



## Original article

# New genera and species of glaessneropsid crabs from the Lower and Middle Jurassic of France and Germany–Austria, and reconsolidation of *Charassocarcinus* Van Straelen, 1925 ☆,☆☆

Barry W.M. van Bakel <sup>a,b,\*</sup>, Danièle Guinot <sup>c</sup><sup>a</sup> Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, the Netherlands<sup>b</sup> Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands<sup>c</sup> Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CP 53, 57 rue Cuvier, F-75231 Paris cedex 05, France

## ARTICLE INFO

## Article history:

Received 17 December 2022

Accepted 1 May 2023

Available online 14 July 2023

## Keywords:

Glaessneropsidae  
Homolodromiidae  
New taxa  
Callovian  
Mesozoic  
Calvados

## ABSTRACT

A new genus, *Meroncarcinus*, and two new species, *M. boursicoti* and *Verrucarcinus marsae*, are described from Callovian (Middle Jurassic) deposits of Calvados and Maine-et-Loire, France. New material of the type species of the genus *Verrucarcinus*, *V. torosus*, is examined, which improves our understanding of the peculiar morphology of this group of crabs. A new genus and species, *Vilsercarcinus keuppi*, is recognised from Lower–Middle Jurassic strata of Germany–Austria. *Charassocarcinus*, a Lower–Middle Jurassic crustacean genus of doubtful taxonomic affinity, is revived and here assigned to the Glaessneropsidae. All of this material forms the basis for a re-examination of the Glaessneropsidae, and an enhanced diagnosis is compiled. The morphology of Glaessneropsidae, one of the oldest known brachyuran families, is discussed; its complex orbital structure is remarkable for such an ancient group of crab and raises questions about its relationship with the basal brachyuran group Homolodromioidea. A solid support for a suprafamilial rank for the Glaessneropsidae is lacking.

© 2023 The Author(s). Published by Elsevier Masson SAS. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

The identification of Middle Jurassic (Callovian) crabs from Saint-Laon and Méron near Montreuil-Bellay, in the Centre–West of France (Nouvelle-Aquitaine region) led us to study the genus *Verrucarcinus* Schweitzer and Feldmann, 2009, and in particular the unique combination of certain characters: the well-developed orbital structures; the wide cervical, postcervical and branchial grooves; and a spatulate rostrum with a triangular axial swelling. The orbital structures in *Verrucarcinus* are remarkable in nature and complexity, a trait not expected in a representative of one of the oldest known brachyuran groups.

Another species of the studied crabs is differentiated by a considerable set of characters, allowing the erection of a new genus within the same family, Glaessneropsidae Patruilius, 1959. In our comparison with other Jurassic decapods from France, we further found that *Charassocarcinus* is morphologically reminiscent of *Verrucarcinus*, but its inclusion in Glaessneropsidae needs to be verified.

The earliest known crabs are of Early and Middle Jurassic age; this is accepted as the dawn era for Brachyura (Jagt et al., 2015). In general, especially Early but also Middle Jurassic crabs are rare, as outlined by Krobicki and Zatoń (2008). Crabs of this age are found in deposits of shallow to moderately deep environments (Müller et al., 2000). Middle Jurassic sediments and outcrops are common in France, leading to several records of Middle Jurassic brachyurans.

From the Bajocian, the following brachyurans are known from France:

- *Abyssophtalmus hebes* (von Meyer, 1840, as *Prosopon hebes*), from the lower Bajocian 'Oolithe ferrugineuse inférieure' near Thionville (Moselle Department, Lorraine, eastern France) (von Meyer, 1840);
- *Planoprosopon major* (Hée, 1924, as *Prosopon major*), from the uppermost Bajocian reefal facies, 'zone à *Stomechinus bigranularis*' at May-sur-Orne (Calvados, north-western France) (Hée, 1924);
- *Pithonoton incisus* Van Straelen, 1925, from the same locality as *Planoprosopon major* (Van Straelen, 1925), late Bajocian (*subfurcatum* ammonite Zone);

\* Corresponding editor: Claude Monnet.

\*\* urn:lsid:zoobank.org:pub:3A5D840B-5B55-4553-87B0-BBA0E3D78DBC.

\* Corresponding author.

E-mail address: [b.w.m.vanbakel@uu.nl](mailto:b.w.m.vanbakel@uu.nl) (B.W.M. van Bakel).

- *Tanidromites maerteni* Fraaije, Van Bakel, Guinot and Jagt, 2013, from the lower upper Bajocian (*niortense* ammonite Zone) of Maizet (Calvados, north-western France) (Fraaije et al., 2013);
- *Bajoprosopon piardi* Van Bakel, Maerten, Jagt and Fraaije, 2021, from the upper Bajocian 'Oolithe ferrugineuse de Bayeux' Fm., Les Fours à Chaux (Calvados, north-western France) (Van Bakel et al., 2021).

From the French Bathonian, the following brachyuran crabs have been recognised:

- *Tanidromites raboeufi* Robin, Van Bakel, d'Hondt and Charbonnier, 2015, from the upper Bathonian (*Retrocostatum* Biozone), La Bigotière, Crannes-en-Champagne (Sarthe, France) (Robin et al., 2015);
- *Abyssopthalmus langrunensis* (Hée, 1924, as *Pithonoton Langrunensis*) from the 'Grande Oolithe' of Langrune (Calvados, north-western France), based on a specimen previously reported as *Pithonoton Meyeri* by Morière (1864: pl.7, figs. 1, 2); also reported from the upper Bathonian of Ranville (Calvados, north-western France) (Hée, 1924; Pezy and Gendry, 2016);
- *Pithonoton moutieri* (Hée, 1924, as *Prosopon Moutieri*) from the upper Bathonian of Moulit (Hée, 1924; Van Straelen, 1925) and Ranville (Pezy and Gendry, 2016), both Calvados, north-western France;
- *Homolus auduini* Eudes-Deslongchamps, 1835, Bathonian, Ranville (Calvados, north-western France) (Eudes-Deslongchamps, 1835; Schweitzer and Feldmann, 2010).

From the Callovian of France, three crabs were described from lower Callovian (*gracilis* ammonite Zone) oolitic limestones of Montreuil-Bellay area, Maine-et-Loire (north-western France) (Crônier and Boursicot, 2009):

- *Abyssopthalmus mainense* (Crônier and Boursicot, 2009, as *Nodoprosopon? mainense*);
- *Abyssopthalmus bellaii* (Crônier and Boursicot, 2009, as *Nodoprosopon? bellaii*);
- *Tanidromites montreuilense* Crônier and Boursicot, 2009.

Apart from the French records, Callovian crabs have been rarely reported so far; Krobicki and Zatoń (2008) pointed out that our knowledge of crabs of Callovian age is extremely poor. The worldwide Callovian transgression resulted in the formation of sponge-microbial mounds and coral reefs on the northern margin of the Tethys Ocean during the Late Jurassic to Early Cretaceous (Oxfordian-Berriasian) times, favouring the diversification of primitive crabs through the development of numerous cryptic habitats (Müller et al., 2000; Krobicki and Zatoń, 2008; Schweigert and Koppka, 2011). But during the Callovian itself, of which sediments are generally very rich in ammonites, only a few brachyuran crabs are known. Krobicki and Zatoń (2008: table 1) reported *Pithonoton* sp. and *Nodoprosopon* sp. from the early Callovian (*koenigi* or *calloviense* ammonite Zone) of the Kraków region, southern Poland. *Tanidromites lithuanicus* Schweigert and Koppka, 2011 was described from the middle Callovian *coronatum* ammonite Zone, Papartinė (Popilani, Lithuania) (Schweigert and Koppka, 2011). These authors also described a single carapace from a Pleistocene glacial boulder of middle Callovian origin from north-eastern Germany: *Planoprosopon quadratum* Schweigert and Koppka, 2011.

In the present paper we describe a new genus, *Meroncarcinus*, and two new species, *M. boursicoti* and *Verrucarcinus marsae*, from the lower-middle Callovian of France, as well as a new genus and species, *Vilsercarcinus keuppi*, from the late Toarcian-Callovian (precise level unknown) of Germany-Austria. These records signif-

icantly add to the knowledge of fossil crabs from the lower-middle Jurassic, and call for a discussion on glaessnerosid crabs.

## 2. Localities and stratigraphy

The material studied in the present paper originates from various localities in France, Germany, and Austria (Fig. 1).

**Saint-Laon, France.** The quarry C.S.L. ('Carrières St Laon') is situated 1.5 km south of Saint-Laon, Vienne department, between Angers and Poitiers. The small quarry yields oolitic lower and middle Callovian limestones, in particular rich in ammonites. Only one crab specimen from this locality was collected by C. Mars.

**Méron, France.** This locality is situated in the industrial area of Méron, near Montreuil-Bellay, Maine-et-Loire department, France (Crônier and Boursicot, 2009). There, Middle Callovian limestone beds of the *anceps* ammonite Zone, *tyranniformis* Subzone, *richei* Horizon, were excavated. The limestones are deposited in a non-reefal, rather deep palaeoenvironment, with low energy bottom settings. Common macrofaunal elements are ammonites, bivalves, and brachiopods. The crab specimens from this locality were collected by P.-Y. Boursicot.

**May-sur-Orne, France.** The historical old quarry of May-sur-Orne, south of Caen (Calvados department, France), is a geologically complex locality. On a massive base of Ordovician sandstones, the Pliensbachian bedded limestones are overlaid by Bajocian limestones; the Aalenian and Toarcian deposits are condensed (Gabilly and Rioult, 1971). The totality of the Jurassic sediments is ca. 2 m thick. Eudes-Deslongchamps (1877) described *Stenochirus? mayalis* from the *Ludwigia murchisonae* ammonite Zone, of late Aalenian age. Hée (1924) described *Prosopon major* from the uppermost Bajocian reef facies, 'zone à *Stomechinus bigranularis*'; Van Straelen (1925) described *Pithonoton incisus* from the Late Bajocian *subfurcatum* ammonite zone; and Van Straelen (1925: p. 356) mentioned *Goniodromites* sp. from the Aalenian 'zone à *Lioceras bradfortense*' [sic] of this locality. However, it is unclear whether these crab specimens were collected in situ, and at what precise level. The material described in these papers is lost, destroyed during the Second World War (Bigot, 1945); the specimens and the surrounding matrix can no more be examined. Theoretically, the material described at this site could be Pliensbachian to Bajocian in age.

**Tuttlingen, Germany.** The 'Eichen' quarry, northwest of Tuttlingen, Baden-Württemberg, Germany, shows thick-bedded cephalopod-bearing limestones with only thin marly layers, of the 'Untere-Felsenkalke-Fm.' (formerly 'Weißjura delta'), which is late Kimmeridgian in age (Schmid et al., 2005). The crabs described in this paper were collected from the upper levels by R. Fraaije.

**Ernstbrunn, Austria.** The Ernstbrunn locality consists of several quarries near Ernstbrunn and near the town of Dörfles (near Ernstbrunn, Niederösterreich), ca. 50 km north of Vienna, Austria. Most specimens of decapod crustaceans in the NHMW collections originate from the Ernstbrunn II, Dörfles I and V quarries (Fraaije et al., 2019: p. 258) but the exact locality and level of the majority of specimens is not recorded. For example, Schweitzer and Feldmann (2008, 2009) described many new primitive brachyuran crabs from the Ernstbrunn localities and postulated, based on ammonite stratigraphy (Zeiss, 2001), that the sediments exposed in Ernstbrunn are middle to late Tithonian (latest Jurassic) in age. Galatheid anomurans from the Ernstbrunn localities have been described by Robins et al. (2012, 2013, 2016). Paguroid anomurans have been described by Fraaije et al. (2019), to which further reference is made for a detailed overview of localities and stratigraphy. Note that Moshhammer and Schlagintweit (1999) stratigraphically studied the benthic Foraminifera and dasycladalean algae, and found middle to late Tithonian up to middle Berriasian (early Cretaceous) sediments.



**Fig. 1.** Map of western Central Europe, showing the localities of material referred to in the text. **1.** May-sur-Orne, Calvados. **2.** Méron, Maine-et-Loire. **3.** Saint-Laon, Vienne. **4.** Tuttlingen, Baden-Württemberg. **5.** Oberjoch, Germany-Austria. **6.** Ernstbrunn, Niederösterreich. Scale bar: 200 km.

