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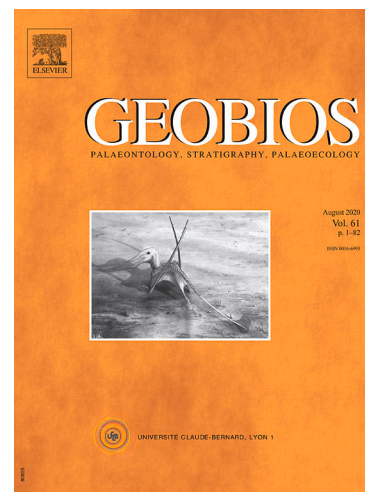
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A new chemosynthetic community (ostracods, foraminifers, echinoderms) from Late Jurassic hydrocarbon seeps, south-eastern France Basin [☆]

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Highlights

- Sahune (Oxfordian, Late Jurassic) in south-eastern France Basin is newly described.
- Carbonate bodies enclosed within Terres Noires Formation formed at cold seeps.
- Associated fauna indicate seepage at bathyal depth ca. 1.500 m.
- Several seep ostracod families have evolved at seeps since the Oxfordian.

- Colonization of bathyal environments occurred earlier than thought.

Abstract

Hydrocarbon seeps represent some of the most extreme marine habitats but are also home to rich communities developed around chemosynthesis rather than photosynthesis. Here we describe the outcrop of Sahune (Drôme department, south-eastern France), that illustrates a new seeping site during the Late Jurassic (middle Oxfordian), as formally demonstrated by geochemical proxies. We report the associated fauna composed of foraminifers, radiolarians, crinoids, echinoids and ostracods that all point to seepage at bathyal depth. The foraminifer assemblage and the occurrence of the irregular echinoid *Tithonia oxfordiana* together point to a middle Oxfordian age. We provide an in-depth analysis of the ostracod community, which is the oldest so far reported in such environments. The new species *Procytherura praecoquum* may be cognate to the seepage site and could illustrate the oldest known example of pore clusters, sometimes proposed as representing ectosymbiosis. The Sahune assemblage demonstrates that cold seep ostracod communities were already a mixture of taxa from platform and deep-sea oligotrophic environments. The post-Jurassic diversification of ostracods at cold seeps was related to colonization events and diversification of families that have been inhabitants of such ecosystems at least since the Oxfordian. The Sahune record changes our current conception of the deep-sea colonization by the ostracods *Tethysia* and *Procytherura* that occurred earlier than traditionally considered.

Keywords:

South-eastern France Basin

Oxfordian

Fluid seepage

Echinoderms

Foraminifers

Ostracods

1. Introduction

Hydrocarbon seeps are sites where low temperature fluids rich in hydrocarbons and hydrogen sulfide are emitted onto the sea floor. Recent examples are known from depths ranging from less than 15 m (Montagna et al., 1987) to more than 7,400 m (Fujikura et al., 1999). They represent some of the most extreme marine habitats but the increased food supply and availability of hard substrate fuel the development of complex ecosystems that are substantially richer in diversity and abundance than in the adjacent non-seep areas and composed of communities dominated by taxa having symbiotic relationships with chemoautotrophic bacteria (Levin, 2005; Levin et al., 2016; Åström et al., 2017). In such environments, fluid flow appears to be controlling the distribution and abundance of benthos through the availability of reduced compounds (Barry et al., 1997; Olu et al., 1997; Sahling et al., 2002; Levin et al., 2003; Tunnicliffe et al., 2003).

The trophic structure of seep communities is similar to that of hydrothermal vent and organic fall communities, and many of the dominant chemosymbiotic macro-organisms are shared at high taxonomic levels but obligate at species level (Van Dover 2000; Van Dover et al., 2002). Because of their reliance on an *in situ* chemosynthetic food source, it has been proposed that these communities may have had an independent evolutionary history compared to those relying on photosynthesis (Tunnicliffe 1992; McArthur et al., 1998). Although major questions remain as to the biodiversity and history of these ecosystems, recent years have seen a growing number of publications providing insights into their fossil record and how they evolved through geological time (Campbell and Bottjer 1993, 1995a; Barbieri et al., 2004; Kiel and Little, 2006; Kiel, 2015; Kaim et al., 2009; Amano et al., 2010; Hryniewicz et al., 2017; Jakubowicz et al., 2017). The oldest seep community with modern structure, i.e., dominated by bivalves, has been reported from the Early Jurassic (Kaim et al., 2016) and numerous taxa composing present-day seeps radiated in the Late Cretaceous and Cenozoic (Amano et al., 2022; Baco et al., 1999; Vrijenhoek, 2013; Herrera et al., 2015; Georgieva and Little, 2022; Kaim, 2022).

Most biological and palaeontological studies of cold seep communities have so far focused on macrofauna and microbiological processes and their fossil record is mostly restricted to groups such as bivalves, gastropods and brachiopods (Campbell and Bottjer, 1995a, 1995b; Kaim and Kelly, 2009; Kiel et al., 2010; Amano and Jenkins, 2013; Kaim et al., 2014; Jenkins et al., 2018). Reports of echinoderms and microfauna as a whole remain scarce (Gaillard et al., 2011; Hayward et al., 2011; Hjálmarsdóttir et al., 2018; Hunter et al., 2016; Kato, 2019; Kato et al., 2017; Meehan et al., 2018; Brezina et al., 2022) so that their diversity, phylogeny, biogeography, ecology and role in trophic chains at cold seeps and more generally chemosynthetic communities are poorly known.

Crustaceans (copepods, decapods, barnacles, ostracods) are common elements of modern vent and seep faunas (Humes, 1988; McArthur and Tunnicliffe, 1998; Van Dover et

al., 2002; Desbruyères et al., 2006), though they remain relatively poorly studied in ancient counterparts (Klompaker et al., 2022). Ostracods are ecologically diverse microcrustaceans inhabiting all types of water bodies, including chemosynthetic environments from hydrothermal vents, cold seeps, and wood falls (Maddocks and Steineck, 1987; Steineck et al., 1990; Kornicker, 1991; Van Harten, 1993; Maddocks, 2005; Kornicker and Harrison-Nelson, 2006; Karanovic and Brandão, 2015; Tanaka and Yasuhara, 2016). In these habitats, they are not obligate at the generic level, as the communities consist of taxa that are found in shallow and oligotrophic deep-sea waters. At the species level, endemism has been confirmed for wood falls and hydrothermal vents, but not for cold seeps (Karanovic and Brandão, 2015). However, the knowledge of ostracods from modern seeps is still in its infancy as they have only been reported from Black Sea (Schornikov and Syrtlanova, 2008), Gulf of Mexico (Degen et al., 2012; Machain-Castillo et al., 2014), Marmara Sea (Ritt et al., 2010), Svalbard margin (Yasuhara et al., 2018), Pelotas Basin (Maia et al., 2022), and Santos Basin offshore Brazil (Bergue et al., 2023). They are noticeably absent from CO₂ seepage in the Zannone Giant Pockmark in the central-eastern Tyrrhenian Sea (Aiello et al., 2022). Fossil cold seeps are increasingly documented but associated ostracods are poorly known with only three reports from the Eocene-Oligocene of USA (Yamaguchi et al., 2016), Miocene of Northern Apennines (Russo et al., 2012) and Quaternary of Ireland (Coles et al., 1996), all displaying taxonomic structure similar to that of more recent seep communities. As a consequence of this major lack of data, central questions are still pending for instance regarding the structure of their diversity, adaptations and possible chemosymbiotic relationships (Maddocks and Steineck, 1987; Van Harten, 1992; Yasuhara et al., 2018; Bergue et al., 2023).

Here we describe the Late Jurassic (middle Oxfordian) Sahune site in the south-eastern France Basin and formally assign it to seep-type fluid circulation. We report the associated fauna composed of ostracods, planktonic and benthic foraminifers, radiolarians, crinoids and echinoids, no other fossil group being found. The diversity and structure of the ostracod assemblage are discussed. They provide the first formal depiction of their communities for all the Jurassic seep deposits of the south-eastern France Basin and the oldest so far reported seep-associated ostracods.

2. Geological context

2.1. The south-eastern France Basin

The south-eastern France Basin is related to the opening of the Liguro-Tethyan Ocean during the Jurassic (Lemoine, 1985; Fig. 1(A)). From the Early to Middle Jurassic (Hettangian to Bathonian), the deposits generally correspond to a shallow-water carbonate platform with frequent subaerial exposure or erosion related to a stable margin with low rates of subsidence. During the Middle Jurassic (Bathonian, Callovian), the subsidence of the southern platform was compensated by sedimentation and environments remained shallow, while cherts and organic-rich marls that deposited along the northern margin indicate a general palaeobathymetric deepening of at least 600 m (Dardeau, 1988). From the Oxfordian onwards, the entire platform was affected by general subsidence that was moderate in the

southern part (as shown by reefal facies and confined environments) and increased in the northern part (represented by deep marl facies and submarine slides). The subsidence reached a maximum during the Bathonian to Oxfordian interval in the deepest, central part of the basin and led to the deposition of thick marly series of the Terres Noires Fm. (2,000–2,500 m thick; Fig. 1(B)). Subsidence was mainly related to basement faults controlled by the withdrawal of salt in the extensional domain of the margin (Masclé et al., 1988).

The Terres Noires Fm. (Bathonian–Oxfordian) contains sedimentary bodies that have long appeared as lithological and palaeontological anomalies. They are calcareous masses that are most of the time fossiliferous, with a volume of a few m³, which contrast very clearly with the surrounding fossil-poor marly deposits (Fig. 2(A, B)). They were first interpreted as sponge bioherms (Artru and Gauthier, 1966; Artru, 1972) but the discovery of hydrothermal ecosystems along present-day ocean ridges (Lonsdale, 1977; Corliss et al., 1979) suggested that hydrothermal activity may have been the source of these anomalous fossil concentrations in sedimentary environments of the south-eastern France Basin (Bourseau, 1977; Macsotay, 1980; Lemoine et al., 1982; Gaillard et al., 1985; Gaillard and Rolin, 1986, 1988). Gaillard et al. (1985) proposed that these limestone bodies, termed pseudobioherms, formed in a context of passive margin with synsedimentary faults allowing the rise of fluids up to the sea bottom. These fluids locally induced limestone concretion and proliferation of ecosystem dependent on bacterial chemosynthesis.

Several sites of such hydrocarbon seep sites have been identified in the south-eastern France Basin; they are related with synsedimentary faults that affected the deposition of the Terres Noires Fm. and allowed fluid circulations debouching at seep sites (Debrand-Passard, 1984; Edon et al., 1991; Guilhaumou et al., 1996). The most famous fossil site within the south-eastern France Basin is that of Beauvoisin, which is now interpreted as a giant pockmark (Gay et al., 2018, 2020). At Beauvoisin, the fluid seep sites are bounded to the west by major salt-rooted faults that enabled the growth of salt diapirs into the marls, as at Condorcet, Propiac and Suzette (Fig. 1(B)). The associated fossil communities were generally dominated by lucinid bivalves locally forming remarkable concentrations, occasionally dominant echinoids (*Tithonia*), together with gastropods, crustaceans, asterids, holothurids, ammonites, belemnites, foraminifers, and ostracods that remain to be fully described (Gaillard et al., 1985, 2011; Rolin et al., 1990; Peckmann et al., 1999; Bouhamdi et al., 2000; Senowbari et al., 2007; Kiel, 2013; Kiel et al., 2010). Rolin et al. (1990) provided the only information on the ostracods so far available, stating that about 15 species are present, dominated by smooth-shelled Cytheruridae.

2.2. The Sahune site

The Sahune site (Drôme department, Auvergne-Rhône-Alpes region) is located in the northern part of the south-eastern France Basin, close to the famous Beauvoisin site. The main sequence crops out on the northern flank of a densely vegetated small hill located about 1.4 km south-east of the Sahune village and 12 km north-east of the Beauvoisin site (44°24'28.188'' N, 5°16'51.96'' E; Fig. 1). The Sahune sequence is composed of four imbricated meter-scale, seep-related, limestone bodies (also termed pseudobioherms),

labelled P1 to P4, cropping out within the Terres Noires Fm. (Fig. 2). One pseudobioherm and one semi-consolidate nodular limestone likely related to an aborted emission of fluid are located laterally. The entire main sequence has been sampled in 2008 and 2022 (Fig. 2(A, B)). Ten samples have been collected from the main sequence (Fig. 2(B)). Lateral samples were also collected from the nodular pseudobioherm bed (22SAH10), underlying marls (22SAH11), likely aborted emission of fluid (22SAH12) and underlying marls (22SAH13).

In the middle Oxfordian deposits of the south-eastern France Basin and its western margin, Gaillard et al. (1996, 2004) defined seven key-beds, labelled R1 to R7 (Fig. 2(C)). These key-beds are present at Beauvoisin where Gaillard et al. (2011) and later Gay et al. (2020) have positioned the pseudobioherm clusters. Gaillard et al. (2011) later described the irregular echinoid *Tithonia oxfordiana* in association with Beauvoisin seeps of R4 key-bed (Transversarium ammonite biozone). Considering the structural context of the Sahune site, its exact stratigraphical position is unclear but the occurrence of *Tithonia oxfordiana* indicates that the described seepage is coeval to R4 key-bed. The foraminiferal assemblage described here provides an additional basis for biostratigraphic scheme.

3. Material and methods

One limestone sample (08SAH01 = 22SAH01, ca. 700 g) collected from the pseudobioherm P1 at Sahune (Fig. 2) was analyzed for characterisation of palaeoenvironment and fossil association. For microfacies analyses, six thin sections of size 47 × 28 mm were prepared (Fig. 3). One of them was stained with Alizarin Red S. Microfacies is described according to classification by Dunham (1962). The sample provided a rich ostracod assemblage together with foraminifers, radiolarians, crinoids and echinoids which is described here. The study of fauna through the entire sequence is in progress but microfaunas from basal (22SAH07) and lateral (22SAH02b) marls are mentioned for comparison. Geochemical analyses have been performed on the entire succession to formally relate this site to fluid seepage.

