geodiversitas

2026 • 48 • 23

A second enigmatic alsasuacaridid (Pancrustacea, Cyclida) from the Maastrichtian type area in The Netherlands (Late Cretaceous)

René H. B. FRAAIJE, Barry W. M. VAN BAKEL, Jonathan J. W. WALLAARD, Maarten DE RIJKE, John W.M. JAGT & Eduard V. MYCHKO



in Adiel A. KLOMPMAKER, Sylvain CHARBONNIER & Fernando A. FERRATGES (eds)

Proceedings of the 9th Symposium on Fossil Decapod Crustaceans, 9-13 June 2025, Denmark

art. 48 (23) — Published on 5 November 2026
www.geodiversitas.com

PUBLICATIONS SCIENTIFIQUES

MUSÉUM NAL HIST NATURELLE

Directeur de la publication / *Publication director* : Gilles Bloch,
Président du Muséum national d'Histoire naturelle

Rédacteur en chef / *Editor-in-chief*: Sylvain Charbonnier

Rédacteur associé / *Associate editor*: Didier Merle

Éditeur technique (suivi éditorial) / *Desk editor (editorial process)*: Emmanuel Côtez (geodiv@mnhn.fr)

Éditeur technique (production) / *Desk editor (production)*: Emmanuel Côtez

Comité scientifique / *Scientific board*:
Christine Argot (Muséum national d'Histoire naturelle, Paris)
Beatrix Azanza (Museo Nacional de Ciencias Naturales, Madrid)
Raymond L. Bernor (Howard University, Washington DC)
Henning Blom (Uppsala University)
Gaël Clément (Muséum national d'Histoire naturelle, Paris)
Ted Daeschler (Academy of Natural Sciences, Philadelphie)
Cédric Del Rio (Muséum national d'Histoire naturelle)
Gregory D. Edgecombe (The Natural History Museum, Londres)
Ursula Göhlich (Natural History Museum Vienna)
Jin Meng (American Museum of Natural History, New York)
Brigitte Meyer-Berthaud (CIRAD, Montpellier)
Zhu Min (Chinese Academy of Sciences, Pékin)
Isabelle Rouget (Muséum national d'Histoire naturelle, Paris)
Sevket Sen (Muséum national d'Histoire naturelle, Paris, retraité)
Stanislav Štamberg (Museum of Eastern Bohemia, Hradec Králové)
Paul Taylor (The Natural History Museum, Londres, retraité)

Couverture / *Cover*:
Réalisée à partir des Figures de l'article/*Made from the Figures of the article*.

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
– Science Citation Index Expanded (SciSearch®)
– ISI Alerting Services®
– Current Contents® / Physical, Chemical, and Earth Sciences®
– Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
– BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par / *Articles and nomenclatural novelties published in* Geodiversitas *are referenced by:*
– ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Adansonia***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie, Comptes Rendus Palevol***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

Les articles publiés dans *Geodiversitas* sont distribués sous licence CC-BY 4.0/*Articles published in* Geodiversitas *are distributed under a CC-BY 4.0 license*.
ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

A second enigmatic alsasuacaridid (Pancrustacea, Cyclida) from the Maastrichtian type area in The Netherlands (Late Cretaceous)

René H. B. FRAAIJE
Barry W. M. VAN BAKEL
Jonathan J. W. WALLAARD
Maarten DE RIJKE
Het Nationaal Oertijdmuseum, Bosscheweg 80, 5283WB Boxtel (The Netherlands)
directie@oertijdmuseum.nl (corresponding author)
barryvanbakel@gmail.com
curator@oertijdmuseum.nl
maarten@oertijdmuseum.nl

John W. M. JAGT
Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht (The Netherlands)
john.jagt@maastricht.nl

Eduard V. MYCHKO
Shirshov Institute of Oceanology, Russian Academy of Sciences,
Nahimovskiy Prospekt 36, Moscow 117997 (Russia)
and Institute of Living Systems, Immanuel Kant Baltic Federal University,
Nevskogo Street 14, Kaliningrad 236016 (Russia)
eduard.mychko@gmail.com

