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ABSTRACT
A new, diminutive arthropod belonging to the cyclidan family Alsasuacarididae Van Bakel, Jagt, Fraaije & Artal, 2011 is described from upper Maastrichtian strata in the type area of that stage. *Alsasuacaris dirkeysermansi* n. sp. is the second member of the genus known to date and extends the stratigraphical and palaeobiogeographical ranges of this genus considerably, the type species, *A. nostradamus* Van Bakel, Jagt, Fraaije & Artal, 2011, having been recorded from the Albian (late Early Cretaceous) of northern Spain. The new species constitutes only the third member of the family Alsasuacarididae, and the first in three-dimensional preservation and with ventral morphology exposed. Morphologically and stratigraphically speaking, alsasuacaridids are quite distinct from other Cyclida recorded to date, but no alternative taxonomic classification is available at the moment. Up to now, in almost all known Mesozoic faunas, the occurrence of cyclidans has been limited to a single species per assemblage. The presence of more than one cyclidan in the diverse faunal assemblages from the Meerssen Member (Maastricht Formation, upper Maastrichtian) in the south-east Netherlands, may suggest that it is feasible that more of such cyclidan taxa will be discovered in strata of Mesozoic age when also millimetre-sized faunal elements are screened in detail. Although cyclidans do have a crab-like appearance, it is highly likely that alsasuacaridids occupied other ecological niches than brachyurans.

KEY WORDS
Cyclida,
Maastrichtian,
Alsasuacaris,
palaeoecology,
new species.

RÉSUMÉ
Un second alsasuacaridid énigmatique (Pancrustacea, Cyclida) provenant de la région type du Maastrichtien aux Pays-Bas (Crétacé supérieur).
Un arthropode nouveau, de petite taille, appartenant à la famille des Cyclida Alsasuacarididae Van Bakel, Jagt, Fraaije & Artal, 2011, est décrit des strates du Maastrichtien supérieur dans le stratotype de cet étage. *Alsasuacaris dirkeysermansi* n. sp. est le second membre connu à ce jour de ce genre et élargit considérablement ses aires de répartition stratigraphique et paléobiogéographique, l'espèce type, *A. nostradamus* Van Bakel, Jagt, Fraaije & Artal, 2011, ayant été répertoriée dans l'Albien (fin du Crétacé inférieur) du nord de l'Espagne. Cette espèce nouvelle ne constitue que le troisième membre de la famille des Alsasuacarididae, et le premier à présenter une conservation tridimensionnelle et une morphologie ventrale exposée. D'un point de vue morphologique et stratigraphique, les alsasuacaridiidés se distinguent nettement des autres Cyclida répertoriés à ce jour, mais aucune classification taxinomique alternative n'est disponible pour l'instant. Jusqu'à présent, dans la quasi-totalité des faunes mésozoïques connues, la présence de Cyclida s'est limitée à une seule espèce par assemblage. La présence de plus d'un réprésentant dans les assemblages faunistiques diversifiés du Membre Meerssen (Formation de Maastricht, Maastrichtien supérieur), dans le sud-est des Pays-Bas, pourrait suggérer qu'il est plausible que d'autres taxons de Cyclida soient découverts dans des strates du Mésozoïque lorsque des éléments faunistiques de taille millimétrique feront également l'objet d'un examen détaillé. Bien que les Cyclida aient effectivement une apparence semblable à celle des crabes, il est très probable que les alsasuacaridiidés occupaient des niches écologiques différentes de celles des brachyoures.

MOTS CLÉS
Cyclida,
Maastrichtien,
Alsasuacaris,
paléoécologie,
espèce nouvelle.