3.1. Geochemical analyses

The elemental composition (major and traces elements) of the bulk-rock samples was analyzed at the CNRS analytical facility Rock and Mineral Analysis Service (SARM) in Vandœuvre-lès-Nancy (see details of the analytical protocol ICP-OES and ICP-MS in Carignan et al., 2001). Thirteen samples were examined (Table 1; Fig. 2) with the focus set on some elements known to be proxies to redox conditions (uranium U, vanadium V and molybdenum Mo), cold seep-associated carbonates (arsenic As, antimony Sb and cadmium Cd) and paleoproductivity (copper Cu, nickel Ni and barium Ba; Tribovillard et al., 2006; Algeo and Tribovillard, 2009; Smrzka et al., 2020; Algeo and Liu, 2020; Gilleaudeau et al., 2021; Tribovillard, 2020, 2021a, b; Sweere et al., 2023). The results are based on enrichment

factors of the elements (EF) that were calculated as: $X\text{-EF} = [(X/Al)_{\text{sample}} / (X/Al)_{\text{upper crust}}]$, where X and Al represent the weight proportion of element X and aluminum (Al), respectively. Samples were normalized using the average composition of the Earth's upper crust (McLennan, 2001). The Al normalization is used to avoid the effects of variable dilution by carbonate and/or biogenic silica, although certain pitfalls sometimes accompany this approach when aluminum content is minimal as may be the case with carbonate rocks (Van der Weijden, 2002; Tribovillard et al., 2006). Any value larger than 1.0 theoretically indicates the enrichment of an element relative to its average crustal abundance but, practically, an enrichment may be considered to be detectable when $EF > 3$ (Algeo and Tribovillard, 2009). According to the recent paper of Wang et al. (2023), titanium (Ti) is a preferable normalization element due to lower mobility relative to Al. However, we kept with Al-normalization to use the U-EF vs. Mo-EF diagram of Algeo and Tribovillard (2009) helping palaeo-redox reconstructions (Fig. 4). Aluminum normalization and the calculation of enrichment factors have been retained in this paper because it is a convenient way to compare geological formations and sediments deposited in very different contexts.

3.2. Preparation of fossils

For the preparation of foraminifers and radiolarians, the rock sample was crushed into 2–3 cm large pieces and dissolved in 5% acetic acid in the laboratory at the Geological Survey of Slovenia. Specimens were collected from the residue under stereomicroscope. Selected specimens were photographed in different orientations under reflective light using VHX-7000 Keyence digital optical microscope. After being coated in carbon, they were further investigated and photographed with a JEOL JSM 6490LV Scanning Electron Microscope (SEM) at the Geological Survey of Slovenia. The mineral composition of the wall was determined in the backscattered electron (BSE) mode in a high vacuum using the Oxford INCA Penta FETx3 Si(Li) detector and INCA Energy 350 processing software. The chemical composition of minerals was measured using the EDS X-ray point analysis.

About 700 g of the limestone sample has been processed using the hot acetolysis technique (Bourdon, 1962; Lethiers and Crasquin-Soleau, 1988) for ostracod extraction. The residue has been sieved through a 0.63 mm mesh, oven dried, and all specimens have been picked under stereomicroscope. Specimens of interest have been gold coated and photographed using the SEM JEOL JCM-600 at the Centre de Recherche en Paléontologie-Paris. Stacked images of uncoated specimens were made using the ZEISS AXIO ZOOM V16 and Camera DELTAPIX USB3 20MP (20 stacks per specimen) using green and red UV light at the CR2P.

Crinoid material was cleaned ultrasonically and platinum coated for observation under a Hitachi SU3500 SEM at the MNHN's technical platform for electron microscopy. All types and figured specimens are deposited in the Palaeontology collections of the MNHN, Paris (France).

4. Results

4.1. Microfacies description

The sample 08SAH01 is texturally a mudstone or wackestone with rare larger intraclasts (Fig. 3(A)), locally loose floatstone. Intraclasts are subrounded to rounded, isometric to semi-elongated, up to 7 mm large. Some contain framboidal pyrite at the margins. A few of the intraclasts show possible signs of boring or burrowing (Fig. 3(E)). Lithologically, intraclasts are wackestone and packstone with calcified spumellarian radiolarians and planktonic foraminifers (Fig. 3(B, C)). Rare ostracods with disarticulated or articulated valves, sponge spicules (locally abundant), small benthic foraminifers, echinoderms, and small sized gastropod shells are also present within intraclasts. The matrix surrounding the intraclasts is recrystallized. Rare grains of glauconite and fossils are visible in the matrix. The fossils comprise spumellarian radiolarians, echinoderms (some ossicles remain articulated), ostracods of different sizes (Fig. 3(D)), small benthic foraminifers (*Ophthalmidiidae* Wiesner, 1920; *Lagenida* Delage and Hérouard, 1896), planktonic foraminifers, ammonoid aptychi, small bivalves (Fig. 3(A)), and fragmented shells, belonging to brachiopods (Fig. 3(G)) and bivalves. Very rare small grains of quartz, most likely of terrigenous origin, are also present.

4.2. Geochemistry

A clearcut Si vs. Al correlation is observed with $R^2 = 0.994$. Only two samples are out of the correlation line (22SAH01 and 22SAH02bis) with an excess in Si compared to Al (Fig. 4). This good correlation suggests that Si and Al are dominantly hosted by aluminosilicate minerals. Therefore, the silica linked with silicified microfossils is of very minor importance. The iron/aluminum (Fe/Al) ratio of the reference used to calculate the enrichment factors (composition of the earth's upper crust) is $Fe/Al = 0.5$. Here, the samples show an Fe/Al ratio close to this reference value (Fig. 4(A)). The points align along the line $Fe/Al = 0.5$, with slightly higher values, which reflects a light iron enrichment in all the samples studied. This ratio is not correlated with the enrichment factors of the trace elements. The enrichment factors of Ba, V, Cr, Co, Cu, Th and Ge (plus Zn except for three samples and Ni for one sample) show a homogeneous distribution, with values below 3, that is, showing no authigenic enrichment. The set contains samples enriched in Cd, As and Sb but not in U and Mo, with some exceptions. Fig. 4(B) shows that the As and Sb enrichment factors are correlated and show a stronger enrichment in As than in Sb. Lastly, Fig. 4(C) shows that the enrichment factors in U and Mo correspond to suboxic conditions of deposition.

4.3. Foraminiferal assemblage

The foraminiferal assemblage from sample 08SAH01 is strongly dominated by planktonic species, representing ca. 95% of the specimens collected. Although apparently well preserved, the mineralogical analysis shows that the wall is preserved in silica, casting some doubt on the authenticity of the texture of the wall surface. In all observed specimens, the outer test surface bears densely set protuberances (Fig. 5(D, H, Q)), which could be replications of original pseudomuricae or a diagenetic artefact. Due to the questionable preservation of the wall surface texture, the taxonomy needs to rely more strongly on the overall test morphology and shape of the chambers, which is a less desired way of determining species (Gradstein et al., 2017a).

Benthic foraminifers are preserved at in very low abundance and low to moderate diversity (Fig. 6). Found in the residue are *Dentalina* sp. (or *Laevidentalina* sp.; Fig. 6(F)), represented by internal casts, and ?*Reophax* spp. (Fig. 6(C–E)), preserving original wall composed of quartz grains and/or replaced by silica. The assemblage further contains planispiral two-chambered foraminifera with wall made of granular quartz (agglutinated or secondarily replaced by silica), tentatively attributed to ?*Ammodiscus* spp. (Fig. 6(A, B)), and some undetermined calcareous species. Specimens are preserved very differently. The wall of the Lagenida is dissolved and the specimens preserved as internal casts made of quartz. The wall of *Ammodiscus* is preserved. The same is probably true for *Reophax*, but the specimen in Fig. 6(C) seems to preserve/consist of only coarse crystals or grains. Beside foraminifers, the residue contains sponge spicules, microgastropods, small bivalves, fragments of echinoderms, and rare spumellarian radiolarians (Figs. 5(U–V), 6(G)).

Some planktonic foraminiferal specimens are depicted in Fig. 5. Specimens shown in Fig. 5(A–Q) are low to medium-high domical in shape, with a trochospiral growth, nearly globular chambers, large last coil, and clearly visible arched apertures. One specimen has a loop-shaped aperture. Although taxonomy is preliminary, awaiting detailed analysis of the assemblage with more specimens using conventional optical and SEM analysis, we are confident that *Globuligerina oxfordiana* (Grigelis) and *Globuligerina bathoniana* (Pazdrowa) are commonly present and that '*Globuligerina*' *balakhmatovae* (Morozova) also occurs in Sahune, but rarely so.

An inferred Oxfordian age of the Sahune samples is compatible with the age of this planktonic foraminiferal assemblage, but could be older also, or slightly younger (Gradstein et al., 2017a, 2017b). More detailed taxonomic analysis is being undertaken.

4.4. Echinoderm assemblage

The Sahune crinoid assemblage (08SAH01) presents high diversity compared to all previously reported assemblages from cold seeps. It is largely dominated by broken *Dolichocrinus* pieces (48% of the crinoid pieces found, N = 450, longest ca. 11 mm in length) that look exactly like the lower part of a *Dolichocrinus aberrans* (de Loriol, 1882) calyx without the articular facets. Several of the latter were found, more or less eroded (N = 79; Fig. 7(A, B)). The second most common finding are balanocrinine-type columnals that have been

assigned to *Balanocrinus dumortieri* de Loriol, 1877 (Fig. 7(D–J)). Only one tenth are pluricolumnals (N = 24, generally two associated columnals) and one fourteenth are nodals (Fig. 7). Several Isocrinida-looking brachials and three Comatulida cirrals have also been found (Fig. 7).

A single specimen of the infaunal irregular echinoid *Tithonia oxfordiana* was discovered (Fig. 7(K–M)). It is the second report of this deposit feeder seep-obligate species, which was so far only known from a dense monospecific assemblage at the top of R4-related pseudobioherm in Beauvoisin (Gaillard et al., 2011). As discussed above, this species might be of lithostratigraphic significance.

4.5. Ostracod assemblage

The sample 08SAH01 provided 22 species distributed into 13 genera and seven families (Table 2; Figs. 8–10). Regarding generic diversity, the Sahune community is largely dominated by Cytheruridae (31%), followed by Pontocyprididae (23%) and Bairdiidae (15%). In terms of number of species per family, the assemblage is co-dominated by Pontocyprididae (27%) and Cytheruridae (23%), Bairdiidae and Paracyprididae each accounting for 18%. Accessory components are Polycopidae, Sigilliidae and Cytherellidae, each being one species, accounting for ca. 5% of the species. About 61% of the genera are represented by one species (*Cytherella*, *Eucytherura*, *Pedicythere*, *Procytherura*, *Polycope*, *Rectangulocyprilla*, *Pseudomacrocypris*, *Cardobairdia*). Conversely, the two most diversified genera are *Pontocyprilla* and *Paracypris*, each being 36% of the species diversity. All species confounded, *Pontocyprilla* largely dominates the assemblage in terms of abundance. *Pontocyprilla* cf. *rara*, *Rectangulocyprilla* cf. *semiquadrata* and *Procytherura praecoquum* Forel nov. sp. are the most abundant species. These observations indicate that Pontocyprididae and Cytheruridae to a less extent were cornerstones of the ostracod community at Sahune. Preliminary observations reveal that marls located below the seep sequence (22SAH07) are barren of fauna while marls deposited laterally (22SAH02b; Fig. 2(A, B)) contain rarer and badly preserved ostracods, foraminifers, micro-gastropods and echinoderm remains.

Here we only provide the full description of *Procytherura praecoquum* Forel nov. sp., likely cognate to cold seep sites. The complete taxonomic list of ostracods species at Sahune is provided in Table 2, and all species are illustrated for future investigations (Figs. 8–10). In the following description, punctuation visible at solum of the exterior reticulate ornament of Cytheruridae is termed “secondary punctuation”. These structures may be pore clusters as discussed below, but until this hypothesis is formally proved, we use descriptive rather than interpretative terms.

4.6. Systematic palaeontology

Phylum Arthropoda Gravenhorst, 1843

Class Ostracoda Latreille, 1806

Suborder Cytherocopina Baird, 1850

Superfamily Cytheroidea Baird, 1850

Family Cytheruridae Müller, 1894

Subfamily Cytherurinae Müller, 1894

Genus *Procytherura* Whatley, 1970 emend. Bate and Coleman, 1975

Type species: *Procytherura tenuicostata* Whatley, 1970, by original description.

***Procytherura praecoquum* Forel nov. sp.**

Fig. 9(F–Y)

Derivation of the name: By apposition of the latin word *praecoquum*, for apricot, referring to the fields of apricot trees surrounding the Sahune site.

Holotype: MNHN.F.F72099, a complete carapace (Fig. 9(U)).

Paratype: MNHN.F.F72100, a complete carapace (Fig. 9(P, Q)).

Additional material: More than fifty complete carapaces.

Type locality and horizon: Sahune, Drôme department, France; sample 08SAH01, middle Oxfordian, Late Jurassic.

Measurements: Length = 300–431 μm ; Height = 142–203 μm .

Diagnosis: Small and delicate species, elongate with tapered posterior ending in a short sub-ventral caudal process. Vento-lateral expansion reduced. Ornamentation dominated by large

and shallow hexagonal reticulation with fine secondary punctuation.

