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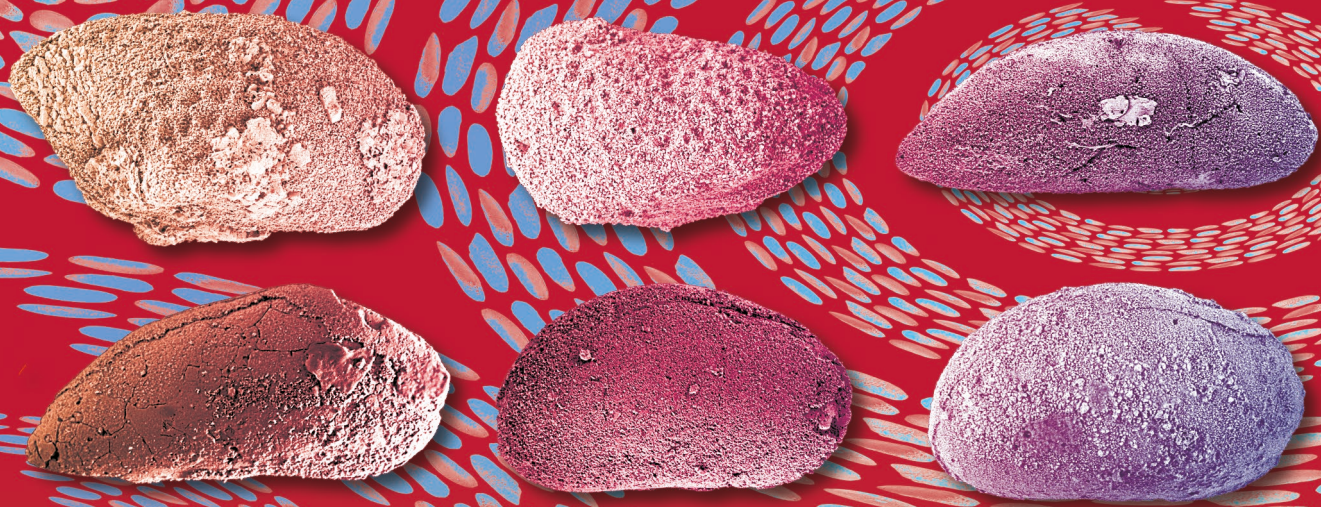

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Ostracod communities through a cold fluid seepage during the Late Jurassic: the Sahune site (Drôme, France)

Marie-Béatrice FOREL
Sylvain CHARBONNIER
Centre de recherche en paléontologie – Paris (UMR 7207, CR2P), CNRS, MNHN, Sorbonne Université, Département Origines et Évolution, Muséum national d'Histoire naturelle, case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
marie-beatrice.forel@mnhn.fr (corresponding author)
sylvain.charbonnier@mnhn.fr

Cristianini Trescastro BERGUE
Centro de Estudos Costeiros, Limnológicos e Marinhos – CECLIMAR, Departamento Interdisciplinar, Universidade Federal do Rio Grande do Sul, Avenida Tramandaí, 976, 95625-000 Imbé, RS (Brazil)
ctbergue@gmail.com

Christian GAILLARD
Université Claude Bernard Lyon 1, Lyon (France)
crisdom.gaillard@orange.fr

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ABSTRACT
The oldest known ostracods from a chemosynthetic community at a cold seep were recently described from an authigenic carbonate lens enclosed within the Upper Jurassic (middle Oxfordian) Terres Noires Formation at Sahune in the south-eastern France Basin. Here we extend the observations to the entire sequence of fluid seepage at Sahune and compare them to those from marls deposited laterally. We report that ostracods are much more abundant throughout the authigenic deposits than within the enclosing marls. The composition of the assemblages is fairly stable over the period of emission of seep-type fluids, likely pointing to their relatively stable chemical composition. Communities are largely dominated by representatives of Pontocyprididae (e.g., *Pontocyprella* Mandelstam *in* Ljubimova, 1955), which seems to be a deep-sea feature within the south-eastern France Basin at least from the Oxfordian to the Early Cretaceous. We suggest that the observed abundance of ostracods within seep deposits, and particularly of pontocyprids, may be related to cold seep fluids and associated complex ecosystems. This complete analysis shows the persistent low diversity and distinct taxonomic composition of Sahune communities compared to contemporaneous plat-

KEY WORDS
Oxfordian,
Ostracoda,
south-eastern France Basin,
Deep-sea,
sequence of fluid seepage,
extreme environments.

form and deep-water communities. For instance, the Cytheroidea *Procytherura*? *praecoquum* Forel *in* Forel, Charbonnier, Gale, Tribovillard, Martinez-Soares, Bergue, Gradstein & Gaillard, 2024 seems to have been adapted and endemic to the active centre of fluid emission, being absent from lateral marly sediments. Well-preserved specimens display morphological characters that were not visible at the time of species description, including fossae arrangement and distribution pattern of normal pores, which are described as a first step toward the clarification of the phylogeny and adaptation of Cytheroidea endemic to cold seeps. Within the limits of the preservation of the material, the valves of this species may display genuine pore clusters and more material may lead to the conclusion that it should be re-attributed to an environment-specific new genus.

RÉSUMÉ

Communautés d'ostracodes au cours de suintements de fluides au Jurassique supérieur : le site de Sahune (Drôme, France).

Les ostracodes les plus anciens connus d'une communauté chimiosynthétique associée à des suintements froids ont été récemment décrits à partir d'une lentille de carbonate authigène contenue dans la Formation des Terres Noires du Jurassique supérieur (Oxfordien moyen) à Sahune dans le bassin sud-est de la France. Nous étendons ici les observations à l'ensemble de la séquence de suintement de fluides à Sahune et les comparons à celles des marnes déposées latéralement. Nous rapportons que les ostracodes sont beaucoup plus abondants dans les dépôts authigènes que dans les marnes encaissantes. La composition des associations est assez stable pendant la période d'émission de fluides, ce qui indique probablement leur composition chimique relativement stable. Les communautés sont largement dominées par des représentants des Pontocyprididae (ex., *Pontocyprella* Mandelstam *in* Ljubimova, 1955), ce qui semble être une caractéristique des eaux profondes du bassin du sud-est de la France, au moins de l'Oxfordien au Crétacé inférieur. Nous suggérons que l'abondance observée d'ostracodes dans les dépôts de suintement, et en particulier des pontocyprides, pourrait plutôt être liée aux fluides de suintements froids et aux complexes écosystèmes associés. Cette analyse complète montre la faible diversité et la composition taxinomique distincte des communautés de Sahune par rapport aux communautés contemporaines des plates-formes et d'eaux profondes. Par exemple, le Cytheroidea *Procytherura*? *praecoquum* Forel *in* Forel, Charbonnier, Gale, Tribovillard, Martinez-Soares, Bergue, Gradstein & Gaillard, 2024 semble avoir été adapté et endémique au centre actif d'émission de fluide, étant absent des sédiments marneux latéraux. Des spécimens bien conservés présentent des caractères morphologiques qui n'étaient pas visibles au moment de la description de l'espèce, notamment la disposition des fossae et la distribution des pores normaux, qui sont décrits comme une première étape vers la clarification de la phylogénie et l'adaptation des Cytheroidea endémiques aux suintements froids. Dans les limites de la préservation du matériel, les valves de cette espèce pourraient posséder de véritables agrégats de pores et davantage de matériel pourrait conduire à la conclusion qu'elle devrait être réattribuée à un nouveau genre, spécifique à ces environnements.

MOTS CLÉS
Oxfordien,
Ostracoda,
bassin du sud-est
de la France,
milieu marin profond,
séquence de suintements
de fluides,
environnements
extrêmes.

INTRODUCTION

Ostracods (Crustacea Brünnich, 1772, Ostracoda Latreille, 1802) inhabit all types of water bodies, including environments from hydrothermal vents, cold hydrocarbon seeps, and wood falls (e.g., Maddocks & Steineck 1987; Steineck *et al.* 1990; Kornicker 1991; Van Harten 1993; Maddocks 2005; Kornicker & Harrison-Nelson 2006; Karanovic & Brandão 2015; Tanaka & Yasuhara 2016). However, ostracods from modern chemosynthetic communities associated with cold seeps have only been seldom reported, namely from Black Sea (Schornikov & 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), São Paulo Plateau and Rio Grande Rise offshore Brazil (Bergue *et al.* 2023). Fundamental questions remain regarding the structure of their taxonomic diversity, their ecological role in these communities and their adaptations to extreme conditions. The evolutionary history of cold seep ostracods is also largely unknown as fossil counterparts have mainly been documented from few Cenozoic deposits, namely from the Eocene-Oligocene of United States (Yamaguchi *et al.* 2016), the Miocene of Italy (Russo *et al.* 2012) and the Quaternary of Ireland (Coles *et al.* 1996) and Svalbard, Norway (Chu *et al.* 2023). Their oldest occurrence in such environments was recently reported in the Late Jurassic, middle Oxfordian, by the description of the entire community (ostracods, radiolarians, benthic and planktonic foraminifers, echinoids, crinoids, comatulids) of a seep-related limestone at the base of the Sahune site in south-eastern France Basin (Forel *et al.* 2024). Here we extend these preliminary observations to the entire sedimentary sequence affected by fluid seepage at Sahune, composed of four successive seep-related limestone masses hereafter termed pseudobioherms, and marls