INTRODUCTION

Cyclidans comprise a diverse, enigmatic group of diminutive to small-sized arthropods, with a subcircular carapace which ranges in age from Early Carboniferous (Tournaisian, Mississippian) to Late Cretaceous (late Maastrichtian) (Schweitzer *et al.* 2020; 2025; Mychko *et al.* 2025). They are exceptionally rare in the fossil record, and each discovery is of major importance for recording and understanding the diversity and stratigraphical development of this group. In terms of appearance, cyclidans share morphological similarities with true crabs (Brachyura Latreille, 1802), but they are only distantly related to these or to any other decapod crustacean groups, having an isolated evolutionary history. Currently, cyclidans are classified as a separate order, the Cyclida Schram, Vonk & Hof, 1997, within the superclass Multicrustacea Regier, Shultz, Zwick. Hussey, Ball, Wetzer, Martin & Cunningham, 2010.

Cyclidans occupied a range of environments: some species are known from either relatively deep-sea shelf or shallow-water deposits, and salinity appears to have ranged from hypersaline to (possibly) freshwater (Schweitzer *et al.* 2020; Mychko 2025). All currently known cyclidan taxa were considered benthic or parasitic (Müller, 1955; Mychko 2022a, b).

At present, the order Cyclida comprises six families with around 60 species in 31 genera (Feldmann & Schweitzer 2019; Schweitzer *et al.* 2020; Tang *et al.* 2021; Mychko 2022b, Mychko 2025; Mychko *et al.* 2025; Schweitzer *et al.* 2025; Sun *et al.* 2025). Each family within the order occupies a distinct morphospace (Schweitzer *et al.* 2020: fig. 26).

The family Alsasuacarididae Van Bakel, Jagt, Fraaije & Artal, 2011 includes the youngest members of the order, with one species, *Alsasuacaris nostradamus* Van Bakel, Jagt, Fraaije & Artal, 2011 from Albian reefal limestones in northern Spain (Van Bakel *et al.* 2011) and two taxa from intra-reefal biocalcarenites of the type-Maastrichtian in the south-east Netherlands (Fraaije *et al.* 2003; present paper). Schweitzer *et al.* (2020: 262) stated that, "The Latin word *caris*, meaning crab, is feminine. The original authors did not designate a gender for *Alsasuacaris*; thus, according to ICZN Article 30.1.1 (ICZN 1999), the gender of the genus name is feminine. We have changed the ending of the trivial name accordingly into *nostradama*". However, Van Bakel *et al.* (2011: 48) had originally offered the following explanation for the spelling *nostradamus*, "The species is named after the Latinised name of Michel de Nostredame (1503-1566), French seer, well known for his prophecies published in his book 'Les Propheties'. His name is used here as a noun in apposition". According to ICZN, Article 31.2.1: "A species-group name that is a simple or compound noun (or noun phrase) in apposition need not agree in gender with the generic name with which it is combined (the original spelling is to be retained), with gender ending unchanged; see Article 34.2.1". Therefore, the correct spellings of the species names of the cyclidan taxa are *Alsasuacaris nostradamus* and *Maastrichtiocaris rostrata* Fraaije, Schram & Vonk, 2003.

Currently, there are no definitive arguments to exclude these three species from the Cyclida, because there is no other higher taxon to which they could be assigned. However, it should be noted that the families Hemitrochiscidae Trauth, 1918 and Alsasuacarididae may not be part of a monophyletic Cyclida (Feldmann & Schweitzer 2019). This is also hinted at in a morphospace analysis, which revealed alsasuacaridids to constitute an outlier in the plot (Schweitzer *et al.* 2020: fig. 26). Alsasuacaridids differ quite significantly from other cyclidan families, mainly in that they show well-developed orbits, a different structure of the frontal region and many other features (Van Bakel *et al.* 2011; this paper). Unfortunately, in



Fig. 1. — Dorsal morphology of the holotype of *Alsasuacaris dirkeysermansi* n. sp. Abbreviations: **r**, rostrum; **or**, orbital rim; **k**, axial keel; **R1**-**R3**, tuberculate ridges. Scale bar: 1 mm. Photo: Barry W. M. van Bakel.

the absence of any pre-mid-Cretaceous representatives and the extremely limited number of finds assignable to this family, more definite conclusions cannot be drawn at this moment.