Description: The carapace is small and delicate, elongate subtriangular in lateral view with maximum of height at the anterior cardinal angle equating between 40% and 50% of maximal length, greatest length around mid-height and greatest width slightly posterior to mid-length. The left valve narrowly overlaps right one at posterior cardinal angle (Fig. 9(P, S, T, W)), right valve overlaps left one along dorsal margin (Fig. 9(I, R)). The carapace is laterally compressed along the anterior cardinal angle and caudal process (Fig. 9(I, L, S–U)). The anterior margin is broadly and asymmetrically rounded, while the posterior margin is narrower and terminates in a blunt and short caudal process located close to ventral margin. The ventral margin is long and straight except for the tenuous oral concavity located around mid-length. The dorsal margin is long, about 70% of maximal length, straight and sloping posteriorly (10–15°) between anterior and posterior cardinal angles. The ventro-lateral expansion is reduced and only marked by postero-ventral termination. The median sulcus is weak and mainly seen in dorsal view by a weak constriction (Fig. 9(O)). Internally, the valves are vestibulate with anterior duplicature wider than posterior one (Fig. 10). Muscle scars and hinge are not seen.

The lateral ornamentation of the carapace is composed of large and shallow hexagonal reticulation subdued both in the antero-median and antero-dorsal areas (Fig. 9(J, K, Q)) that turns into fine longitudinal ridges at the ventro-lateral expansion (Fig. 9(R–V)) and over the entire ventral surface (Fig. 9(N)). The solum of the exterior reticulate ornament displays dense secondary punctuation that is only developed within reticules and not along the ventral surface (Fig. 9(L, M)). Each reticule contains between 48 and 55 secondary punctae, with a size ranging from 1.2 to 2.1 μm . The anterior-most row of reticules anteriorly delimitates an important marginal ridge that runs parallel to the anterior margin. A short, straight ridge emerges in the posterior area around mid-height of anterior marginal ridge and extends upward over about 15% of the total length of the valve (Fig. 9(T, U)).

Remarks: The carapace of *Procytherura* is small, laterally subtriangular to subovate with right valve overlapping left one dorsally, displaying an ornamentation from almost smooth to reticulate or striate, and internally vestibulate with lophodont hinge (Whatley, 1970; Bate and Coleman, 1975; Ballent and Whatley 2009). *Procytherura praecoquum* nov. sp. conforms to all characters, with the restriction that hinge and muscle scars could not be observed because all specimens are complete carapaces. The use of green UV light has allowed the observation of anterior and posterior duplicatures (Fig. 9(Y)) that are otherwise hardly visible by transparency through the fossil valves.

Specimens of *P. praecoquum* nov. sp. display one morphology with wide posterior end (Fig. 9(I, P, R–V)) and a second one with tapered posterior border (Fig. 9(W, X)). Most males of modern Cytheruridae are more elongate and inflated than females (Ramos et al., 1999) although counter-examples exist (Jöst et al., 2022). In the fossil record, males of *Eocytheropteron immodicus* Ballent and Whatley, 2009 from the Hauterivian of Argentina are more elongate than females (Ballent and Whatley, 2009) and length variations of *Procytherura? cuneata* Majoran, 1989 from the middle Cretaceous of Algeria have been related to sexual dimorphism (Majoran, 1989). The males of *Metacytheropteron sutherlandensis* Whatley, 1970 from the Callovian of UK are larger, longer and more parallel-

sided than females (Whatley, 1970). The first morphology of *P. praecoquum* nov. sp. may thus correspond to males, the second being females.

Among all reported *Procytherura* species, the new species is very close to *Procytherura serangodes* Ballent and Whatley, 2000 from the Middle Jurassic of Argentina (Ballent and Whatley, 2000) in terms of morphology, outline and ornamentation, including secondary punctation. However, the ventro-lateral rib of *P. serangodes* extends along the entire ventral margin until anterior margin where it merges with all muri to form a thick area, the entire structure delimiting a flat venter which is lacking in *P. praecoquum* nov. sp. *P. serangodes* also has a narrow, smooth and flat dorsal plateau that is lacking at the new species. In dorsal view, the median sulcus is more visible in *P. praecoquum* nov. sp. and the anterior portion of the carapace is more serrate. The ventral contact between the valves is straight in *P. praecoquum* nov. sp. while an important offset of left valve over right one is visible at *P. serangodes*. Finally, the ventral surface of *P. serangodes* is flat while it is composed of two posterior bulges separated from the contact line by a narrow concavity in *P. praecoquum* nov. sp.

5. Discussion

5.1. Palaeoenvironmental implications

5.1.1. The cold seep of Sahune

Regarding geochemical data, the vertical distribution of iron is disconnected from that of other enrichment factors. This implies that the possible enrichments in trace elements were not guided by their capture by iron oxy-hydroxides during sedimentation. In other words, the authigenic enrichments observed are independent of the iron supply and the latter was clearly supplied in detrital form, as indicated by the correlation with aluminum (Fig. 4). This implies that the trace-element enrichments may be ascribed to paleoenvironmental conditions and, therefore, the redox-sensitive elements may be considered to be reliable proxies.

The distribution of the values of the enrichment factors in U and Mo indicates that the oxygenation conditions are distributed along a trend going from oxic to suboxic conditions. The correlation of the enrichments in As and Sb, accompanied by a more marked enrichment in As than in Sb, is an argument allowing to propose that the Sahune site recorded the influence of cold seep-type circulations (Tribovillard, 2021a). Cadmium shows a good correlation with As and Sb (in terms of enrichment factors). These Cd enrichments can also be interpreted as a signature of the influence of fluid circulations. Indeed, several works mention that Cd enrichments are observed in sediments impacted by cold seeps and in associated fauna (Smrzka et al., 2020). To summarize, the geochemical data are consistent with what is generally known for cold seeps. What matters here is the fact that the conditions prevailing close to the sediment-water interface were not drastically reducing, which did not prevent benthic life. Therefore, the sulfate-dependent anoxic oxidation of methane, a

phenomenon commonly associated with cold seeps, and occurring at the so-called sulfate-methane transition zone (Smrzka et al., 2016, 2020; Zwicker et al., 2018), was taking place at a distance below seafloor large enough not to prevent the development of fauna.

5.1.2. Palaeobathymetry: evidence from crinoids, foraminifers and ostracods

Crinoids support a deep environment. As discussed for the Middle Jurassic La Voulte Lagerstätte and the Chénier Ravine (Charbonnier et al., 2007; Charbonnier, 2009), *Dolichocrinus aberrans*, with its very long radials, has been linked by some authors to modern deep-sea Bathycrinidae Bather, 1899 (Rasmussen, 1978; Bourseau et al., 1991). Indeed, *Naumachocrinus hawaiiensis* Clark, 1912 also possesses very long radials and has been found at depths ranging from ca. 500 to ca. 1,500 m (Tunnicliffe et al., 2016). *Dolichocrinus aberrans* is a rare species found in low numbers in Jurassic deposits of the Portugal (Algarve; de Loriol, 1891), France (Ardèche; de Loriol, 1882; Charbonnier et al., 2007; Hess, 2012), Switzerland (Ausich et al., 1999) and Crimea (Klikushin, 1996). Therefore, finding large amounts of radials is quite remarkable. It is worth noting that its identification from Polish sites remains uncertain and should be reanalysed (Pisera and Dzik, 1979; Salamon and Gorzelak, 2007). Similarly, finding large numbers of columnals of small balanocrinines is also indicative of deep environments based on bathymetric models on Jurassic stalked crinoids (Roux et al., 1988). Extant Isocrinida rarely exceed 2,000 m water depth (Améziane et al., ongoing work). To conclude, the presence of *Dolichocrinus* at Sahune is indicative of deep-water setting and its abundance may be related to the emission of seep fluids and/or to the availability of seep carbonate as hard substrate for attachment.

The foraminiferal assemblage is massively dominated by planktonic species, being ca. 95% of the specimens collected. The high proportion of planktonic species confirms a deep-water setting (van der Zwaan et al., 1990).

The ostracod community is largely dominated by complete carapaces, attesting for an hydrodynamically quiet environment and limited to absent post-mortem transportation. Several taxa provide significant information on palaeoenvironmental conditions. Among them, members of *Cardobairdia* lived on muddy bottoms of the sublittoral zone during the Early Jurassic and later survived mainly in the bathyal zone of the Tethyan Ocean (Ainsworth, 1986, 1987; Lord and Boomer, 1988; Boomer, 1991; Lord et al., 1993; Tabuki and Hanai, 1999). They were important components of deep-water assemblages in the Cenozoic, for example at depths exceeding 2,500 m in the Biscay Abyssal Plain during the Late Eocene and 1,000–1,500 m in Jamaica during the Early Miocene (van den Bold, 1974; Benson, 1975, 1977; Ducasse and Peypouquet, 1978, 1979; Steineck, 1981; Aumond et al., 2009). Another significant example is that of *Pontocyprrella* representatives that were common in Middle Jurassic bathyal communities of Hungary, accompanied by *Cardobairdia* (Monostori, 1995). During the Early Cretaceous, *Pontocyprrella* dominated upper bathyal environments of North Sea and off Norway (Ayress and Gould, 2018) as well as lower bathyal conditions of Aubenais area, western margin of the south-eastern France Basin (Scarenzi-Carboni, 1984).

The occurrence of *Tethysia* and *Procytherura* at Sahune is also noticeable. *Tethysia* was a typical Tethyan genus that occurred from the Bathonian of Normandy, northern France and UK (Middle Jurassic) to the Hauterivian (Early Cretaceous) of south-eastern France Basin (Donze, 1975; Sheppard, 1981; Tesakova, 2003). During the Tithonian-Hauterivian time interval, it was found at bathyal to sub-bathyal water depth and was proposed as a biostratigraphical tool for deep-sea facies (Donze 1975). It may have derived from bathyal or shallower littoral species earlier in the Jurassic, shallow water Bathonian species from Normandy (France) and UK being hypothesised as this original stock (Donze 1975; Sheppard, 1981). The two *Tethysia* species at Sahune (Fig. 9(Z–AE)) demonstrate that in its southward migration since the Bathonian, *Tethysia* had already reached south-eastern France Basin and bathyal depth in the Oxfordian. *Procytherura* first occurred in south-western Tethys (North Africa) during the Sinemurian, Early Jurassic (Ballent and Whatley 2000) and subsequently migrated to epicontinental shelf seas of northern Europe where it diversified (Ainsworth, 1986). It then went through the Hispanic Corridor between eastern Pacific and western Tethys and progressively became restricted to southern hemisphere (Boomer and Ballent, 1996; Ballent and Whatley, 2000). It was considered that *Procytherura* may only have colonized bathyal and abyssal waters in the Early Cretaceous, with the downslope migration having initiated in Europe (Donze 1977). *Procytherura praecoquum* nov. sp. at Sahune pushes back this event to the Oxfordian.

At Sahune, the co-occurrence of *Cardobairdia*, dominance of *Pontocyprilla*, presence of *Tethysia* and absence of otherwise widespread Cytheroidea families, as discussed below, point to a bathyal depositional setting, ca. 1,500 m. b.s.l.

5.2. Palaeoautecology of ostracods

5.2.1. Pore clusters: evidence of palaeochemosymbiosis?

The notion of pore clusters in ostracods was introduced by Maddocks and Steineck (1987) to accommodate pores at the surface of recent Cytheruridae that differ from other types of lateral pores (normal, sieve-type and exocrine pores). They are described as “occupying each solum or puncta of the exterior reticulate ornament, all or most of which penetrate the carapace, producing on the interior a pattern of clustered perforations that directly corresponds to the exterior reticulate ornament, without accompanying setae” (Maddocks and Steineck, 1987: p. 321). Pore clusters are found at recent Eucytherurinae Puri, 1974 from deep-sea chemosynthetic environments where they have been proposed to illustrate relationship with chemosynthetic bacteria, though this remains to be formally demonstrated (Van Harten, 1993; Maddocks, 2005; Karanovic and Brandão, 2015; Yasuhara et al., 2018; Tanaka et al., 2019, 2021).

Distinguishing pore clusters from secondary punctation in the fossil record is challenging. Secondary punctation is frequent at *Procytherura* species, for instance *Procytherura celtica* Ainsworth, 1986 and *Procytherura reticulata* Ainsworth, 1986 (Toarcian–Bajocian, Fastnet Basin; Ainsworth, 1986), *Procytherura amygdala* Ballent and

Whatley, 2009 (Valanginian, Argentina: Ballent and Whatley, 2009), *Procytherura ippolitovi* Tesakova and Seltser, 2022 (Callovian, Russia: Tesakova and Seltser, 2022). Pore clusters have also been hypothesized in other Cytheroidea families such as Cytheridae from the Albian–Cenomanian of Jordan (Bergue et al., 2016). However, it remains unclear whether they correspond to pore clusters or surface ornamentation.

At Sahune, such structures are seen in *Eucytherura* sp. (Fig. 9(D–H); three to four punctae of 2.5–4.5 μm) and *Procytherura praecoquum* nov. sp. (Fig. 9(I–X); 48 to 55 punctae of 1.2–2.1 μm). At *P. praecoquum* nov. sp., punctae are filled with sediment that seems directly related to the infill of carapaces (Fig. 9(K)), indicating that they may be canals going through the valve thickness that were filled upon death of the animal. These patterns may be the oldest pore clusters so far reported, which could be coherent with the cold seep environment at Sahune though taxa displaying pore clusters are not systematically reported from such setting (Bergue et al., 2023). Pore clusters are diagnostic of Eucytherurinae (Maddocks and Steineck, 1987; Mazzini and Gliozzi, 2000; Danielopol et al., 2023) but until the present hypothesis is confirmed, we follow the traditional attribution to Cytherurinae.

5.2.2. Comparison with non-seep Oxfordian assemblages

Our knowledge of Jurassic deep-water ostracod communities is still limited and comparison with Sahune remains preliminary. Outside of the south-eastern France Basin, an Early Jurassic (Pliensbachian) community from Turkey dominated by *Ptychobairdia* Kollmann, 1960 and lacking cosmopolitan Metacopina and Cytheroidea was hypothesized as illustrating bathyal conditions (Lord and Lambourne, 1991). Another Early Jurassic (Sinemurian–Pliensbachian) community from the Northern Calcareous Alps dominated by Bairdiidae and lacking typical members of contemporaneous platform communities was considered as inhabiting outer neritic-upper continental slope (Honigstein et al., 2014). Finally, a bathyal community from the Late Jurassic of Italian Apennine was entirely composed of Bairdiidae (Oertli, 1967). These bairdiid-dominated communities drastically differ from Sahune assemblage.