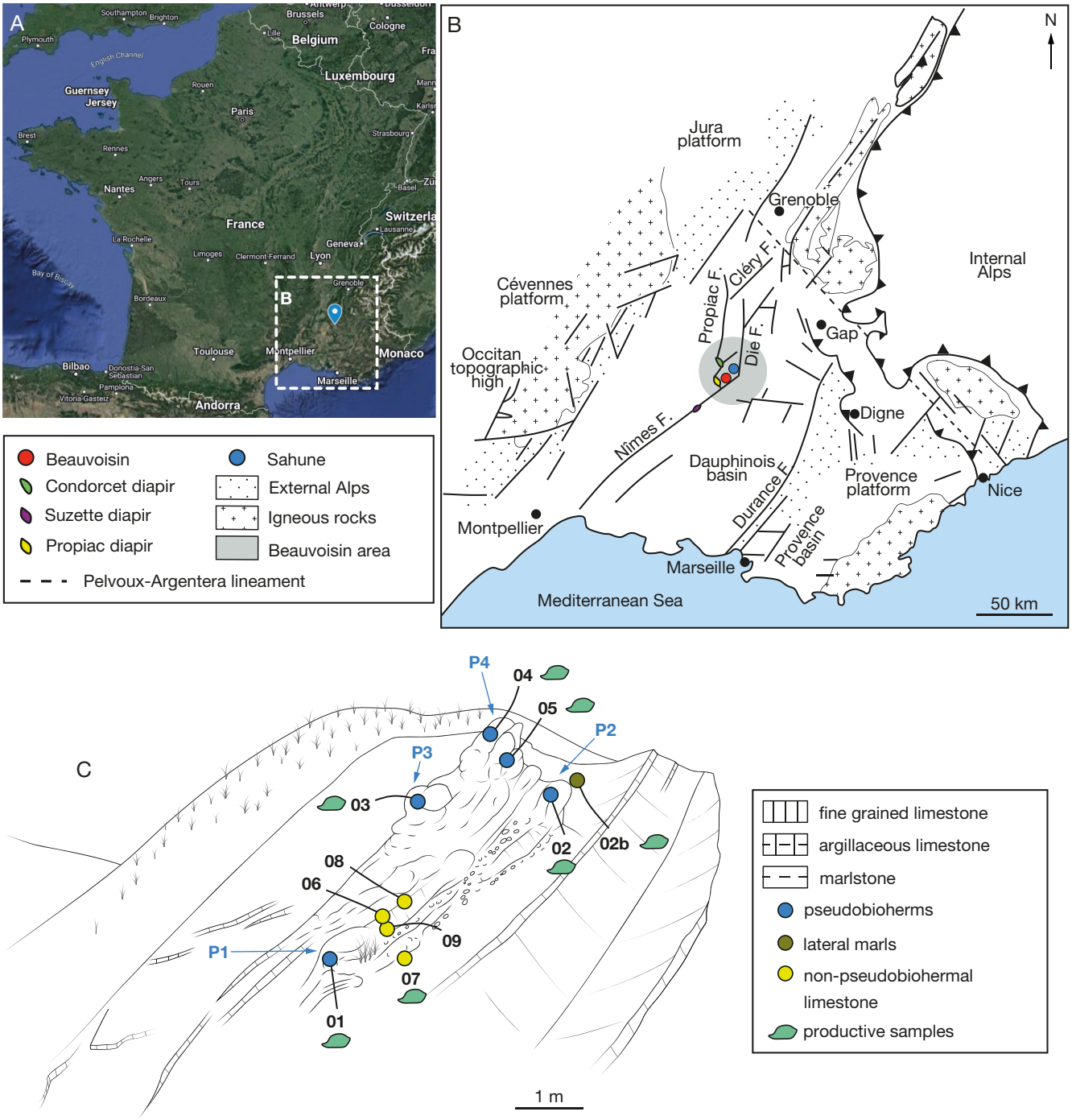


FIG. 1. — **A**, Geographical map of France showing Sahune locality in Drôme, south-eastern France Basin (Google Maps, 2023); **B**, simplified structural map of the south-eastern France Basin with the location of Sahune in the Natural Regional Park of Baronnies provençales (modified from Tribovillard *et al.* 2013). Circle represents Beauvoisin area; abbreviation: **F**, fault; **C**, interpretative scheme of the Sahune sequence (modified from Forel *et al.* 2024). P1-P4, pseudobioherms; numbers: **01**-**09**, studied samples, labelled 08SAH (collected in 2008, studied in Forel *et al.* 2024) and 22SAH (sampled in 2022, newly studied here). Samples 22SAH10 to 22SAH13, of which only 22SAH12 produced unidentifiable specimens, were collected from the opposite side of the main sequence, they are not shown on the present sketch.

deposited laterally. The present analysis provides insights into ostracod assemblages over the whole period of seep fluid circulation and spatially when compared with lateral marls. The discovery of well-preserved specimens of *Procytherura*? *praecoquum* Forel *in* Forel, Charbonnier, Gale, Tribovillard, Martinez-Soares, Bergue, Gradstein & Gaillard, 2024 allows the thorough re-description of its morphological features and possible pore-clusters. Because this species may turn out to represent an environment-specific new genus, we here consider its attribution to *Procytherura* Whatley, 1970 as uncertain. A particular attention is paid to the reticular pattern of its lateral surface, with the aim of laying the foundation for the future understanding the phylogeny of Cytheroidea Baird, 1850 from cold seeps.

GEOLOGICAL CONTEXT

The Sahune site is located within the south-eastern France Basin, the history of which is linked to the opening of the Liguro-Tethyan Ocean during the Jurassic (Lemoine 1985; Fig. 1A). Following the Early to Middle Jurassic (Hettangian to Bathonian), characterized by low subsidence and deposition of shallow-water carbonate platform, the Bathonian to Oxfordian interval (Middle to Late Jurassic) recorded the maximum of subsidence of the deepest, central part of the basin, due to basement faults controlled by the withdrawal of salt in the extensional domain of the margin (Mascle *et al.* 1988). It led to the deposition of a 2000 to 2500 m thick marly series, the Terres Noires Formation (Bathonian-Oxfordian; Fig. 1B), which encloses fossiliferous calcareous masses contrasting with the surrounding fossil-poor deposits. Their origin was long debated, with hypotheses ranging from sponge bioherms (Artru & Gauthier 1966; Artru 1972) to hydrothermal activity (Bourseau 1977; Macsotay 1980; Lemoine *et al.* 1982). These limestone bodies, termed pseudobioherms, have finally been related to a context of passive margin with synsedimentary faults affecting the Terres Noires Formation allowing the upward migration of fluids to the sea bottom (Gaillard *et al.* 1985; Gaillard & Rolin 1986, 1988). This circulation of seep-type fluids locally induced the formation of authigenic limestone and sustained an ecosystem relying on bacterial chemosynthesis.

The Sahune site is located in the Drôme department, Auvergne-Rhône-Alpes region (44°24'28.188"N, 5°16'51.96"E; Fig. 1A, B), in the northern part of the south-eastern France Basin. It is exposed on the northern flank of a hill about 1.4 km from the Sahune village and 12 km north-east from the well-known Beauvoisin site, today considered as a giant pockmark (Gay *et al.* 2018, 2020). The Sahune sequence was described in Forel *et al.* (2024): it is composed of four imbricated meter-scale, seep-related pseudobioherms labelled P1 to P4, enclosed within the Terres Noires deposits (Fig. 1C). Another pseudobioherm and a semi-consolidate nodular limestone likely related to an aborted emission of fluid occur laterally.

The relation of Sahune pseudobioherms to the circulation of seep fluids was demonstrated by geochemical proxies (Forel *et al.* 2024). Pseudobioherm P1 at the base of the sequence yielded a rich and diverse community composed of abundant ostracods together with benthic and planktonic foraminifers, radiolarians, crinoids, echinoids and comatulids. The analysis of the P1 community indicates that the fluid seepage occurred at bathyal depth. The occurrence of the irregular echinoid *Tithonia oxfordiana* Gaillard, Néraudeau & Thierry, 2011 clarified that Sahune site is coeval to the R4 key-bed, which is one of the seven key-beds (R1 to R7) recognized for middle Oxfordian deposits of the south-eastern France Basin and its western margin (Gaillard *et al.* 1996, 2004). The planktonic foraminiferal assemblage containing *Globuligerina oxfordiana* (Grigelis, 1958), *Globuligerina bathoniana* (Pazdrowa, 1969) and '*Globuligerina*' *balakhmatovae* (Morozova *in* Morozova & Moskalenko, 1961) is in line with the Oxfordian age (Forel *et al.* 2024).

MATERIAL AND METHODS

Ten samples were collected from the main sequence at Sahune, labelled 22SAH01 to 22SAH09 (Fig. 1C):

Five samples from the four pseudobioherms P1 to P4: 22SAH01 (= 08SAH01 collected at the same position in 2008 and studied in Forel *et al.* 2024; P1), 22SAH02 (P2), 22SAH03 (P3), 22SAH04 and 22SAH05 (P4).