**Germany-Austria.** Only one specimen studied here comes from the ‘Vilser Kalk’ debris of the southwestern slope of the Sorgschrofen near Oberjoch, a 1635 m high mount near the boundary between Germany (Bavaria) and Austria (Tyrol) (H. Keupp, pers. comm. July 2021). [Krobicki and Zatoń \(2016: 710\)](#) discussed *Abyssopthalmus? vilsense* [Stolley, 1914](#), from the Vilser Alps, Vils, Austria, and concluded a ‘most probable’ early Callovian age for this species, based on the co-occurrence of ammonites and brachiopods. The geology of the ‘Vilser Kalk’ is complex, spanning the Lower and Middle Jurassic, from late Toarcian to Callovian ([Heissel, 1937](#); [Gschwend, 1988](#); [Leuprecht and Moshhammer, 2010](#); G. Schweigert pers. comm. January 2023).

### 3. Systematic palaeontology

We follow the higher classification of the Brachyura advocated by [Guinot et al. \(2013\)](#).

Thoracic somites are numbered from 1 to 8; pleonal somites are numbered from 1 to 6; thoracic sternal sutures are designated by the number of the two thoracic sternites that they involve, and thus are numbered from 1/2 to 7/8.

**Repositories and institutional abbreviations:** **SNSB-BSPG:** Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **C.C.M.:** Carter County Museum, Ekalaka, Montana, USA; **IGPUW:** Institute of Geology, University of Warsaw, Poland; **IGR:** Institutul Geologic al României, Bucharest, Romania; **LPBIIlart:** Laboratory of Paleontology, Department of Geology and Paleontology, University of Bucharest, Romania; **MAB k.:** Oertijdmuseum, Boxtel, the Netherlands; **MNH.N.F.:** Collection de Paléontologie, Muséum national d’Histoire naturelle, Paris, France.

**Abbreviations used in the text:** CL: carapace length (as preserved); CW: carapace width (as preserved); G2: second gonopod;

mxp1, mxp3: first or third maxillipeds, respectively; P1–P5: pereopods 1–5, respectively.

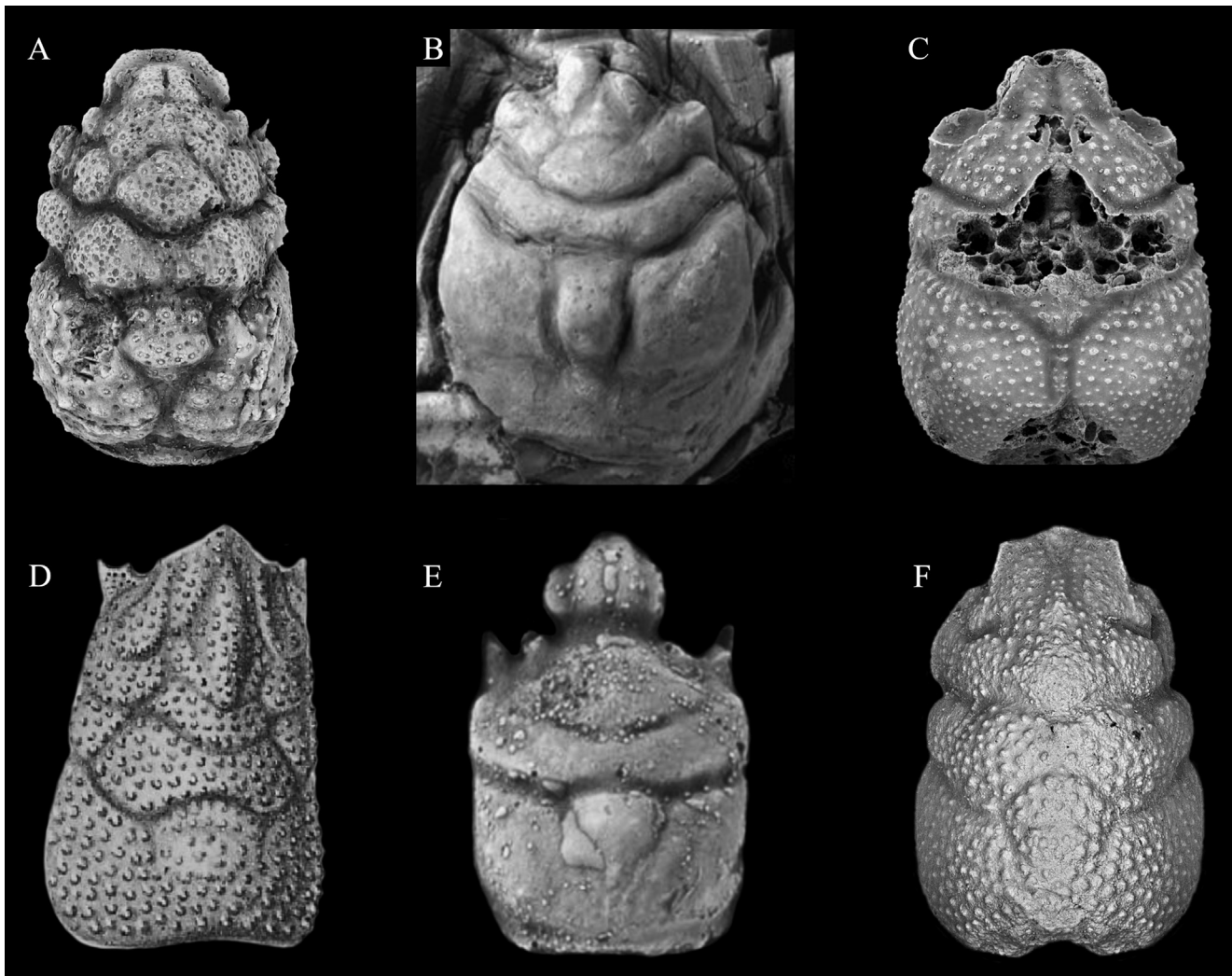
Phylum Arthropoda [von Siebold, 1848](#)  
 Subphylum Crustacea [Brünnich, 1772](#)  
 Class Malacostraca [Latreille, 1802](#)  
 Order Decapoda [Latreille, 1802](#)  
 Infraorder Brachyura [Latreille, 1802](#)  
 Family Glaessneropsidae [Patrulius, 1959](#)

**Type genus:** *Glaessneropsis* [Patrulius, 1959](#), by original designation.

**Included genera** ([Fig. 2](#)): *Charassocarcinus* [Van Straelen, 1925](#); *Ekalakia* [Bishop, 1976](#); *Glaessneropsis* [Patrulius, 1959](#); *Meroncarcinus* nov. gen.; *Verrucarcinus* [Schweitzer and Feldmann, 2009](#); *Vilsercarcinus* nov. gen.

**Diagnosis:** Carapace tumid in longitudinal and transverse sections, elongated, longer than wide, suboval in outline, widest at posterior branchial region, may be weakly constricted at epibranchial region; lateral margins undefined, rounded; hepatic and epibranchial margins may be developed into spine or tubercle. Dorsal carapace surface densely granular, central and anterior regions may have low nodes or tubercles. Surface of carapace tripartite, crossed by well-separated, complete, distinct cervical and branchial grooves. Cervical groove wide, divided into three arcs; branchial grooves at steeper angle. Fronto-orbital margin wide; rostrum wide, about one third of maximum carapace width, complex, much projected beyond orbits, orbital margin oblique to subhorizontal, with two coarse, shallow notches; orbital fossae large, subdivided by arched rim; orbits directed anteriorly or weakly anterolaterally. Anterior carapace regions usually inflated; mesogastric region completely delineated, with large, broadly triangular base; protogastric region not completely subdivided by oblique groove; metagastric region as distinct lobe, commonly axially restricted; cardiac region well defined, inverted triangular or





**Fig. 2.** Genera included herein in the Glaessneropsidae [Patrulius, 1959](#). **A.** *Verrucarcinus* [Schweitzer and Feldmann, 2009](#); *V. torosus* ([von Meyer, 1860](#)). **B.** *Ekalakia* [Bishop, 1976](#); *E. lamberti* [Bishop, 1976](#), holotype, C.C.M. 5590, modified from [Feldmann et al. \(2008: fig. 1.1\)](#). **C.** *Meroncarcinus* nov. gen.; *M. boursicoti* nov. gen., nov. sp. (this study). **D.** *Charassocarcinus* [Van Straelen, 1925](#); *C. mayalis* ([Eudes-Deslongchamps, 1877](#)), Pliensbachian-Bajocian (precise level unknown), May-sur-Orne, Calvados (northwest France), modified from [Eudes-Deslongchamps \(1877: pl. 1, fig. 10\)](#). **E.** *Glaessneropsis* [Patrulius, 1959](#); *G. heraldica* ([Moericke, 1897](#)), holotype, SNSB-BSPG AS III 306, Tithonian Štramberk Limestone, Štramberk, Czech Republic, modified from [Schweitzer and Feldmann \(2009: fig. 4.1\)](#). **F.** *Vilsercarcinus* nov. gen.; *V. keuppi* nov. gen., nov. sp. (this study). Not to scale.

scutiform, completely delineated. Posterior margin sinuous or W-shaped (or ‘biconvex’), with concave median portion, and occupying entire carapace width. Elements other than carapace unknown.

**Remarks:** The original diagnosis of Glaessneropsidae by [Schweitzer and Feldmann \(2009: p. 83\)](#) was based on two genera: *Glaessneropsis* and *Verrucarcinus*, but the elevation of the family to a higher rank, Glaessneropsoidea, and the inclusion of several other genera ([Schweitzer et al., 2012](#)) may challenge the nature of its distinctive morphological characters and composition (see below for further discussion on the family). The revision of the genus *Verrucarcinus*, with the addition of a new species, is a first step to better delineate Glaessneropsidae.

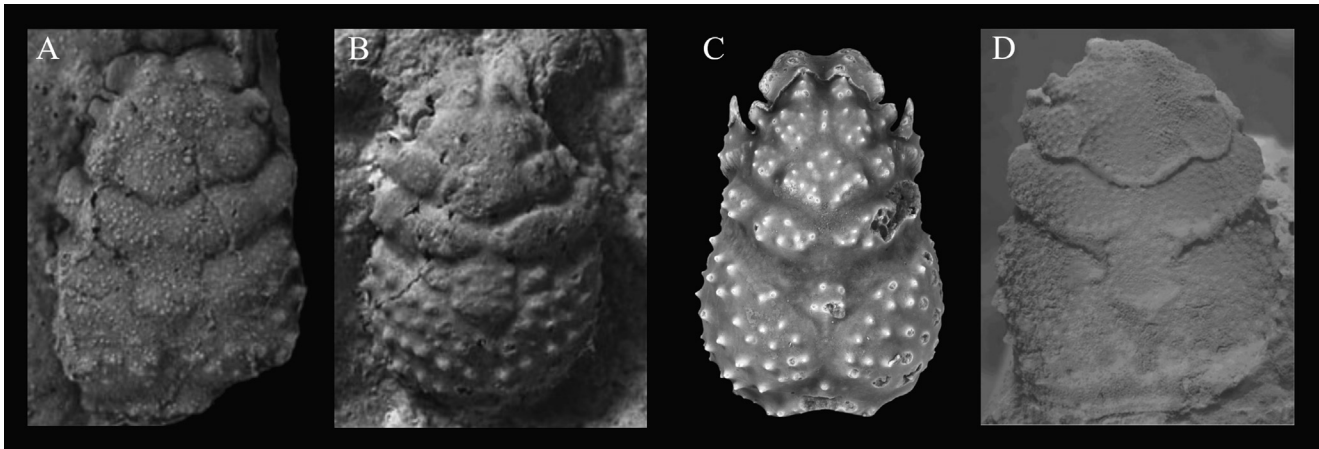
Based on morphological similarity to *Verrucarcinus* in particular (see discussion below), *Charassocarcinus* is here added to the Glaessneropsidae, together with two new genera: *Meroncarcinus* and *Vilsercarcinus*.

Genus *Verrucarcinus* [Schweitzer and Feldmann, 2009](#).

**Type species:** *Prosopon torosum* [von Meyer, 1860](#), by original designation.

**Included species** ([Fig. 3](#)): *Verrucarcinus cutifrontis* [Frantescu, 2011](#); *Verrucarcinus marsae* nov. sp.; *Verrucarcinus ordinatus* (Collins in [Collins and Wierzbowsky, 1985](#), as *Nodoprosopon ordinatum*); *Verrucarcinus torosus* ([von Meyer, 1860](#), as *Prosopon torosum*).