Within the south-eastern France Basin, the Terres Noires deposited at outer neritic to bathyal depth during the Middle and Late Jurassic were alternatively dominated by *Bairdia* and *Pontocyprilla* (Oertli, 1972). More precisely, a poorly diversified fauna with abundant dwarf species related to unfavourable environment occur in Buis-les-Baronnies (Drôme; Oertli, 1960). Oertli (1963) listed ‘*Bairdia*’, *Bythocypris*, *Krausella* (= *Cardobairdia*), *Paracypris* and *Pontocyprilla* from the early Oxfordian of the nearby Lauzière Mountain, although the identification of modern genera as *Bythocypris* Brady, 1880 would require a re-observation of the specimens (Lord, 2020). All genera from the Oxfordian of the Terres Noires Fm. were therefore also members of the Sahune community, indicating that at least at the generic level, ‘*Bairdia*’, *Cardobairdia*, *Paracypris* and *Pontocyprilla* were also members of the deep-sea background community within the south-eastern France Basin.

It is also worth discussing how much Sahune community differs from coeval platform

assemblages. To do so, data from the literature was gathered, illustrating Oxfordian platform localities without seepage from France (Besançon, Calvados, Isère, Jura), Switzerland, Germany, Poland, UK and Israel. Their relative proportions of genera per superfamilies and families are shown in Fig. 10 (complete dataset in Table S1, Appendix A). This analysis first shows that all superfamilies and families from Sahune were also present in contemporaneous platform assemblages. The same is true for genera with the most distinctive at Sahune being largely documented, for instance from UK (*Procytherura*; Whatley, 1970), France (*Cardobairdia*: Donze and Enay, 1962; Gaillard, 1983; *Pontocyprilla*: Oertli, 1963), Poland (*Cardobairdia*; Bielecka and Styk, 1966), Germany (*Cardobairdia*; Glashoff, 1964) and Russia (*Pontocyprilla*: Tesakova, 2003; *Tethysia*: Tesakova, 2003).

The superfamilial richness of Sahune community is comparable to coeval platform assemblages that range from five to nine (Fig. 10(A)). However, it differs by higher proportions of Pontocypridoidea, and Bairdioidea to a lesser extent, as well as lower proportions of Cytheroidea. Conversely, the familial richness is well below that observed at other localities (Fig. 10(B)), where it ranges from 10 (Besançon, Poland) to 20 (Germany). More specifically, Sahune displays a high proportion of Pontocyprididae (27%) while they never exceed 8% in other communities with the exception of Besançon area (13%). Today, Pontocyprididae are widespread from shallow littoral to deep-sea, generally in low abundance (van den Bold, 1974; Maddocks, 1969, 1977; Karanovic, 2019) so their high abundance in Sahune could relate to fluid seepage. Additionally, Sahune significantly lacks otherwise widespread Cytheroidea families as Progonocytheridae, Bythocytheridae, Cytherideidae, Protocytheridae, Schulerideidae and Trachyleberididae (Fig. 10(B)). Of special notice is the absence of Macrocyprididae that are today most abundant where high biological productivity produces food-rich bottom sediments, i.e., on coral reefs, near the edges of continental shelves, in the oxygen-minimum zone, in bathyal and abyssal depths, and beneath cold or upwelling surface currents (Maddocks, 1991; Brandão, 2005). They have been documented since the Late Ordovician (Kellett, 1935; Swain, 1987; Milhau, 1988) but their presence in pre-Jurassic assemblages remains unverified. They became abundant since the Early Jurassic (Harloff and Jäger, 1994; Bodergat et al., 1998; Gómez and Arias, 2010; Mitta et al., 2018), including in basinal environments (Boomer et al., 1998). Although it remains hard to state when Macrocyprididae radiated, they were largely distributed in terms of environments during the Jurassic and their absence from Sahune community may relate to fluid seepage.

Overall, the Sahune record shows that cold seep communities were already a mixture of taxa found in coeval platform and deep-sea oligotrophic environments during the Oxfordian. Conversely, some important Jurassic taxa were excluded, possibly by the interplay of water-depth and seep fluid chemistry to which they may not have been adapted.

5.2.3. Comparison with younger cold seep assemblages

Three assemblages from ancient cold seeps have been reported in the literature and Sahune is the oldest documented so far. Chronologically, the oldest one corresponds to a deep-sea slope seepage during the Eocene and Oligocene in USA (Yamaguchi et al., 2016). Russo et al. (2012) reported ten species from a Miocene seep in Northern Apennines

developed in an open-shelf to deep-water context. The seep nature of this assemblage was questioned in Karanovic and Brandão (2015) but recently validated based on the nature of carbonate deposits and carbonate stable C isotopes (Hryniewicz, 2022). It is worth emphasizing that the absence of obligate taxa at this site may well be related to its putative shallow context, as it is now widely acknowledged that shallow water seeps display few to none seep-specific taxa and are mainly inhabited by background taxa (Levin, 2005; Dando, 2010; Hryniewicz et al., 2014, 2015; Kaim et al., 2017). Finally, Coles et al. (1996) reported 48 species from Quaternary seeps in the Porcupine Basin, western Ireland. Reports of recent seeps are slightly more abundant and provide a larger geographic coverage: 18 species from Black Sea (Schornikov and Syrtlanova 2008), 16 from the Gulf of Mexico (Degen et al., 2012; Machain-Castillo et al., 2014), four from brackish water cold seep in Marmara Sea (Ritt et al., 2010), eight from a mud volcano in the Mediterranean Sea (Ritt et al., 2012), seven from mud volcano and pockmark from the Nile deep-sea fan (Ritt et al., 2011), and 89 from deep-water seepage on the São Paulo Ridge in southwestern Atlantic (Bergue et al., 2023). All data from these fossil and recent communities have been gathered and their compositions are shown in Fig. 11 (complete dataset in Table S2, Appendix A). For the discussion of general trends in ostracod diversity through time, the communities of four time bins are considered: Oxfordian, Eocene–Oligocene, Miocene, Quaternary–Recent.

The superfamilial richness at Sahune is comparable to that of post-Jurassic seeps that ranged from two in the Eocene–Oligocene to nine in the Quaternary–Recent (Fig. 11(A)). All superfamilies associated with post-Jurassic seeps were already present in Sahune with the exception of Macrocypridoidea that may have colonized deep-water seeps quite recently as they only occur in Quaternary–Recent counterparts, in low proportion. The superfamilial composition at Sahune is thus comparable to that of post-Jurassic seeps and the major differences are to be found in their relative proportions. The familial diversity of seep assemblages displays a major diversification through time, from five in the Eocene–Oligocene to 24 in the Quaternary–Recent (Fig. 11(B)). It seems to be correlated with the global diversification of marine ostracods, mainly Cytheroidea (see Forel and Crasquin, 2022). Overall, all families from Sahune except Macrocyprididae have been associated with seeps until present days. The modern diversity of ostracods at cold seeps was therefore shaped by the diversification of families that have been inhabitants of such ecosystems at least since the Oxfordian and colonization events.

An important point is the fossil record of families from post-Jurassic seeps that are absent from Sahune: can their colonization of seeps be discussed? Among them, Eucytheridae, Hemicytheridae, Leptocytheridae, Paracytheroidea and Xestoleberididae have all been reported from Miocene to Recent seeps but radiated from the Late Cretaceous to the Miocene (van den Bold, 1957; Bertels, 1974; Guernet, 1985; Ayress, 1995; Aiello and Szczechura, 2004; Bergue and Govindan, 2010; Babinot and Colin, 2011). Representatives of Krithidae have been part of cold seep assemblages since the Eocene–Oligocene while their oldest non-seep occurrence has been reported from the Aptian–Albian, Early Cretaceous (Antonietto et al., 2016). Krithidae did not radiate before the Cretaceous and migrated into deeper or colder environments in a retrothermal adaptation (Dingle, 2009). The absence of all these families from Sahune therefore relates to their post-Oxfordian radiation.

Three families may conversely provide food for thoughts regarding seep colonization. Of them, Paradoxostomatidae have been reported from Quaternary–Recent seeps. Their oldest

non-seep occurrences date back to the Early Jurassic, Sinemurian and Pliensbachian (Herrig, 1969; Michelsen, 1975; Exton, 1979; Boomer, 1991) and they mostly diversified in the Cenozoic (Mandelstam, 1960). As far as we know, Paradoxostomatidae have never been reported from Oxfordian sediments. As they have only been found in Quaternary–Recent seeps, they may illustrate relatively recent events of colonization. Loxoconchidae have been reported from Eocene–Oligocene and Quaternary–Recent seeps and are known from non-seep Oxfordian in Germany and France (Malz, 1958; Glashoff, 1964; Bodergat, 1997). Similarly, Trachyleberididae occur in seeps since the Eocene–Oligocene and are well known from non-seep Oxfordian beds of Germany, France, Madagascar, Israel, Saudi Arabia (Malz, 1958; Glashoff, 1964; Lutze, 1960; Bodergat, 1997; Dépêche et al., 1987; Rosenfeld et al., 1987; Mette, 2004). The absence of Loxoconchidae and Trachyleberididae from Sahune may also indicate that they colonized seeps later on, between the Oxfordian and their first seep occurrence in Eocene–Oligocene.

6. Conclusions

The Terres Noires Formation cropping out in the south-eastern France Basin preserves limestone bodies related to cold seep-type circulations during the Oxfordian (Late Jurassic). Here we described the new site of Sahune in the Drôme department and demonstrated its link to fluid seepage with trend going from oxic to suboxic conditions. We described and discussed its middle Oxfordian age and the associated fauna dominated by foraminifers, echinoderms and ostracods. Altogether, they indicate that the Sahune seepage occurred at a bathyal water-depth, ca. 1,500 m. The ostracod assemblage is the oldest so-far reported from such environments and has been thoroughly analyzed. The new species *Procytherura praecoquum* may display the first known pore clusters that are highly debated structures possibly related to ectosymbiosis. The taxonomic structure of the assemblage shows that today's seep-ostracod taxa (families, superfamilies) have evolved in such environments at least since the middle Oxfordian, echoing reports of seep macro-invertebrate communities with modern structure since the Early Jurassic. Events of colonization of seep environments by ostracods are hypothesized for future research. More work is needed to characterize the diversity, evolution and adaptations of ostracods to such environments in deep time, being today an entire new field of ostracodology.

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Appendix A. Supplementary information

Supplementary information (including Tables S1 and S2) associated with this article can be found, in the online version, at:

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Table and Figure captions

Table 1. Chemical composition and enrichment factors of the 13 samples from Sahune section. <LD stands for below limit of detection. Major elements are expressed in weight %, trace elements are in $\mu\text{g/g}$ (or ppm). Enrichment factors are dimensionless. P, samples from the carbonate mass of the pseudobioherms; NP, non-pseudobiohermal limestone; LM, samples from lateral marls.

Table 2. Taxonomic list of all ostracod species identified from Sahune (sample 08SAH01), Drôme, south-eastern France Basin, Oxfordian, Late Jurassic.

Fig. 1. **A.** Geographical map of France showing Sahune locality in Drôme, south-eastern France Basin (Google Maps, 2023). **B.** Insight simplified structural map of the south-eastern France Basin. shows the position of Sahune in the Natural Regional Park of Baronnies provençales (modified from Tribovillard et al., 2013). Circle represents Beauvoisin area; F, fault.

Fig. 2. **A.** Field photography of the Sahune sequence (C. Gaillard). **B.** Interpretative scheme of the Sahune sequence. P1-P4, pseudobioherms; 01-09, studied samples, labelled 08SAH and 22SAH. **C.** Key-beds R1 to R7 along the middle Oxfordian of the Beauvoisin section (modified from Gaillard et al., 1996) showing the stratigraphic distribution of pseudobioherms in south-eastern France Basin (from Rolin et al., 1990).

Fig. 3. Microfacies of cold seep deposits at Sahune, Drôme, south-eastern France Basin, Oxfordian, Late Jurassic, sample 08SAH01. **A.** Wackestone with large intraclast. White arrow: radiolarian; grey arrow: cast of a small bivalve. **B.** Intraclast of a packstone, bearing radiolarians (black arrows) and planktonic foraminifers (white arrow). **C.** View of an intraclast rich in planktonic foraminifers (white arrows). Black arrow: barely visible, micritized radiolarian. **D.** Detail of the matrix surrounding the intraclasts. White arrow: ostracod. **E.** Possible boring/burrowing within the intraclast, associated with early lithification surface. **F.** Aptichus. **G.** Fragment of a brachiopod shell (see its lamellar structure). Scale bars: 1 mm (A), 0.5 mm (B–G).

Fig. 4. Crossplots opposing the Al vs. Fe contents (**A**), the As vs. Sb contents (**B**), the enrichment factors of U and Mo (**C**), and the Si vs. Al contents (**D**) for the 13 samples analyzed of the Sahune section. For explanations about the insert of C, see Algeo and Tribovillard (2009). SW: seawater.

Fig. 5. Planktonic foraminifers and radiolaria from the deposits at Sahune, Drôme, south-eastern France Basin, middle Oxfordian, Late Jurassic. **A–D.** *Globuligerina bathoniana* (Pazdrowa). A: spiral view; B: umbilical view; C: side view; D: detail of the wall (MNHN.F.F72112–MNHN.F.F72115). **E–Q.** *Globuligerina oxfordiana* (Grigelis). E, I, M: spiral view; F, J, K, N, O: umbilical view; G, L, P: side view; H, Q: detail of the wall (MNHN.F.F72116–MNHN.F.F72128). **R–T.** *Globuligerina* sp. R: spiral view; S: umbilical view; T: side view (MNHN.F.F72129–MNHN.F.F72131). **U, V.** Spumellarian radiolaria (MNHN.F.F72132, MNHN.F.F72133). Scale bars: 100 µm (A–C, E–G, I–P, R–V; white), 20 µm (D, H, Q; black).