Abbreviations

Institutional abbreviation

MAB — Het Nationaal Oertijdmuseum Boxtel, The Netherlands (formerly Museum de Ammonietenhoeve, Boxtel).

SYSTEMATIC PALAEONTOLOGY

Infraphylum PANCRUSTACEA Zrzavý & Štys, 1997
Class MULTICRUSTACEA Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Order CYCLIDA Schram, Vonk & Hof, 1997
Family Alsasuacarididae
Van Bakel, Jagt, Fraaije & Artal, 2011
[*nom. corr.* Schram & Koenemann, 2022]

Included genera. — *Alsasuacaris* and *Maastrichtiocaris* Fraaije, Schram & Vonk, 2003.

Genus *Alsasuacaris* Van Bakel, Jagt, Fraaije & Artal, 2011

Included species. — *Alsasuacaris nostradamus* Van Bakel, Jagt, Fraaije & Artal, 2011 and *Alsasuacaris dirkeysermansi* n. sp.

Diagnosis. — Carapace diminutive to very small, oval to round; wide, large, dorsally oriented orbits; rostrum very large, fan-shaped; prominent upraised orbital tooth or rim; front anteriorly widened, with central depression; posterior margin rounded, with distinct shelf; carapace surface areolated with swellings, granular posterior part covered with multiple subcircular ornamented ridges parallel to posterior margin. Ventral side with large basal plate anteriorly and ventral cavity posteriorly.

Alsasuacaris dirkeysermansi n. sp.
(Figs 1; 2)

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Diagnosis. — Dorsal carapace diminutive, round; large, slightly quadratic orbits, directed outwardly and dorsally, orbital margin thickened, orbital rim strong; very large, fan-shaped rostrum; with raised crest and

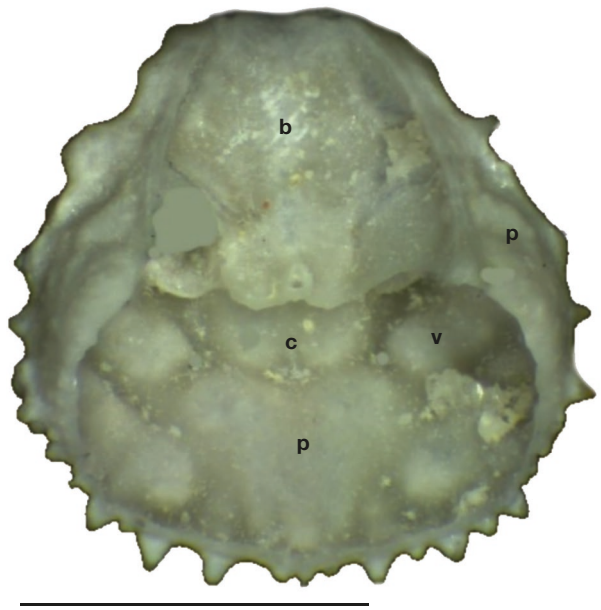


Fig. 2. — Ventral morphology of the holotype MAB16877 of *Alsasuacaris dirkeysermansi* n. sp. Abbreviations: **b**, basal plate; **c**, central plate; **p**, posterior plate; **v**, ventral cavity. Scale bar: 1 mm. Photo: Barry W. M. van Bakel.

central depression; granular axial keel on central and posterior carapace portions, posterior margin rounded, with sloping shelf; carapace surface areolated, posterior portion covered with multiple subcircular, parallel ridges; cuticle granular. Flattened ventral carapace with large basal plate anteriorly and ventral cavity posteriorly. Basal plate bounded laterally by pterygostomial regions. Relatively small central plate. Cordate posterior plate. Lateral edge of posterior carapace highly tuberculate.