**Diagnosis** (modified after [Schweitzer and Feldmann, 2009: p. 89](#)): Carapace strongly convex in longitudinal and transverse sections, longer than wide, CL/CW = 1.5, outline shape pyriform, widest at posterior branchial regions about three-quarters the distance posteriorly on carapace; dorsal regions inflated to bulbous, ornamented with large granules, especially large on branchial regions. Lateral margins undefined, completely rounded. Rostrum, which occupies entire front, wide, about half maximum carapace width, (sub)triangular, long downturned, projected well in advance of orbits, flanged, lined with small spinules, with single (axial) or paired (admedial) longitudinal swelling(s). Eyestalk appearing to have arisen beneath rostrum. Fronto-orbital width 72–80% maximum carapace width; orbit directed forward, bounded on inner angle by rostrum; upper orbital margin formed by subrectangular intraorbital spine bounded by deep, open fissures; fissures and spine directed anterolaterally; outerorbital angle formed by



**Fig. 3.** All known species of *Verrucarcinus* Schweitzer and Feldmann, 2009. **A.** *Verrucarcinus torosus* (von Meyer, 1860), neotype SNSB-BSPG 1881 IX 686, Kimmeridgian (Upper Jurassic), Bavaria (Germany), photograph from Schweitzer and Feldmann (2009). **B.** *V. ordinatus* (Collins in Collins and Wierzbowsky, 1985), holotype IGPUW/C/1/6, Oxfordian (Upper Jurassic), Silesia (Poland), photograph from Schweitzer and Feldmann (2009). **C.** *V. marsae* nov. sp., holotype MNHN.F.A86392, Callovian (Middle Jurassic), Calvados (France). **D.** *V. cutifrontis* Frantescu, 2011, holotype LPBillart-160, Oxfordian-Kimmeridgian (Upper Jurassic), Dobrogea (Romania), photograph from Frantescu (2011). Not to scale.

triangular, forward-directed spine that wraps around laterally into cup-shaped structure. Anterior mesogastric process narrow; posterior mesogastric region large, rhomboidal; metagastric region large, wide, bilobed; cervical and branchial grooves well developed, complete, well separated; postcervical groove absent. Cardiac region small, scutiform, positioned well anterior to posterior margin. Posterior margin W-shaped, nearly as wide as carapace.

**Remarks:** *Verrucarcinus* is only known from the Jurassic, and from the oldest to the youngest: Callovian of France (present study); Oxfordian of France (Gendry et al. in prep.) and Poland (Collins in Collins and Wierzbowsky, 1985); Kimmeridgian of Germany (Schweigert et al., 2016; Schweigert and Kuschel, 2018) and Romania (Frantescu, 2011); and Tithonian of Czech Republic and Austria (Schweitzer and Feldmann, 2009; and present study).

*Verrucarcinus* species are readily recognised by their conspicuously convex, pyriform, and coarsely granular carapaces; prominent, wide, spatulate and downturned rostrum; and small but complex orbits. Their bulbous, elongated, pyriform appearance and the shape of rostrum are reminiscent of some majoid crabs, such as the extant inachoidid *Esopus* A. Milne-Edwards, 1875 (Guinot and Van Bakel, 2020). Guinot (2019: p. 749) noted the resemblance of *Verrucarcinus* with the Eocene *Wilsonimaia* Blow and Manning, 1996, referred to the Majidae Samouelle, 1819. However, we do not consider Glaessneropsidae as closely related to the Majoidea Samouelle, 1819. The degree of branchial condensation (i.e., the distance between the cervical and branchial grooves, and their separation from each other) in *Verrucarcinus* and other Glaessneropsidae (e.g., *Charassocarcinus*, *Ekalakia*, *Glaessneropsis*, and *Vilsercarius* nov. gen.) is weak, which is considered a basal trait (for discussion, see Van Bakel et al., 2020: p. 13). For example, the weak branchial condensation in *Verrucarcinus* is approximately similar to that of, e.g., Homolodromiidae. In a cladistic analysis and phylomorphospace, *Verrucarcinus* showed to “exhibit plenty of primitive character states” (Van Bakel et al., 2020: p. 19).

In general appearance, *Verrucarcinus* is reminiscent of the Viaiidae Artal, Van Bakel, Fraaije, Jagt and Klomp maker, 2012 (Artal et al., 2012: figs. 1, 2), but members of the Viaiidae show some highly peculiar characters: a pointed rostrum, laterally placed orbits, and deep concavities on the lateral sides of the carapace. Artal et al. (2012: p. 400) noted for *Viaia* Artal, Van Bakel, Fraaije, Jagt and Klomp maker, 2012: “front triangular, fairly advanced, stout, massive, [...] ventral portion of front strongly downturned from the tip of the rostrum”. The same diagnosis was maintained

in a recent study (Gašparič et al., 2022) while adding two new species. The latter remarked (p. 9) the complexly formed orbits of Viaiidae, and general resemblance of Viaiidae with majoid crabs; they stated (Gašparič et al., 2022: p. 9) that it “seems possible that the palaeoecology of viaiids corresponded to that of certain extant majoids in that both inhabited branched coral thickets”.

Authorship of *Verrucarcinus torosus* (von Meyer, 1860, as *Prosopon torosum*) was hitherto regularly noted (e.g., Schweitzer and Feldmann, 2009; Frantescu, 2011) as from von Meyer, 1857 (and not 1860). However, von Meyer’s (1857) names must be considered *nomina nuda*, and 1860 is noted as the correct year of authorship (Van Bakel et al., 2021: p. 5). This applies in particular to *Prosopon torosum* von Meyer, 1860 (instead of 1857).

#### *Verrucarcinus torosus* (von Meyer, 1860)

##### Fig. 4

1857. *Prosopon torosum* - von Meyer, p. 555.

1860. *Prosopon torosum* - von Meyer, pl. 23, fig. 30.

1936. *Nodoprosopon beurleni* - Kuhn, fig. 1.

1985. *Nodoprosopon torosum* - Collins in Collins and Wierzbowski, pl. 1, fig. 7.

1988. *Nodoprosopon torosum* - Wehner, pl. 3, figs. 6-9.

2000. *Nodoprosopon torosum* - Müller et al., fig. 17H.

2007. *Prosopon torosum* - Schweitzer et al., fig. 2.10.

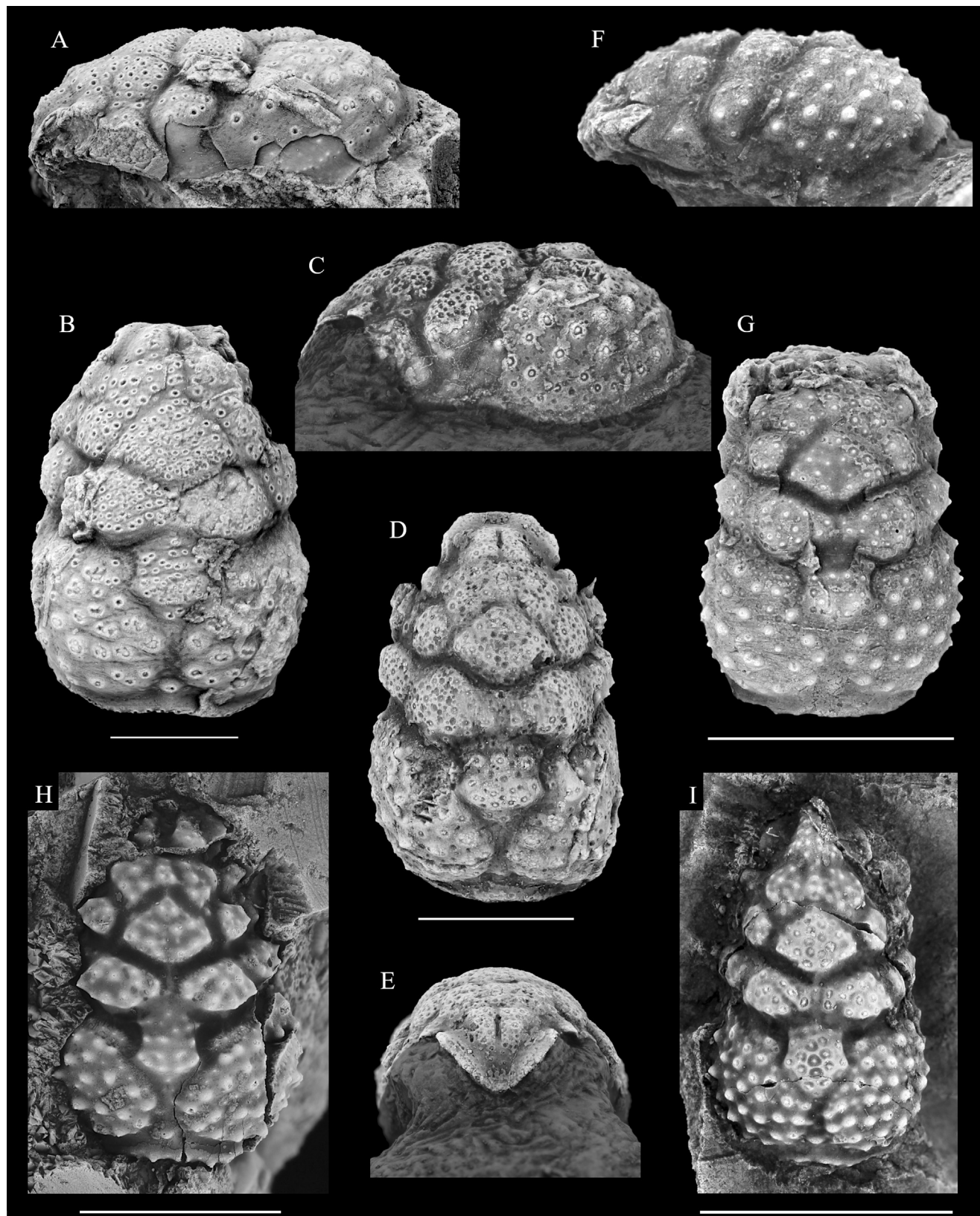
2009. *Verrucarcinus torosus* - Schweitzer and Feldmann, fig. 1.5 (neotype), figs. 5.1-2 and 5.4-5.

2018. *Verrucarcinus torosus* - Schweigert and Kuschel, fig. 21.

**Material and measurements:** Three isolated carapaces from the Kimmeridgian of the ‘Eichen’ quarry, NW of Tuttlingen, Germany: MAB k.3775 (CL: 12.6 mm, CW: 8.2 mm), MAB k.3776 (CL: 15.9 mm, CW: 10.9 mm), MAB k.3777 (CL: 7.6 mm, CW: 5.2 mm); these specimens are preserved with endocuticle. Two isolated carapaces preserved as internal moulds from the Tithonian of Ernstbrunn, Austria: NHMW 1990/0041/3476 (CL: 7.3 mm, CW: 4.3 mm), NHMW 2014/0194/0963 (CL: 9.1 mm, CW: 6.3 mm), and NHMW 1990/0041/3597 (fragment).

**Diagnosis:** Carapace strongly convex in longitudinal and transverse sections, longer than wide, CL/CW = 1.5, outline shape oval to pyriform, widest at posterior branchial regions, about three-quarters the distance posteriorly on carapace; dorsal regions inflated, ornamented with large granules, especially large on posterior branchial regions. Lateral margins undefined, completely rounded. Rostrum, which occupies entire front, wide, about half





**Fig. 4.** *Verrucarcinus torosus* (von Meyer, 1860). **A-G.** Kimmeridgian, 'Eichen' quarry, northwest of Tuttlingen (Germany). **A, B:** MAB k.3776 (CL: 15.9 mm, CW: 10.9 mm) in left lateral and dorsal views, respectively; **C-E:** MAB k.3775 (CL: 12.6 mm, CW: 8.2 mm) in left lateral, dorsal and frontal views, respectively; **F, G:** MAB k.3777 (CL: 7.6 mm, CW: 5.2 mm) in left lateral and dorsal view, respectively. Specimens preserved with endocuticle. **H, I.** Tithonian, Ernstbrunn (Austria). **H:** NHMW 2014/0194/0963 (CL: 9.1 mm, CW: 6.3 mm); **I:** NHMW 1990/0041/3476 (CL: 7.3 mm, CW: 4.3 mm). Specimens preserved as internal moulds. All specimens coated with ammonium chloride sublimate prior to photography. Scale bars: 5 mm.

the maximum carapace width, (sub)triangular, strongly downturned, projected in advance of orbits, flanged, lined with minute spinules, with closely paired longitudinal swellings. Fronto-orbital width approximately 80% of maximum carapace width; orbit directed forward; upper orbital margin formed by subrectangular intraorbital spine bounded by open fissures; fissures and spine directed anterolaterally; outerorbital angle formed by triangular, forward-directed spine that wraps around laterally into cup-shaped structure. Anterior mesogastric process short, narrow; posterior mesogastric region large, rhomboidal; metagastric region large, wide, bilobed; cervical and branchial grooves well developed, complete, well separated; cervical groove sinuous, formed by three arcs; postcervical groove absent. Cardiac region rather small, scutiform, positioned well anterior to posterior margin. Posterior margin wide, nearly as wide as carapace, rimmed with a line of minute spinules. Branchiostegite well-developed, conspicuously high; cervical and branchial grooves continuing and uniting on lateral carapace flanks.

