and Hjoula fossils correspond to accumulations in, deep “holes” in the seafloor at the time of their formation (e.g. 600m diameter and 150m deep in Haqel). A thermocline probably formed above the anoxic seafloor, and when fish and other animals reached the bottom, perhaps by fleeing or dying from algal blooms, they perished and were preserved on the azoic seafloor. We consider that the “holes” described by Hückel (1970) may correspond small pull apart basins in a tectonic active area. These structures resemble sinkholes, which are quite common on present-day seafloors, and have been the subject of numerous studies over the past decades. Interestingly, Baumberger et al. (2010) recorded in a sinkhole off the coast of Florida an aggregation of spawning barbfish, *Polymixia lowei*, which is a basal acanthopterygian phylogenetically related to *Pycnosteroides* and *Aipichthys* (Davesne et al., 2016) present at Hjoula for the former, and at Hjoula and Hakel for the latter. In addition to *Polymixia*, eleven species of fish and a variety of invertebrates were observed at the Florida site. Although these sinkholes, formed from submerged freshwater seeps and excavated nearly 150 m below the seafloor, located approximately 280 m below sea level, no longer appeared active, as there was no evidence of salinity or temperature anomalies, the similarity with the Lebanese site is noteworthy. Shallower sinkholes (less than 100 m deep) off the Brazilian coast are hotspots for biodiversity and bioproductivity, particularly for fish (Cavalcanti et al., 2013).

An alternative to sinkholes are pockmarks, i.e. large circular depressions on the seafloor, formed by the release of gases and fluids (Betzler et al., 2011). The evolution of these structures begins with dome-shaped bodies caused by fluid migration and ends with bowl-shaped concavities filled with sediment drifted from the margin of the structure, an arrangement similar to that described by Hückel (1970) for Haqel and Hjoula. Although generally present in siliciclastic depositional environments, pockmarks also occur on carbonate platforms, as is the case today in the Maldives (Betzler et al., 2011). However, both current and ancient hydrocarbon seeps harbor very rich life assemblages based on chemosynthesis, with microbes at the base of food chains supporting a diverse benthic life of macroinvertebrates (Campbell, 2006), a situation not observed at Lebanese sites except in some beds that preserved large accumulations of

crabs or other crustaceans, such as the "crab layer" located in the upper part of the Haqel series which can contain up to 100 individuals per square meter (P.A.S, personal observations).

A detailed interpretation of the life and fossilization environment of the Haqel and Hjoula sites is beyond the scope of this article. However, some major features can be highlighted for future work: (1) The abundance and diversity of macrofauna (especially fish) indicate that the original environment consisted of natural traps for these organisms, such as canyons or, favored here, more restricted depressions such as sinkholes or pockmarks of probable tectonic origin; (2) The quality of macrofauna preservation and the scarcity of benthic invertebrates indicate an anoxic seabed, although there are exceptions; (3) In partial contradiction to the previous point, the fish assemblage contains ecomorphotypes typical of a variety of environments (pelagic, demersal, benthic); (4) If the cause of the mass mortality is algal blooms, as is generally accepted, the reason for the preservation of the assemblage is due to local conditions (point 1) because the frequent calciphaerulid rich sediments worldwide are (very) rarely associated with Lagerstätten fossil sites.

Importance of the Lebanese Cenomanian Lagerstätte

The Cenomanian Lebanese fossiliferous deposits, such as Haqel, Hjoula and Nammoura, have provided a wealth of well-preserved and diverse fossils that offer invaluable insights into the ancient marine ecosystems and the evolution of life during that time, making them indisputably important in the palaeontological world. The reasons for these deposits holding such a significant position in palaeontology are discussed hereafter.

First, the fossils found in these deposits are often exquisitely preserved, showcasing intricate details of various organisms (Forey et al., 2003; Gayet et al., 2003; Elgin & Frey, 2011). This exceptional preservation includes soft tissues and delicate structures (Martínez-Delclòs et al., 2004) and even evidence of behaviors (e.g. the fish motion leaving a wavy trace made by the impression of the caudal fin) (personal observations, P.A.S), which are usually rare in the fossil record.

Furthermore, Lebanon is reputed for its diverse array of Cenomanian fossil assemblages, including marine invertebrates, fishes, plants and occasionally insects and tetrapods, such as marine reptiles (e.g. Elgin & Frey, 2011; Campbell et al., 2019) or rare pterosaurs (Dalla Vecchia et al., 2001). Fossil fishes, in particular, from Lebanon, form one of the oldest historical record of fossil fishes in the world, reputed not only for their diversity but the abundance of material as well (Capasso, 2017); add to that, despite the extensive collection for several centuries now, with multitude of species described over this period, even more new species are still being excavated and described at a 1/5 rate of taxa per year (Capasso, 2017), making the Lebanese fossil deposits, in particular Haqel, one the richest ichthyofaunal deposits in the world (Capasso et al., 2010).

In summary, the Lebanese Cenomanian deposits with their exceptionally preserved and diverse fossils provide important data for understanding the marine palaeoecosystems, the evolutionary history of several organisms, and the reconstruction of palaeoenvironments. Many of these characteristics are also found in other *Lagerstätte* around the world, mainly those from the Central Tethys, however, none has comparable fish assemblages to that of the Lebanese deposits. Several fish groups reached their highest morphological diversification in the Cenomanian, with most ones documented from Lebanese deposits (example of fish groups are the Pycnodontomorpha (Marramà et al., 2015) and the Tselfatiiformes (Taverne & Gayet, 2004).

CONCLUSION

Following recent ammonite data (Lehmann et al. 2024) Haqel and Hjoula are both deposited in the lowermost Late Cenomanian. This age is not in accordance with the age provided by the foraminifers giving a slightly older one, i.e., Middle Cenomanian. The solution of this enigma may be solved by further field studies and new stratigraphic fossil findings, with their precise location in the stratigraphic series.

Small cuvette like tectonic basin as evidenced by the field work of Hückel (1970) contains the *Lagerstätten* in thin laminated mudstones containing planktonic foraminifers, very abundant calcispheres, and some benthic foraminifers, some of which appear in laminae.

Although known for over 1,500 years and constituting immense collections in museums worldwide, the ecology and taphonomy of Cenomanian fish assemblages from Lebanon remain largely understudied. Our study provides new information but nevertheless leaves an open question. The main paradox lies in the difficulty of interpreting the living and depositional environments. Some pelagic fish living in the water column may have thrived vertically above the fossil sites. However, other elements of the assemblage, particularly species living near the bottom, did not benefit from favourable living conditions at the site, as benthic macroinvertebrates were rare except in some layers. The bottom was likely anoxic, as indicated, among other things, by the near absence of predation on corpses. This situation could be explained by post-mortem transport of bodies, but sedimentological evidence of such events is evident at the sites. We believe that the exceptional richness of these two spatially restricted sites corresponds to exceptional environmental and topographical conditions, a hypothesis that remains to be explored. The best model currently proposed is that localized sinkholes, offering conditions highly favourable to life, experienced mass mortality at certain times, probably due to poisoning from algal blooms. The corpses settled to the bottom and were preserved thanks to the anoxic conditions.

Declarations

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Author Contribution

SM and DA conceived the project.SM, DA, AP, and LC wrote the main manuscript.DA, SM, LC, and TEH conducted the fieldwork and sampling.PAS provided the material for study.SM prepared Figures 1–16 and Table 1.LC prepared Figures 17–19 and Table 2.All authors reviewed and approved the final manuscript.