Submitted on 15 December 2025 | accepted on 26 January 2026 | published on 5 November 2026

urn:lsid:zoobank.org:pub:1F8425D2-C942-4A3E-ABD2-81F869A2A090

Fraaije R. H. B., Van Bakel B. W. M., Wallaard J. J. W., De Rijke M., Jagt J. W. M. & Mychko E. V. 2026. — A second enigmatic alsasuacaridid (Pancrustacea, Cyclida) from the Maastrichtian type area in The Netherlands (Late Cretaceous), *in* Klompmaker A. A., Charbonnier S. & Ferratges F. A. (eds), Proceedings of the 9th Symposium on Fossil Decapod Crustaceans, 9-13 June 2025, Denmark. *Geodiversitas* 48 (23): 547-554. https://doi.org/10.5252/geodiversitas2026v48a23. http://geodiversitas.com/48/23

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

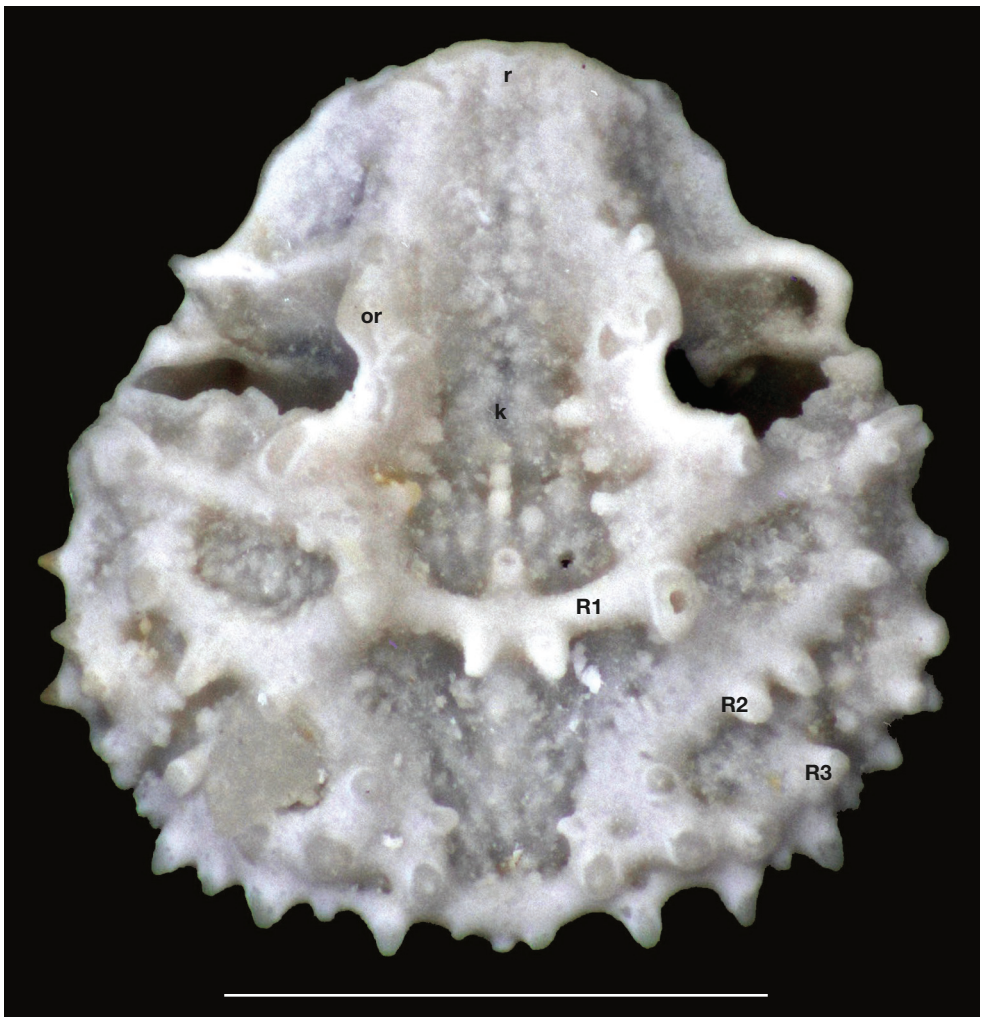


Fig. 1. — Dorsal morphology of the holotype of *Alsasuacaris dirkeysermansi* n. sp. Abbreviations: **r**, rostrum; **or**, orbital rim; **k**, axial keel; **R1**-**R3**, tuberculate ridges. Scale bar: 1 mm. Photo: Barry W. M. van Bakel.

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)

urn:lsid:zoobank.org:act:557DC4DF-2CAC-4881-8D8D-0A88B0926210

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

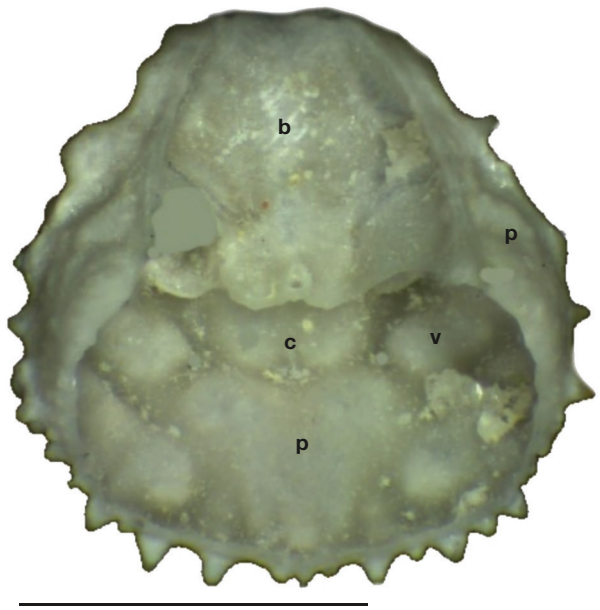


Fig. 2. — Ventral morphology of the holotype MAB16877 of *Alsasuacaris dirkeysermansi* n. sp. Abbreviations: **b**, basal plate; **c**, central plate; **p**, posterior plate; **v**, ventral cavity. Scale bar: 1 mm. Photo: Barry W. M. van Bakel.