One sample from marls deposited laterally to P2: 22SAH02b (hereafter noted LM).

Four samples from bedded non-pseudobiohermal limestone: 22SAH06 to 22SAH09.

Four additional samples were collected from the opposite side of the main sequence, from the nodular pseudobioherm bed (22SAH10), underlying marls (22SAH11), likely aborted emission of fluid (22SAH12) and underlying marls (22SAH13).

About 700 g of sediment of each of the 14 studied samples were processed by hot acetolysis technique (Bourdon 1962; Lethiers & Crasquin-Soleau 1988) for ostracod extraction. All residues were sieved through a 0.63 mm mesh, oven dried, and specimens were picked under a stereomicroscope. Specimens of interest have been gold coated and photographed using the SEM JEOL JCM-600 at the Centre de Recherche en Paléontologie-Paris (CR2P). All ostracod specimens figured here are deposited in the Palaeontology collections of the Muséum national d'Histoire naturelle, Paris (France).

Most species reported here, including those that were not found in Forel *et al.* (2024), are kept in open nomenclature because of their rarity and/or overall poor preservation. Only the five newly found species are illustrated (Fig. 2A-F) as well as specimens of *Procytherura*? *praecoquum* that are well-preserved enough to allow an in-depth discussion of their characters (Fig. 2G-W). The complete taxonomic list of all Sahune species is provided in Appendix 1; their distribution and abundance through the seep sequence is summarized in Table 1.

RESULTS AND DISCUSSION

Insights into *Procytherura*? *praecoquum*

Procytherura? *praecoquum* was described from P1, it is only known from Sahune and was hypothesized as ecologically restricted to seeps (Forel *et al.* 2024). At the time of its description, only characters of its outer surface were visible, and green UV light permitted the observation of duplicatures and vestibules through slightly translucent valves. Some of the newly obtained specimens are much better preserved and provide further details on the general morphology, surface reticulation, muscle scars and normal pores of *Procytherura*? *praecoquum*. The very likely presence of pore clusters through its valves differs from all *Procytherura* species known so far, and this species may rather represent a new genus, specifically related to peculiar environmental conditions. For this reason, we choose to consider the generic attribution of this species as uncertain, noted here as *Procytherura*? *praecoquum.*

TABLE 1. — Distribution and abundance of ostracod species (upper part) and summary of the observed richness and diversity (lower part) through the five studied communities at Sahune, Drôme, south-eastern France Basin, Oxfordian, Late Jurassic. Abbreviations: **P1**-**P4**, pseudobiohermal communities; **LM**, lateral marl community. **In bold**, species newly reported in the present work.

Family	Species	P1	P2	LM	P3	P4
Polycopidae	*Polycope pelta* Fischer, 1961	15	4	–	3	2
Sigilliidae	*Cardobairdia* cf. *argoviensis* Oertli, 1959	15	1	–	1	1
Bairdiidae	'*Bairdia*'? sp. 1	15	–	2	1	1
Bairdiidae	'*Bairdia*' cf. *major* Donze, 1964	8	1	–	2	2
Bairdiidae	*Isobythocypris*? sp. 1	5	1	1	1	–
Bairdiidae	*Isobythocypris*? sp. 2	1	–	–	–	1
Paracyprididae	***Paracypris* cf. *acuta* (Cornuel, 1848)**	1	–	–	–	–
Paracyprididae	*Paracypris* cf. *siliqua* Jones & Hinde, 1890	2	–	–	–	3
Paracyprididae	*Paracypris* cf. *stripta* Ljubimova, 1956	8	1	–	2	2
Paracyprididae	*Paracypris*? sp. 1	2	–	1	–	–
Paracyprididae	*Paracypris*? sp. 2	1	–	–	–	–
Paracyprididae	***Paracypris*? sp. 3**	1	1	–	–	–
Pontocyprididae	*Pontocyprella vescusa* Ljubimova, 1956 *in* Tesakova, 2003	7	–	–	–	–
Pontocyprididae	***Pontocyprella* cf. *cavata* Donze, 1967**	1	2	3	–	–
Pontocyprididae	*Pontocyprella* cf. *rara* Kaye, 1965a	107	7	6	13	14
Pontocyprididae	*Pontocyprella* sp. 1	1	–	–	–	–
Pontocyprididae	*Pontocyprella* sp. 2	7	2	–	2	1
Pontocyprididae	*Pseudomacrocypris* sp.	3	–	–	–	–
Pontocyprididae	*Rectangulocyprella* cf. *semiquadrata* (Kaye, 1965b)	42	2	2	1	9
Cytheruridae	*Eucytherura* sp.	2	–	–	3	–
Cytheruridae	***Eucytherura* sp. 2**	2	–	–	–	–
Cytheruridae	***Cytheropterina* sp.**	1	–	–	–	–
Cytheruridae	*Pedicythere*? sp.	1	–	–	–	–
Cytheruridae	*Procytherura*? *praecoquum* Forel *in* Forel *et al.*, 2024	75	2	–	4	11
Cytheruridae	*Tethysia* cf. *bathonica* Sheppard *in* Brand, 1990	4	–	–	–	–
Cytheruridae	*Tethysia* sp. 1	7	–	–	2	–
Cytherellidae	*Cytherella* sp.	1	–	–	–	–
Observed richness and diversity	Number of specimens	335	24	15	35	47
	Number of species	27	11	6	12	11
	Number of genera	14	8	5	10	8
	Number of families	7	6	3	6	6

CARAPACE MORPHOLOGY

Two well-preserved carapaces retrieved from P3 provide thorough insights into their free margin, that was not visible with such fine details on the previous specimens. The anterior and posterior margins are bordered by thin bevelled flanges (Fig. 2G, I, O, S). The posterior flange extends ventrally within the oral concavity in front of mid-length, while the anterior one is shorter and does not develop within the oral concavity. The anterior and posterior flanges of both valves are parallel and closely set together into a sort of narrow funnel when the valves are closed (Fig. 2I, S). The surface of the anterior flange appears serrate in lateral view (Fig. 2G, I, S).

MUSCLE SCARS

In the new material as in Forel *et al.* (2024), no isolated valve was found and most specimens are recrystallized carapaces or steinkerns, precluding the observation of their inner structures. However, the outer surface of the right valve of the two carapaces from P3 displays adductor muscle scars (AMS; Fig. 2G, H, J). The AMS are located close to mid-length and below mid-height, just below the sulcus (Fig. 2G, H). They are composed of four elongate, ovoid individual scars oriented postero-ventrally, tightly packed into an oblique row oriented antero-ventrally (Fig. 2H, J). This pattern is in line with the original description of the AMS of *Procytherura* provided by Whatley (1970) and emended by Bate & Coleman (1975). However, the heart-shape frontal scar located antero-dorsally to the adductor row of *Procytherura* is not visible on the outer surface of the Sahune specimens. This may indicate that the associated muscle was weaker than the others and may have left a fainter mark on the outer lateral surface.

ORNAMENTATION

The lateral surface of *Procytherura*? *praecoquum* is characterized by a large and shallow polygonal, mostly hexagonal reticulation that fades in the antero-median and antero-dorsal areas and turns into fine longitudinal ribs ventrally (Forel *et al.* 2024). The reticulation of most specimens originally studied was partly eroded, which limited observations. The better-preserved specimens recovered here allow the description of fossae arrangement and the identification of homologous fossae. As a comparison, the pattern seen on the holotype (see Forel *et al.* 2024: Fig. 9U) is reproduced as a line drawing in Figure 2T.

One carapace from P3 displays a nearly complete reticular pattern, the only missing part corresponding to its broken posterior end (Fig. 2G, I). On its dorsal and median surfaces, fossae are hexagonal (Fig. 2K) and organized in sinuate rows. They turn to sub-rectangular to rectangular ventrally below the AMS where they are organized in elongate, sub-straight rows. Overall, 120 fossae are seen on the lateral and ventral surfaces of the right valve of this carapace (Fig. 2G-I, N).