Derivation of name. — Named after Diederik ('Dirk') Eysermans of Vosselaar (Belgium), a highly esteemed collector of type-Maastrichtian fossils over the last four decades, who discovered numerous museum-quality fossils inclusive of the sole specimen of this new species of *Alsasuacaris*.

Type material. — **Holotype**. **The Netherlands** • Maastricht, Sint-Pietersberg, former ENCI-HeidelbergCement Group quarry; late Maastrichtian; middle Meerssen Member (unit IVf-4) of the Maastricht Formation; D. Eysermans leg.; MAB16877.

Type locality. — The Netherlands, Maastricht, Sint-Pietersberg.

Additional information on type material. — The holotype, and sole specimen known to date, is MAB16877, from the former ENCI-HeidelbergCement Group quarry (Sint-Pietersberg, Maastricht), stemming from a coarse-grained biocalcarenitic level within the middle Meerssen Member (unit IVf-4) of the Maastricht Formation. At this level there are discontinuous scleractinian coral- and rudist bivalve-dominated, bioherm-like structures, and remains of sea grasses (Baron-Szabo & Leloux 2024; Mitchell *et al.* 2024). The diminutive carapace was hand-picked from sieve residues by Diederik Eysermans.

Description

Dorsal carapace diminutive (maximum length and width, 1.6 mm), round; large, slightly quadratic orbits, directed outwardly and dorsally, orbital margin thickened, orbital rim strong with large orbital process; very large, fan-shaped rostrum; with raised crest and central depression; granular axial keel on central and posterior carapace portions, posterior margin rounded, with sloping shelf; carapace surface areolated, posterior portion covered with multiple subcircular, parallel and tuberculate ridges; cuticle granular.

Flattened ventral carapace with large basal plate anteriorly and ventral cavity posteriorly. Basal plate outlined laterally by pterygostomial regions. Relatively small bilobed central plate posteriorly bordered by heart-shaped posterior plate and anteriorly by a wavy edge of transverse ventral cavity. In between the posterior part of the pterygostomial region and the heart-shaped posterior plate is a region covered by three angular protuberances. Lateral edge of posterior carapace highly tuberculate.

DISCUSSION

All currently known alsasuacaridids are relatively small sized in comparison to most of the other cyclidans recorded in the literature. The maximum carapace length of *Maastrichtiocaris rostrata* is 4.8 mm, while that of *A. nostradamus* is 2.6 mm and that of *A. dirkeysermansi* n. sp. 1.6 mm. However, the large, dorsally orientated, ornamented orbits, the pronounced and grooved rostrum, the post-rostral depression, the lobation of the anterior carapace and the multiple rimmed posterior carapace of members assigned to the family Alsasuacarididae differ from those of other known cyclidan families (Fig. 3). The morphology of the ventral side also deviates considerably as can be seen from the description above.

Similar to the late Maastrichtian forms (Fig. 4), the majority of Palaeozoic and Mesozoic members of the order Cyclida are confined to reef and near-reef facies (Schweitzer *et al.* 2020).

Invertebrate faunas from the Meerssen Member of the Maastricht Formation comprise larger benthic foraminifera, decapod crustaceans, ostracods, radiolitid and hippuritid bivalves, red algae, sponges, bryozoans and echinoderms (stalkless crinoids, asteroids, ophiuroids and echinoids), all indicative of water temperatures of about 20°C and shallow depths (0-10 m). This particular level within the upper part of the Maastricht Formation corresponds to a notable warm-water influx (see e.g. Liebau 1978; Fraaye 1996, 1997). Other records of warm-water immigrant taxa include the brachyuran genera *Cretachlorodius* Fraaye, 1996 and *Xanthosioides* Collins & Breton, 2009, as well as large myodocopid ostracods (Kornicker *et al.* 2006). Strata assigned to the middle Meerssen Member consist of sheets of coarse- to fine-grained biocalcarenites in-between small-sized and discontinuous bioherms, vertically and laterally alternating with hardgrounds. These strata have been interpreted as spillovers and tempestite sheets, indicative of high-energy and storm-generated deposition (Zijlstra 1994).