**Remarks:** In *Verrucarcinus torosus*, the very tumid carapace with inflated regions and complex orbitofrontal structures is commonly left concealed by surrounding matrix at the front and lateral margins. For this reason, the rostrum, orbits, lateral margins and branchiostegites have been prepared in detail in the three studied German specimens, allowing a more confident diagnosis.

*Verrucarcinus torosus* is widespread: specimens are known from Germany (e.g., Wehner, 1988; present study), Poland (Wehner, 1988), France (Gendry et al., in prep.) and Austria (e.g., Schweitzer and Feldmann, 2009; present study). This species was previously reported from 'Eichen' by Wehner (1988: pp. 53, 131). The studied specimens from Austria are preserved without cuticle and, as a result, the grooves appear more acutely defined (Fig. 4(H, I)). Reference to Klompmaker et al. (2015) is made to illustrate their significant variation in appearance due to the presence and preservation differences of the cuticle; in addition, *V. torosus* appears to have some intraspecific variation of ornamentation.

*Verrucarcinus marsae* nov. sp.

Fig. 5

urn:lsid:zoobank.org:act:12CD70B4-29CE-4ACC-BA93-2723330  
D8EBA

**Derivation of the name:** Species dedicated to Chantal Mars (Sémelay, Bourgogne-Franche-Comté region, France), who collected the holotype and sole specimen.

**Material and measurements:** Holotype, MNHN.F.A86392 (CL: 16.2 mm, CW: 10.8 mm), a well-preserved dorsal carapace, collected in November 2016 in an ammonite-rich block of oolitic limestone, Callovian in age (lower and middle Callovian, *gracilis*, *anceps*, *coronatum* ammonite Zones) of the Saint-Laon quarry, Vienne Department, France. The specimen is 3D-preserved with portions of the cuticle only preserved on the front; MAB k.3778 represents a cast. The paratypes, MNHN.F.A86393 (CL: 14.2 mm, CW: 10.1 mm) and MAB k.3779 (CL: 14.0 mm, CW: 9.6 mm), both preserved as internal moulds, come from the locality of Méron near Montreuil-Bellay, Maine-et-Loire, France.

**Diagnosis:** A *Verrucarcinus* with conspicuously wide grooves on dorsal carapace and rostrum with wide median depression and dual prominent longitudinal ridges, dorsally visible. Coarse granulation consisting of spaced, sharp granules on all vaulted regions. Whole posterior margin distinctly concave, with a wide, depressed flange.

**Description:** Carapace longer than wide, CL/CW = 1.56, widest at posterior branchial region ca. 30% the distance posteriorly; carapace distinctly tumid in transverse and longitudinal cross-sections; regions well marked by deep, broad grooves; regions ornamented with coarse, subevenly spaced, sharp granules.

Fronto-orbital width ca. 72% maximum carapace width. Rostrum wide and prominent, projected well beyond orbits, strongly downturned distally, with bluntly triangular tip; lateral margins sinuous, basal part expanded; surface with two strong diverging ridges and deep axial depression.

Orbits small, directed forwards; supra-orbital margin with two distinct, sub-open, anteriorly and outwardly directed notches; intraorbital lobe subquadrate, directed anterolaterally; outerorbital spine sharp, anteriorly directed, with broad, flattened base extending outwards.

Lateral margins of carapace undefined, blunt and rounded, sinuous in dorsal view, constricted at the level of the two main grooves and divided into three bulbous portions by cervical and branchial grooves, epibranchial portion smallest; small spiniform granules along all three portions.

Posterior margin wide, slightly wider than orbitofrontal margin, concave, W-shaped; as a flange with thickened margin, lined with small granules on arched latero-posterior portions and larger granules along median portion.

Mesogastric region subdivided into two distinct portions: anterior mesogastric process relatively short, conspicuously narrow, tip pointed; posterior mesogastric region large, diamond-shaped, inflated, with chevron-shaped depression parallel to posterior margin. Protogastric regions elongated, subdivided into two subequal portions by oblique groove halfway pointing towards orbits. Metagastric region as two axially separated lobes; epibranchial region laterally inflated and granular. Cardiac region conspicuously small, isolated; posterior branchial region very large, obliquely elongated, surface undifferentiated, inflated, bulbous.

Grooves deep and very wide, smooth; cervical groove V-shaped, complete and continuous; branchial groove parallel to cervical groove, extremely wide, branching into narrower branchiocardiac grooves, bounding cardiac region, extending posteriorly into wide, deep groove, posteriorly bifurcate by axial intestinal tubercle, and continuing posterolaterally above posterior margin (flange).

**Remarks:** *Verrucarcinus marsae* nov. sp. differs from the type species *V. torosus* (Kimmeridgian, Bavaria, Germany; Tithonian, Stramberk, Czech Republic, and Ernstbrunn, Austria; Müller et al., 2000: fig. 17H, as *Nodoprosopon torosum*; Fig. 4) by the following characters: evenly granulated carapace, with spaced granules (more weakly granulated in central regions in *V. torosus*); posterior margin concave, with depressed flange; branchial, cervical grooves wider; and a more prominent and deeper axial depression on the rostrum, with more isolated, separated and prominent epigastric ridges.

*Verrucarcinus marsae* nov. sp. differs from *V. cutifrontis* (late Oxfordian to early Kimmeridgian, Dobrogea, Romania; Frantescu, 2011) by a more bulbous carapace, with more inflated regions; steeper, V-shaped and wider branchial and cervical grooves; a much coarser granulated carapace surface; and a distinctly defined anterior mesogastric region, with central frontal depression.

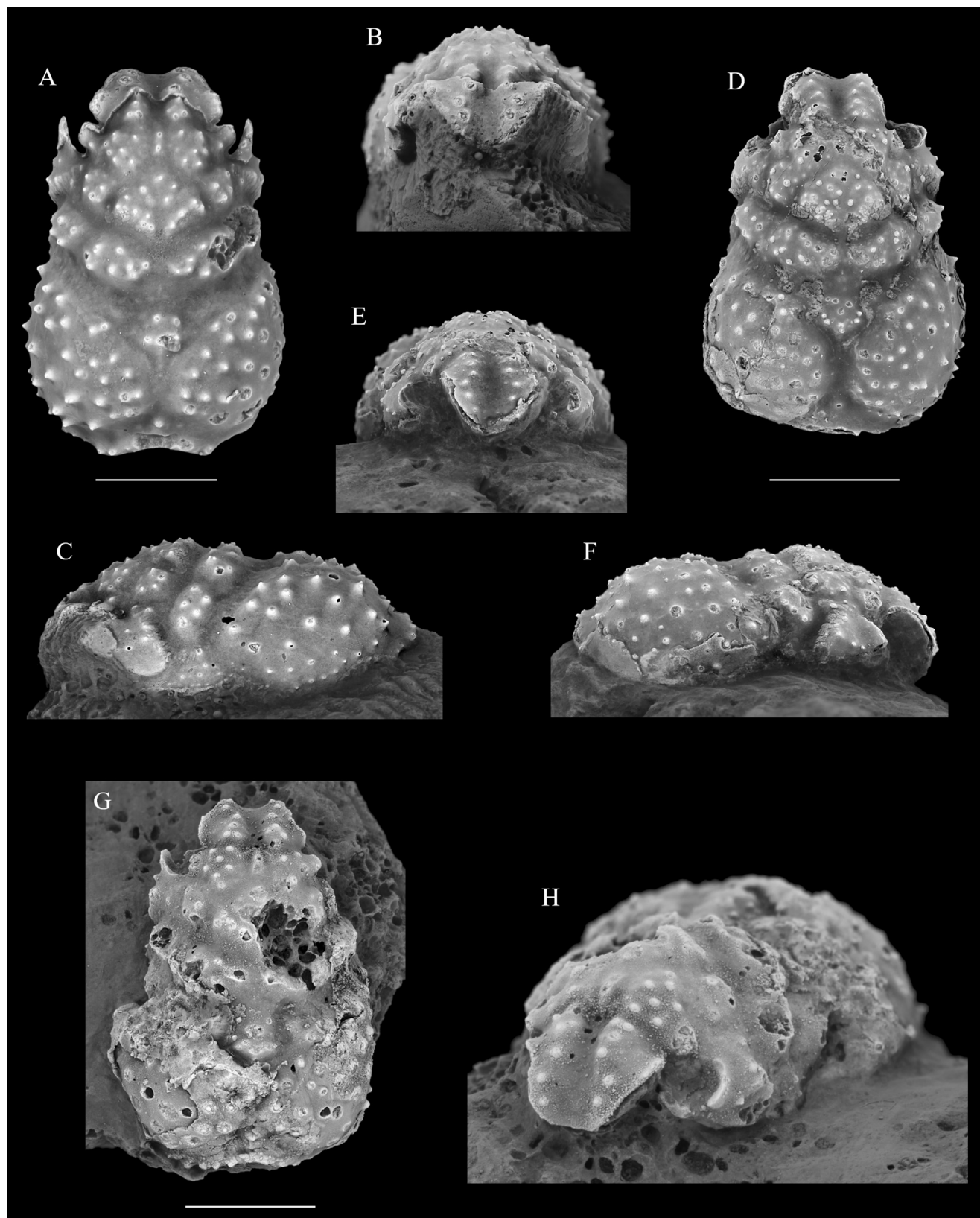
*V. marsae* nov. sp. differs from *V. ordinatus* (Oxfordian, Silesia, Poland; Collins and Wierzbowsky, 1985) by the entire dorsal carapace surface with coarse granules (vs. only posteriorly, on the posterior branchial regions in *V. ordinatus*); wider branchial and cervical grooves; and more elongated and distinct epigastric regions.

Genus *Charassocarcinus* Van Straelen, 1925.

**Type and only species:** *Stenochirus? mayalis* Eudes-Deslongchamps, 1877.

**Occurrence:** Pliensbachian-Bajocian (precise level unknown) of France.

**Diagnosis:** Carapace longer than wide, elongated trapezoidal in outline, widest at posterior margin; carapace regions inflated,



**Fig. 5.** *Verrucarcinus marsae* nov. sp. **A-C.** Holotype, MNHN.F.A86392, (CL: 16.2 mm, CW: 10.8 mm) in dorsal, frontal and left lateral views, respectively. Lower to middle Callovian, (*gracilis*, *anceps*, *coronatum* ammonite biozones), Saint-Laon quarry, Vienne Department (France). **D-F.** Paratype, MNHN.F.A86393 (CL: 14.2 mm, CW: 10.1 mm) in dorsal, frontal and right lateral views, respectively. Middle Callovian (*anceps* ammonite biozone, *tyranniformis* subzone, *richei* horizon) from Méron near Montreuil-Bellay, Maine-et-Loire (France). **G, H.** Paratype, MAB k.3779 (CL: 14.0 mm, CW: 9.6 mm) in dorsal and oblique frontal views, respectively, showing deep, well-defined orbit. Same locality and level as D-F. All specimens coated with ammonium chloride sublimate prior to photography. Scale bars: 5 mm.



ornamented with fine granules, evenly spaced. Lateral margins undefined, completely rounded. Rostrum wide, about half orbito-frontal width, (sub)triangular, projected in advance of orbits, lacking longitudinal swellings. Fronto-orbital width ca. 75% maximum carapace width; orbit directed forward, bounded on inner angle by rostrum; upper orbital margin simple, lacking pronounced spines or fissures; outerorbital angle weakly projected, anterolaterally directed. Anterior mesogastric process triangular, separated from broadly V-shaped posterior mesogastric region; metagastric region large, wide, bilobed; protogastric region with vertical groove; cervical and branchial grooves well developed, complete, acute, well separated; postcervical groove absent. Cardiac region low, wide, positioned quite posteriorly, near posterior margin. Posterior margin concave, nearly as wide as maximum carapace width.