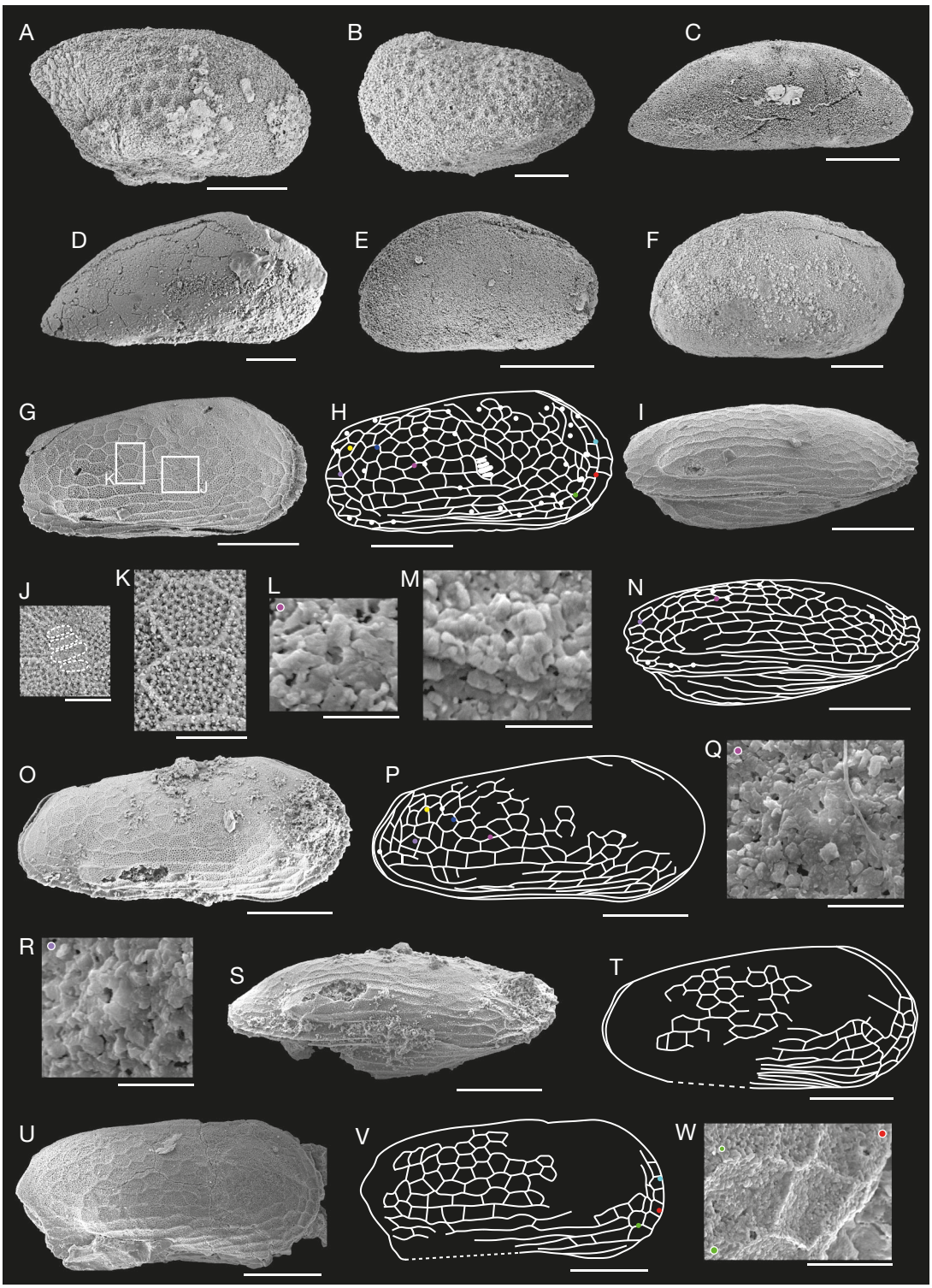
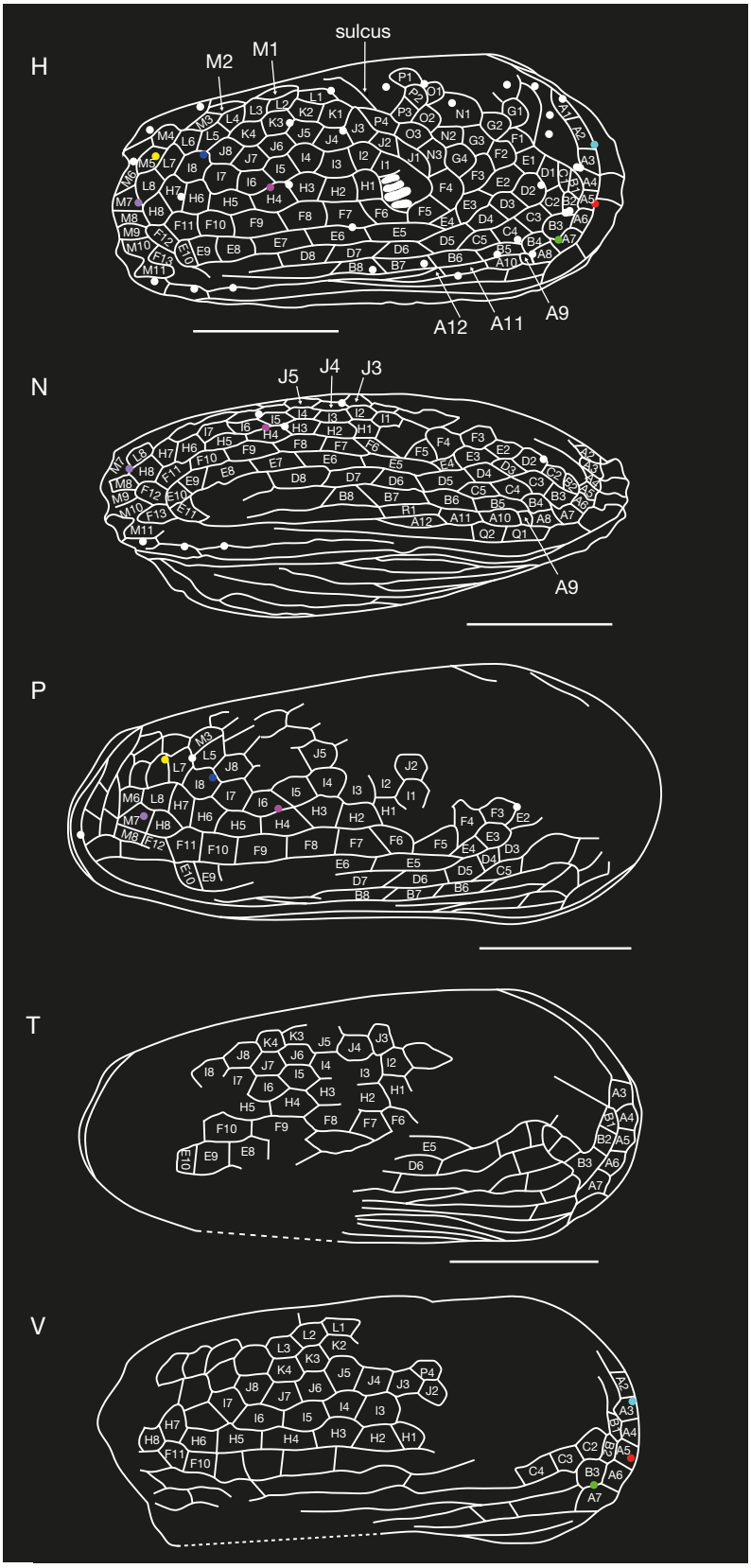


Fig. 2. — Ostracods from the deposits at Sahune, Drôme, south-eastern France Basin, middle Oxfordian, Late Jurassic: **A**, *Cytheropterina* sp., right view of a complete carapace, sample 22SAH01 (MNHN.F.F73027); **B**, *Eucytherura* sp. 2, left view of a complete carapace, sample 22SAH01 (MNHN.F.F73028); **C**, *Paracypris* cf. *acuta* (Cornuel, 1848), right view of a complete carapace, sample 22SAH01 (MNHN.F.F73029); **D**, *Paracypris*? sp. 3, right view of a complete carapace, sample 22SAH02 (MNHN.F.F73030); **E**, **F**, *Pontocyprella* cf. *cavata* Donze, 1967; **E**, right view of a complete carapace, sample 22SAH02 (MNHN.F.F73031); **F**, right view of a complete carapace, sample 22SAH02 (MNHN.F.F73032); **G**-**W**, *Procytherura*? *praecoquum* Forel *in* Forel, Charbonnier, Gale, Tribovillard, Martinez-Soares, Bergue, Gradstein & Gaillard, 2024; **G**, right view of a complete carapace broken posteriorly, sample 22SAH03 (MNHN.F.F73033); **H**, sketch of the same specimen showing fossae arrangement and normal pores; **I**, same specimen in sub-ventral view; **J**, close-up on AMS; **K**, close-up on fossae I4 and H3; **L**, close-up on mural pore conuli associated with muri between fossae H4 and I6; **M**, close-up on mural pore conuli associated with muri between fossae F7 and E6; **N**, sketch of the same specimen in sub-ventral showing fossae arrangement and normal pores; **O**, right view of a complete carapace, sample 22SAH03 (MNHN.F.F73034); **P**, sketch of the same specimen showing fossae arrangement and normal pores; **Q**, close-up on mural pore conuli associated with muri between fossae H4 and I6; **R**, close-up on solar pore conuli associated with fossa M7; **S**, same specimen in sub-ventral view; **T**, sketch of the holotype (see Forel *et al.* 2024: fig. 9U)



showing fossae arrangement; **U**, right view of a complete carapace, sample 22SAH02 (MNHN.F.F73035); **V**, sketch of the same specimen showing fossae arrangement and normal pores; **W**, close-up on solar pore conuli associated with fossa A5 and mural pore conuli associated with muri between fossae A7 and B3. **H**, **L**, **N**, **P**-**R**, **T**, **V**, **W**, white dots indicate the position of normal pores, homologous pores being colour-coded. **H**, **N**, **P**, **T**, **V**, corresponding drawings in larger size. SEM images and line drawings: M.-B. Forel. Scale bars: 100 µm, except L, M, Q, R: 5 µm, J, K: 10 µm, W: 20 µm.