Unfortunately, the appendages of alsasuacaridids are not preserved, which is why their morphological and palaeoenvironmental characteristics cannot be fully assessed (see also Schram & Koenemann 2022). Schweitzer *et al.* (2020) concluded, by analogy with modern small-sized dwellers of reefs, that cyclidans fed on organic debris in ancient reefs, crawling between various reef-forming biota. With such a great diversity and number of decapod crustacean taxa in the Maastrichtian

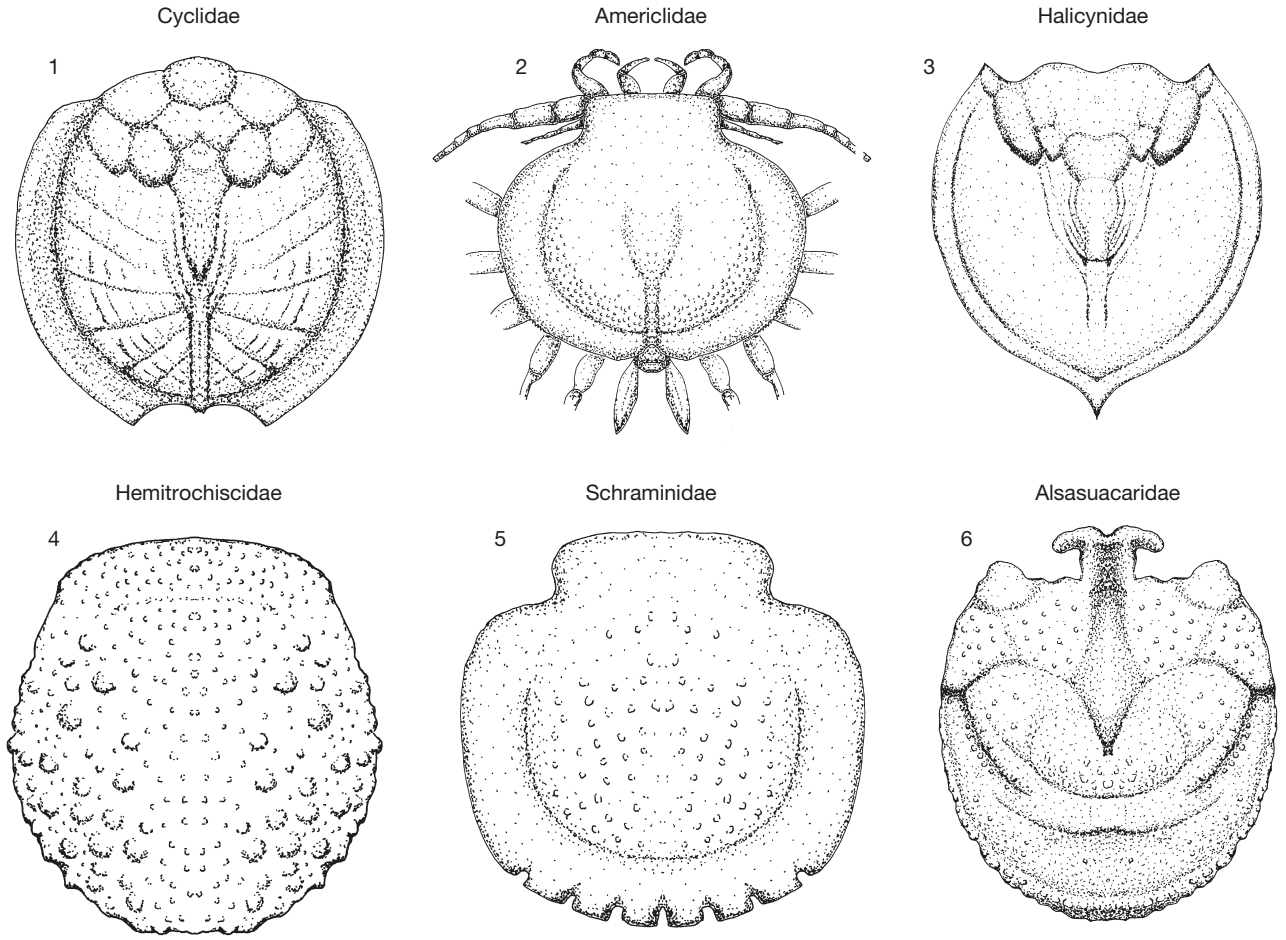


FIG. 3. — Reconstructed morphologies of representatives of the six families of the order Cyclida (modified from Schweitzer *et al.* 2020): **1**, *Cyclus radialis* (Phillips, 1836); **2**, *Americlus americanus* (Packard, 1885); **3**, *Halicyne ornata* Trümpy, 1957; **4**, *Oonocarcinus insignis* Gemmellaro, 1890; **5**, *Opolanka decorosa* Dzik, 2008; **6**, *Maastrichtiocaris rostrata* Van Bakel, Jagt, Fraaije & Artal, 2011. Not to scale. Drawing: Eduard V. Mychko.

type area (e.g. Fraaije 2003), it would appear that cyclidan ecology differed from that of brachyurans and anomurans. Their primary paucity also hints at this.

It is interesting to note that, despite the fact that they belong to different families, reefal cyclidans were almost invariably small in overall size, with carapaces with a range of ornamental features, quite unlike non-reefal Palaeozoic and Mesozoic species. A similar range in ornament and sculpture of carapaces characterises numerous extant crabs and other decapod crustaceans that inhabit reefs. This may be linked to peculiarities of their habitats and the need for camouflage or mimicry.