**Remarks:** *Stenochirus? mayalis* was described by Eudes-Deslongchamps (1877: p. 9, pl. I, figs. 9, 10) from the Pliensbachian-Bajocian (precise level unknown, see under ‘Localities and stratigraphy’) of May-sur-Orne, France (Hée, 1924: p. 127). The holotype material consisted of a complete cephalothorax (13 × 8 mm) in the collection of Eugène Eudes-Deslongchamps, but this material was destroyed during the Second World War (Bigot, 1945; Rioult, 1964), and no further material has been published or is known to the authors at present.

The frontal characters were described in detail (Eudes-Deslongchamps, 1877: p. 370): “Le bord frontal est étiré en un rostre large mais court, à la base duquel il y a une carène médiane. Les échancrures orbitaires sont larges et semi-circulaires, limitées par des angles orbitaires très développés. [...] La carène médiane est limitée par des sillons dessinant un losange, s’étendant depuis l’origine du rostre jusqu’au sillon cervical.” [The frontal margin is stretched into a broad but short rostrum, at the base of which there is a median carina. The orbital fossae are wide and semicircular, bounded by well-developed orbital angles. [...] The median carina is bounded by diamond-shaped grooves, extending from the origin of the rostrum to the cervical groove].

Van Straelen (1925: p. 369) erected *Charassocarcinus* to monotypically embrace *Stenochirus? mayalis*, and placed it “at the end of [à la suite des] the Homolodromiidae”. Glaessner (1933: p. 183) noted that *Charassocarcinus* was “probably a Galatheoid”; in the Treatise (Glaessner, 1969: p. R532), it is included in the section ‘Decapoda of uncertain systematic position or validity’; it was not quoted in the Systematic list of fossil decapod crustacean species (Schweitzer et al., 2010) and not addressed since. Here we assign *Charassocarcinus* to the Glaessneropsidae, based on its defined orbits, well-developed front, lack of lateral margins (thus carapace flanks completely rounded, as in the Homolodromiidae), complete and parallel cervical and branchial grooves, and its morphological similarity with *Verrucarcinus*. *Charassocarcinus* is morphologically most similar to *Verrucarcinus* and *Vilsercarcinus* nov. gen., due to its conspicuously wide, completely delineated and bilobed metagastric region, and the grooves on the anterior carapace.

The characters that separate *Charassocarcinus* from *Verrucarcinus* are the following: the carapace outline is elongated trapezoidal in *Charassocarcinus*, whereas it is pyriform in *Verrucarcinus*. The dorsal carapace surface of *Charassocarcinus* bears small, evenly spaced granules, instead of coarse granules especially on the branchial region in *Verrucarcinus*. The rostrum in *Charassocarcinus* is not so projected and as downturned, not sulcate (only a median carina at the base) and it lacks longitudinal swellings (compared to the rostrum of *Verrucarcinus*). Another diagnostic difference is the cardiac region, which in *Charassocarcinus* is positioned posteriorly, close to the posterior margin, whereas in *Verrucarcinus* it is distant from the posterior margin; the typical configuration of glaessneropsids.

*Charassocarcinus* differs from *Glaessneropsis* by: a more convex carapace in transverse cross-section, a less prominent and pro-

jected rostrum, a more posteriorly positioned cardiac region, and steeper angle of cervical and branchial grooves.

*Charassocarcinus* differs from *Ekalakia* by: a more convex carapace in transverse cross-section, a more elongated carapace (CL/CW = 1.45 in *Charassocarcinus mayalis*, vs. 1.3 in *Ekalakia lamberti*), and the cardiac region and branchial groove much more posteriorly placed.

*Charassocarcinus*, being recorded from the Pliensbachian-Bajocian (precise level unknown) of France (*C. mayalis*), is likely the oldest member of the Glaessneropsidae. It is among the oldest Brachyura known to date (for age comparison with the oldest brachyurans known, see Krobicki and Zatoń, 2008; Schweitzer and Feldmann, 2010; Jagt et al., 2015; Guinot, 2019).

Genus *Vilsercarcinus* nov. gen.

urn:lsid:zoobank.org:act:A75D3856-5933-44EF-AB93-50AA7559E5F2

**Derivation of the name:** Named after the ‘Vilser Kalk’, the geological unit in which the sole specimen known to date was collected.

**Type and only species:** *Vilsercarcinus keuppi* nov. gen., nov. sp.

**Diagnosis:** Carapace longer than wide, CL/CW = 1.5, elongated trapezoidal in outline, widest at branchial region at about a third the maximum carapace length from posterior; carapace subcircular in transverse cross-section; carapace regions inflated, ornamented with evenly spaced fine granules. Lateral margins undefined, completely rounded. Rostrum wide, occupying most of orbitofrontal width, projected in advance of orbits, lacking longitudinal swellings, margins steep, sharp-edged. Fronto-orbital width ca. 80% maximum carapace width; orbit directed anterolaterally, lacking outer orbital corner. Anterior mesogastric process pointed, triangular, merged with rhomboidal posterior mesogastric region; metagastric region conspicuously large, wide, bilobed. Protogastric region with acute oblique groove. Cervical and branchial grooves well developed, complete, acute, well separated; branchial groove W-shaped; postcervical groove absent. Cardiac region relatively narrow, scutiform, positioned posteriorly. Posterior margin broken.

**Remarks:** *Vilsercarcinus* nov. gen. is assigned to the Glaessneropsidae because its morphology fits well with the familial diagnosis (see above). In particular, the elongate trapezoidal carapace outline, the wide orbitofrontal margin, the wide and developed rostrum, and the well-separated, complete, sinuous cervical and branchial grooves favour placement of *Vilsercarcinus* nov. gen. in the Glaessneropsidae. *Vilsercarcinus* nov. gen. is morphologically reminiscent in particular of *Verrucarcinus* and *Charassocarcinus* by the prominent bilobed metagastric region.

*Vilsercarcinus* nov. gen. differs from *Verrucarcinus* by the rostrum having steep lateral margins, the mesogastric region formed in a unified triangular shape, the prominent oblique groove on the protogastric region, the scutiform cardiac region, and the fine granular carapace ornamentation. *Vilsercarcinus* nov. gen. is equal in age, or geologically older, than *Verrucarcinus* (Table 1).

*Vilsercarcinus* nov. gen. differs from *Charassocarcinus* by having the rostrum more projected and elongated, the protogastric region with a deep oblique groove (vs. an arched vertical groove in *Charassocarcinus*), the anterior and posterior mesogastric region merged (vs. separated by a groove in *Charassocarcinus*), and a narrow, scutiform cardiac region (vs. wider and subsquare in *Charassocarcinus*). *Vilsercarcinus* nov. gen. is geologically younger than *Charassocarcinus* (Table 1).

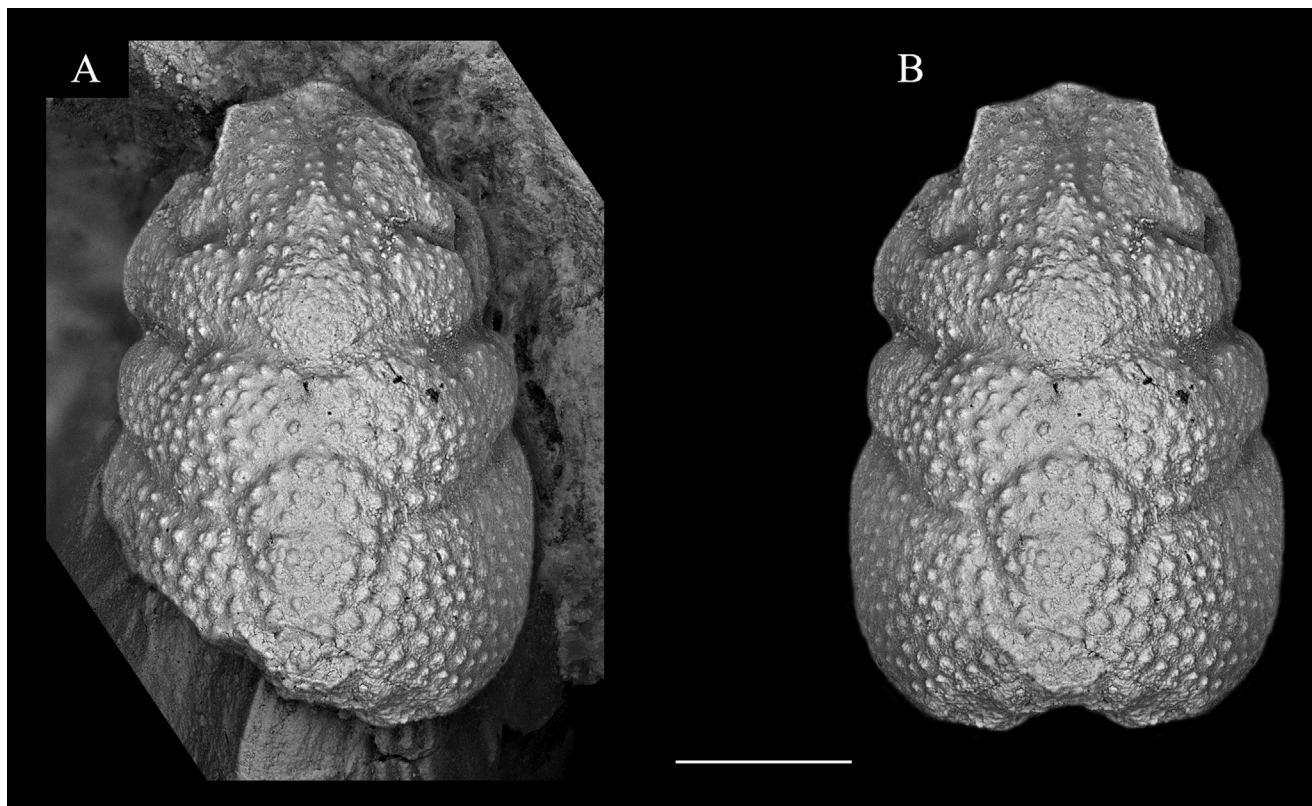
*Vilsercarcinus keuppi* nov. gen., nov. sp.