Two other carapaces (P2 and P3; Fig. 2O, P, S, U, V) and the holotype (P1; Fig. 2T) preserve partial fossae arrangements. To build hypotheses of homology, all fossae visible on the best-preserved specimen (Fig. 2G-I, N) have been labelled by the combination of a letter (corresponding to a row) and a number (corresponding to its position in the row) in lateral and sub-ventral views (Fig. 2H and Fig. 2N respectively). Although reticulation fades in front of the sulcus, muri between fossae could still be mapped in most of this area; on the ventral surface, reticulation is mostly absent and replaced by well-developed ridges. The comparison of the four examined right valves illustrates the relative stability of the fossae arrangement on *Procytherura*? *praecoquum* as most visible fossae can be homologized on the studied specimens (Fig. 2H, N, P, T, V). This stability applies to the number and position of fossae, as well as to the shape of most of them. Some fossae are characteristically higher than others on all specimens, such as H7 and L7 (Fig. 2H, N, P, V), while other fossae are significantly bevelled on one side, such as C5 (Fig. 2H, N, P). Among the remarkable features of the lateral surface, the row of fossae A1-A12 borders the anterior flange: the fossae are relatively small, rectangular to sub-rectangular, elongate along the margin curvature and separated by thin and sharp muri corresponding to the flange serrations (Fig. 2H, N, T, V). Another remarkable feature is that of the rows D and E covering the lateral surface of the reduced ventro-lateral expansion: they are composed of elongate sub-rectangular fossae and end with the easily recognizable hemispherical E10 (Fig. 2H, P, T). Overall, the close observation of the lateral surface of these specimens reveals fossae with fairly constant shape and size, with tenuous variations that may relate to ontogeny and/or interspecific variability. The arrangement of fossae on ostracods being correlated with the arrangement of epidermal cells (Okada 1981), their description on *Procytherura*? *praecoquum* could be the first step toward the understanding of the phylogeny of Cytheroidea taxa from cold seeps (e.g., Benson 1972; Liebau 1991).

Normal pores

The valves of ostracods are penetrated by normal pore canals through which setae are connected to nerve cells of the underlying epidermal layer and act as touch receptors, chemoreceptors or mechanoreceptors. Their significance in the taxonomy, systematics and phylogeny of Podocopida Sars, 1866, mostly Cytheroidea, is widely acknowledged (e.g., Sandberg 1964; Puri & Dickau 1969; Hanai 1970; Benson 1972; Puri 1974; Keyser 1980; Tsukagoshi & Ikeya 1987; Ikeya & Tsukagoshi 1988; Tsukagoshi 1990; Danielopol *et al.* 2018; Lord *et al.* 2020). Normal pores on the surface of the type species *Procytherura tenuicostata* Whatley, 1970 were not illustrated but described as few, small, and widely spaced (Whatley 1970). Pores were not seen on the type specimens of *Procytherura*? *praecoquum* and the newly recovered ones allow observation of their characteristics and distribution. Visible pores are most abundant on specimen in Fig. 2G where they are spread all over the lateral (Fig. 2H) and ventral surfaces (Fig. 2N), being more numerous anteriorly. Normal pores observed on *Procytherura*? *praecoquum* are of two types: those emerging through mural pore conuli (Fig. 2L, M, Q, W) and those emerging through solar pore conuli (Fig. 2R, W). They are all of small diameter, ranging from 0.7 to 1.2 µm, not considering conuli margin, and their preservation precludes the observation of possible sieve structures. However, we favour them being simple normal pores rather than small sieve-type pore canals (StPCs) as 1) they would be smaller than micro-StPCs reported from Jurassic and Cretaceous Cytheroidea as ranging *c.* 5-7 µm (Lord *et al.* 2020), and 2) simple normal pores of similar small dimensions have for instance been reported from the Early Cretaceous *Dolocythere amphistiela* Lord, Cabral & Danielopol, 2020.

Several homologous pore systems are tracked on the surface of *Procytherura*? *praecoquum* specimens and are colour-coded in Fig. 2H, L, N, P-R, V, W. Their position is conservative on the surface of the valves, but is slightly variable in relation to fossae, as for instance pores associated with fossae M7 (purple: Fig. 2H, P, R), M5 (yellow: Fig. 2H, P) and A2/A3 (light blue: Fig. 2H, V) that are alternatively solar or mural. The dimensions of the four specimens displaying pores are similar, indicating that they may all roughly correspond to the same ontogenetic stage (Fig. 2G-N: length not measurable, height = 168 µm; Fig. 2O-S: length = 395 µm, height = 169 µm; Fig. 2T, holotype: length = 380 µm, height = 177 µm; Fig. 2U-W: length, incomplete = 395 µm, height = 181 µm). The observed differences in the position of pores in relation to fossae may thus not be related to ontogeny, so that their mural or solar position may be of rather low significance. However, more well-preserved specimens of *Procytherura*? *praecoquum* need to be analysed to confirm these observations and a larger investigation of other *Procytherura* species should be undertaken to unravel generic vs specific patterns.

As for the arrangement of fossae on the lateral surface of ostracods, the number and organization of pores are genetically controlled (Benson 1972) and the evolution of pores and ornament are correlated within a species (Liebau 1978). The present preliminary observations are complementary with those related to fossae arrangement and altogether will be important to unravel the phylogeny of Cytheroidea taxa at cold seeps.

Pore clusters – a comment

Among Sahune species, *Procytherura*? *praecoquum* is of peculiar importance as it may be endemic to seeps and may display the oldest known pore clusters (Forel *et al.* 2024). Pore clusters have been proposed to illustrate relationship with chemosynthetic bacteria (e.g., Van Harten 1993; Maddocks 2005; Karanovic & Brandão 2015; Yasuhara *et al.* 2018; Tanaka *et al.* 2019, 2021) and it is here important to clarify some problematic reports in the literature that may obscure future discussions on their recognition, characteristics and functions.

Pore clusters occupy the solum of reticulate ornament; they lack setae, entirely penetrate the valve thickness and produce clustered perforations on the interior surface (Maddocks &

Steineck 1987). Van Harten (1993) first reported the close association of the external surface of pore clusters of recent specimens of *Xylocythere* Maddocks & Steineck, 1987 with bacteria and proposed that they may represent ectosymbiosis. Spherical structures were later observed within the internal openings of pore clusters of recent *Xylocythere sarrazinae* Tanaka, Lelièvre & Yasuhara, 2019 from hydrothermal vent field on the Juan de Fuca Ridge (Pacific), their shape and size being similar to those of chemosynthetic bacteria engaged in a symbiosis with other invertebrates (see Tanaka *et al.* 2019: fig. 6g). Oviducts with eggs were pressed against the dorsal surface of *Xylocythere vanharteni* Maddocks, 2005 from hydrothermal vent fields on the East Pacific Rise, which is uncommon in Cytheroidea and might accommodate the higher oxygen needs of eggs in relation to pore clusters (Maddocks 2005). Finally, the co-occurrence of *Rosaliella svalbardensis* Yasuhara, Sztybor, Rasmussen, Okahashi, Sato & Tanaka, 2018 with bacterial mats from seepage sites on the Svalbard margin, being otherwise absent from tubeworm field and non-seepage zone, could confirm a close relationship between such taxa with pore-clusters and bacterial populations (Yasuhara *et al.* 2018). *Rosaliella svalbardensis* was proposed as a proxy for past methane release (Chu *et al.* 2023). Work is still needed to further characterize the occurrence of taxa with pore clusters from Pleistocene and Holocene seepage areas on the São Paulo Plateau and Rio Grande Rise as they were reported but not discussed in Bergue & Coimbra (2008; *Xylocythere*, *Microceratina* Swanson, 1980) and not found at any site in Bergue *et al.* (2023). Overall, the hypothesis of pore clusters being related to ectosymbiosis still requires investigations, including histological, physiological, and biochemical evidence, as stated by Tanaka & Yasuhara (2016).