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

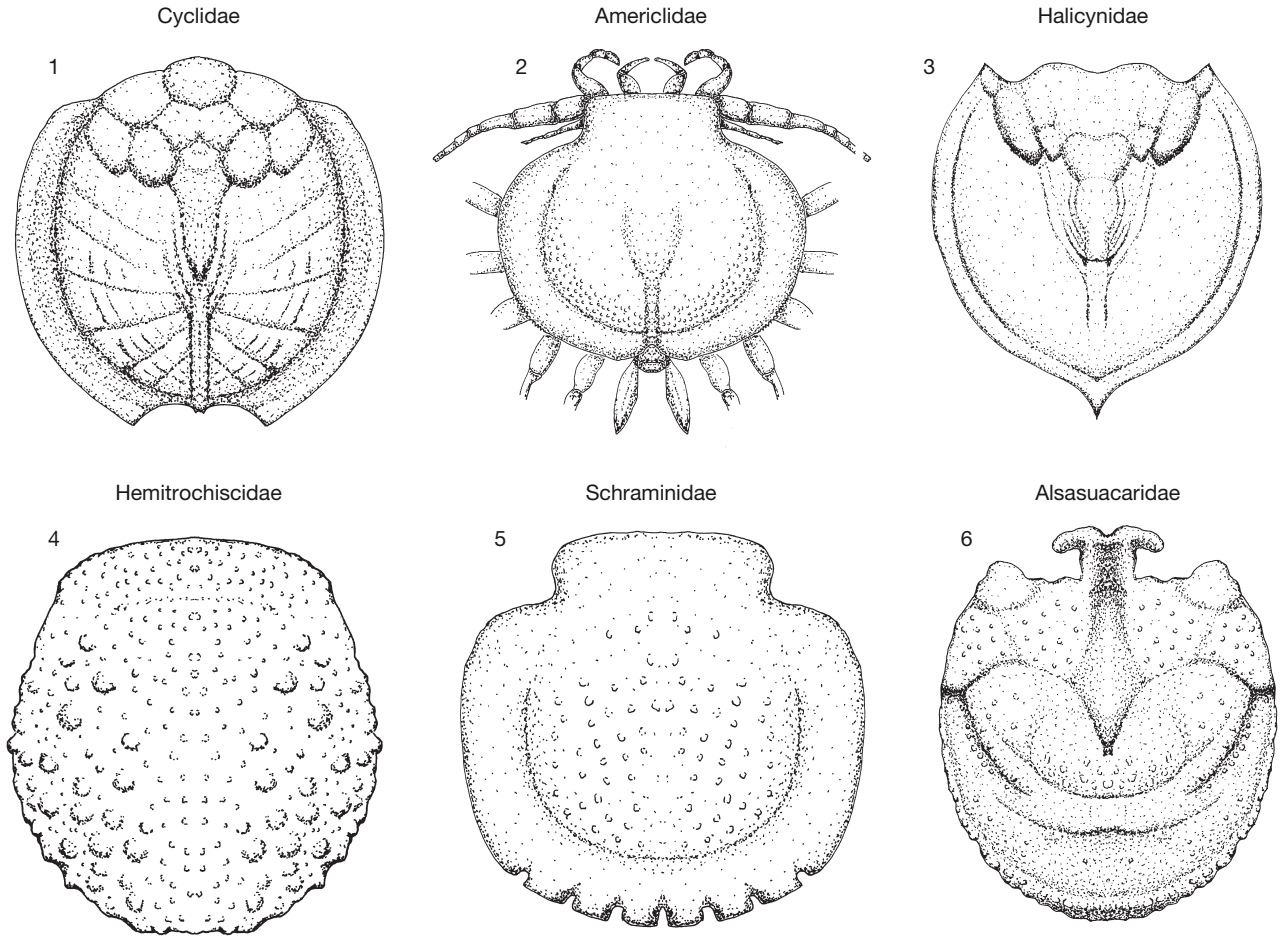


FIG. 3. — Reconstructed morphologies of representatives of the six families of the order Cyclida (modified from Schweitzer *et al.* 2020): **1**, *Cyclus radialis* (Phillips, 1836); **2**, *Americlus americanus* (Packard, 1885); **3**, *Halicyne ornata* Trümpy, 1957; **4**, *Oonocarcinus insignis* Gemmellaro, 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.