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Figures

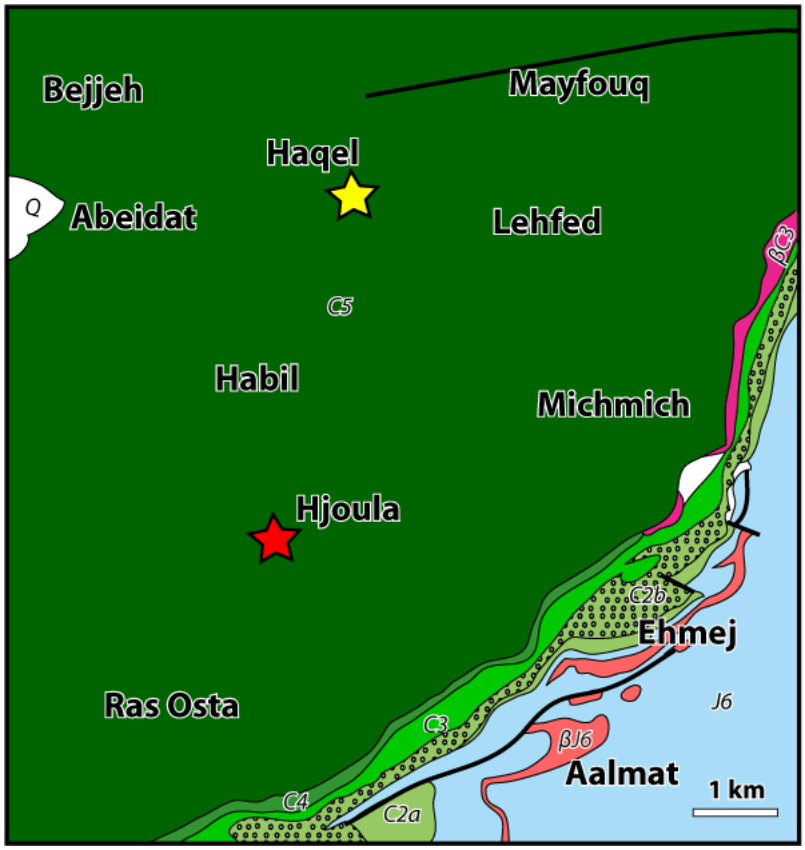


Figure 1

Geological map showing the localities of Haqel (yellow star) and Hjoula (red star) outcrops.

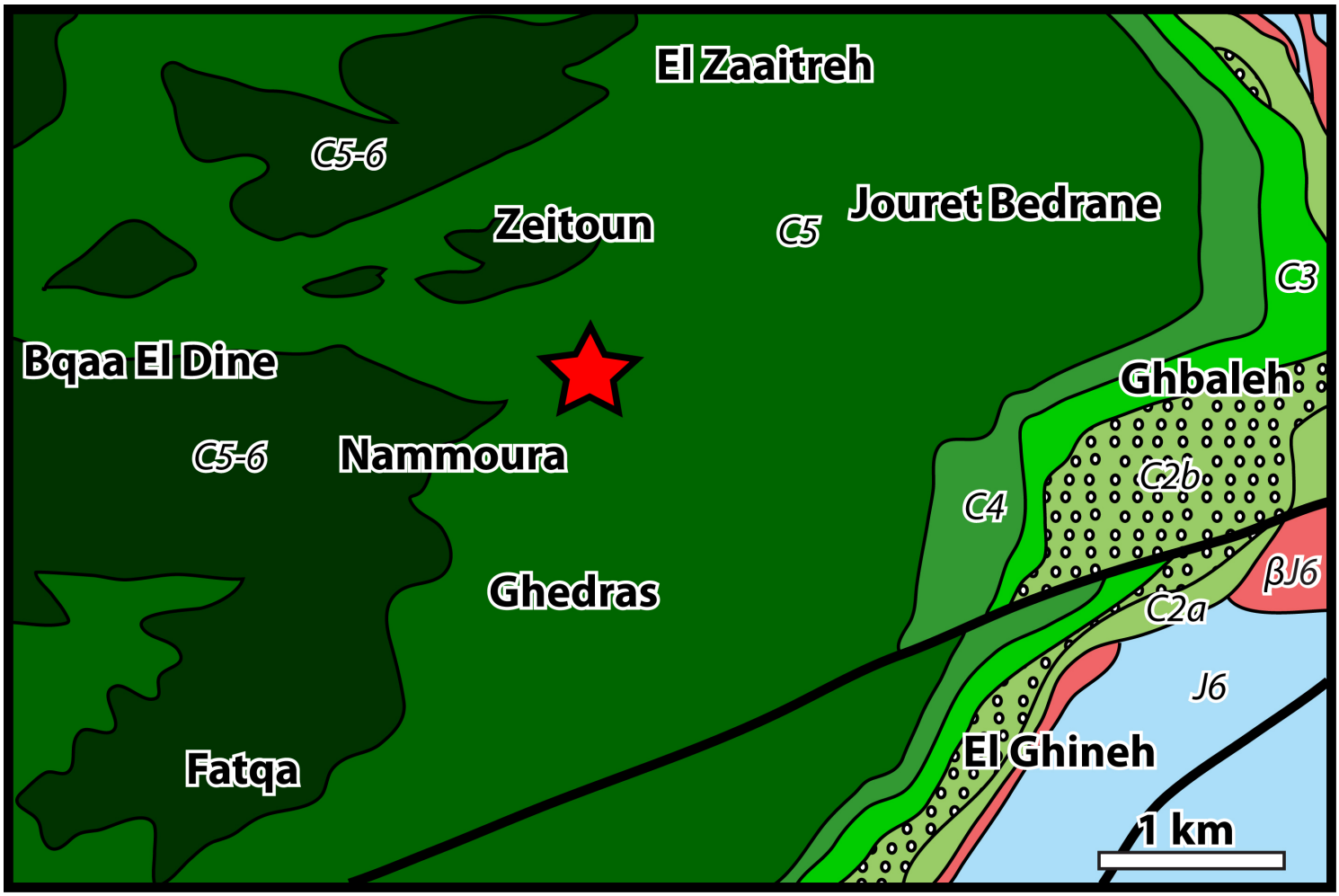


Figure 2

Geological map showing the locality of Nammoura outcrop (red star).

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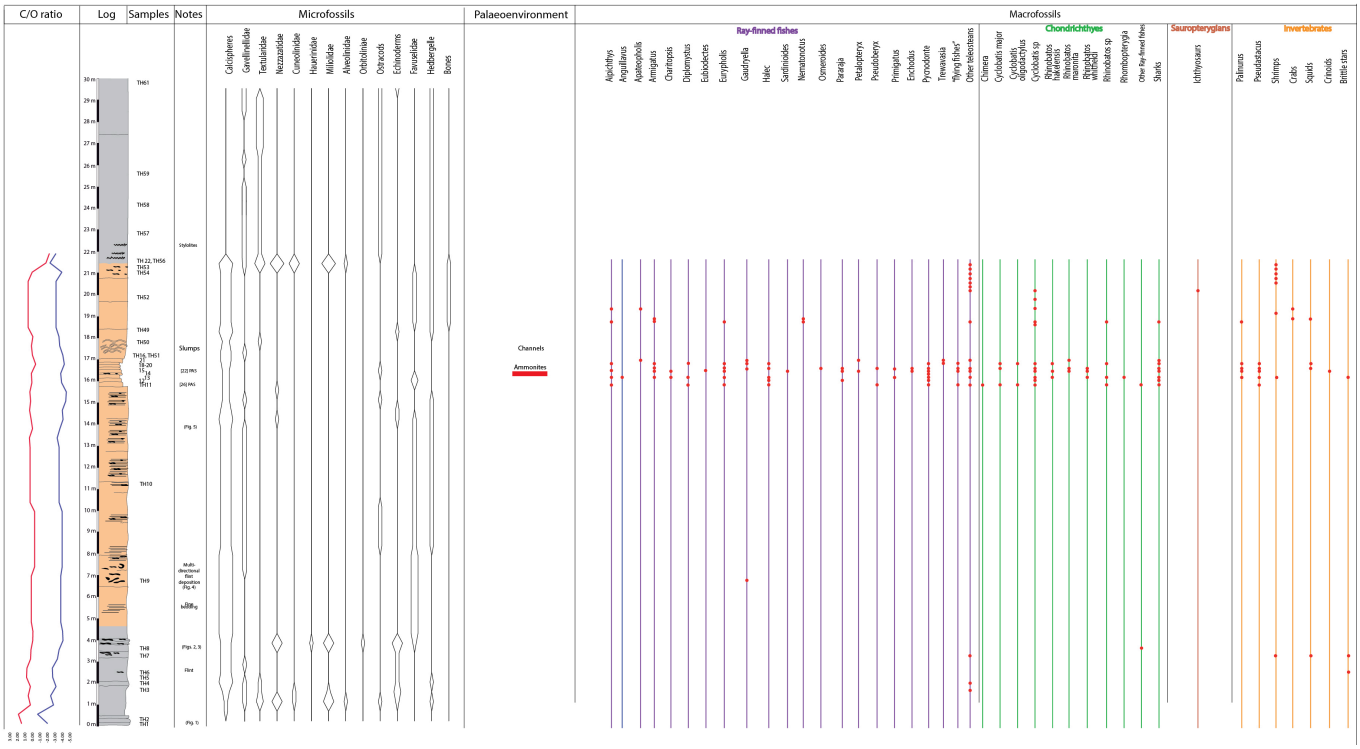