In practice, pore clusters are complex to identify with certainty, and more particularly on fossil specimens. Of special notice, the statement that pore clusters are equivalent to secondary reticulation (see Yasuhara *et al.* 2018: 141, 143) is problematic as reticulation, should it be primary or secondary, does not cross the thickness of the valves and thus does not open directly on the inner surface as pore clusters do. Considering that pore clusters are equivalent to secondary reticulation, Yasuhara *et al.* (2018) noted that they occur on *Cluthia cluthae* (Brady, Crosskey & Robertson, 1874), *Cytheropteron carolinae* Whatley & Coles, 1987 and *Polycope bireticulata* Joy & Clark, 1977 from modern seeps from the western Svalbard margin. However, the secondary reticulation on the solum of the reticulate ornament of the illustrated specimen of *Polycope bireticulata* does not cross the valve thickness (see Yasuhara *et al.* 2018: Fig. 4i). Joy & Clark (1977) similarly did not originally mention, nor illustrate, the secondary reticulation as crossing the valve thickness. In that case, and until further notice, these features are not pore clusters and rather correspond to true secondary reticulation. Similarly, secondary reticulation crossing the valve thickness of *Cytheropteron carolinae* is not verifiable and so far, these species can hardly be considered as displaying pore clusters. Internal views of valves of *Cluthia cluthae* in the original description of the genus by Neale (1973) are clear that it lacks 'pore clusters' *sensu* Maddocks & Steineck (1987). Yasuhara *et al.* (2018) considered that the occurrence of these species at cold seepage on the Svalbard margin may suggest that "these secondary reticulation and pit clusters are related to ectosymbiosis of chemoautotrophic bacteria, like the pore clusters in *Xylocythere*" (see Yasuhara *et al.* 2018: 146), here implying that secondary reticulation and pore clusters are different features. Should secondary reticulation be associated with ectosymbiosis, it may imply different physiological processes, if any, as the proposed enhanced oxygen uptake by fluid flow through the pore clusters (Van Harten 1993) is unlikely in the case of secondary reticulation as it does not cross the thickness of the valves. We further consider that the association of secondary reticulation with ectosymbiosis of chemoautotrophic bacteria is highly questionable as such feature is quite common in taxa from non-chemosynthetic environments (e.g., *Eucytherura mayressi* Yasuhara, Okahashi & Cronin, 2009, *Eucytherura spinicorona* Yasuhara, Okahashi & Cronin, 2009 from Quaternary deep-sea deposits from northwestern Atlantic Ocean; *Eucytherura hazeli* Yasuhara, Okahashi & Cronin, 2009 from the same area being considered as a shelf species transported downslope).

The newly recovered specimens of *Procytherura*? *praecoquum* at Sahune are better preserved and further support the hypothesis of the presence of pore clusters proposed in Forel *et al.* (2024). Except anterodorsally, the solum of each fossa is pierced by very tiny deep holes that apparently cross the thin valve wall (Fig. 2G, K). They were slightly larger, apparently more dissolved in the previously studied specimens, each opening exhibiting a "cork" of sediment likely crossing the entire valve thickness (see Forel *et al.* 2024: fig. 9J, K). The new specimens display similar tiny corks within each opening: they are apparently related to sediment filling the carapace rather than to encrustation from outside which is coarser and randomly set on the surface. This observation reinforces the hypothesis of pore clusters on *Procytherura*? *praecoquum*, and the analysis of more material may lead to the description of a new genus to accommodate this unique species. Nonetheless, the possible presence of pore clusters on *Procytherura*? *praecoquum* is not a reasonable argument for the straightforward assumption that they are related to seepage and thus to ectosymbiosis. Similar structures occur on numerous other Jurassic taxa, including from non-chemosynthetic environments as discussed in Forel *et al.* (2024), and future works may focus on further characterizing their morphology. We consider it dangerous to state that the presence of pore clusters is an indicator of past seepage but *Procytherura*? *praecoquum* appears restricted to Sahune seepage, being only found within pseudobioherms and absent from lateral marls as detailed below. This could qualify it as a proxy for seepage during the Late Jurassic as was recently proposed for *Rosaliella svalbardensis* from Quaternary seep deposits of western Svalbard margin (Chu *et al.* 2023). A verification of this assumption may come from the analysis of ostracod communities from the nearby Beauvoisin site.

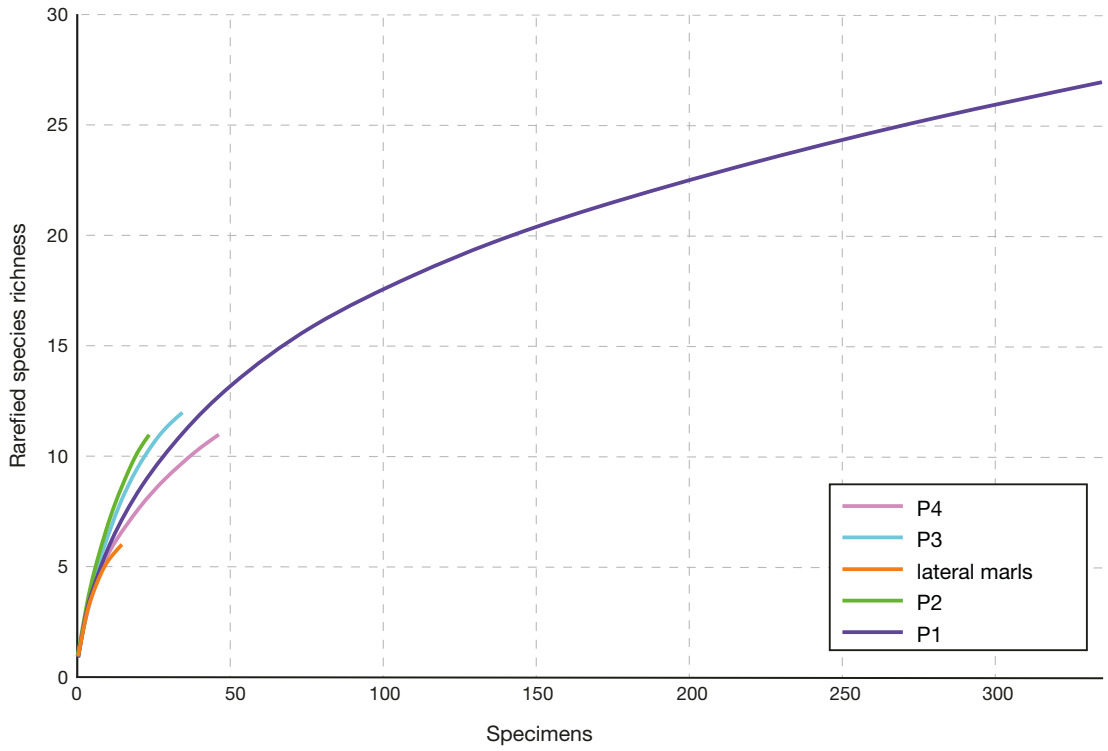


Fig. 3. — Individual rarefaction curves for ostracod assemblages from the deposits at Sahune, Drôme, south-eastern France Basin, middle Oxfordian, Late Jurassic.

Observed ostracod diversity and taphonomy

Eight of the 14 studied samples were productive (22SAH01, 02, 02b, 03-05, 07, 12, the latter being located on the opposite side of the main sequence; Fig. 1C) but ostracods were rare, badly preserved and not identifiable in 22SAH07 and 12. As a consequence, ostracods from Sahune are only reported from the main pseudobiohermal limestone masses (22SAH01-05, corresponding to P1 to P4) and lateral marls (22SAH02b, LM). In the following, five communities are thus analysed and compared: those associated with each of the pseudobioherms P1 to P4 and that derived from marls deposited laterally to P2 (Fig. 1C). Overall, twenty-seven species are here recognized, distributed in 14 genera from seven families (Appendix 1). Their distribution through the sequence and observed taxonomic richness of each community is summarized in Table 1. Within pseudobioherms, the observed familial diversity ranges from six (P2-P4) to seven (P1), generic diversity ranges from eight (P2, P4) to 14 (P1) and species diversity ranges from 11 (P2, P4) to 27 (P1). The diversity is much lower in the lateral marls, with only six species from five genera and three families. Overall, the present investigation of the entire Sahune succession does not yield significant additional taxa in comparison to the preliminary analysis of P1 (Forel *et al.* 2024; Appendix 1). At the genus level, only the rare *Cytheropterina* Mandelstam, 1956 (P1) is newly reported. Similarly, only five rare species are new, mainly from P1: cytherurids *Cytheropterina* sp. (P1; Fig. 2A) and *Eucytherura* sp. 2 (P1; Fig. 2B), paracyprids *Paracypris* cf. *acuta* (Cornuel, 1848) (P1; Fig. 2C) and *Paracypris*? sp. 3 (P1, P2; Fig. 2D) and pontocyprid *Pontocyprella* cf. *cavata* Donze, 1967 (P1, P2, LM; Fig. 2E, F). When considering the taxonomic diversity of P1 community in particular, the newly studied material adds nothing at the familial level, while it increases genera from 13 to 14, and species from 22 to 27.

To discuss the significance of these diversity patterns among Sahune ostracod assemblages, their taphonomy and representativeness need to be assessed. As a first indicator, the proportion of complete carapaces *versus* isolated valves and the demographic structure of populations provide information as to the autochthonous or allochthonous nature of ostracod assemblages (e.g., Oertli 1971; Boomer *et al.* 2003). At Sahune, all specimens are complete, articulated carapaces, no disarticulated valve being found neither in Forel *et al.* (2024) nor in the present analysis. Numerous species are rare (n<5; Appendix 1) and their preservation as complete carapaces precludes the observation of inner characters to determine ontogenetic series and whether they are adults or juveniles. However, the large size range of the three most abundant species, namely *Pontocyprella* cf. *rara* Kaye, 1965a (n = 147; length = 247-674 µm; height = 135-338 µm), *Procytherura*? *praecoquum* (n = 92; length = 301-431 µm; height = 142-204 µm), and *Rectangulocyprella* cf. *semiquadrata* (Kaye, 1965b) (n = 56; length = 260-684 µm; height = 139-335 µm), demonstrates that several ontogenetic stages co-occur. It is thus likely that most assemblages at Sahune are composed of a mixture of complete carapaces of adults and juveniles, therefore largely corresponding to autochthonous communities.