Fig. 6

urn:lsid:zoobank.org:act:25963848-094E-42BF-8789-39E9D9B69C46

**Table 1**Members of the family Glaessneropsidae *Patrulius*, 1959 considered in the present paper. \*: Type species of the genus.**Charassocarcinus** Van Straelen, 1925*Charassocarcinus mayalis*\* (Eudes-Deslongchamps, 1877) (as *Stenochirus?* *mayalis*); Pliensbachian-Bajocian (precise level unknown); Calvados (northwest France)**Ekalakia** Bishop, 1976*Ekalakia exophthalmops* Feldmann, Schweitzer and Wahl, 2008; Maastrichtian; Wyoming, Montana (USA)*Ekalakia lamberti*\* Bishop, 1976; Campanian-Maastrichtian; Montana, North Dakota (USA)**Glaessneropsis** Patrulius, 1959*Glaessneropsis bucegiana* Patrulius, 1959; Tithonian (?); Carpathians (Romania)*Glaessneropsis heraldica*\* (Moericke, 1897) (as *Prosopon heraldicum*); Tithonian; Stramberk (Czech Republic), Ernstbrunn (Austria)*Glaessneropsis myrmekia* Schweitzer and Feldmann, 2009; Tithonian; Stramberk (Czech Republic)*Glaessneropsis tribulosa* Schweitzer and Feldmann, 2009; Tithonian; Ernstbrunn (Austria)**Meronicarcinus** nov. gen.*Meronicarcinus boursicoti*\* nov. gen., nov. sp.; Callovian; Maine-et-Loire (France)**Verrucarcinus** Schweitzer and Feldmann, 2009*Verrucarcinus cutifrons* Frantescu, 2011; Oxfordian-Kimmeridgian; Dobrogea (Romania)*Verrucarcinus marsae* nov. sp.; Callovian; Calvados, Maine-et-Loire (France)*Verrucarcinus ordinatus* (Collins in Collins and Wierzbowsky, 1985) (as *Nodoprosopon ordinatum*); Oxfordian; Silesia (Poland)*Verrucarcinus torosus*\* von Meyer, 1860 (as *Prosopon torosum*); Oxfordian; Cher Department (France), Silesia (Poland), Kimmeridgian, Bavaria (Germany);

Tithonian; Stramberk (Czech Republic), Ernstbrunn (Austria)

**Vilsercarcinus** nov. gen.*Vilsercarcinus keuppi*\* nov. gen., nov. sp.; late Toarcian-Callovian (precise level unknown); Germany-Austria bordern. 1914. *Prosopon Vilsense* - Stolley, p. 680, pl. 40, fig. 4.1988. *Nodoprosopon?* *vilsense* - Wehner, p. 39, pl. 2, fig. 4.2007. *Nodoprosopon?* *vilsense* - Schweitzer et al., p. 101, fig. 2.4.**Derivation of the name:** Named after its collector, Dr. Helmut Keupp (Berlin), who donated this specimen to the SNSB-BSPG.**Material and measurements:** The single specimen was collected in the 1960s from the late Toarcian-Callovian (precise level unknown) 'Vilser Kalk' debris of the southwestern slope of the Sorgschrofen near Oberjoch, a 1635 m high mount near the boundary between Germany and Austria (H. Keupp, pers. comm., July 2021) by H. Keupp (Berlin), and is currently housed in the BSPG.The specimen, formerly registered as KEU-a 111 7, currently labeled as SNSB-BSPG 2014 XXV 328 (CL: 7.2 mm, CW: 4.9 mm; cuticle not preserved), was relocated in May 2021 by Mike Reich (at that time BSPG) in the collection of the late Dr. Reinhard Förster. This specimen was figured by Wehner (1988: pl. 2, fig. 4, as '*Nodoprosopon?* *vilsense* [Stolley]') and by Schweitzer et al. (2007: fig. 2.4, as *Nodoprosopon?* *vilsense*).**Diagnosis:** As for the genus, by monotypy.**Description:** Carapace longer than wide, elongated trapezoidal in outline, widest posteriorly near posterior margin; carapace regions inflated, ornamented with fine granules, evenly spaced,**Fig. 6.** *Vilsercarcinus keuppi* nov. gen., nov. sp., holotype, SNSB-BSPG 2014 XXV 328 (CL: 7.2 mm, CW: 4.9 mm), upper Toarcian-Callovian 'Vilser Kalk' (precise level unknown), southwestern slope of the Sorgschrofen, near Oberjoch, Germany-Austria. **A.** Dorsal view. **B.** Mirror-image reconstruction. Photograph by Imelda Hausmann (BSPG); specimen coated with ammonium chloride sublimate prior to photography. Scale bar: 2 mm.

posteriorly granules larger. Lateral margins undefined, completely rounded. Rostrum wide, incompletely preserved but apparently well projected in advance of orbits, anteromedially depressed. Fronto-orbital width ca. 75% maximum carapace width; orbits directed forward. Anterior mesogastric process sharply triangular, continuous with rhomboidal posterior mesogastric region; meta-gastric region conspicuously large, wide, distinctly bilobed; cervical and branchial grooves well developed, deep, well separated; postcervical groove absent. Cardiac region rather narrow, scuti-form, positioned relatively posteriorly on carapace. Posterior margin incompletely preserved.

**Remarks:** The single specimen that is described here as *Vilsercarcinus keuppi* nov. gen., nov. sp., was initially assigned to *Prosopon vilsense* Stolley, 1914 by Wehner (1988: p. 39, pl. 2, fig. 4), a species being originally described from the ‘alpinen Doggerkalk’ (Stolley, 1914: p. 680, pl. 40a, b).

*Prosopon vilsense* has a long taxonomical history: it was placed in *Avihomola* Van Straelen, 1925 (Van Straelen, 1925), *Pithonoton von Meyer*, 1842 (Beurlen, 1928), *Prosopon von Meyer*, 1840 (Lörenthey and Beurlen, 1929), *Protocarcinus* Woodward, 1866 (Glaessner, 1929), *Nodoprosopon* Beurlen, 1928 (Glaessner, 1933; Müller et al., 2000; Schweitzer et al., 2007; Krobicki and Zatoń, 2008; Crônier and Boursicot, 2009), and in *Abyssopthalmus* Schweitzer and Feldmann, 2009 (Krobicki and Zatoń, 2016). Krobicki and Zatoń (2016: p. 710, fig. 7) tentatively assigned this species to *Abyssopthalmus* and noted that ‘*Abyssopthalmus? vilsense*’ was collected from the upper part of the Vils Limestone. Therefore, these authors concluded that this species is most probably Early Callovian in age. Klomp maker et al. (2020) did not list *A. vilsense* in their review of many Jurassic genera. At this moment we adopt here the taxonomic position concluded by Krobicki and Zatoń (2016) for the type specimen of *Prosopon vilsense*.

*Vilsercarcinus keuppi* nov. gen., nov. sp. shows a strongly areolated carapace, with deep and distinct branchial and cervical grooves; an oblique, anteriorly and outwardly directed groove subdividing the protogastric region; and two axial tubercles on the mesogastric region. These significant characters distinguish it from *Abyssopthalmus vilsensis*.

*Vilsercarcinus keuppi* nov. gen., nov. sp., differs from *Charassocarcinus mayalis* (Eudes-Deslongchamps, 1877) by having an undifferentiated mesogastric region, and by lacking distinct outerorbital corners. The rostrum is incomplete in *V. keuppi* nov. gen., nov. sp., and it may also have been incomplete in *C. mayalis*. We hope that additional material will become available in the near future.

Genus *Meronecarcinus* nov. gen.

urn:lsid:zoobank.org:act:55939B11-7F18-43DC-A907-65A5510E53D0

**Derivation of the name:** Named after Méron (Maine-et-Loire department, France), the type locality of the sole specimen known.

**Type and only species:** *Meronecarcinus boursicoti* nov. gen., nov. sp.

**Diagnosis:** Carapace gently arched in transverse section, longer than wide, CL/CW = 1.3, outline shape subrectangular, widest at posterior branchial regions, about two-thirds the distance posteriorly on carapace; dorsal regions flattened, ornamented with granules, evenly sized across carapace. Lateral margins undefined, bluntly rounded. Rostrum occupying entire front, wide, about one quarter maximum carapace width, rounded (sub)triangular, stout, slightly downturned, projected well in advance of orbits, margins simple, with paired (admedial) longitudinal granular swellings. Eyestalk appearing to have arisen beneath rostrum. Fronto-orbital width ca. 80% maximum carapace width; orbit large, directed forward, slightly outward and upward, bounded on inner angle by rostrum; upper orbital margin concave, sharp, granular,

lacking strong intraorbital spine and fissures; outerorbital angle subtle. Anterior mesogastric process narrow, posterior mesogastric and metagastric regions damaged; cervical and branchial grooves well developed, complete, notching lateral carapace margins, well separated. Cardiac region small, diamond-shaped, well separated from posterior margin by elongated, narrow intestinal region. Posterior margin incompletely preserved, nearly as wide as maximum carapace width.

**Remarks:** *Meronecarcinus* nov. gen. is morphologically reminiscent to *Verrucarcinus* by: the prominent rostrum; well-separated, complete and subparallel cervical and branchial grooves; undefined, rounded lateral carapace margins; large, anteriorly placed, and well delineated orbital fossae; and granular carapace surface. *Meronecarcinus* nov. gen. is distinguished from *Verrucarcinus* by the stouter, subrectangular carapace outline (CL/CW = 1.3 in *Meronecarcinus* nov. gen., vs. 1.5 in *Verrucarcinus*); clearly less convex carapace in transverse section; the flatter carapace regions; the dorsally visible and slightly upward directed orbits; and the lack of a distinct tooth and prominent fissures on the orbital margin.

*Meronecarcinus boursicoti* nov. gen., nov. sp.

Fig. 7

urn:lsid:zoobank.org:act:5E1D1463-1975-4701-B4AB-5E65A358F10F

**Derivation of the name:** Species dedicated to Pierre-Yves Boursicot (Villedieu-la-Blouère, Mayuges region, France), who collected the holotype and sole specimen.

**Holotype and only specimen:** MNHN.F.A86394, a well-preserved dorsal carapace (CL: 10.8 mm, CW: 8.3 mm), preserved as internal mould, from the locality of Méron near Montreuil-Bellay, Maine-et-Loire, France. MAB k.3780 represents a cast.

**Diagnosis:** As for the genus, by monotypy.

**Description:** Carapace longer than wide, CL/CW = 1.3, widest at posterior branchial region ca. 30% the distance posteriorly; carapace gently arched in transverse section, weakly arched to flattened in longitudinal cross-section; regions well marked by deep, broad grooves; dorsal carapace surface ornamented with evenly granules.

Fronto-orbital width ca. 79% maximum carapace width; rostrum wide, prominent, projected well beyond orbits, in line with carapace, slightly downturned, tip blunt, lateral margins convex, surface with two converging keels and shallow axial depression.

Orbits large, directed forwards and laterally; supra-orbital margin with only a single, very small median dent, basal to an upward curve towards the outerorbital corner; intraorbital lobe rounded, directed anteriorly and slightly outward; outerorbital corner weakly developed, reclined.

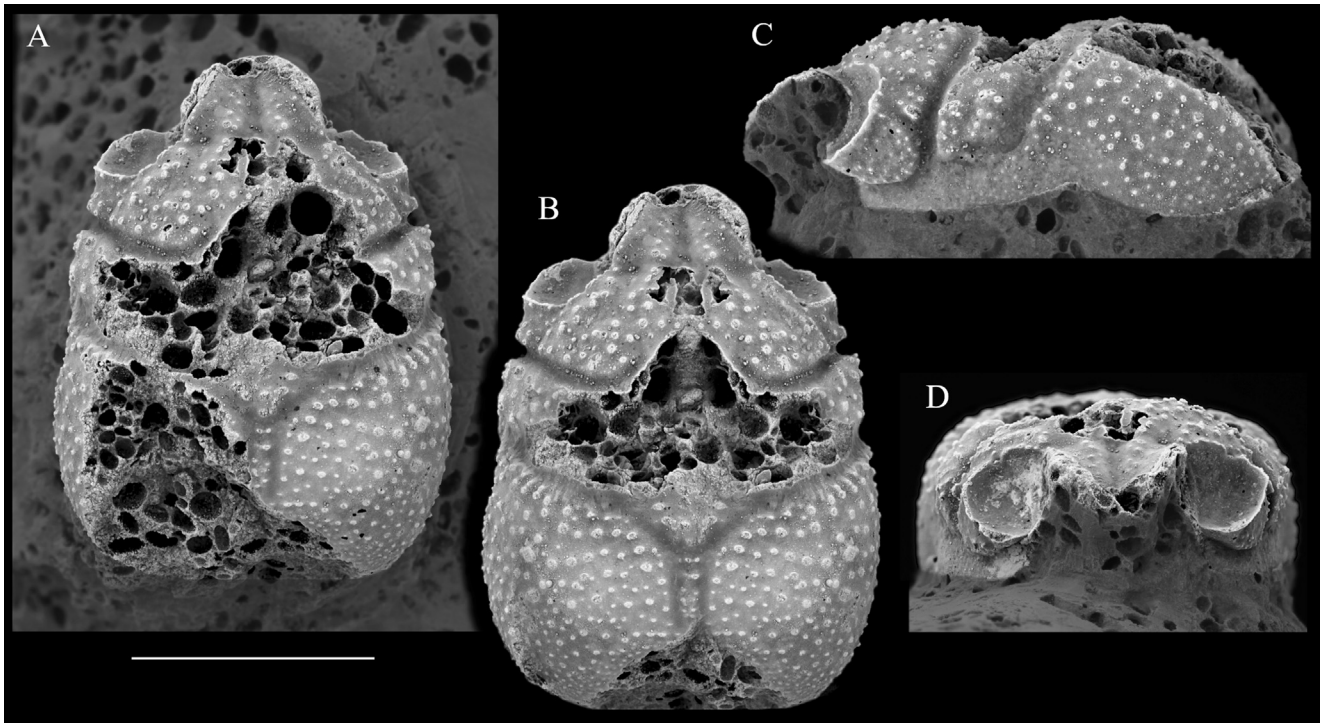
Lateral margins of carapace undefined, rounded, continuously convex in dorsal view, incised by the branchial and cervical grooves, and divided into three portions: anteriormost smallest, posterior portion distinctly largest; small spiniform granules along anterior two portions.