Figure 3

Detailed geological section of Haqel outcrop

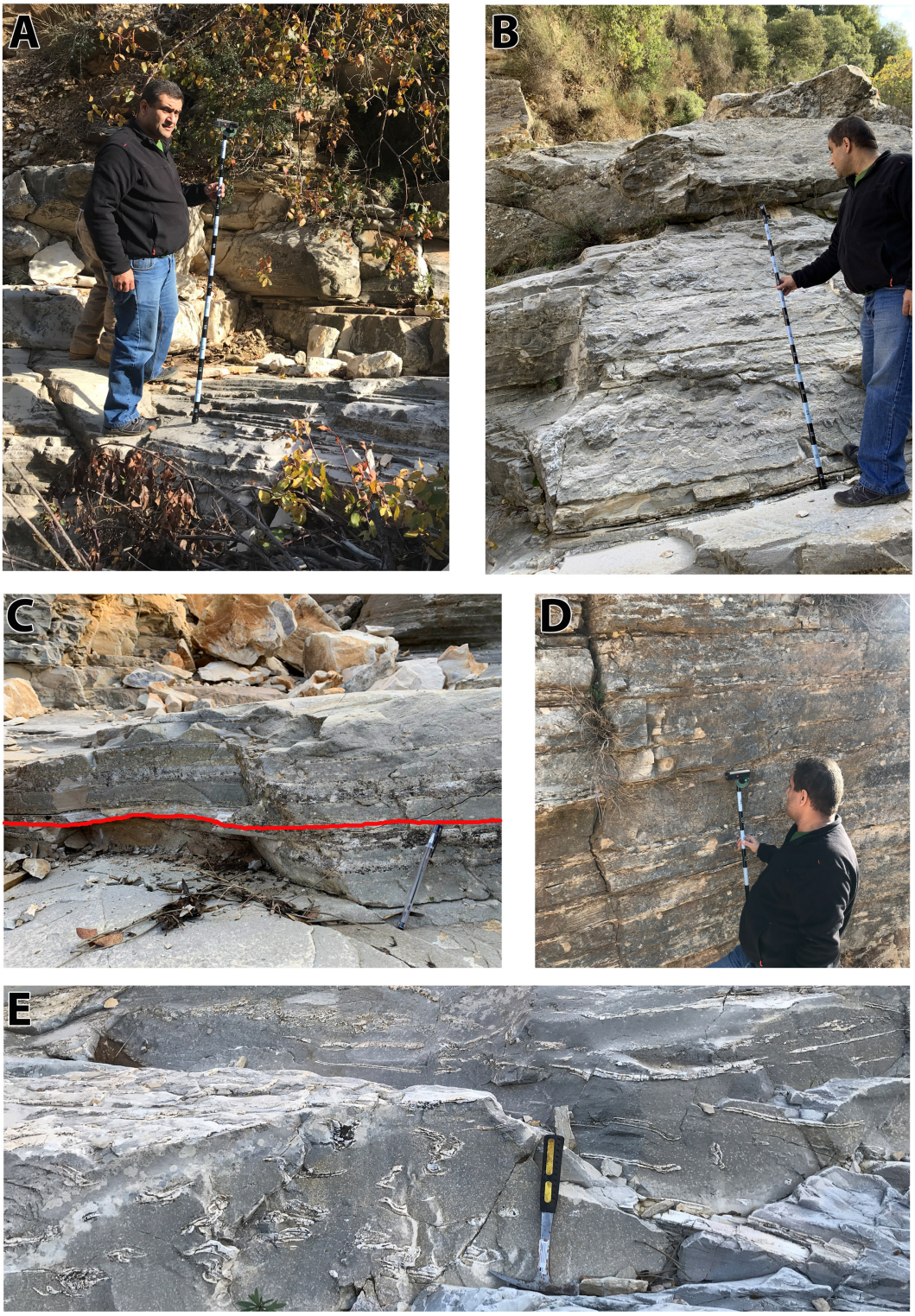


Figure 4

Haqel section

A- Starting level of the section

B- Measuring with Jacob Stuff the first 1.5 meters of the blue grey massive limestone unit, directly above the level rich in Orbitolinids

C- Level rich in Orbitolinids marked in red

D- Chert laminations

E- Chert nodules and centimetric lenses in the blue grey massive limestone unit of the section