As a second indicator, individual rarefaction has been calculated with PAST version 4.04 (Hammer *et al.* 2001; Hammer & Harper 2005), showing the expected number of

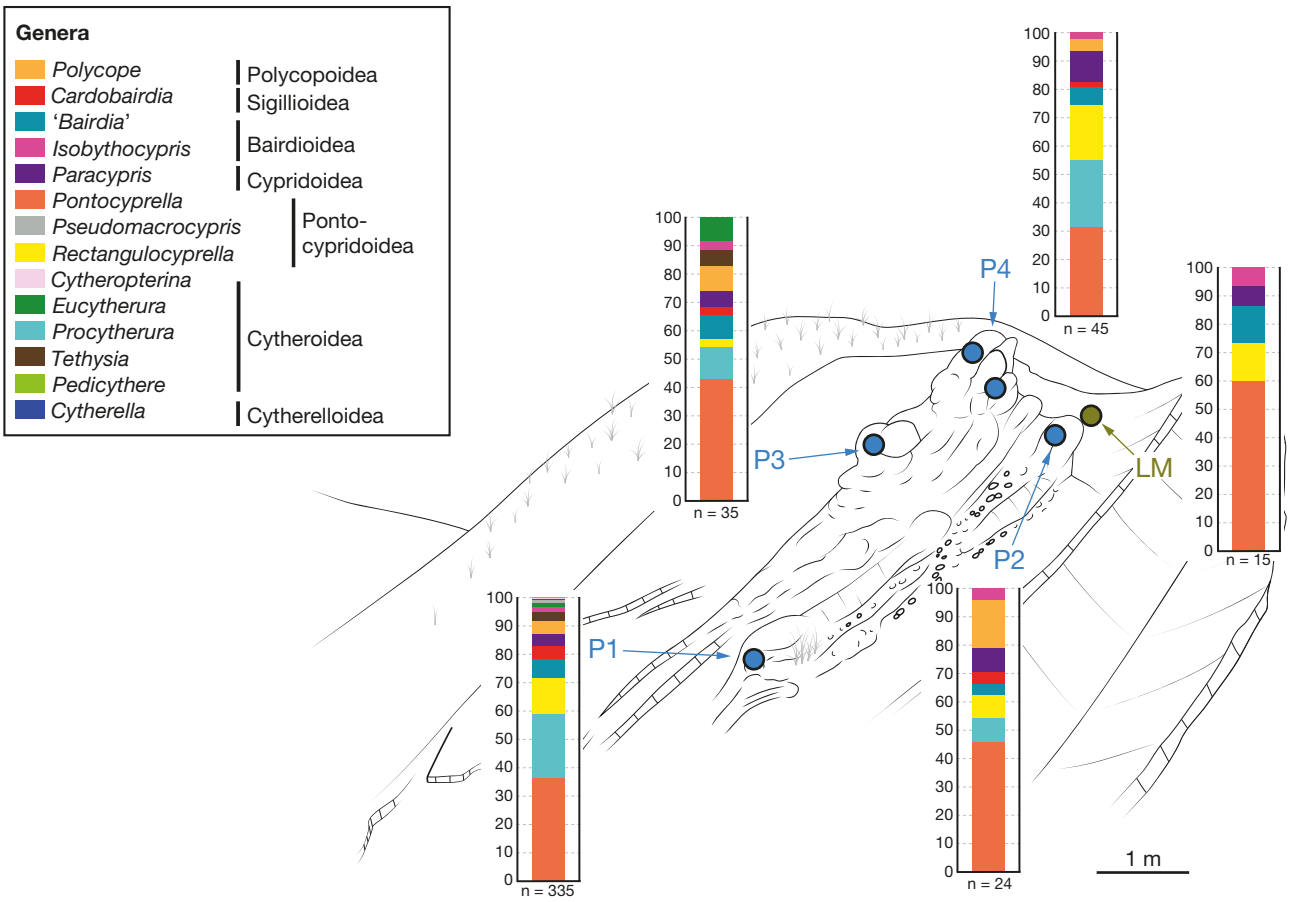


Fig. 4. — Proportion of specimens per genus at each pseudobioherm (P1 to P4) and lateral marls (LM) exposed at Sahune.

species as a function of the number of specimens in each community (Fig. 3). To do so, the number of articulated carapaces of each species per sample were counted, as no isolated valves were found in the course of this analysis (Fürsich & Wendt 1977; Nützel & Kaim 2014; Haussmann & Nützel 2015; Table 1). The rarefaction curves indicate that taxa count is not representative of the entire fauna for assemblages associated with P2, P3, P4 and lateral marls (LM), and that larger samples would have given better counts and higher diversity levels. Although curves are far from flattening out, all have passed or are around their maximum of slope, indicating that the assemblages nonetheless gather an important proportion of species. On the other hand, the curve corresponding to assemblage P1 flattens out gradually, which demonstrates that further sampling would not have provided a significant number of additional species. The P1 assemblage thus relatively faithfully represents the original diversity of the ostracod fauna, while others provide a partial representation of communities that need to be cautiously considered. Interestingly, the curves associated with P2 and P3 are above that of P1 with steeper slopes, indicating that further sampling may lead to higher diversity levels in P2 and P3 than in P1. Because of the incompleteness of most assemblages, their diversity and structure cannot be quantified by indices such as Shannon diversity and Taxonomic Distinctness. They are thus discussed based on the observed features, *mutatis mutandis*. Based on these observations, three major features of ostracod communities through the Sahune sequence are distinguished and discussed below.

Taxonomic diversity and structure of ostracod communities

A first important feature is that of the taxonomic diversity of ostracod communities at Sahune, which is considerably lower within lateral marls than within pseudobioherms, even those with fewer specimens (Table 1; Fig. 4). The rarefied curve of LM community is located well below that of each pseudobioherm, indicating that the observed difference in diversity may illustrate an original feature. The same amount of sediment was prepared and observed for all samples, so that this pattern may not relate to differences in sample size.

All ostracod taxa reported from P2, P3, P4 and LM occur in P1 (Appendix 1; Table 1; Fig. 4), so that all Sahune assemblages appear as subsamplings of P1. All in all, all pseudobiohermal communities are more diverse and complex than that of lateral marls. Forel *et al.* (2024) have summarized information available on ostracods from the Terres Noires Formation, with early Oxfordian communities composed of '*Bairdia*', *Bythocypris* Brady, 1880, *Cardobairdia* van den Bold, 1960 emend. McKenzie (1967), *Paracypris* Sars, 1866 and *Pontocyprella* Man-

delstam *in* Ljubimova, 1955 (Oertli 1963; see Forel *et al.* 2024 for taxonomic discussion). The poor Sahune LM assemblage composed of pontocypridids (*Pontocyprella* cf. *rara*, *Rectangulocyprella* cf. *semiquadrata*, *Pontocyprella* cf. *cavata*) with few bairdiids (*Isobythocypris*? sp. 1) and paracypridids (*Paracypris*? sp. 1) partly aligns with previous observations. A robust comparison of seep *versus* deep-sea background communities during the middle Oxfordian clearly requires the full characterization of ostracods from the Terres Noires Formation, as suggested by the rarefaction curve. The present data nonetheless extend the observation of Forel *et al.* (2024) to the entire Sahune sequence and show that seepage communities were composed of members of the nearby deep-sea background community, and adds *Isobythocypris* Apostolescu, 1959 and *Rectangulocyprella* Wilkinson, 1990 to the background taxa in the area. Two main differences are noticeable when comparing pseudobiohermal and LM communities:

1) Cytheroidea (Cytheruridae Müller, 1894) are absent from marls while they are members of all pseudobiohermal communities, even those undersampled;

and 2) while no taxa appear restricted to LM, 22 species are restricted to pseudobiohermal communities, as further discussed below.

When compared with contemporaneous platform populations, typical cytheroid ostracod families such as Progonocytheridae Sylvester-Bradley, 1948, Protocytheridae Ljubimova, 1956, Schulerideidae Mandelstam, 1959 and Trachyleberididae Sylvester-Bradley, 1948 (e.g., Bizon 1958; Donze 1962; Whatley 1970; Piotelat 1984; Schudack & Schudack 2000), are absent from all Sahune samples, as was previously noted for P1. The absence of such typical Jurassic taxa is thus a characteristic of the entire Sahune sequence including lateral marls, likely in relation to bathyal water depth, as discussed below. The overall Sahune familial diversity (7) is comparatively lower than contemporaneous platform populations, which ranges from 10 to 20 in localities without seepage from France, Switzerland, Germany, Poland, UK and Israel (see Forel *et al.* 2024: fig. 10). Ostracod communities from the entire Sahune seep sequence are thus comparatively of low diversity at the familial level, and this feature is not only a character of P1.