Fig. 6. Benthic foraminifers from the deposits at Sahune, Drôme, south-eastern France Basin, middle Oxfordian, Late Jurassic. **A.** ?*Ammodiscus* sp. A (MNHN.F.F72134). **B.** ?*Ammodiscus* sp. B (MNHN.F.F72135). **C.** ?*Reophax* sp. A (MNHN.F.F72136). **D.** ?*Reophax* sp. B (MNHN.F.F72137). **E.** ?*Reophax* sp. C (MNHN.F.F72138). **F.** *Dentalina* sp. or *Laevidentalina* sp. (MNHN.F.F72139). **G.** A single chamber of a lagenid (?) foraminifera (MNHN.F.F72140). **H.** Polyaxon sponge spicule (MNHN.F.F72141). Scale bar: 100 µm.

Fig. 7. Crinoids from the deposits at Sahune, Drôme, south-eastern France Basin, middle Oxfordian, Late Jurassic. **A, B.** *Dolichocrinus aberrans* (De Loriol, 1882), lateral view of the incomplete radials with articular facets (MNHN.F.A89406; MNHN.F.A89407). **C.** Unidentified Comatulida cirral (MNHN.F.A89408). **D–J.** *Balanocrinus dumortieri* De Loriol, 1877. D, E: isolated columnals with their symplexial articulation (MNHN.F.A89409; MNHN.F.A89410); F: isolated nodal with its cryposymplexy (MNHN.F.A89411); G: pluricolumnal with nodal and its cryposymplexy (MNHN.F.A89412); H: proximal symplexial articulation on an axillary brachial (MNHN.F.A89413); I: distal muscular synarthy on an axillary brachial articulation (MNHN.F.A89414); J: distal muscular synarthy on a brachial (MNHN.F.A89415). **K–M.** *Tithonia oxfordiana* Gaillard et al., 2011 (MNHN.F.A89416). K: lateral view; L: posterior view; M: oral view. Scale bars: 1 mm (A–J), 1 cm (K–M).

Fig. 8. Ostracods from the deposits at Sahune, Drôme, south-eastern France Basin, middle Oxfordian, Late Jurassic. **A.** *Polycope pelta* Fischer, 1961, ?left view of a complete carapace (MNHN.F.F72061). **B–D.** *Cardobairdia* cf. *argoviensis* Oertli, 1959. B: right view of a complete carapace (MNHN.F.F72062); C: right view of a complete carapace (MNHN.F.F72063); D: right view of a complete carapace (MNHN.F.F72064). **E, F.** ‘*Bairdia*’? sp. 1. E: right view of a complete carapace (MNHN.F.F72065); F: right view of a complete carapace (MNHN.F.F72066). **G.** ‘*Bairdia*’ cf. *major* Donze, 1964, right view of a complete carapace (MNHN.F.F72067). **H.** *Isobythocypris*? sp. 1, right view of a complete carapace (MNHN.F.F72068). **I.** *Isobythocypris*? sp. 2, right view of a complete carapace (MNHN.F.F72069). **J.** *Paracypris*? sp. 1, right view of a complete carapace

(MNHN.F.F72070). **K.** *Paracypris?* sp. 2, right view of a complete carapace broken anteriorly (MNHN.F.F72071). **L.** *Paracypris* cf. *siliqua* Jones and Hinde, 1890, right view of a complete carapace (MNHN.F.F72072). **M, N.** *Paracypris* cf. *stripta* Lubimova, 1956. **M:** right view of a complete carapace (MNHN.F.F72073); **N:** right view of a complete carapace (MNHN.F.F72074). **O–W.** *Pontocyprrella* cf. *rara* Kaye, 1965a. **O:** right view of a complete carapace (MNHN.F.F72075); **P:** right view of a complete carapace (MNHN.F.F72076); **Q:** right view of a complete carapace (MNHN.F.F72077); **R:** right view of a complete carapace (MNHN.F.F72078); **S:** right view of a complete carapace (MNHN.F.F72079); **T:** right view of a complete carapace (MNHN.F.F72080); **U:** right view of a complete carapace (MNHN.F.F72081); **V:** right view of a complete carapace (MNHN.F.F72082); **W:** right view of a complete carapace (MNHN.F.F72083). **X.** *Pontocyprrella vescusa* Lubimova in Tesakova, 2003, right view of a complete carapace (MNHN.F.F72084). **Y.** *Pontocyprrella* sp. 1, right view of a complete carapace (MNHN.F.F72085). **Z.** *Pontocyprrella* sp. 2, right view of a complete carapace (MNHN.F.F72086). **AA.** *Pseudomacrocypris* sp., left view of a complete carapace (MNHN.F.F72087). Scale bars: 100 μ m.

Fig. 9. Ostracods from the deposits at Sahune, Drôme, south-eastern France Basin, middle Oxfordian, Late Jurassic. **A–C.** *Rectangulocyprrella* cf. *semiquadrata* (Kaye, 1965b). **A:** right view of a complete carapace (MNHN.F.F72088); **B:** right view of a complete carapace (MNHN.F.F72089); **C:** right view of a complete carapace (MNHN.F.F72090). **D–H.** *Eucytherura* sp. **D:** right view of a complete carapace (MNHN.F.F72091); **E, F:** detail of the posterior end of the same specimen; **G:** detail of the anterior end of the same specimen; **H:** right view of a complete carapace (MNHN.F.F72092). **I–Y.** *Procytherura praecoquum* Forel nov. sp. **I:** left view of a complete carapace (MNHN.F.F72093); **J, K:** detail of the posterior portion of the same specimen showing hexagonal reticules and “pore” at the bottom of solum; **L:** detail of the posterior end of the same specimen in sub-ventral view; **M:** detail of the anterior end of the same specimen in sub-ventral view; **N:** ventral view of a complete carapace (MNHN.F.F72094); **O:** dorsal view of a complete carapace (MNHN.F.F72095); **P:** right view of a complete carapace (MNHN.F.F72096); **Q:** detail of the posterior end of the same specimen in sub-ventral view; **R:** left view of a complete carapace (MNHN.F.F72097); **S:** right view of a complete carapace (MNHN.F.F72098); **T:** right view of a complete carapace, holotype (MNHN.F.F72099); **U:** right view of a complete carapace, paratype (MNHN.F.F72100); **V:** left view of a complete carapace (MNHN.F.F72101); **W:** right view of a complete carapace (MNHN.F.F72102); **X:** left view of a complete carapace (MNHN.F.F72103); **Y:** complete carapace seen in green UV light with white arrows showing the limits of the anterior calcified inner lamella (MNHN.F.F72104). **Z–AB.** *Tethysia* cf. *bathonica* Sheppard in Brand, 1990. **Y:** right view of a complete carapace (MNHN.F.F72105); **Z, AA:** details of normal pores of the same specimen; **AB:** right view of a complete carapace (MNHN.F.F72106). **AC–AE.** *Tethysia* sp. **AC:** left view of a complete carapace (MNHN.F.F72107); **AD:** right view of a complete carapace (MNHN.F.F72108); **AE:** right view of a complete carapace (MNHN.F.F72109). **AF.** *Pedicythere?* sp., right view of a complete carapace (MNHN.F.F72110). **AG.** *Cytherella* sp., right view of a complete carapace (MNHN.F.F72111). Scale bars: 100 μ m (A–D, H–K, N–P, R–AG), 20 μ m (E–G, Q), 50 μ m (L, M).

Fig. 10. Taxonomic composition of seep vs. non-seep Oxfordian ostracod communities. **A.** Generic composition of superfamilies. **B.** Generic composition of families. Database and references in Table S1 (Appendix A).

Fig. 11. Taxonomic composition of cold seep ostracod communities through time. **A.** Generic composition of superfamilies. **B.** Generic composition of families. Database and references in Table S2 (Appendix A).

								5	1							1	3		1	3	8	5		2	1	9	
22SA H09	N P	8.78	40.11	0.54	0.06	0.11	3.56	19.80	1.59	4.94	3.27	0.39	0.75	< L.D.	1.78	3.14	2.27	3.50	1.98	0.17	2.52	0.47	29.687	0.25	1.96	0.98	
22SA H10	P	7.43	33.35	0.59	0.05	0.36	3.47	17.66	1.46	5.85	3.01	0.40	0.66	< L.D.	0.55	2.72	1.68	4.51	1.76	0.23	2.51	0.46	34.105	0.22	1.75	0.74	
22SA H11	L M	8.29	26.11	0.45	0.06	0.53	2.04	13.98	1.18	7.81	2.46	0.32	0.50	< L.D.	0.92	2.14	1.83	4.90	1.44	0.28	2.44	0.40	33.340	0.17	1.42	0.75	
22SA H12	P	10.65	51.36	0.54	0.06	0.42	6.75	22.13	1.85	8.06	3.97	0.58	0.72	< L.D.	3.34	3.09	2.82	1.29	2.27	0.58	3.92	0.59	35.174	0.24	2.24	1.74	
22SA H13	L M	2.00	90.44	0.73	0.07	0.20	2.05	28.08	2.66	8.63	5.19	0.79	0.98	< L.D.	1.34	3.93	2.02	4.00	3.10	0.22	5.16	0.72	33.728	0.32	2.88	1.77	
Samp les	T y p e	V	W	Y	Zn	Z r	L a	C e	P r	N d	S m	E u	G d	Tb	D y	H o	E r	T m	Y b	L u							
22SA H01	P	29.22	< L.D.	12.45	18.07	3.25	2.15	3.04	4.03	1.52	2.49	0.51	1.97	0.2816	1.66	0.34	0.90	0.02	0.77	0.11	0.12						
22SA H02	P	18.25	< L.D.	4.37	8.5081	1.75	5.38	8.46	1.07	4.18	0.79	0.17	0.66	0.0962	0.57	0.12	0.32	0.04	0.28	0.04							
22SA H02b is	L M	63.97	< L.D.	15.16	43.05	7.87	2.26	3.70	4.63	1.75	3.04	0.62	2.43	0.3622	2.17	0.45	1.22	0.18	1.14	0.17							
22SA H03	P	28.89	< L.D.	7.22	16.73	3.05	1.02	1.67	2.20	8.56	1.46	0.30	1.18	0.1691	0.99	0.21	0.55	0.08	0.49	0.08							
22SA H04	P	20.50	< L.D.	5.18	22.7307	1.51	6.45	9.01	1.26	5.01	0.88	0.18	0.74	0.1074	0.64	0.13	0.36	0.05	0.31	0.05							
22SA H05	P	20.6	< L.D.	7.24	14.59	2.00	8.4	1.33	1.7	6.8	1.2	0.2	1.07	0.1529	0.9	0.1	0.5	0.0	0.4	0.0							

22SA H10	N P	0. 4 0	1. 61	1. 42	1.3 6	2. 5 3	1. 5 6	3. 7 7	0 .8 8	1. 7 6	2. 4 3	1. 0 9	24 .5 5	32.95 00001 7	7. 7 4	1 .6 8	1. 7 7	3. 8 6	1. 2 1	0 .9 7	0 .0 2	0 .5 4	33 .5 3	0 .0 8	0 .3 0	0 .0 7
22SA H11	P	0. 4 0	1. 64	1. 42	1.0 1	3. 5 8	2. 6 3	6. 4 6	0 .8 4	2. 2 5	5. 1 4	1. 1 2	45 .2 9	46.44 50000 6	1 1. 5 3	1 .6 9	2. 4 3	3. 1 9	0. 9 5	0 .8 8	0 .0 2	0 .6 0	34 .6 6	0 .0 8	0 .2 4	0 .0 5
22SA H12	L M	0. 4 6	1. 35	1. 31	1.9 5	3. 2 1	1. 5 8	4. 0 8	0 .6 8	3. 0 5	1 0. 9 2	1. 0 3	21 .1 4	34.77 26552 2	1 4. 1 3	1 .7 8	3. 7 4	4. 8 8	1. 6 4	1 .6 5	0 .0 2	0 .6 3	31 .8 7	0 .0 9	0 .3 9	0 .0 8
22SA H13	P	0. 6 2	1. 44	1. 27	0.4 5	1. 7 4	1. 3 0	2. 2 5	0 .7 2	2. 3 7	3. 3 6	1. 0 1	7. 61	5.005 90888 6	4. 1 0	1 .8 5	0. 8 9	6. 0 1	2. 1 4	1 .5 7	0 .0 2	0 .6 3	30 .4 5	0 .0 8	0 .5 3	0 .1 1

Table 2.