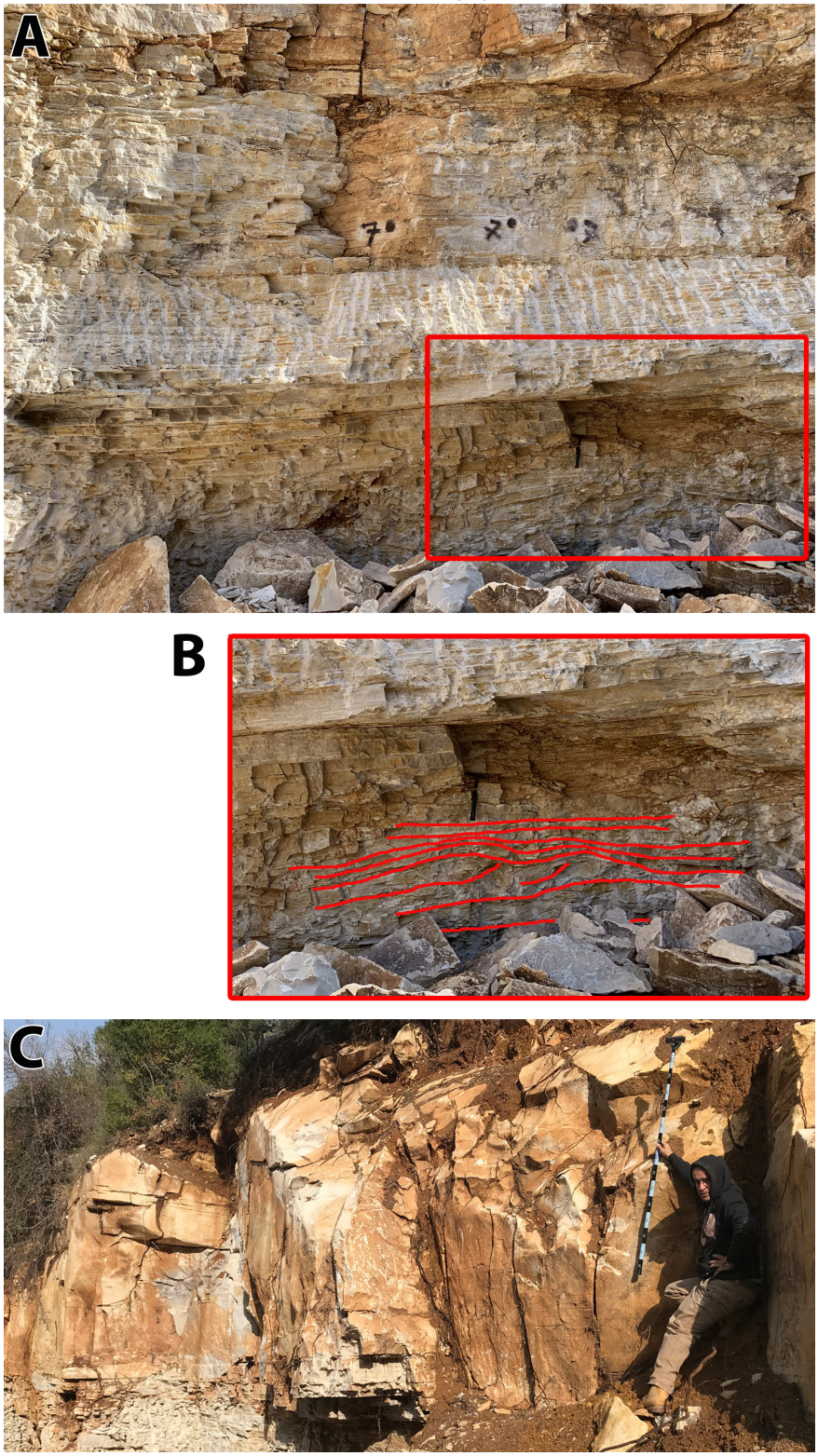


Figure 5

Haqel section

A- Slump in the light-yellow limestones' unit

B- Slump marked in red

C- Stylolitic bed in the massive grey limestones' unit

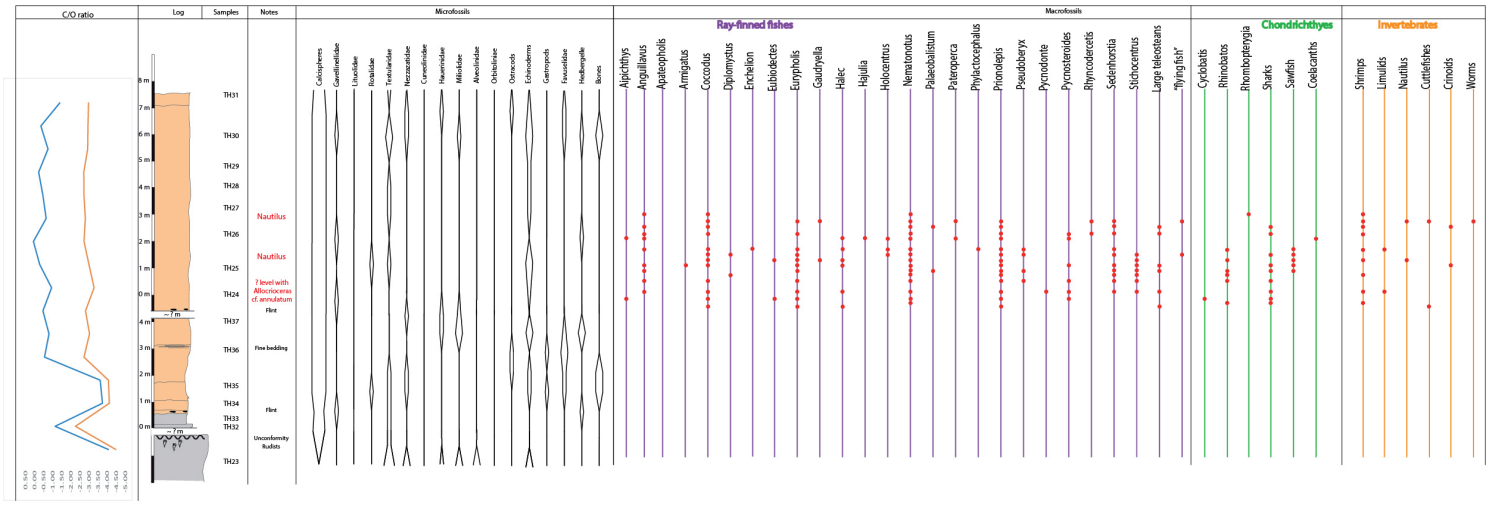


Figure 6

Detailed geological section of Hjoula outcrop



Figure 7

Hjoula section

A- Eroded surface marking the lower unconformity

B- Blue grey limestones unit with shells and rudists

C- The contact between the eroded surface and the first beds of the fish layers

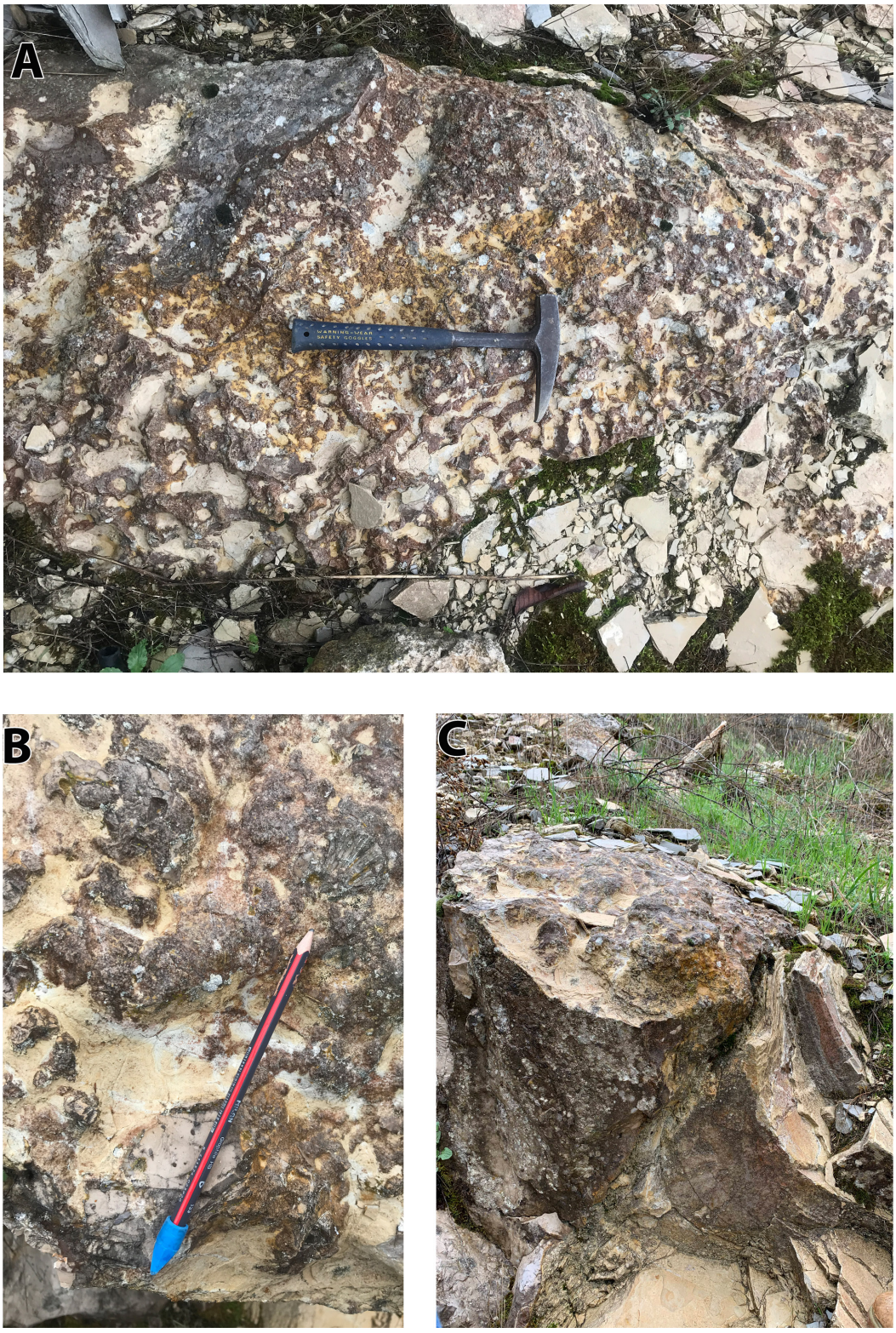


Figure 8

Hjoula section

A- The contact between the eroded surface of the blue grey limestones' unit and the first beds of the fish layers (light-yellow and grey limestones' unit) viewed from the top

B- Starting level of the section

C- The succession of the first meters of the light-yellow and grey limestones unit, followed by a gap



Figure 9

Hjoula section

A- Measuring the layers holding the macrofauna (provided by P.A.S.) directly above the bed with chert

B- Topmost layers of the section

C- The random excavation of the fish beds making difficult to follow the layers successions

D- Measuring the layers holding the macrofauna (provided by P.A.S.) directly above the bed with chert

E- Topmost layers of the section

F- The random excavation of the fish beds making difficult to follow the layers successions