Posterior margin wide, majority not preserved.

Mesogastric region partially preserved; anterior mesogastric process narrow; posterior mesogastric and metagastric regions damaged. Protogastric regions flattened, undivided, laterally separated from small, subtrapezoidal hepatic area by short depression. Epibranchial region flattened, granular. Posterior portion of cardiac region as a wide triangle with apex pointed downward; posterior branchial region very large, oblique pyriform, surface undifferentiated, inflated, bulbous.

Grooves wide, smooth; lateral portions of cervical groove deep and widely V-shaped, complete, strongly incising lateral carapace flanks; branchial groove subparallel to cervical groove, wide, curved posteriorly extending into elongated, closely spaced grooves on intestinal region.





**Fig. 7.** *Meroncarcinus boursicoti* nov. gen., nov. sp., holotype, MNHN.F.A86394 (CL: 10.8 mm, CW: 8.3 mm) in dorsal (A, B (mirror-image reconstruction)), left lateral (C) and frontal (D) views, middle Callovian (*anceps* ammonite biozone, *tyranniformis* subzone, *richei* horizon) from Méron, near Montreuil-Bellay, Maine-et-Loire (France). Specimen preserved as internal mould. Specimen coated with ammonium chloride sublimate prior to photography. Scale bar: 5 mm.

**Remarks:** *Meroncarcinus boursicoti* nov. gen., nov. sp. co-occurs in the same locality and same level as *Verrucarcinus marsae* nov. sp. but it can be easily distinguished by its less convex and proportionally shorter carapace, the dorsally visible and slightly upwardly directed orbital fossae, and a finer granulation.

*Abyssopthalmus mainense* (Crônier and Boursicot, 2009, as *Nodoprosopon? mainense*), from the lower Callovian *gracilis* Zone near Montreuil-Bellay (Maine-et-Loire, France) and included in *Abyssopthalmus* by Schweitzer et al. (2018: 320), can be distinguished by its longer anterolateral margin (margin anterior the cervical groove longer than margin between cervical and branchial grooves in *Abyssopthalmus mainense*, vs. the opposite in *Meroncarcinus boursicoti* nov. gen., nov. sp.); a shorter and more downturned rostrum; forward directed orbits, not upward; and a central tubercle on the cardiac region and each epibranchial region (vs. smooth regions in *M. boursicoti* nov. gen., nov. sp.).

*Abyssopthalmus bellaii* (Crônier and Boursicot, 2009, as *Nodoprosopon? bellaii*), from the lower Callovian *gracilis* Zone near Montreuil-Bellay (Maine-et-Loire, France), tentatively included in *Abyssopthalmus* by Schweitzer et al. (2018: p. 321), has a more elongated carapace (CL/CW = 1.4, vs. 1.3 in *Meroncarcinus boursicoti* nov. gen., nov. sp.); an oblique orbital margin with orbits directed laterally and not upward; the anterior mesogastric process well extended on the rostrum (in *Meroncarcinus boursicoti* nov. gen., nov. sp. only a depressed gutter beyond the level of the outerorbital corners); and the cervical and branchial grooves not parallel, more diverging.

#### 4. Discussion

##### 4.1. Remarks on the diagnosis of Homolodromioidea/Homolodromiidae Alcock, 1900

Schweitzer and Feldmann (2009: p. 82) proposed the superfamily Glaessneropssoidea Patruilius, 1959 as sister group of Homolo-

dromioidea Alcock, 1900. They noted (Schweitzer and Feldmann, 2009: pp. 64, 65): “To our knowledge, no succinct definition of the characteristics of the Homolodromioidea has been presented” and cited only Guinot (1978) and Martin (1990). A diagnosis of the family was given in the revision of Guinot (1995) based on Recent taxa but with non-negligible palaeontological data (Guinot, 1995: pp. 188, 265); a key was provided by Guinot and Tavares (2003: p. 120) that differentiated Homolodromioidea from Dromioidea De Haan, 1833; a series of articles by Martin, and Martin et al. (e.g., Martin et al., 2001), as well as other contributions (e.g., Ng and McLay, 2005; Ng and Naruse, 2007; Tavares and Lemaître, 2014; Ng and Yang, 2021) have since been published and expanded the family, and give us a clear idea of its outlines. The characters from the key to Homolodromiidae provided by Guinot and Tavares (2003) are as follows:

- both P4 and P5 modified, reduced, subdorsal or dorsal, with terminal prehensile apparatus (Guinot, 1995: fig. 3);
- male pleopodal formula complete (i.e., presence of vestigial pleopods on pleonal somites 3 to 5 in addition to the gonopods on pleonal somites 1 and 2; see Guinot, 1995: fig. 5A-D);
- uropods showing as ventral lobes, never involved in pleonal holding;
- male pleon with distinct pleurae;
- telson very long, reaching mxp3;
- axial skeleton regularly layered, with phragmata interfingered to each other;
- female sternal sutures 7/8 short, spermathecal apertures lying close to gonopores on P3;
- exopod absent on G2;
- male P5 coxa modified, elongated, prolonging into hard process enclosing penis.

To a large extent, this diagnosis applies also to the higher rank Homolodromioidea.

It is clear that the majority of these characters are not visible in fossil remains and that the use of the carapace is the only possible way of identification, especially for Jurassic and Early Cretaceous crabs. The carapace of extant homolodromiids (known only from *Homolodromia* A. Milne-Edwards, 1880 and *Dicranodromia* A. Milne-Edwards, 1880), are characterised by: a proepistome (=antennular somite) non-existent (plesiomorphy) or weak; a rostrum that is absent or only represented by a median small spine; a pair of pseudo-orbital teeth; the absence of a true orbit; the presence of only a supra-orbital tooth or of both supra- and sub-orbital teeth; and flanks developed, undemarcated (Guinot, 1995: p. 171, fig. 2A-C). The carapace in extant Homolodromioidea is characterised by a very weak areolation, to varying degrees: in fact, no carapace region is indicated. The carapace appears smooth, sometimes furry, or finely granular/spinulate, and seems continuously and evenly swollen. In most fossil forms assigned at some time to Homolodromioidea, the regions are defined by distinct grooves and/or bulges, and are easily recognisable.

Guinot (1995: p. 168) noted for the Homolodromiidae that “The body is thick, with subvertical flanks; there is no lateral edge delimiting the dorsal side surface from the flanks, nor any marginal armature; no trace of a lateral line (linea dromica) as in Dromiidae; no homolid line is present”. A major carapace feature of the Homolodromiidae is in fact the presence in the branchiostegal region of a large poorly calcified area that extends ventrally (well shown by Schweitzer et al., 2012: fig. 1c). It can be considered as the resorption zone during moulting, replacing the linea along which the carapace breaks open during ecdysis, which exists in other crabs (linea homolica in Homolidae H. Milne Edwards, 1837; linea dromica or linea dromiida in Dromiidae De Haan, 1833; lateral line in Eubrachiura Saint Laurent, 1980). It is admittedly difficult to recognise this poorly calcified area in the fossils, but this feature is closely related to the lack of a well-defined lateral margin of the carapace at this level. It is therefore questionable, if not unlikely, that crabs with well-defined lateral carapace margins are really homolodromioids.

The known Jurassic and early to mid-Cretaceous families that have been assigned to Homolodromioidea are to date based solely on dorsal carapaces. These additional fossil families are as follows in Karasawa et al. (2011) and Schweitzer et al. (2012; 2018): Buculentidae Schweitzer and Feldmann, 2009; Goniodromitidae Beurlen, 1932; Prosopidae von Meyer, 1860; Tanidromitidae Schweitzer and Feldmann, 2009. Carapaces of members of the abovementioned families are quite variable in characters; as a result of the inclusion of these families, the characters of the superfamily Homolodromioidea (extant + extinct families considered) have become highly diversified, as outlined above. The inclusion of many extinct families into the Homolodromioidea may have distorted the definition of this high-rank taxon, making the resulting diagnosis very problematic; a new diagnosis of Homolodromioidea including the fossil families should be updated and established on solid basis.

The Prosopidae is consensually considered a homolodromioid family (see Van Bakel et al., 2021: p. 10, with further references). The diagnosis of the Prosopidae was revised by Van Bakel et al. (2021: p. 5), providing a solid basis to compare it with the diagnosis of the Glaessneropsidae (see below). These authors stressed (op. cit.: p. 10) that “differences between homolodromiids and prosopids are few”.

#### 4.2. Remarks on fossil Homolodromioidea

*Homolus auduini* Eudes-Deslongsamps, 1835, from the Middle Jurassic (Bathonian) of France (Pezy and Gendry, 2016) and England, was included in Homolodromiidae by Bouvier (1896: pp. 47-52, fig. 36, as *Protocarcinus* (=Palaeinachus) *longipes*

Woodward and Salter, 1865) and Guinot (1995: pp. 164, 265), then referred to as *Foersteria auduini* by Wehner (1988), a name replaced by *Gabriella Collins, Ross, Genzano and Manzian, 2006* (Collins et al., 2006). It is the perfect example of a true fossil homolodromiid. Thanks to the examination of the lectotype, Schweitzer and Feldmann (2010: fig. 2) adhered to the idea that *Homolus auduini* could be referable to the Homolodromiidae, based on the possession of a large extra-orbital area ('augenrest' *sensu* these authors) protected by spines, and that of two pseudo-orbital spines, and a pleon partially exposed in dorsal view. Guinot (2019: p. 766), Klompaker et al. (2020: p. 12) and Van Bakel et al. (2021: p. 7) agreed that the extant family Homolodromiidae is represented by *Homolus auduini* in the Jurassic; also Krobicki and Zatoń (2016: p. 705) considered it to be the oldest homolodromiid. The affiliation to Homolodromiidae of certain well-preserved fossil forms by Guinot (1995) is now in doubt, and their family assignment is to be reconsidered: *Antarctiprosopon chaneyi* (Feldmann and Wilson, 1988), Eocene, Antarctica; *Antarctidromia inflata* Förster, Gaździcki and Wrona, 1985, Lower Miocene, Antarctica; and *Notiodromia novaezelandica* (Feldmann, 1993), Upper Cretaceous, New Zealand.

The Prosopidae is one of the oldest brachyuran families, with *Bajoprosopon piardi* Van Bakel, Maerten, Jagt and Fraaije, 2021 from the upper Bajocian, Middle Jurassic of the 'Les Fours à Chauv' locality, Calvados, northwestern France, as the oldest known member. This record is only slightly older than the Bathonian homolodromiid *Homolus auduini* (see above).

#### 4.3. Remarks on Glaessneropsidae/Glaessneropsidae

By elevating the Glaessneropsidae to a suprafamilial rank, Schweitzer and Feldmann (2009: p. 82) stated that the distinguishing features diagnosing the Glaessneropsidae were: 'orbits well developed; usually ornamented with supra- and sub-orbital spines, fronto-orbital width always occupying entire frontal margin of carapace; augenrest absent'. They included *Verrucarcinus* in Glaessneropsidae, whose type genus *Glaessneropsis* Patruilius, 1959 contains Jurassic species “united by the distinctive rostrum and orbital configuration, which are unique among Brachyura of any age” (Schweitzer and Feldmann, 2009: p. 84). The Glaessneropsidae is known only from the fossil record (lower Jurassic [*Charassocarcinus*] – upper Cretaceous [*Ekalakia*]; Table 1), unlike Homolodromidae or Homolodromioidea, which is known from the lower Jurassic until Present day, making it the oldest lineage of brachyurans. No elements other than the carapace are known for Glaessneropsidae, making a direct functional comparison difficult. However, carapace characters exclude the Glaessneropsidae from the Homolodromioidea. The presence of a single, enlarged rostrum, well-defined deep orbits with distinct orbital notches, prevents the assignment of *Verrucarcinus* to Homolodromiidae, based on the diagnostic characteristics of the family, and even to the superfamily Homolodromioidea *sensu stricto*. It should also be noted that no living homolodromiid has a dorsal surface with so pronounced, inflated and clearly defined regions. In contrast, the undefined, blunt and rounded lateral margins of the carapace of *Verrucarcinus* are typically homolodromiid.