Class OSTRACODA Latreille, 1806

Subclass MYODOCOPA Müller, 1894

Order HALOCYPRIDA Dana, 1853

Suborder CLADOCOPINA Sars, 1866

Superfamily POLYCOPOIDEA Sars, 1866

Family POLYCOPIDAE Sars, 1866

Genus *Polycope* Sars, 1866

Polycope pelta Fischer, 1961 (Fig. 8(A))

Subclass PODOCOPA Müller, 1894

Order PODOCOPIDA Sars, 1866

Suborder SIGILLIOPINA Martens, 1992

Superfamily SIGILLIOIDEA Mandelstam, 1960

Family SIGILLIIDAE Mandelstam, 1960

Genus *Cardobairdia* van den Bold, 1960 emend. McKenzie, 1967

Cardobairdia cf. *argoviensis* Oertli, 1959 (Fig. 8(B–D))

Suborder BAIRDIOCOPINA Gründel, 1967

Superfamily BAIRDIOIDEA Sars, 1888

Family BAIRDIIDAE Sars, 1865

Genus '*Bairdia*' M'Coy 1844

'Bairdia'? sp. 1 (Fig. 8(E, F))

'Bairdia' cf. *major* Donze, 1964 (Fig. 8(G))

Genus *Isobythocypris* Apostolescu, 1959

Isobythocypris? sp. 1 (Fig. 8(H))

Isobythocypris? sp. 2 (Fig. 8(I))

Suborder CYPRIDOCOPINA Jones, 1901

Superfamily CYPRIDOIDEA Baird, 1845

Family PARACYPRIDIDAE Sars, 1923

Genus *Paracypris* Sars, 1866

Paracypris? sp. 1 (Fig. 8(J))

Paracypris? sp. 2 (Fig. 8(K))

Paracypris cf. *siliqua* Jones & Hinde, 1890 (Fig. 8(L))

Paracypris cf. *stripta* Lubimova, 1956 (Fig. 8(M, N))

Superfamily PONTOCYPRIDOIDEA Müller, 1894

Family PONTOCYPRIDIDAE Müller, 1894

Genus *Pontocyprella* Mandelstam in Lubimova, 1955

Pontocyprella cf. *rara* Kaye, 1965a (Fig. 8(O–W))

Pontocyprella *vescusa* Lubimova in Tesakova, 2003 (Fig. 8(X))

Pontocyprella sp. 1 (Fig. 8(Y))

Pontocyprella sp. 2 (Fig. 8(Z))

Genus *Pseudomacrocypris* Michelsen, 1975

Pseudomacrocypris sp. (Fig. 8(AA))

Genus *Rectangulocyprella* Wilkinson, 1990

Rectangulocyprella cf. *semiquadrata* (Kaye, 1965b) (Fig. 9(A–C))

Suborder CYTHEROCOPINA Baird, 1850

Superfamily CYTHEROIDEA Baird, 1850

Family CYTHERURIDAE Müller, 1894

Subfamily CYTHERURINAE Müller, 1894

Genus *Eucytherura* Müller, 1894 emend. Ayress *et al.*, 1995

Eucytherura sp. (Fig. 9(D–H))

Genus *Procytherura* Whatley, 1970 emend. Bate & Coleman, 1975

Procytherura praecoquum Forel nov. sp. (Fig. 9(I–Y))

Genus *Tethysia* Donze, 1975

Tethysia cf. *bathonica* Sheppard in Brand, 1990 (Fig. 9(Z–AB))

Tethysia sp. (Fig. 9(AC–AE))

Subfamily CYTHEROPTERINAE Hanai, 1957

Genus *Pedicythere* Eager, 1965

Pedicythere? sp. (Fig. 9(AF))

Order PLATYCOPIDA Sars, 1866

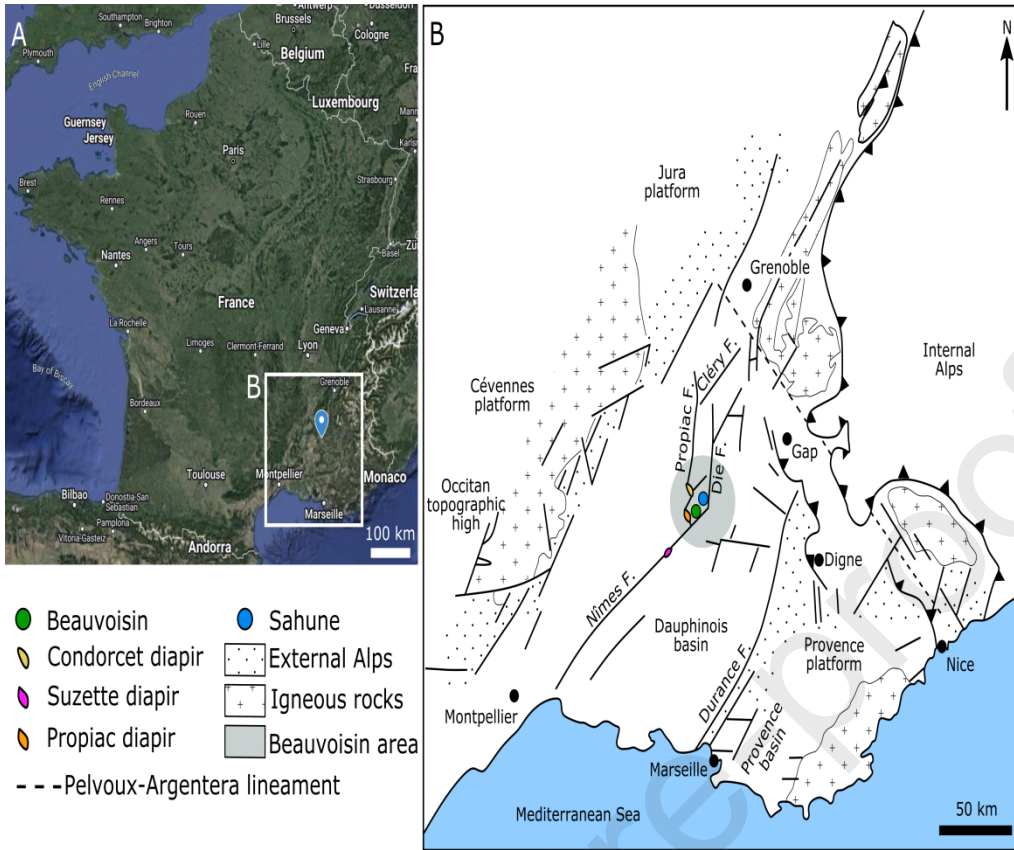
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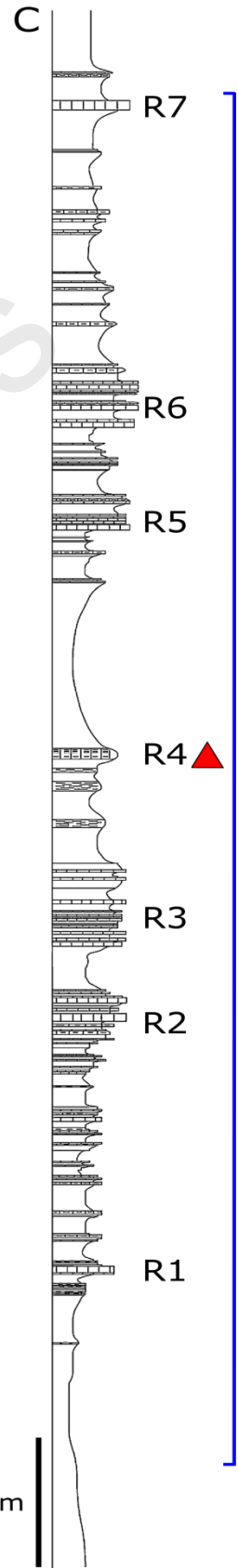
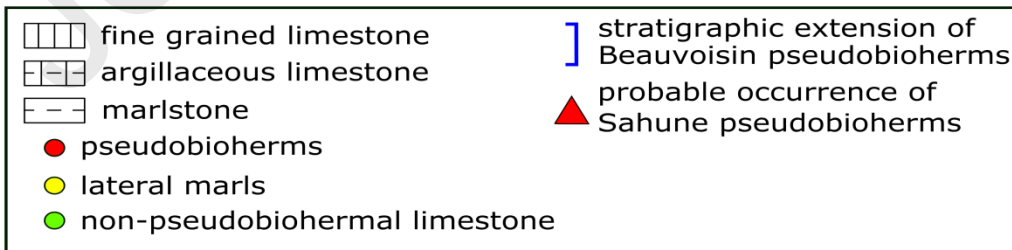
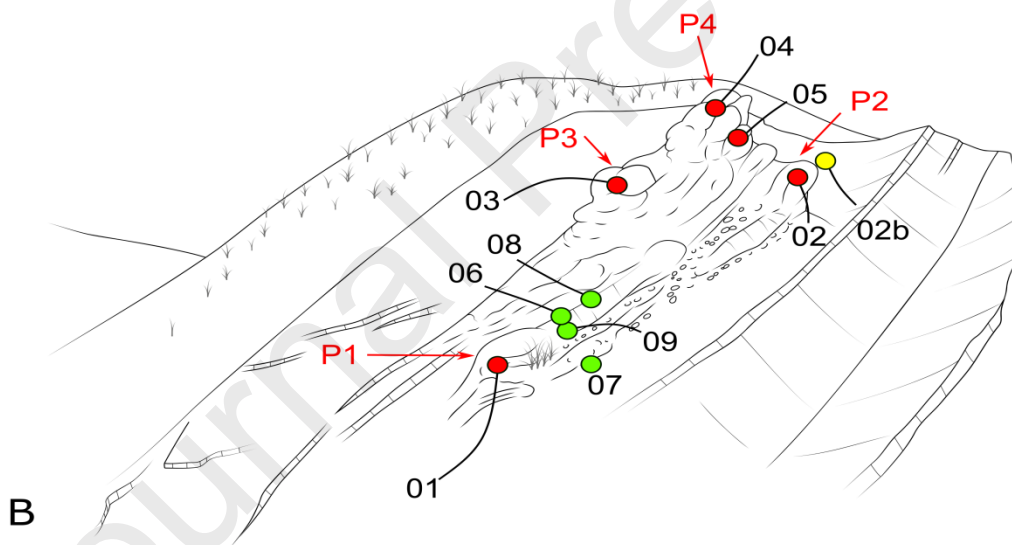
Superfamily CYTHERELLOIDEA Sars, 1866