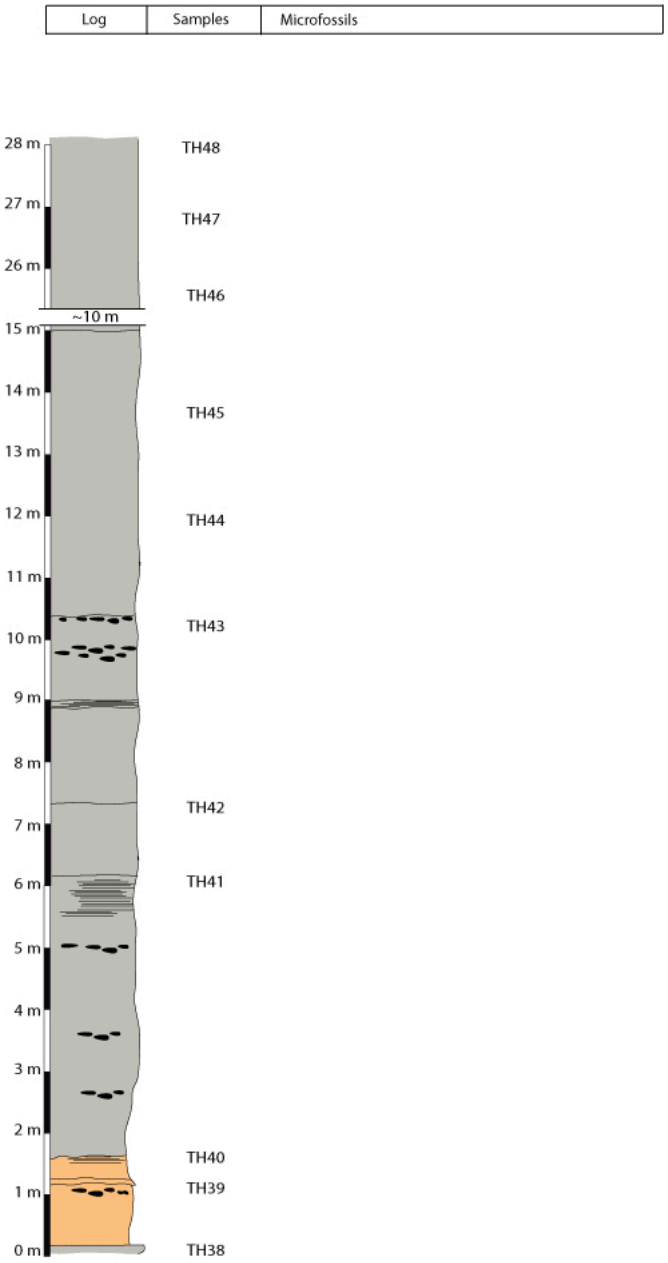


Figure 10

Detailed geological section of Nammoura outcrop

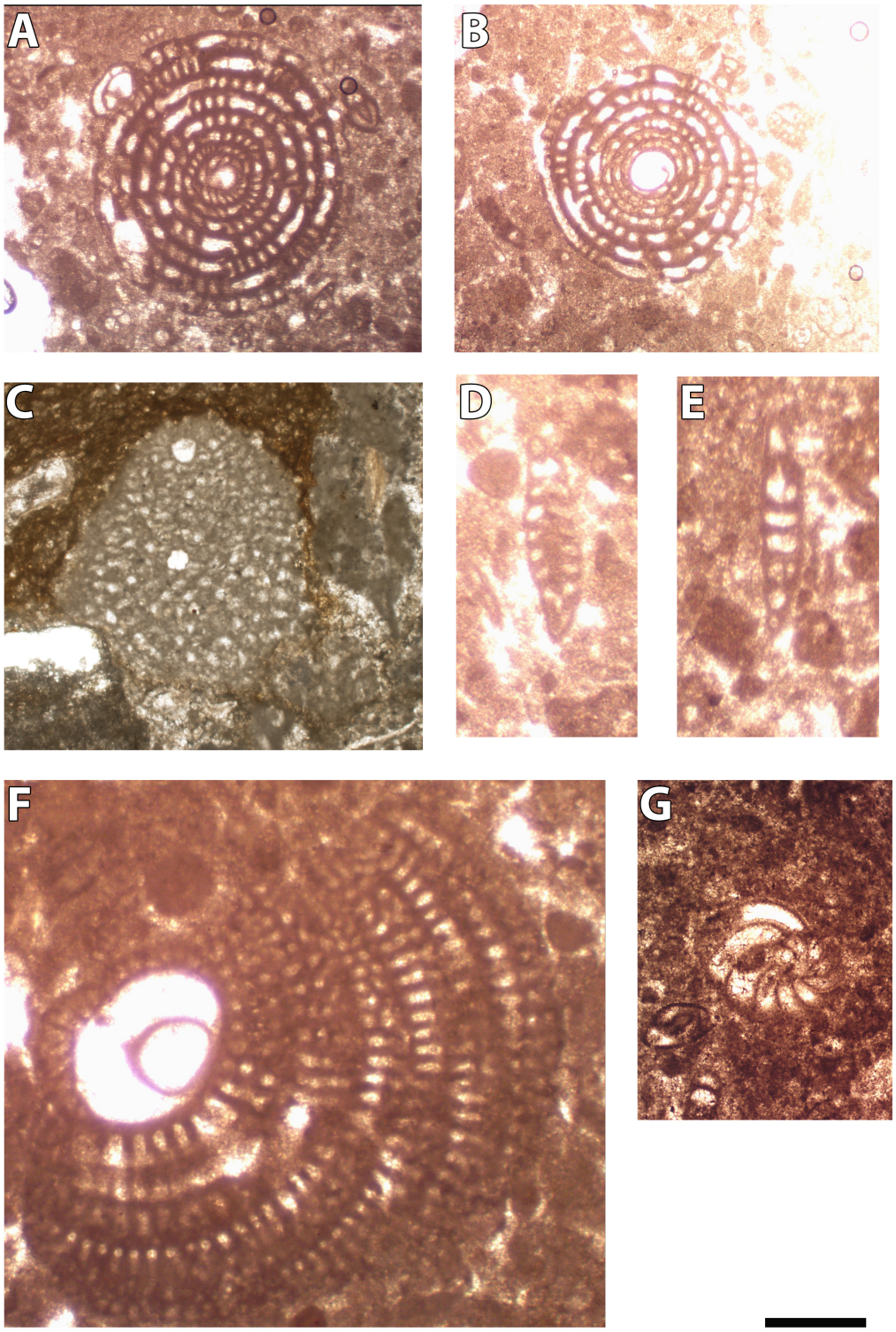


Figure 11

Benthic Forams

A-B- *Simplalveolina simplex* (Reichel, 1936). *Thin sections: DA7*, Hjoula; and *DA2*, Hjoula

C- *Orbitolina (Conicorbitolina) conica* (D'Archiac, 1837). *Thin section: TH7*, Haqel and *Thin section DA_Ch*, Haqel