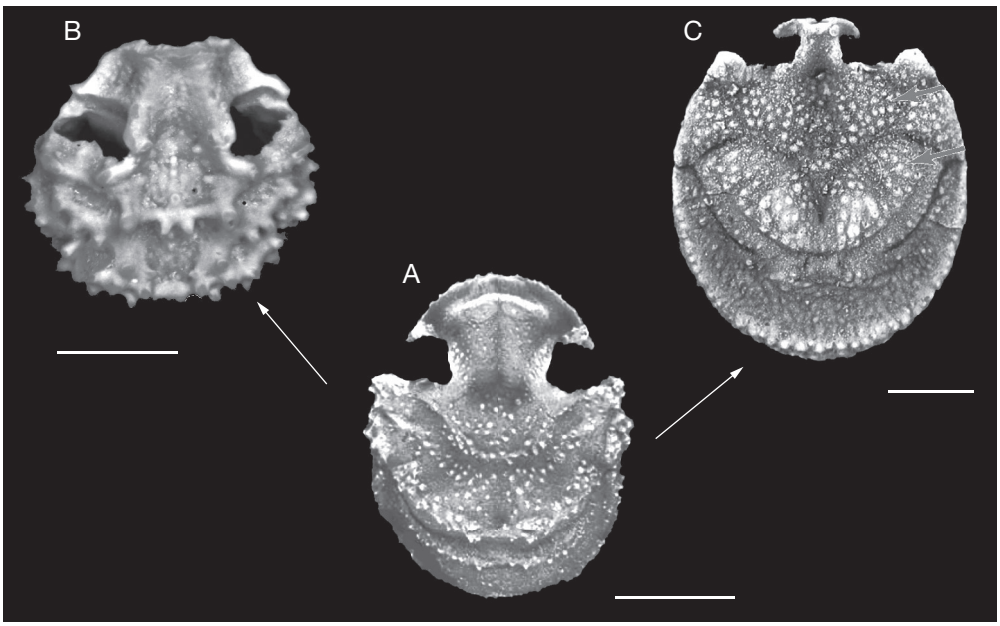


FIG. 4. — All currently known members (holotypes) of the family Alsasuacarididae Van Bakel, Jagt, Fraaije & Artal, 2011, with indication of possible evolutionary relationships: **A**, *Alsasuacaris nostradamus* Van Bakel, Jagt, Fraaije & Artal, 2011, Albian, north-east Spain; **B**, *Alsasuacaris dirkeysermansi* 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.

Acknowledgements
We thank Diederik ('Dirk') Eysermans of Vosselaar (Belgium), for donating the studied specimen. The journal reviewers, Dr Carrie E. Schweitzer (Kent State University, Kent, Ohio, United States) and Dr Günter Schweigert (Staatliches Naturhistorisches Museum, Stuttgart, Germany) are gratefully acknowledged for their valued input.

REFERENCES

Baron-Szabo R. C. & Leloux J. 2024. — Distribution and palaeoecology of scleractinian corals during the Maastrichtian (Late Cretaceous), *in* Jagt J. W. M., Fraaije R. H. B., Jagt-Yazykova E. A. & Vellekoop J. (eds), Aspects of Maastrichtian (Late Cretaceous) palaeontology and stratigraphy. *Netherlands Journal of Geosciences* 103: e14. https://doi.org/10.1017/njg.2024.7

Bicknell R. D. C., Klompmaker A. A., Edgecombe G. D., Mccoy V. E., Young A., Lauer B., Lauer R. & Cuomo C. 2025. — Gregarious behaviour in Carboniferous cyclidan crustaceans. *Biology Letters* 21: 20240734. https://doi.org/10.1098/rsbl.2024.0734

Brambilla S., Garassino A., Pasini G. & Teruzzi G. 2002. — Studies on Permo-Trias of Madagascar. 6. First record of Cycloidea from the Lower Triassic (Olenekian) of Ambilobe´ region (Nw Madagascar). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milan* 143: 105-115.

Collins J. S. H. & Breton G. 2009. — New crabs (Crustacea, Decapoda) from the Cenomanian stratotype (western Paris Basin, France). *Bulletin of the Mizunami Fossil Museum* 35: 43-50.

Dzik J. 2008. — Gill structure and relationships of the Triassic cycloid crustaceans. *Journal of Morphology* 269: 1501-1519. https://doi.org/10.1002/jmor.10663

Feldmann R. M. & Schweitzer C. E. 2019. — The enigmatic Cyclidae (Pancrustacea): morphological terminology and family-level classification. *Journal of Crustacean Biology* 39: 617-633. https://doi.org/10.1093/jcbiol/ruz053

Fraaye R. H. B. 1996. — A new Tethyan migrant: *Cretachlorodius enciensis* n. gen., n. sp. (Crustacea, Decapoda), from the Maastrichtian type area. *Journal of Paleontology* 70: 293-296. https://doi.org/10.1017/s0022336000023374

Fraaye R. H. B. 1997. — Swimming crabs from the Maastrichtian type area: radiation, migration, competition and extinction. *Acta Geologica Polonica* 47 (for 1996): 269-278.