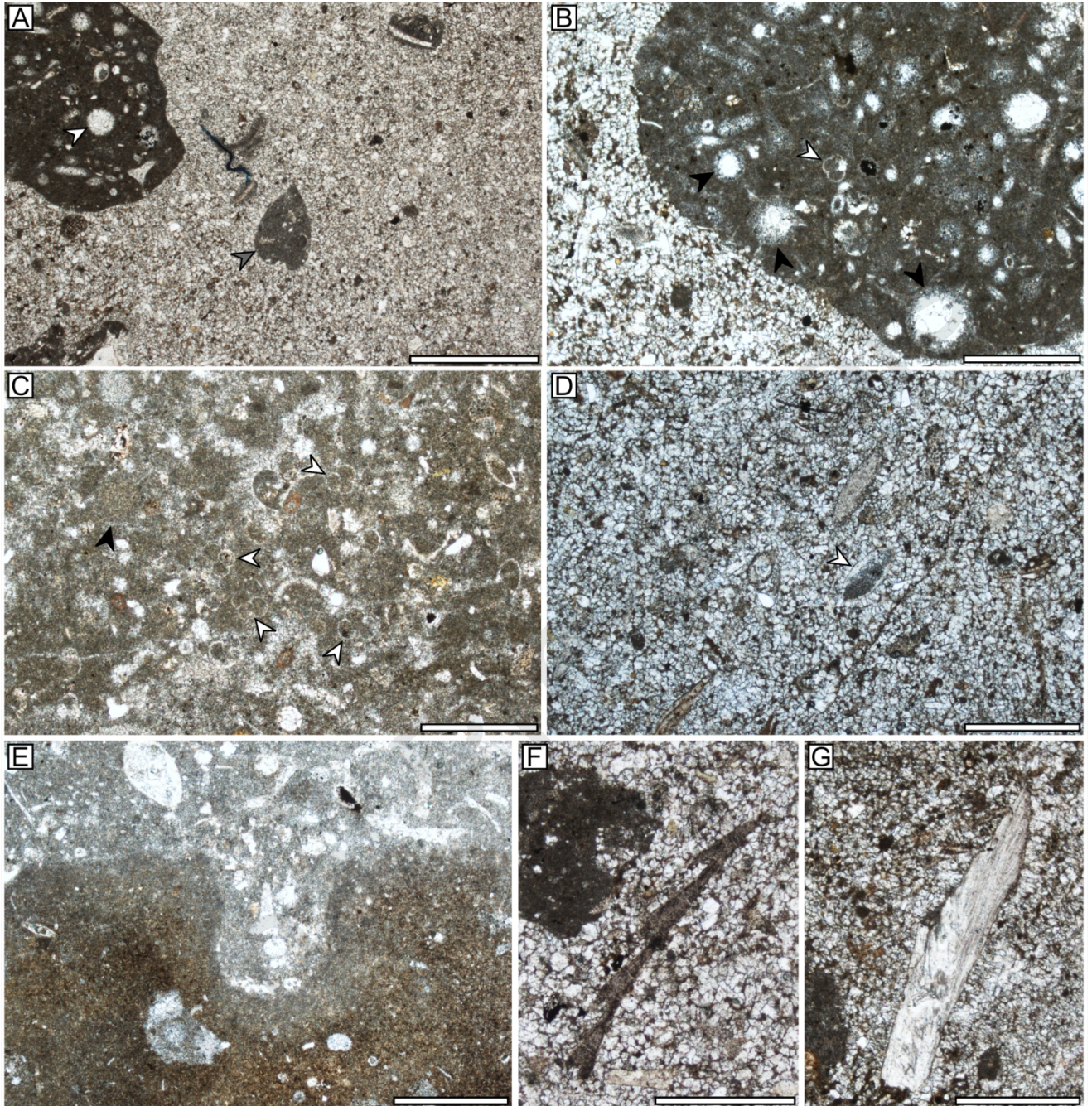
Family CYTHERELLIDAE Sars, 1866

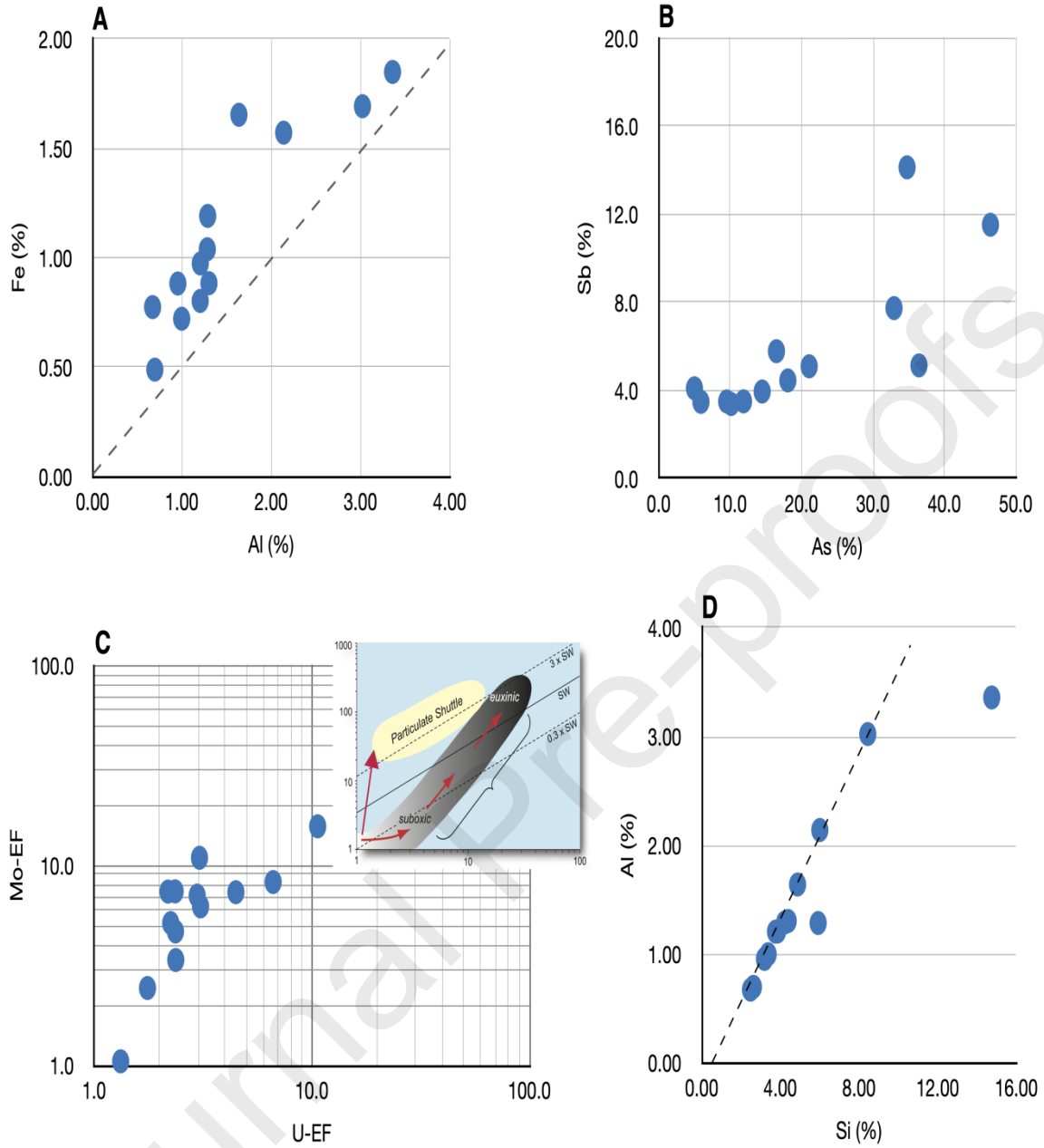
Genus *Cytherella* Jones, 1849

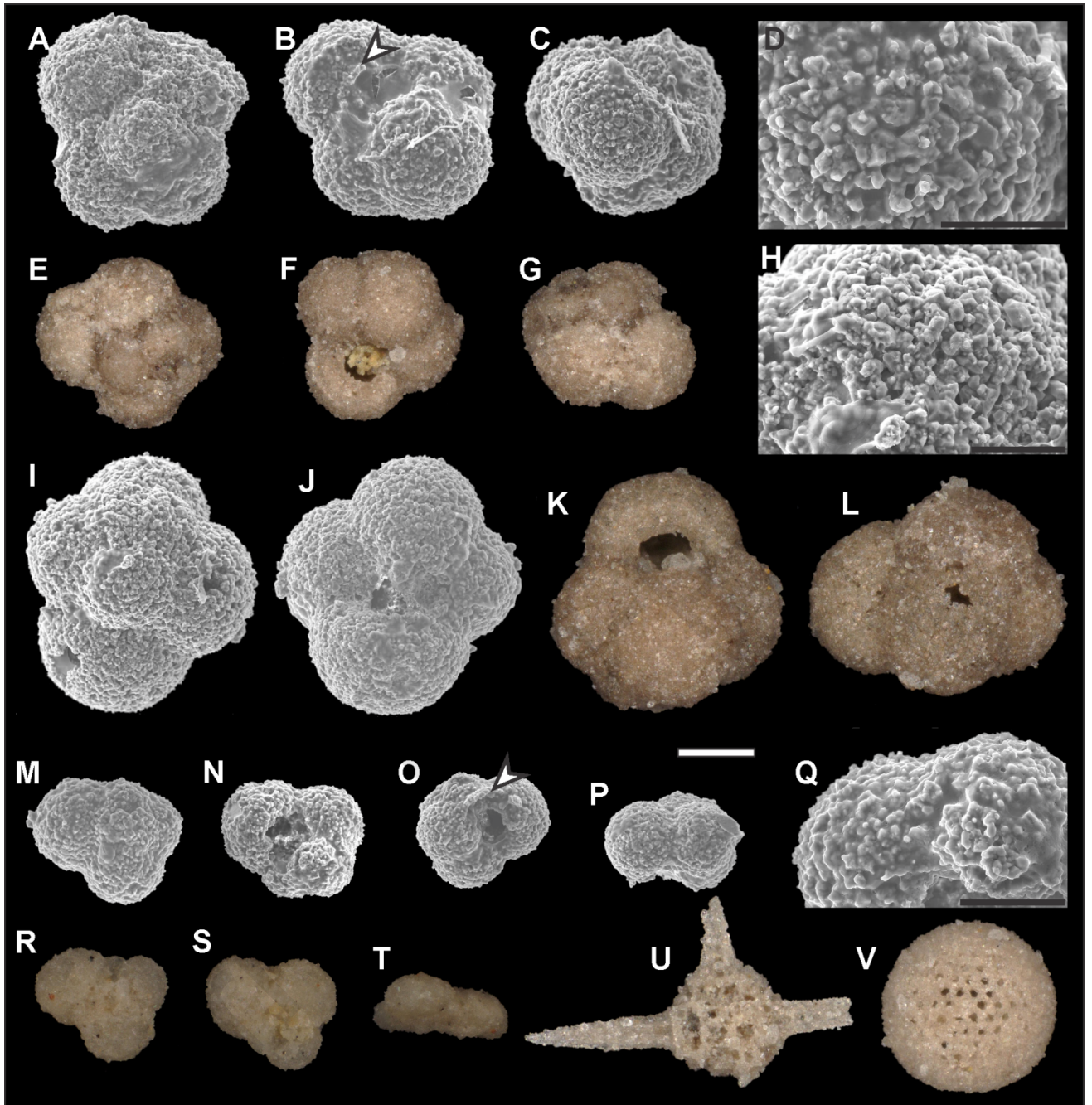
Cytherella sp. (Fig. 9(AG))