D- *Biconcava* ? *Thin section: DA2*, Hjoula

E-*Merlingina* ? *Thin section: DA7*, Hjoula

F- *Dicyclina* sp. *Thin section: DA5*, Hjoula

G- *Neodubrovnikella turonica* ? *Thin section: DA3*, Hjoula

Scale bar = 0.25 mm

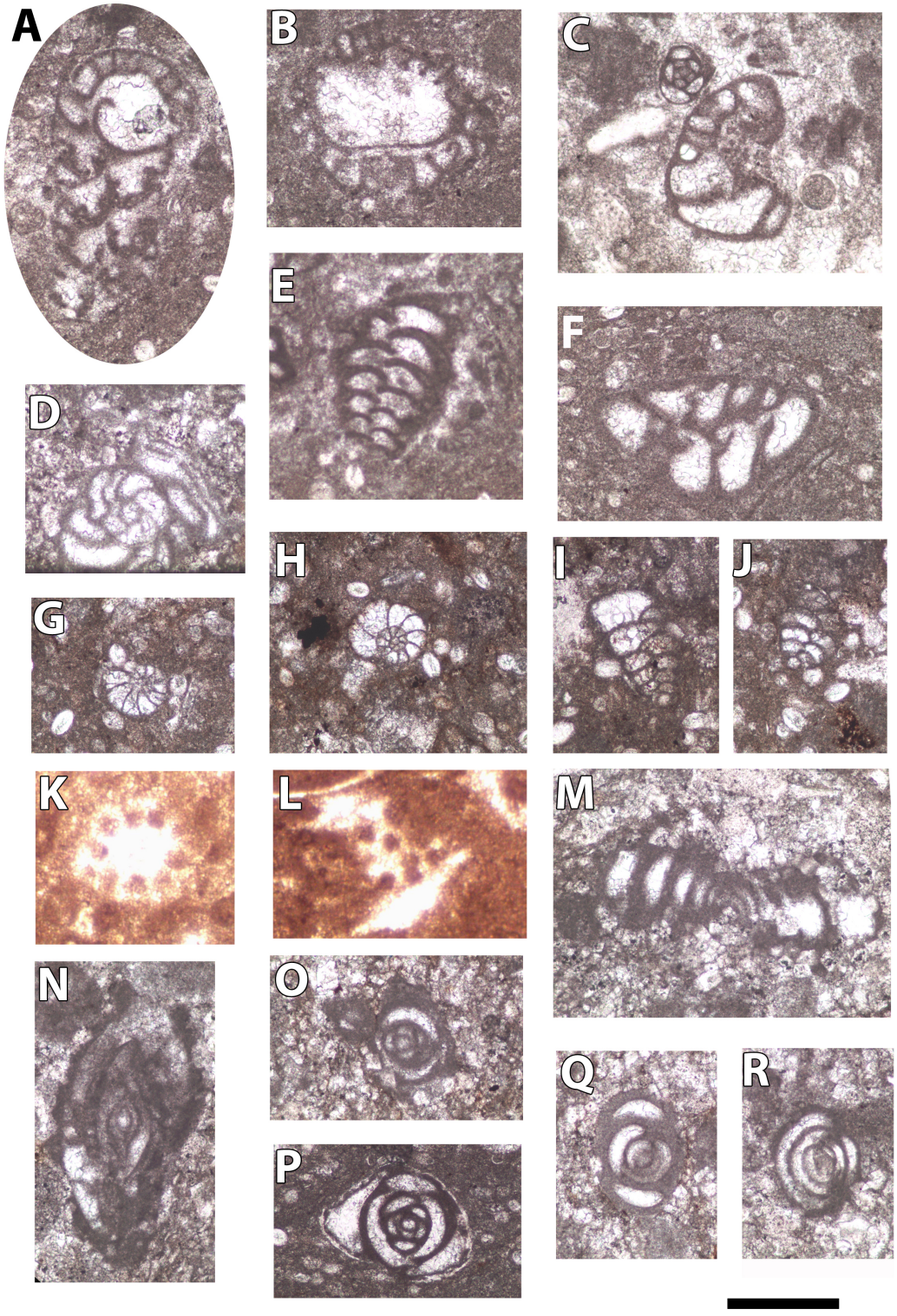


Figure 12

Benthic Forams

A, B- *Cuneolina* sp. Henson, 1948 *Thin section: TH22*, Haqel

C- Nezzazatidae, *Nezzazatinella* sp. *Thin section: TH22*, Haqel

D- cf. *Neodubrovnikella turonica Thin section: TH3*, Haqel

E- *Spiroplectammina* ? *Thin section: TH2*, Haqel

F- *Nezzazata simplex* Omara, 1956 *Thin section: TH22*, Haqel

G-H- Gavellinellidae *Thin section: TH30*, Hjoula

I-J- *Spiroplectammina* sp. *Thin section: TH30*, Hjoula

K-L- *Terquemella* sp. *Thin section: DA6,* Hjoula

M-N- *Spiroloculina* sp. *Thin section: TH3*, Haqel. N- transverse section, *Thin section TH3*, Haqel

O-P- Nummuloculinas" *Thin sections: TH4*, Haqel; and *TH31*, Hjoula

Q- *Istriloculina* sp. *Thin section: TH4*, Haqel

R- *Pyrgo* sp. *Thin section: TH3*, Haqel

Scale bar = 0.25 mm

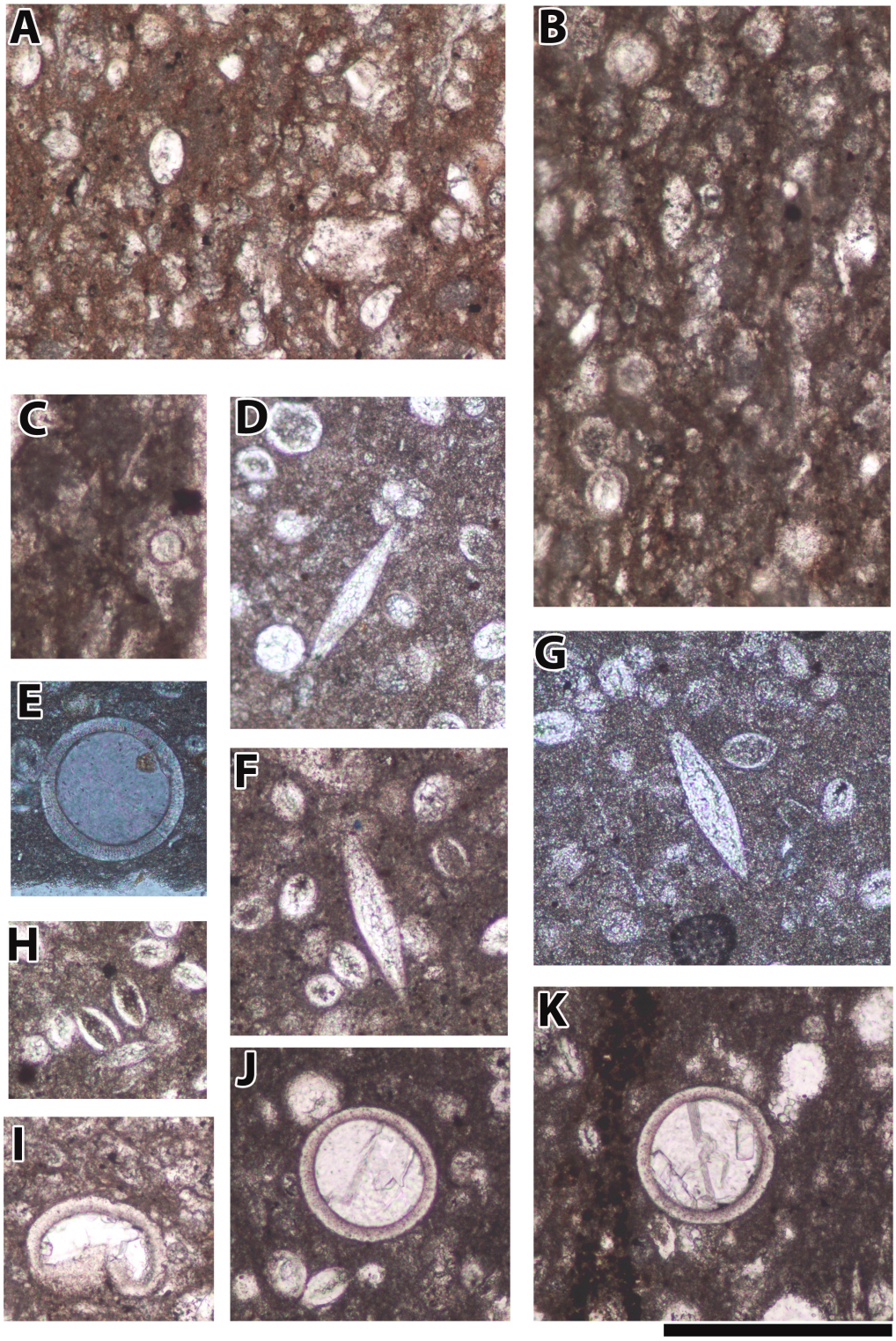


Figure 13

Calcispheres

A- *Pithonella ovalis* (Kaufmann, 1865) *Thin section: TH21*, Haqel

B- *Pithonella sphaerica* (Kaufmann, 1865) *Thin section: TH11, Haqel*

C- *Stomiosphaera ? V*ogler, 1941 *Thin section: TH21, Haqel*

D, F, G- *Pithonella trejoi* Andri, 1972 *Thin sections: TH26,* Hjoula; *TH29*, Hjoula and *TH30*, Hjoula

H- *Pithonella perlonga* Borza, 1972 *Thin section: TH29, Hjoula*

E, I-K- *Stomiosphaera sp.* **E-** *Thin section*: *TH25,* Hjoula; **I-** Thin section: *TH13*, Haqel; **J, K**: *Thin section: TH36,* Hjoula