Müller (1955) tentatively assumed a parasitic lifestyle for cyclidans, with a diet of fish. Such would be in accordance with the abundance of fish and other nektonic vertebrates in sedimentary rocks in which benthic organisms are almost lacking (Schweigert 2007). In view of their small size and rounded morphology, we currently believe that a parasitic lifestyle on fish is a best fit, at least for the Cretaceous alsasuacaridids (Fig. 5). However, what role the markedly large, dorsally orientated, "orbits" played is not yet fully understood.

Dzik (2008), who developed the notion of cyclidans being related to the Branchiura Thorell, 1864, correlated some cyclidan structures with possible organs necessary for parasitism. He compared the pre-oral structure of the Triassic cyclid *Schramine gondwanae* (Brambilla *et al.* 2002) with the pre-oral spine of extant Branchiura of the genus *Argulus* Müller, 1785. Although such an assumption is curious, it does give rise to questions. Besides, in comparison to other cyclidans, *Opolanka decorosa* Dzik, 2008 was a true giant,. Interestingly these Triassic cyclidans co-occurred with various large temnospondyl amphibians. In most species of the families Cyclidae Packard, 1885 and Hemitrochiscidae, it is difficult to imagine what host species such an animal would parasitise on. The carapace was convex, while some species even carried hooked structures under the carapace (ventral lugs, for example as found in *Skuinocyclus juliae* Mychko & Alekseev, 2018). It is logical to assume that such adaptations on the ventral carapace surface would simply interfere with sucking onto the host's body. However, the very small size and flattened carapace of alsasuacaridids suggest a parasitic lifestyle. In the type-Maastrichtian region there was a wide variety of nektonic vertebrates such as bony and cartilaginous fish, turtles and mosasaurs to attach to (Fig. 5). Perhaps the dorsally oriented "orbits" had a suction function in living between and on the gills of fish.