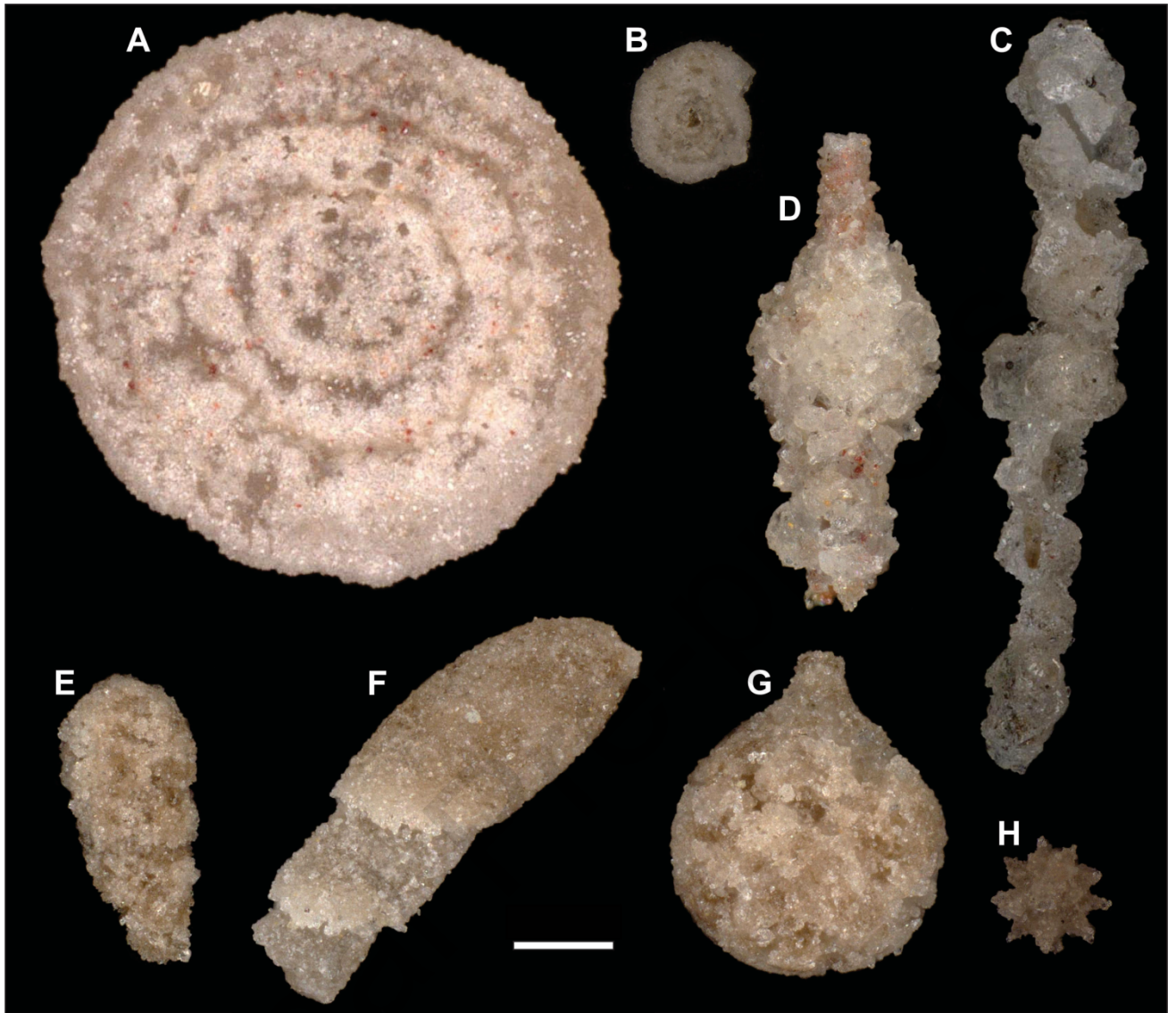


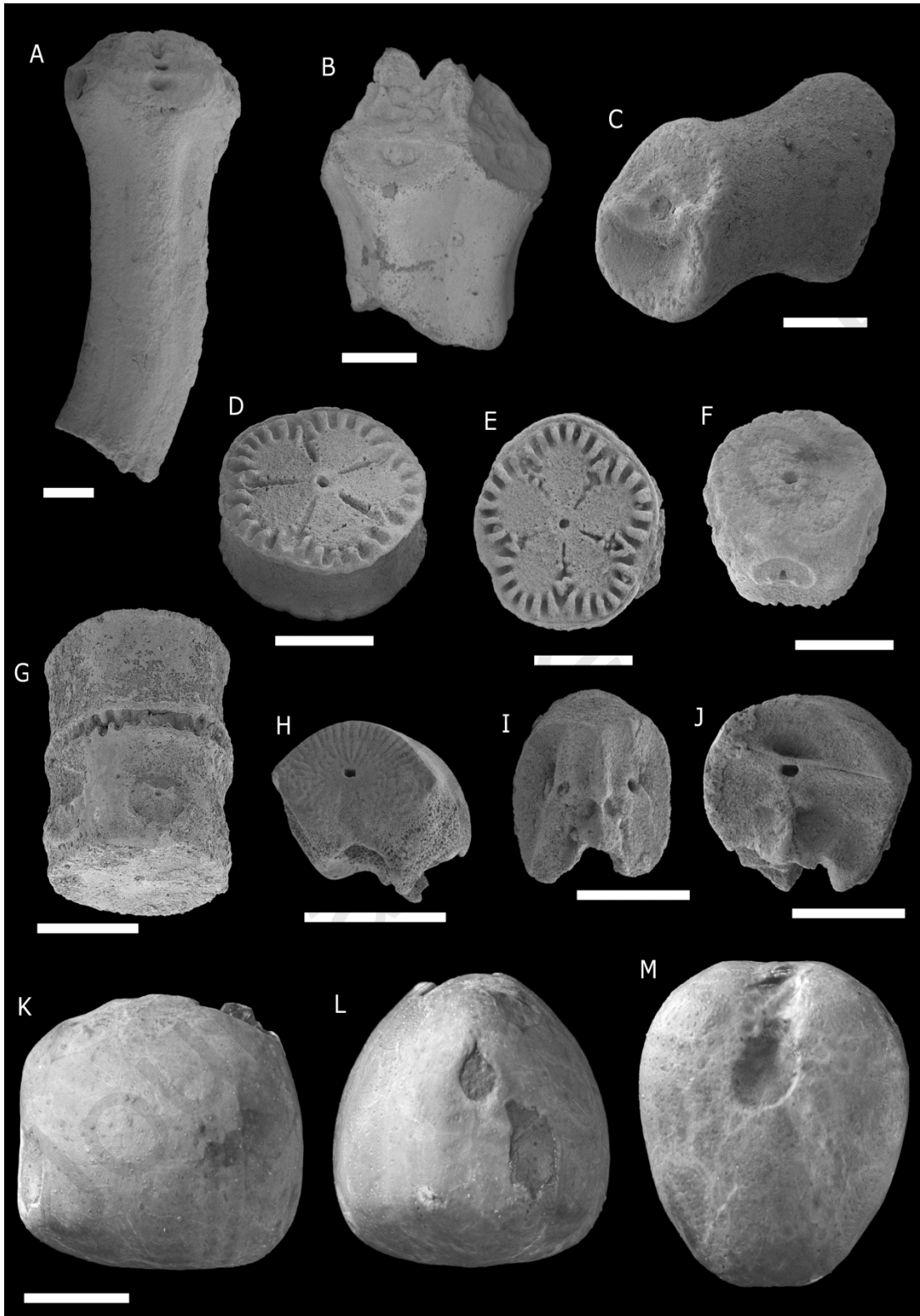


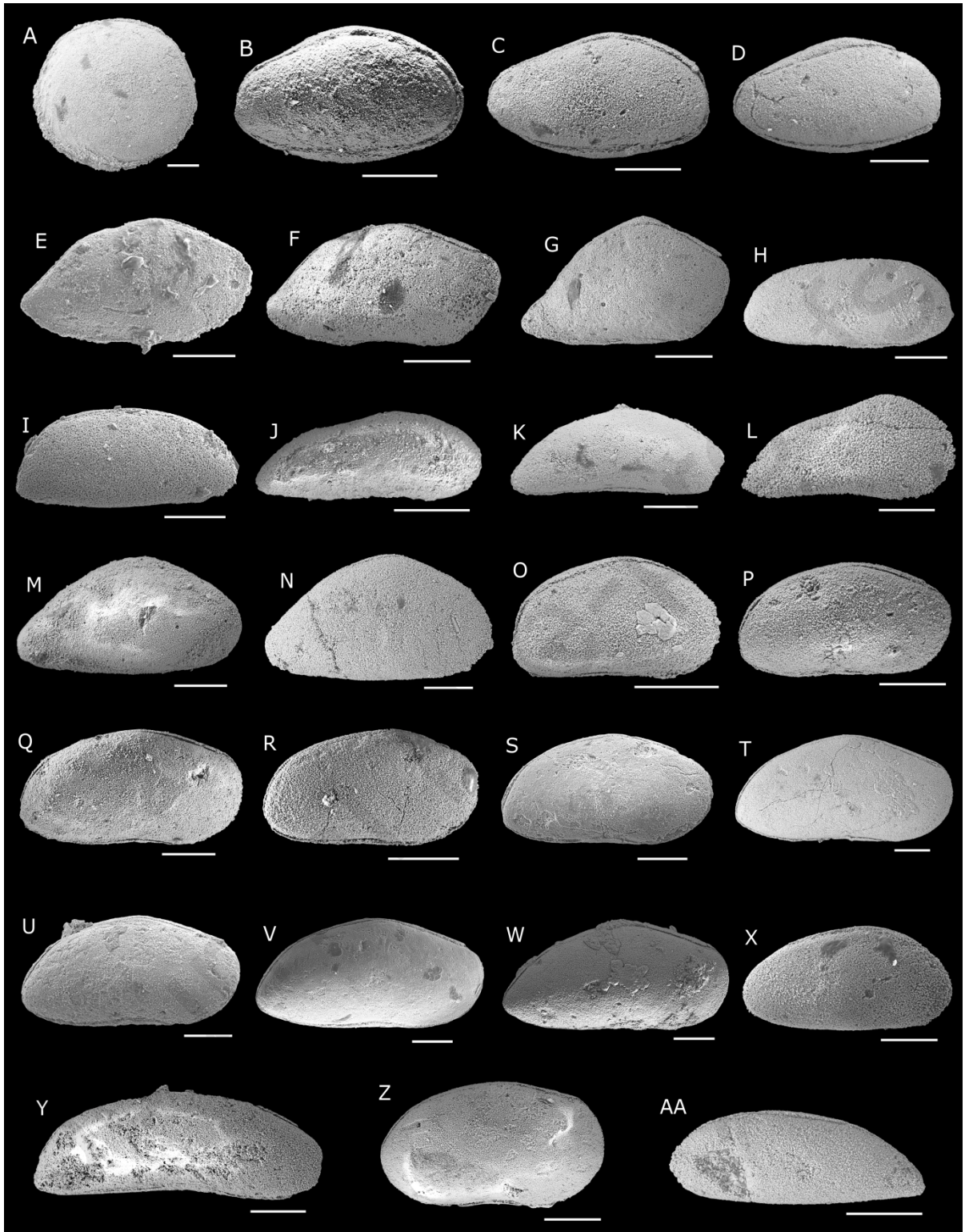


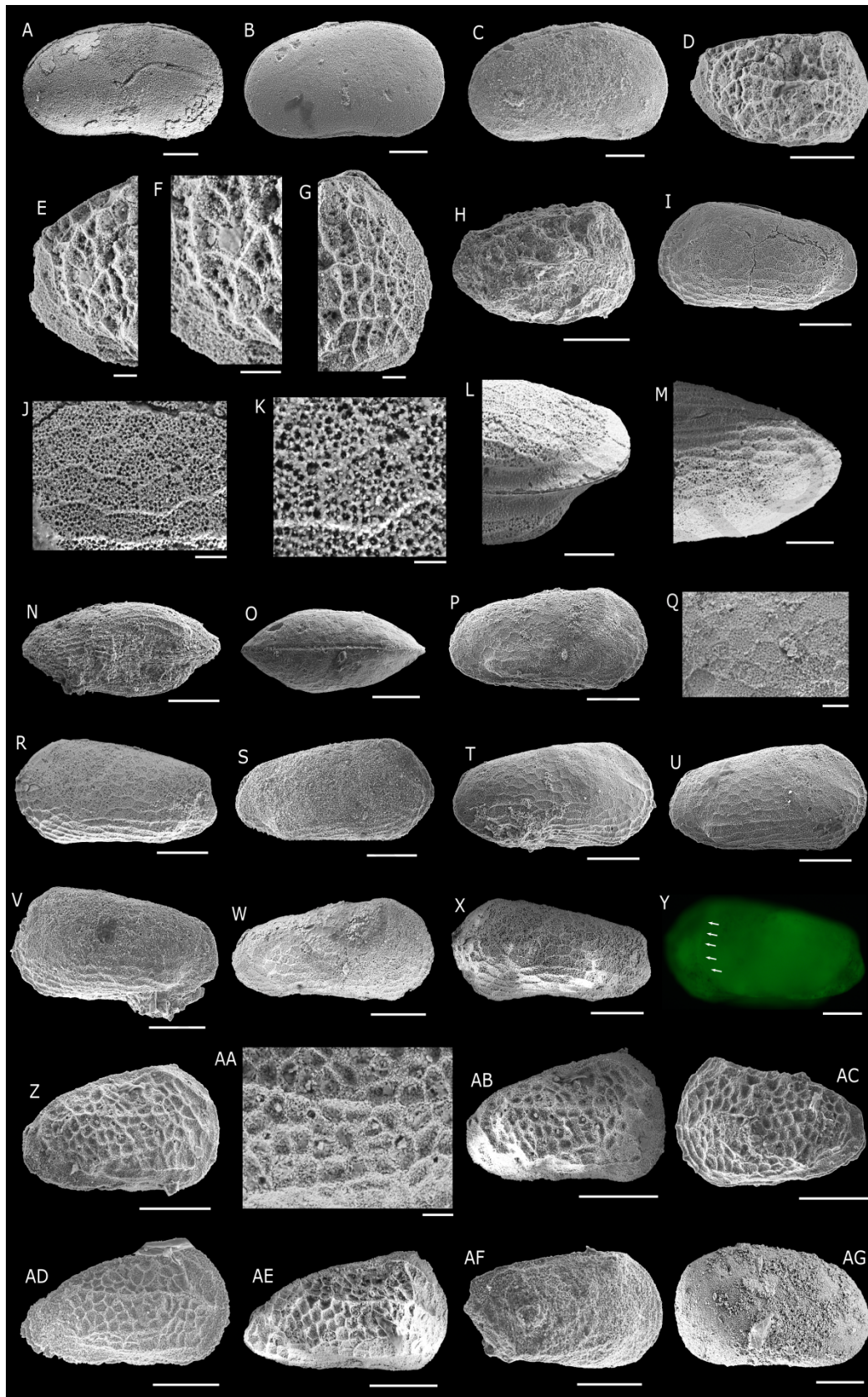




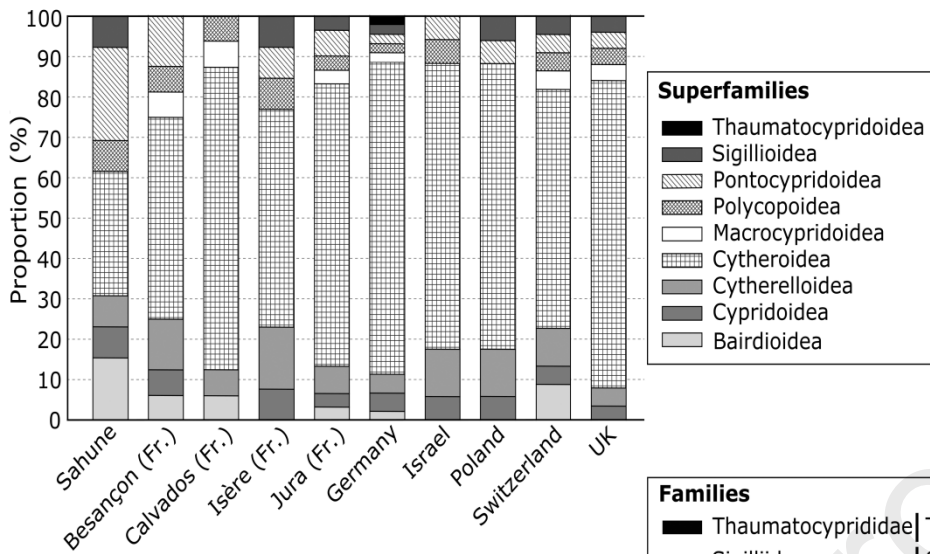




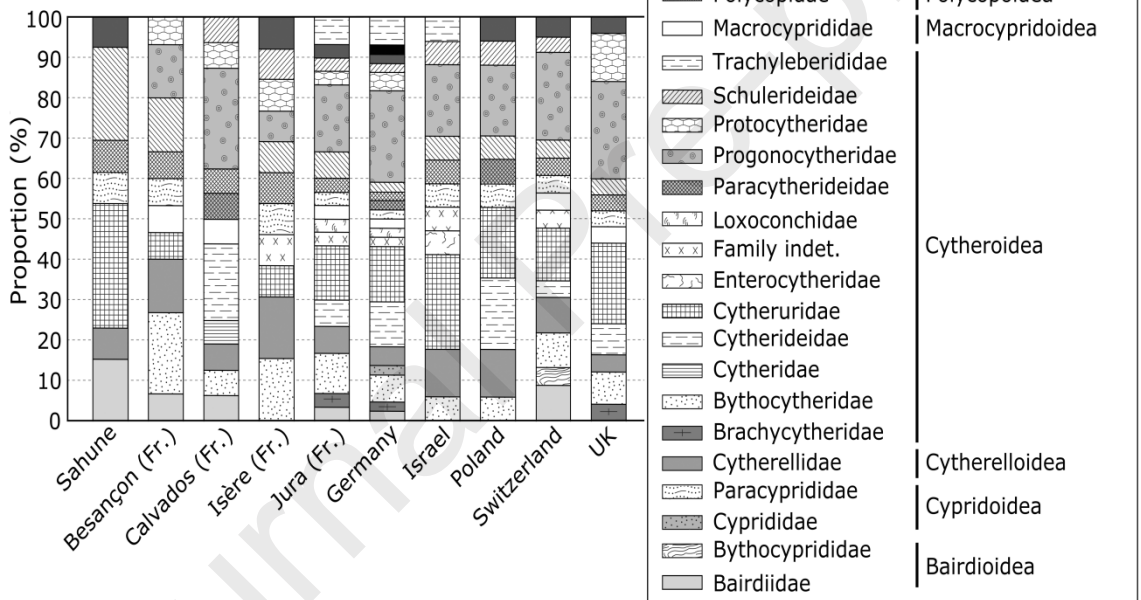




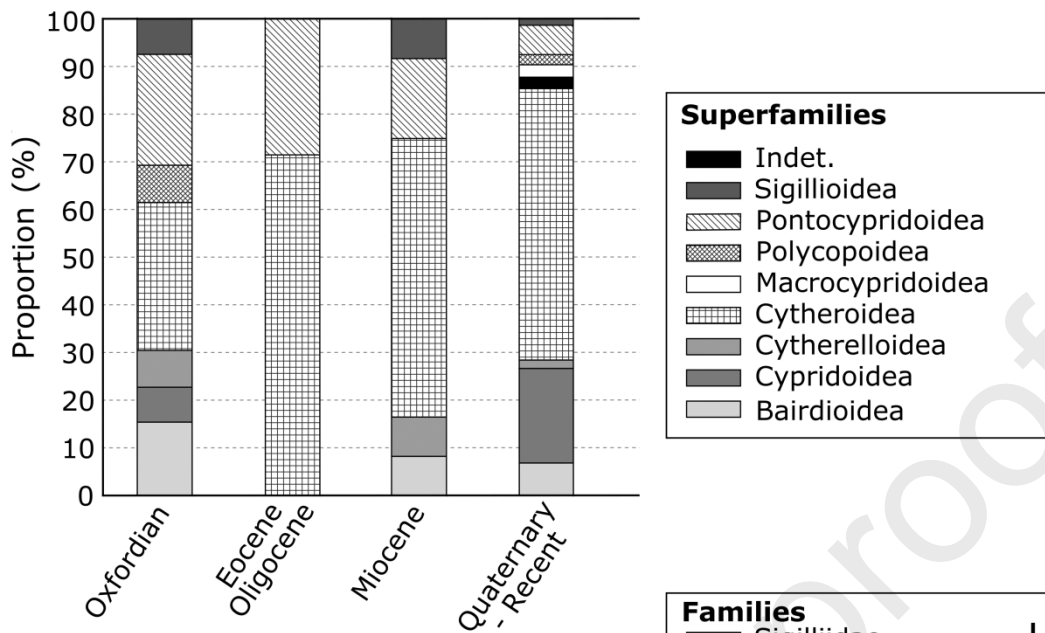
A Genera per superfamily



B Genera per family



A Genera per superfamily



B Genera per family