Scale bar = 0.25 mm

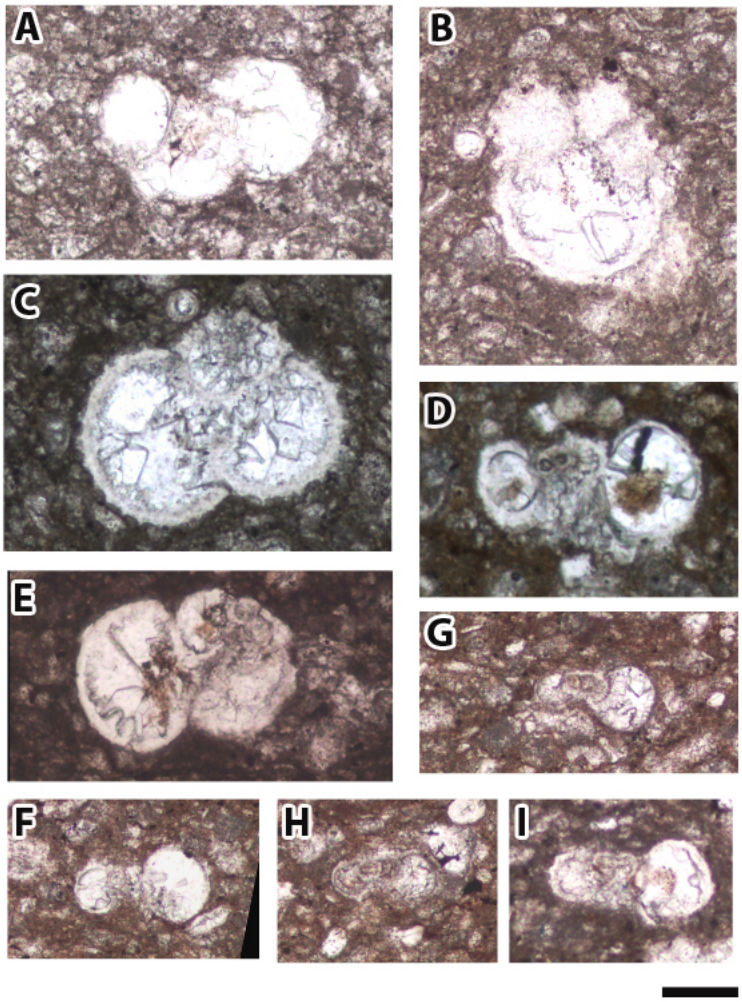


Figure 14

Planktonic foraminifera, Haqel

A- *Whiteinella* sp. *Thin section: TH7*

B-C- *Favusella washitensis* (Carsey, 1926) *Thin section: TH8*

D, F- Hedbergellidae (*Laeviella*?) *Thin section: TH21*

E- Hedbergellidae: *Whiteinella* cf. *baltica Thin section: TH11*

G, H- *Muricohedbergella planispira* (Tappan, 1940) *Thin section: TH11, TH21*

I- *Muricohedbergella* cf. *delrioensis* (Carsey, 1926) *Thin section: TH12*

Scale bar = 0.1 mm

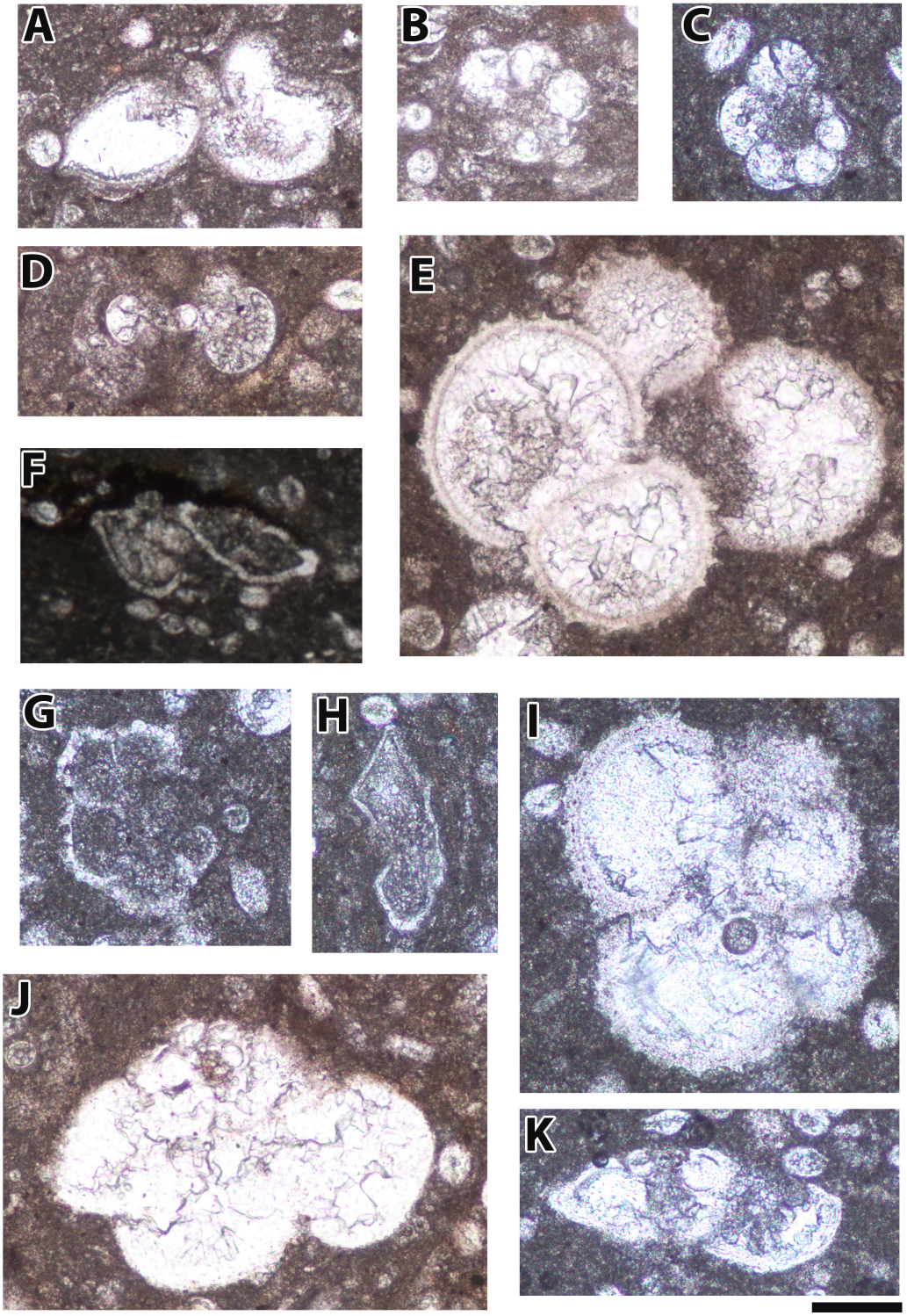


Figure 15

Hjoula planktonic foraminifera

A- Undetermined. *Thin section: TH24*. Tangential section.

B, C- *Muricohedbergella* cf. *planispira* (Tappan, 1940). *Thin sections: TH25* and *TH28*. Equatorial sections

D- Globigerinelloididae (*Laeviella*?). *Thin section: TH30*

E, I- *Favusella washitensis* (Carsey, 1926), *Thin sections: TH30* and *TH28*

F-H- *Thalmanninella* cf. *appenninica* (Renz, 1936). *Thin sections: TH25* and *TH26*

J- *Whiteinella* sp. *Thin section: TH30.* Oblique section.

K- *Praeglobotruncana* cf. *delrioensis*(Plummer, 1931). *Thin section: TH27*. Axial section.



Figure 16

Mantelliceras mantelli (Sowerby, 1817)