Dominance of Pontocyprididae

The second important feature of Sahune communities is that of the dominance of pontocypridids (*Pseudomacrocypris* Michelsen, 1975, *Pontocyprella* and *Rectangulocyprella*) that are between 46% (P3) and 55% (P2) of the specimens within pseudobioherms. The observed 73% of the specimens in LM community is biased by its overall low abundance. Among the three pontocypridid genera occurring at Sahune, *Pontocyprella* is the most abundant, ranging from 32% (P4) to 46% (P2) within pseudobiohermal communities (Fig. 4). They are 60% in LM, a value which is here also likely overestimated. This overall dominance corresponds to the abundance of *Pontocyprella* cf. *rara* that accounts for 66% (P2) to 90% (P1, P3, P4) of all *Pontocyprella* specimens. Although quantifications have to be considered with care, the observed dominance of Pontocyprididae (*Pontocyprella*) thus appears as a characteristic of the entire sequence of the fluid seep at Sahune. The record of LM assemblage may illustrate the lateral influence of seep fluids, owing to the close proximity of the studied LM sample and the pseudobioherm succession (Fig. 4). In modern environments, the vertical and lateral extent of seep fluid influence is at the origin of successive habitats around the emission area, although likely weaker than at hydrothermal vents (e.g., Levin *et al.* 2016; Sisma-Ventura *et al.* 2022). Additional samples collected at increasing distances laterally from the pseudobioherms at Sahune should permit further evaluation of the extent of seep fluid influence and characterize the structure of successive communities.

In modern marine environments, Pontocyprididae are widespread from shallow littoral to deep-sea, generally in low abundance (e.g., van den Bold 1974; Maddocks 1969, 1977; Karanovic 2019). In the fossil record, ostracod communities with such taxonomic structure and proliferation of Pontocyprididae have never been reported from any contemporaneous marine deposit, as preliminarily analyzed in Forel *et al.* (2024). This feature echoes the composition of ostracod communities from the deepest parts of the south-eastern France Basin (also called Vocontian Basin) during the Early Cretaceous, characterized by low taxonomic diversity and overall dominance of Pontocyprididae (Donze 1971; Babinot *et al.* 1985). Pontocyprididae thus appear as members of communities of deep-sea oligotrophic environments through most of the history of the south-eastern France Basin. Their abundance at Sahune may thus rather illustrate the influence of seep fluids through the development of complex ecosystems providing food supply in otherwise oligotrophic conditions (Forel *et al.* 2024). Their pattern of abundance possibly extending within closely located lateral marls strengthens this hypothesis.

Endemic species

The third feature of Sahune communities relates to *Procytherura*? *praecoquum*, that was hypothesized as endemic to the seepage based on the analysis of P1 assemblage (Forel *et al.* 2024). The present dataset confirms that *Procytherura*? *praecoquum* occurs throughout the seep succession, ranging from 8% (P2) to 22 and 23% of the specimens in P1 and P4 respectively (Fig. 4). With the exception of P2, *Procytherura*? is the second most abundant component of pseudobiohermal communities, all corresponding to specimens of *Procytherura*? *praecoquum*. This species is absent from the lateral marls, the same amount of pseudobiohermal and LM material being processed and observed for ostracod analysis.

As mentioned above, marly material collected at increasing distance laterally to the main sequence may provide an indication of the extent of seep fluid influence. It would also illustrate the successive, concentric populations around the active zone of fluid emission, encompassing species endemic to direct seepage within pseudobioherms while those adapted to more diffuse fluid would occur laterally. The absence of *Procytherura*? *praecoquum* from LM community and from previously Terres Noires studies (Oertli 1963) indicates that it may be adapted to the active, direct seep area. All other species shared between LM and pseudobioherms (Table 1) may be adapted to both areas, from direct active seepage to more diffuse influence laterally.

CONCLUSION

Pseudobioherms enclosed within the Terres Noires Formation at Sahune in the south-eastern France Basin provide the oldest known ostracod communities associated with hydrocarbon seepage, of middle Oxfordian age. Following the preliminary analysis of the pseudobioherm at the base of the section (P1), we here extend the discussion to ostracod communities spanning the sequence of seepage, which is recorded in four carbonate bodies. The structure of pseudobioherm ostracod communities is stable throughout the period of seep-fluid emission, with the pervasive dominance of Pontocyprididae specimens. We propose that Pontocyprididae were members of deep-sea ostracod communities at least from the Oxfordian to the Early Cretaceous, and that their abundance pattern at Sahune illustrates the influence of seep fluids. The marls deposited laterally are poor in ostracods but may display the same dominance pattern, likely illustrating the lateral influence of fluids. *Procytherura*? *praecoquum* is an important component of all pseudobiohermal communities but absent from the lateral marls, leading to the hypothesis that it was adapted and endemic to the area of active fluid emission. The newly obtained specimens of *Procytherura*? *praecoquum* allow observations of its morphology, muscle scars, ornamentation and normal pores, as a first step towards understanding of the phylogeny of Cytheroidea at cold seeps. An important point of comparison will be the analysis of the roughly coeval Beauvoisin area exposing a succession of pseudobioherms spanning the Oxfordian.

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APPENDIX 1. — Taxonomic list of all ostracod species identified at Sahune, Drôme, south-eastern France Basin, Oxfordian, Late Jurassic, including sample numbers and abundance. **In bold**, species newly reported in the present work; all other species were already reported in Forel *et al.* (2024) from P1 only.

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 (P1, P2, P3, P4; n=24)

Subclass PODOCOPA Müller, 1894
Order PODOCOPIDA Sars, 1866
Suborder SIGILLIOCOPINA Martens, 1992
Superfamily SIGILLIOIDEA Mandelstam, 1960
Family SIGILLIIDAE Mandelstam, 1960
Genus *Cardobairdia* van den Bold, 1960 emend. McKenzie, 1967
Cardobairdia cf. *argoviensis* Oertli, 1959 (P1–P4; n=18)

Suborder BAIRDIOCOPINA Gründel, 1967
Superfamily BAIRDIOIDEA Sars, 1888
Family BAIRDIIDAE Sars, 1865
Genus '*Bairdia*' M'Coy, 1844
'*Bairdia*'? sp. 1 (P1, P3, P4, LM; n=19)
'*Bairdia*' cf. *major* Donze, 1964 (P1-P4; n=13)
Genus *Isobythocypris* Apostolescu, 1959
Isobythocypris? sp. 1 (P1-P3, LM; n=8)
Isobythocypris? sp. 2 (P1, P4; n=2)

Suborder CYPRIDOCOPINA Jones, 1901
Superfamily CYPRIDOIDEA Baird, 1845
Family PARACYPRIDIDAE Sars, 1923
Genus *Paracypris* Sars, 1866
***Paracypris* cf. *acuta* (Cornuel, 1848)** (P1; n=1)
Paracypris cf. *siliqua* Jones & Hinde, 1890 (P1, P4; n=5)
Paracypris cf. *stripta* Ljubimova, 1956 (P1–P4; n=13)
Paracypris? sp. 1 (P1, LM; n=3)
Paracypris? sp. 2 (P1; n=1)
***Paracypris*? sp. 3** (P1, P2; n=2)

Superfamily PONTOCYPRIDOIDEA Müller, 1894
Family PONTOCYPRIDIDAE Müller, 1894
Genus *Pontocyprella* Mandelstam *in* Ljubimova, 1955
Pontocyprella vescusa Ljubimova, 1956 *in* Tesakova, 2003 (P1; n=7)
***Pontocyprella* cf. *cavata* Donze, 1967** (P1, P2, LM; n=6)
Pontocyprella cf. *rara* Kaye, 1965a (P1–P4, LM; n=147)
Pontocyprella sp. 1 (P1; n=1)
Pontocyprella sp. 2 (P1–P4; n=12)
Genus *Pseudomacrocypris* Michelsen, 1975
Pseudomacrocypris sp. (P1; n=3)
Genus *Rectangulocyprella* Wilkinson, 1990
Rectangulocyprella cf. *semiquadrata* (Kaye, 1965b) (P1–P4, LM; n=56)

Suborder CYTHEROCOPINA Baird, 1850
Superfamily CYTHEROIDEA Baird, 1850
Family CYTHERURIDAE Müller, 1894
Genus *Eucytherura* Müller, 1894 emend. Horne & Lord (2024)
Eucytherura sp. (P1, P3; n=5)
***Eucytherura* sp. 2** (P1; n=2)
Genus *Cytheropterina* Mandelstam, 1956
***Cytheropterina* sp.** (P1; n=1)
Genus *Pedicythere* Eager, 1965
Pedicythere? sp. (P1; n=1)
Genus *Procytherura* Whatley, 1970 emend. Bate & Coleman, 1975
Procytherura? *praecoquum* Forel *in* Forel *et al.*, 2024 (P1–P4; n=92)
Genus *Tethysia* Donze, 1975
Tethysia cf. *bathonica* Sheppard *in* Brand, 1990 (P1; n=4)
Tethysia sp. 1 (P1, P3; n=9)

Order PLATYCOPIDA Sars, 1866
Suborder PLATYCOPINA Sars, 1866
Superfamily CYTHERELLOIDEA Sars, 1866
Family CYTHERELLIDAE Sars, 1866
Genus *Cytherella* Jones, 1849
Cytherella sp. (P1; n=1)