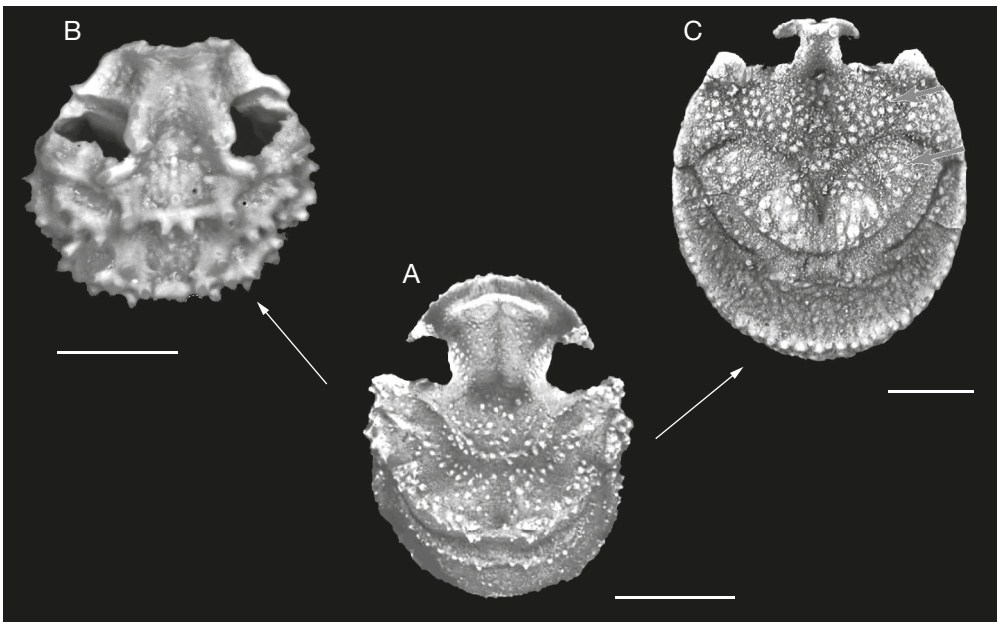


Fig. 4. — All currently known members (holotypes) of the family Alsasuacarididae Van Bakel, Jagt, Fraaije & Artal, 2011, with indication of possible evolutionary relationships: **A**, *Alsasuacaris nostradamus* Van Bakel, Jagt, Fraaije & Artal, 2011, Albian, north-east Spain; **B**, *Alsasuacaris dirkeysermansi* n. sp., late Maastrichtian, The Netherlands; **C**, *Maastrichtiocaris rostrata* Fraaije, Schram & Vonk, 2003, late Maastrichtian, The Netherlands. Scale bars: 1 mm. Photos: Barry W. M. van Bakel.



Fig. 5. — Possible lifestyle of the Late Cretaceous (late Maastrichtian) alsasuacarid, *Alsasuacaris dirkeysermansi* n. sp., parasitic on a mosasauroid host (AI generated reconstruction, René H. B. Fraaije).

Our insight into cyclidan palaeoecology is poor. A cluster of 50 individuals of *Schramine montanaensis* (Schram, Boere & Thomas, 2006) from the Serpukhovian-aged Bear Gulch Limestone of Montana, United States, supports the interpretation of carcasses that were preserved during a rapid burial event. This particular example records either a mass moulting event or clustering for shelter, and represents one of the oldest records of crustacean gregariousness (Bicknell *et al.* 2025).

Only at a few localities yielding Palaeozoic and Triassic cyclidans has more than one species been found (Schweitzer *et al.* 2020). The presence of a multi-taxon cyclidan assemblage in the highly diverse crustacean faunas of the Meerssen Member in the Maastrichtian type area (e.g. Fraaije 2003), would suggest that they are commoner in the fossil record, and additional cyclidans may be discovered in other upper Mesozoic strata, and possibly also Paleogene deposits, when the focus will shift to millimetre-sized faunal elements.

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