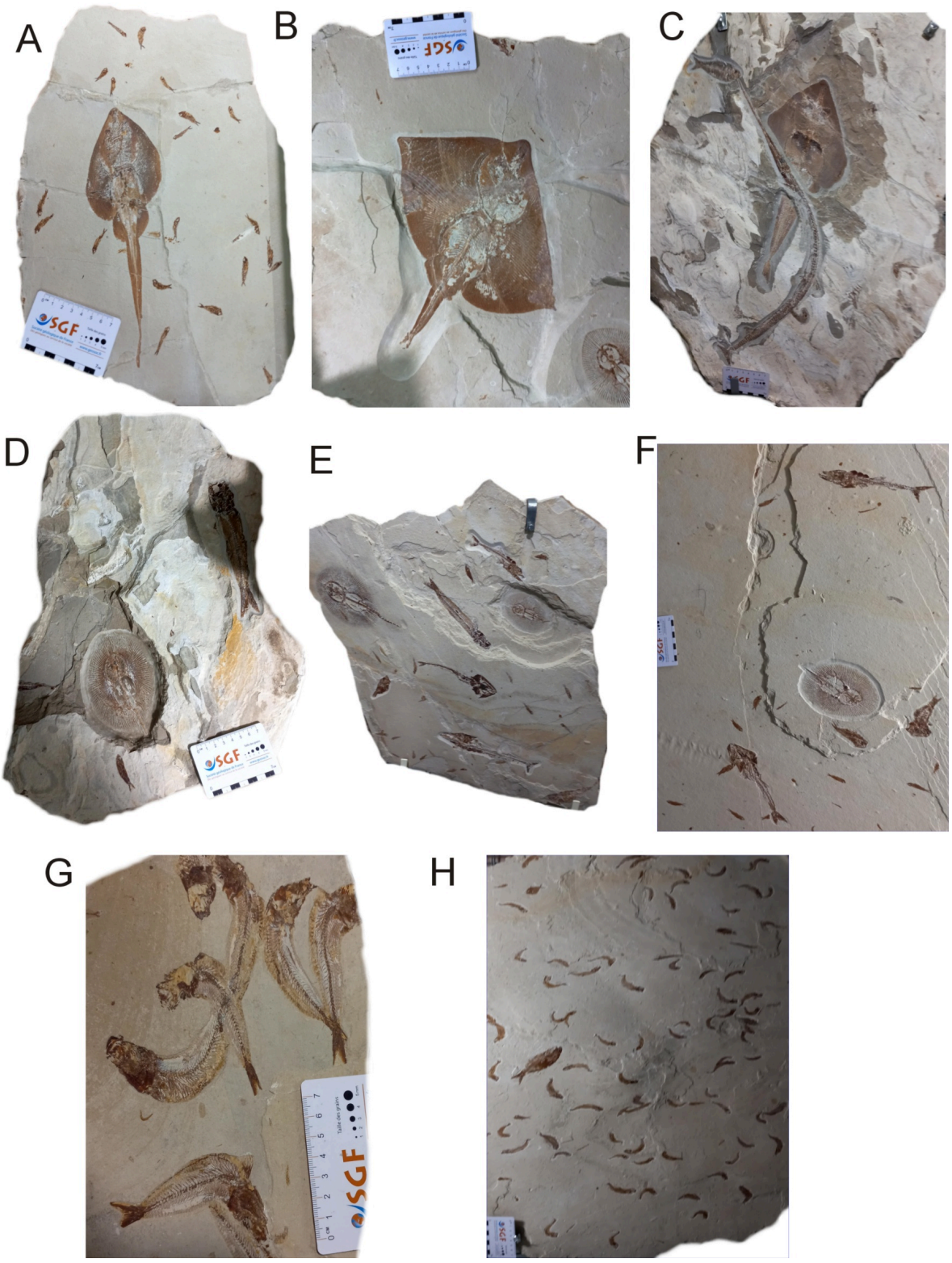


Figure 17

Examples of different taphonomic situations

A- C- level 26 [PAS] = TH11

D- Level 24 [PAS] = TH13

E-F- level 19 [PAS] = TH21

G -H- level 18 [PAS] = TH22

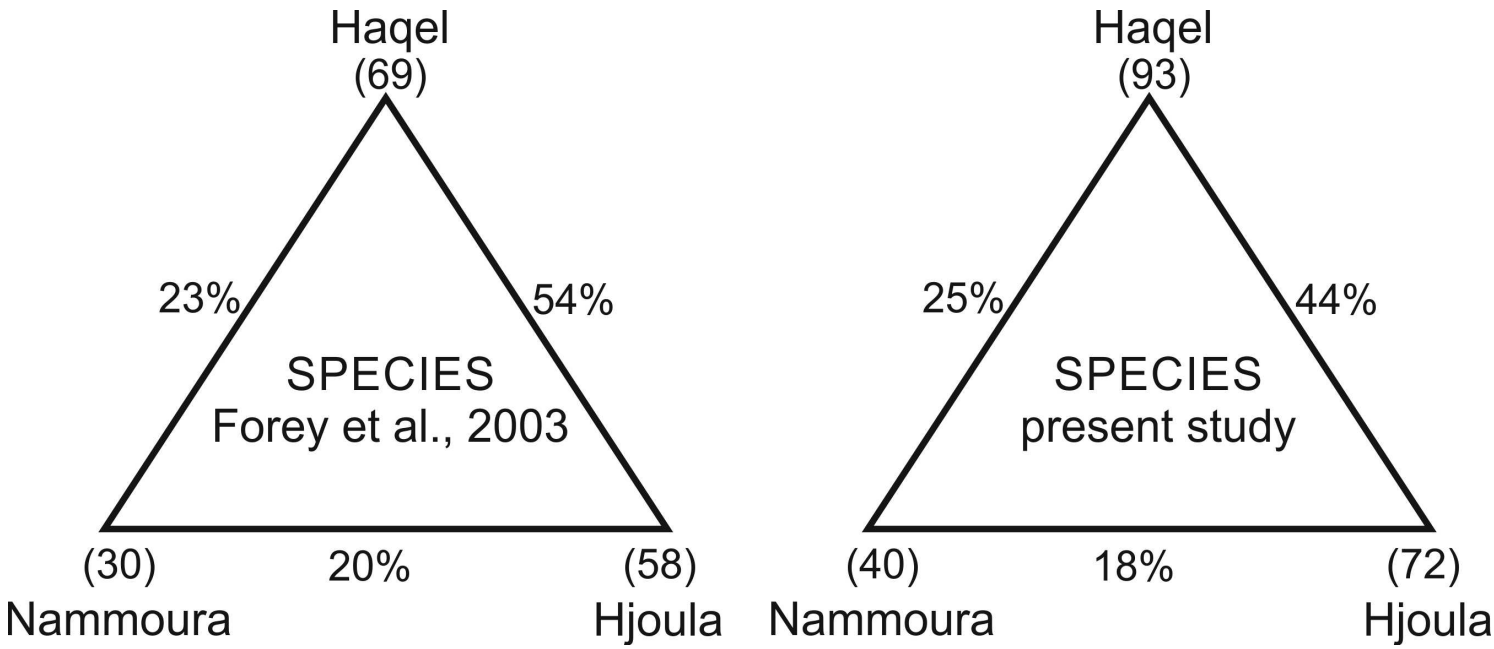


Figure 18

Three-way comparison between the species from of Hakel, Hjoula and Namoura based on data from Forey et al. (2003) (left) and on updated data (right). The numbers in parentheses are the actual number of taxa. The numbers along the sides of the triangles are the percentage overlap between the localities subtended by the line.

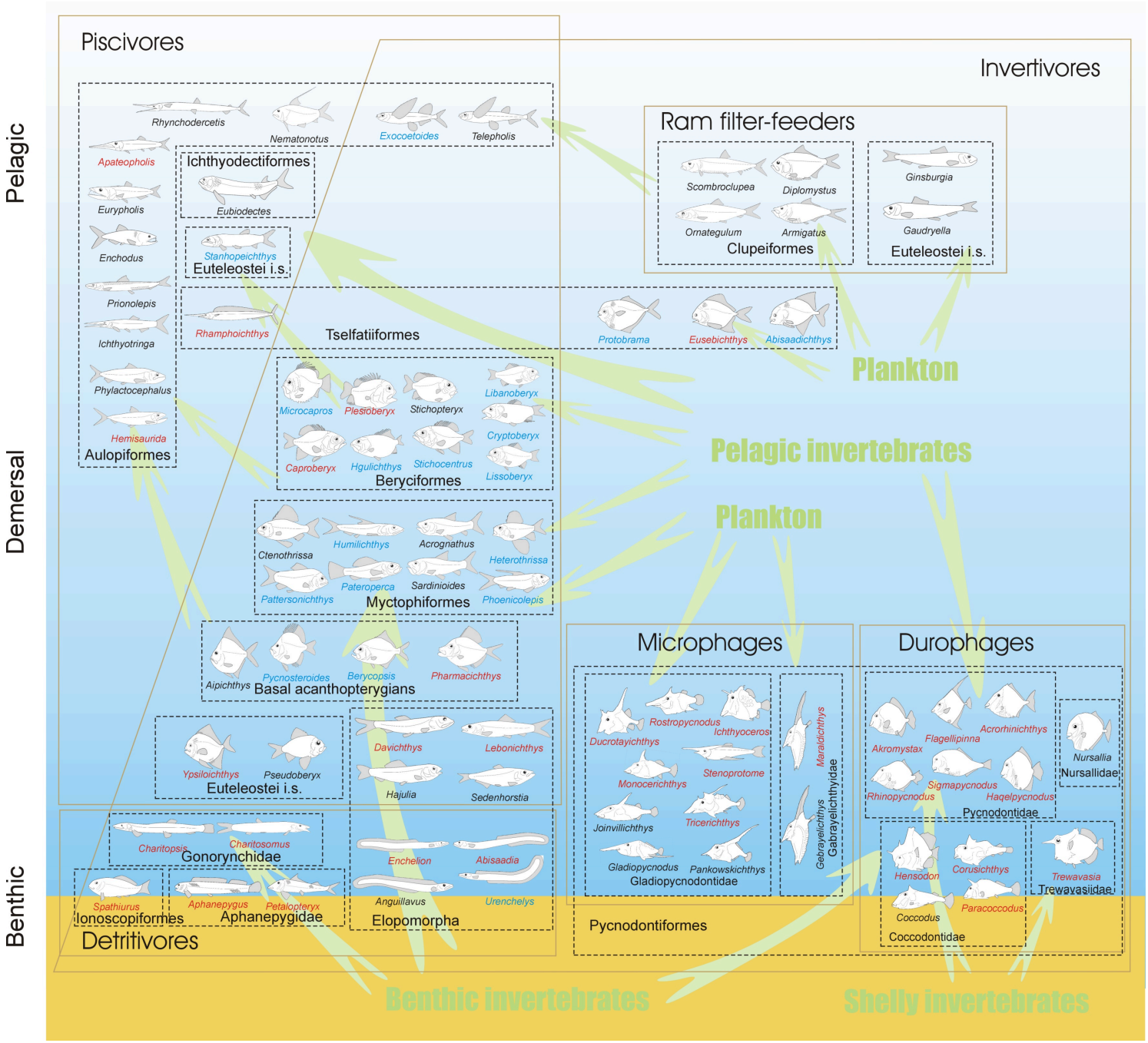


Figure 19

Actinopterygian assemblages from the Haqel and Hjoula sites. Genera are grouped by clades and their presumed habitat. Genera in black are found at both sites, in red only at Haqel, and in blue only at Hjoula. Trophic relationships are indicated in green in the background.