Fraaije R. H. B. 2003. — Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. *Contributions to Zoology* 72: 119-130. https://doi.org/10.1163/18759866-0720203010

Fraaije R. H. B., Schram F. R. & Vonk R. 2003. — *Maastrichtiocaris rostratus* new genus and species, the first Cretaceous cycloid. Journal of Paleontology 77: 386-388. https://doi.org/10.1666/0022-3360(2003)077<0386:MRNGAS>2.0.CO;2

Gemmellaro G. G. 1890. — I crostacei dei calcari con *Fusulina* della valle del fiume Sosio nella Provincia di Palermo in Sicilia. *Memorie della Società Italiana delle Scienze* 8 (1): 1-40.

Kornicker L. S., Van Bakel B. W. M., Fraaije R. H. B. & Jagt J. W. M. 2006. — Revision of Mesozoic Myodocopina (Ostracoda) and a new genus and species, *Mesoleberis hollandica*, from the Upper Cretaceous of Belgium and The Netherlands. *Zootaxa* 1246: 15-54. https://doi.org/10.5281/zenodo.172935

Liebau A. 1978. — Paläobathymetrische und paläoklimatische Veränderungen im Mikrofaunenbild der Maastrichter Tuffkreide. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 157: 119-122.

Mitchell S. F., Steuber T. & Jagt J. W. M. 2024. — Comment on Dubicka *et al.* (2024): Multi-proxy record of the mid-Maastrichtian event in the European Chalk Sea: paleoceanographic implications. *Gondwana Research* 129: 1-22. *Gondwana Research* 134: 410-412. https://doi.org/10.1016/j.gr.2024.07.012

Müller A. H. 1955. — Über einen Neufund von *Halicyne plana* und die systematische Stellung von *Halicyne* (Crustacea?). *Paläontologische Zeitschrift* 29: 131-135.

Müller O. F. 1785. — *Entomostraca seu Insecta Testacea, quae in aquis Daniae et Norvegiae reperit, descripsit et iconibus illustravit Otho Fridericus Müller*. F.W. Thiele, Leipzig/København (Lipsiae/Havniae), 134 p.

Mychko E. V. 2022a. — Amazing cyclidans — the witnesses of the Great Extinction: Part I. *Priroda* 9: 12-23 [in Russian]. https://doi.org/10.7868/S0032874X22090022

Mychko E. V. 2022b. — Amazing cyclidans — the witnesses of the Great Extinction: Part II. *Priroda* 10: 26-35 [in Russian]. https://doi.org/10.7868/S0032874X22100039

Mychko E. V. 2025. — The first Triassic cyclidan (Multicrustacea: Cyclida) from Russia. *Historical Biology*. https://doi.org/10.1080/08912963.2025.2592987

Mychko E. V. & Alekseev A. S. 2018. — Two new genera of Cyclida (Crustacea: Maxillopoda: Branchiura) from the Cisuralian (Lower Permian) of southern Urals. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 289: 23-34. https://doi.org/10.1127/njgpa/2018/0747

Mychko E. V., Alekseev A. S. & Schweitzer C. E. 2025. — New Carboniferous and Permian cyclidans (Multicrustacea: Cyclida) from the Urals (Russia): unpublished collection of B.I. Chernyshev at the Cnigr museum in St. Petersburg. *Journal of Paleontology* 99 (3): 567-581. https://doi.org/10.1017/jpa.2024.85

Packard A. S. Jr 1885. — On the Carboniferous xiphosurous fauna of North America. *Memoirs of the National Academy of Sciences* 3: 143-157.

Phillips J. 1836. — *Illustrations of the Geology of Yorkshire*. II. – *The Mountain Limestone District*. London, John Murray, 331 p.

Regier J. C., Shultz, J. W., Zwick, A., Hussey A. B., Ball B., Wetzer R., Martin J.W. & Cunningham C. W. 2010. — Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* 463 (7284): 1079-1083. https://doi.org/10.1038/nature08742

Schram F. R. & Koenemann S. 2022. — Cyclida, *in* Schram F. R. & Koenemann S. (eds), *Evolution and Phylogeny of Pancrustacea: a Survey of Scientific Method*. Oxford University Press, Oxford: 229-238. https://doi.org/10.1093/oso/9780195365764.003.0018

Schram F. R., Vonk R. & Hof C. J. 1997. — Mazon Creek Cycloidea. *Journal of Paleontology* 71: 261-283. https://doi.org/10.1017/s0022336000039172

SCHRAM F. R., BOERE A.C. & THOMAS N. 2006. — Cycloidea of the Mississippian Bear Gulch Limestone of central Montana. *Natural History Museum of Los Angeles County Contribution to Science* 504: 1-8.

SCHWEIGERT G. 2007. — *Juracyclus posidoniae* n. gen. and sp., the first cycloid arthropod from the Jurassic. *Journal of Paleontology* 81 (1): 213-215. https://doi.org/10.1666/0022-3360(2007)81[213:jpngas]2.0.Co;2

SCHWEITZER C. E., MYCHKO E. V. & FELDMANN R. M. 2020. — Revision of Cyclida (Pancrustacea, Multicrustacea), with five new genera. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 296 (3): 245-303. https://doi.org/10.1127/njgpa/2020/0905

SCHWEITZER C. E., MYCHKO E. V. & LEHNERT M. S. 2025. — North American midcontinental cyclidans (Pancrustacea, Multicrustacea: Cyclida) revisited. *Journal of Crustacean Biology* 45 (3). https://doi.org/10.1093/jcbiol/ruaf045

SUN X., SCHWEITZER C. E., DAI X., YUAN Z., BAI R., TIAN L., CHU D., GUO W., CHEN J., LIU X., JIANG S., LIU Y., LI Z. & SONG H. 2025. — A new Induan (Early Triassic, Dienerian) cyclidan crustacean from the Guiyang biota. *Papers in Palaeontology*, 11 (6): e70052. https://doi.org/10.1002/spp2.70052

TANG H. Y., MYCHKO E. V., FELDMANN R. M., SCHWEITZER C. E., SHAARI, H. & SONE M. 2021. — *Malayacyclus* gen. nov., the first southeast Asian Cyclida (Crustacea) from the Early Carboniferous of Terengganu, Malaysia. *Geological Journal* 2021: 1-9. https://doi.org/10.1002/gj.4128

TRAUTH F. 1918. — Über einige Krustazeenreste aus der alpinmediterranen Trias. *Annalen des Kaiserlichen und Königlichen Naturhistorischen Hofmuseums in Wien* 32: 172-192.

TRÜMPY R. 1957. — Ein Fund von *Halicyne* (Crustacea incertae sedis) im mittleren Muschelkalk des Wutachtales. *Eclogae geologicae Helvetiae* 23: 544-553.

VAN BAKEL B. W. M., JAGT J. W. M., FRAAIJE R. H. B. & ARTAL P. 2011. — A new family, genus and species of cyclid (Crustacea, Branchiura, Cyclida) from mid-Cretaceous reefal deposits in northern Spain. *Bulletin of the Mizunami Fossil Museum* 37: 47-49.

ZIJLSTRA J. J. P. 1994. — Sedimentology of the Late Cretaceous and Early Tertiary (tuffaceous) chalk of northwest Europe. *Geologica Ultraiectina* 119: 1-192.

ZRZAVÝ J. & ŠTYS P. 1997. — The basic body plan of arthropods: insights from evolutionary morphology and developmental biology. *Journal of Evolutionary Biology* 3: 353-367. https://doi.org/10.1046/j.1420-9101.1997.10030353.x

Submitted on 15 December 2025;
accepted on 26 January 2026;
published on 5 November 2026.