An example of the difficulty of assigning particular families to a higher rank is illustrated by the case of Viaiidae. While Artal et al. (2012: p. 402) tentatively assigned Viaiidae to the superfamily Glaessneropsidae, Gašparič et al. (2022: p. 9) concluded that “the higher-level taxonomic position remains obscure” and left Viaiidae without higher systematic placement. Guinot (2019: pp. 764, 782) examined different possibilities for the position of Glaessneropsidae, hypothesising that some members could be included in Eubrachiura, in particular in Majoidea. A good diagnosis of Glaessneropsidae is available (see above) but a solid diagno-

sis of Glaessneropsoidea differentiating it from other superfamilies is still lacking. We therefore leave Glaessneropsidae, like Viiidae, without a higher systematic placement.

### Data availability

The data used for this paper are palaeontology specimens held in museum collections, as described in the paper under 'material'.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgements

Chantal Mars (Sémelay, France) donated the holotype specimen of *Verrucarcinus marsae* nov. sp.; Pierre-Yves Boursicot (Villedieu-la-Blouère, France) donated the paratypes of *V. marsae* nov. sp. and the holotype of *Meronarcinus boursicoti* nov. gen., nov. sp.; Jean Louis Bonnin (Méron, France) and Bertrand Chasle (Angers, France) assisted Pierre-Yves Boursicot in the field. Alexander Nützel and Mike Reich (Bavarian State Collection of Palaeontology and Geology Munich, Germany) located the specimen of *Vilsercarcinus keuppi* nov. gen., nov. sp., and Imelda Hausmann (same institute) provided the photographs. Helmut Keupp (Berlin) pointed us towards the type material of *Vilsercarcinus keuppi* nov. gen., nov. sp. and provided details of the locality and stratigraphy. We are grateful to Dr. Andreas Kroh (Naturhistorisches Museum Wien, Vienna, Austria) for supplying silicone rubber moulds of material from Ernstbrunn (Figs. 4(H, I)). Sylvain Charbonnier (Muséum national d'Histoire naturelle, Centre de Recherche en Paléontologie; Paris, France) kindly provided museum registration numbers. René Fraaije (Oertijdmuseum, Boxtel, the Netherlands) provided material of *Verrucarcinus torosus* from Germany. We thank the reviewers, Guenter Schweigert (Staatliches Museum für Naturkunde, Stuttgart, Germany) and Carrie Schweitzer (Kent State University, North Canton, Ohio, USA), for their thorough reviews and constructive comments that improved the manuscript. All these individuals and institutions are warmly thanked for their invaluable contributions.

### References

- Alcock, A., 1900. Materials for a carcinological fauna of India, No. 5. The Brachyura Primigenia or Dromiacea. *Journal of the Asiatic Society of Bengal* 68, 123–169.
- Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M., Klompmaker, A.A., 2012. New Albian–Cenomanian crabs (Crustacea, Decapoda, Podotremata) from Monte Orobe, Navarra, northern Spain. *Revista Mexicana de Ciencias Geológicas* 29, 398–410.
- Beurlen, K., 1928. Die fossilen Dromiaceen und ihre Stammesgeschichte. *Paläontologische Zeitschrift* 10, 144–183.
- Beurlen, K., 1932. Brachyurenreste aus dem Lias von Bornholm mit Beiträgen zur Phylogenie und Systematik der brachyuren Dekapoden. *Paläontologische Zeitschrift* 14, 52–66.
- Bigot, A., 1945. La destruction des collections et des bibliothèques scientifiques de Caen. *Bulletin de la société linnéenne de Normandie*, vol. suppl. Année 1945, 1–75.
- Bishop, G.A., 1976. *Ekalakia lamberti* n. gen., n. sp. (Crustacea: Decapoda) from the Upper Cretaceous Pierre Shale of eastern Montana. *Journal of Paleontology* 50, 398–401.
- Blow, W.C., Manning, R.B., 1996. Preliminary descriptions of 25 new decapod crustaceans from the middle Eocene of the Carolinas, U.S.A. *Tulane Studies in Geology and Paleontology* 29, 1–26.
- Bouvier, E.-L., 1896. Sur l'origine homarienne des Crabes : étude comparative des Dromiacés vivants et fossiles. *Bulletin de la Société philomathique*, 8ème série, 8 (2) (for 1895), 34–110.
- Brünnich, M.T., 1772. *Zoologiae fundamenta praelectionibus academicis accommodata*. Grunde i Dyrelaeren. Copenhagen & Leipzig (F.C. Pelt), 254 p.
- Collins, J.S.H., Ross, A.J., Genzano, G., Manzian, H., 2006. *Earleria* gen. nov. and *Gabriella* gen. nov., replacement names for *Foersteria* Arai and Brinkmann-Voss, 1980 (Cnidaria, Hydrozoa, Mitrocomidae) and *Foersteria* Wehner, 1988 (Crustacea, Decapoda, Prosopidae), junior homonyms of *Foersteria* Szépligeti, 1896 (Insecta, Hymenoptera, Braconidae). *Bulletin of the Mizunami Fossil Museum* 33, 125–126.
- Collins, J.S.H., Wierzbowski, A., 1985. Crabs from the Oxfordian sponge megafacies of Poland. *Acta Geologica Polonica* 35, 73–88.
- Crônier, C., Boursicot, P.-Y., 2009. A new decapod crustacean faunule from the Middle Jurassic of north-west France. *Palaeontology* 52, 1275–1289.
- De Haan, W., 1833–1850. Crustacea. In: Siebold, P.F. von (Ed.), *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summun in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*. Lugduni-Batavorum, Leiden, pp. 1–243.
- de Saint Laurent, M., 1980. Sur la classification et la phylogénie des Crustacés Décapodes Brachyours. I. Podotremata Guinot 1977 et Eubrachiura sect. nov. *Comptes rendus de l'Académie des Sciences (Paris)* 290, 1265–1268.
- Eudes-Deslongchamps, J.A., 1835. Mémoire pour servir à l'histoire naturelle des Crustacés fossiles. *Mémoires de la Société Linnéenne de Normandie* 5, 37–46.
- Eudes-Deslongchamps, E., 1877. Le Jura normand. Études paléontologiques des divers niveaux jurassiques de la Normandie. Deuxième livraison. F. Savy, Paris, et Le Blanc-Hardel, Caen.
- Feldmann, R.M., 1993. Additions to the fossil decapod crustacean fauna of New Zealand. *New Zealand Journal of Geology and Geophysics* 36, 201–211.
- Feldmann, R.M., Wilson, M.T., 1988. Eocene decapod crustaceans from Antarctica. In: Feldmann, R.M., Woodburne, M.O. (Eds.), *Geology and paleontology of Seymour Island, Antarctic Peninsula*, vol. 169. Geological Society of America, Memoir, pp. 465–488.
- Feldmann, R.M., Schweitzer, C.E., Wahl, W.R., 2008. *Ekalakia* (Decapoda: Brachyura): the preservation of eyes links Cretaceous crabs to Jurassic ancestors. *Journal of Paleontology* 82, 1030–1034.
- Förster, R., Gaździcki, A., Wrona, R., 1985. Homolodromid crabs from the Cape Melville Formation (Lower Miocene) of King George Island, West Antarctica. *Acta Palaeontologica Polonica* 49, 147–161.
- Fraaije, R.H.B., Van Bakel, B.W.M., Guinot, D., Jagt, J.W.M., 2013. A new Middle Jurassic (Bajocian) homolodromiid crab from northwest France; the earliest record of the Tanidromitidae. *Boletín de la Sociedad Geológica Mexicana* 65, 249–254.
- Fraaije, R.H.B., Robins, C.M., Van Bakel, B.W.M., Jagt, J.W.M., Bachmayer, F., 2019. Paguroid anomurans from the Tithonian Ernstbrunn Limestone, Austria - the most diverse extinct paguroid assemblage on record. *Annalen des Naturhistorischen Museums in Wien, Serie A* 121, 257–289.
- Frañescu, O.D., 2011. Brachyuran decapods (including five new species and one new genus) from Jurassic (Oxfordian–Kimmeridgian) coral reef limestones from Dobrogea, Romania. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 259, 271–297.
- Gabilly, J., Rioult, M., 1971. Le Bajocien inférieur et le Toarcien supérieur sur les Bordsures du Massif Armoricaire. Limite entre le Jurassique inférieur et moyen. Problème de l'Aalénien. In: *Colloque du Jurassique - Luxembourg* 1967. Mémoires du Bureau des recherches géologiques et minières, vol. 75, pp. 385–396.
- Gašparič, R., Van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M., 2022. First record of viaiid crabs (Decapoda, Podotremata) from the Lower Cretaceous of Slovenia, with the description of two new species. *Cretaceous Research* 138, 105293.
- Glaessner, M., 1929. Dekapodenstudien. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B, Beilageband* 63, 137–176.
- Glaessner, M.F., 1933. Die Krabben der Juraformation. *Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B* 3, 178–191.
- Glaessner, M.F., 1969. Decapoda. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology (R, Arthropoda)* 4(2). The Geological Society of America/The University of Kansas Press, Lawrence, Kansas, pp. R399–R533.
- Gschwend, D., 1988. Brachiopoden aus dem Oberostalpin der Allgäuer Alpen, Teil III: Brachiopoden aus dem Unterdogger/Vilserkalk (Forts. v. Heft 1984/2 u. 1984/4). *Berichte des Naturwissenschaftlichen Vereins für Schwaben, Augsburg* 92, 5–11.
- Guinot, D., 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyours. *Bulletin biologique de la France et de la Belgique* 112, 211–292.
- Guinot, D., 2019. New hypotheses concerning the earliest brachyurans (Crustacea, Decapoda, Brachyura). *Geodiversitas* 41, 747–796.
- Guinot, D., Tavares, M., 2003. A new subfamilial arrangement for the Dromiidae de Haan, 1833, with diagnoses and description of new genera and species. *Zoosystema* 25, 43–129.
- Guinot, D., Tavares, M., Castro, P., 2013. Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa* 3665, 1–414.
- Guinot, D., Van Bakel, B.W.M., 2020. Extraordinary majoid crabs: the genus *Esopus* A. Milne-Edwards, 1875 in the new subfamily *Esopinae* subfam. nov., and erection of *Paulitinae* subfam. nov. (Crustacea, Decapoda, Brachyura, Majoidea, Inachoididae Dana, 1851). *Zootaxa* 4766, 101–127.
- Guinot, D., 1995. Crustacea, Decapoda, Brachyura: Révision des Homolodromiidae Alcock, 1900. In: Crosnier, A. (Ed.), *Résultats des campagnes MUSORSTOM*, Volume 13. Mémoires du Muséum national d'Histoire naturelle Paris, vol. 163, pp. 155–282.
- Hée, A., 1924. Catalogue critique des Crustacés jurassiques du Calvados et de l'Orne. *Bulletin de la Société Linnéenne de Normandie* 7 (6), 126–157.
- Heissel, W., 1937. Geologie der Vilser Alpen. *Jahrbuch der Geologischen Bundesanstalt* 87, 235–273.



- Jagt, J.W.M., Van Bakel, B.W.M., Guinot, D., Fraaije, R.H.B., Artal, P., 2015. Fossil Brachyura. In: Castro, P., Davie, P.J.F., Guinot, D., Schram, F., von Vaupel Klein, C. (Eds.), *Treatise on zoology – anatomy, taxonomy, biology – the Crustacea*, complementary to the volumes translated from the French of the *Traité de Zoologie 9(C) (I), Decapoda: Brachyura (Part 1)*. E.J. Brill, Leiden, pp. 847–920.
- Karasawa, H., Schweitzer, C.E., Feldmann, R.M., 2011. Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families. *Journal of Crustacean Biology* 31, 523–565.
- Klompaker, A.K., Hyžný, M., Jakobsen, S.L., 2015. Taphonomy of decapod crustacean cuticle and its effect on the appearance as exemplified by new and known taxa from the Cretaceous–Danian crab *Caloxanthus*. *Cretaceous Research* 55, 141–151.
- Klompaker, A.A., Starzyk, N., Fraaije, R.H.B., Schweigert, G., 2020. Systematics and convergent evolution of multiple reef-associated Jurassic and Cretaceous crabs (Decapoda, Brachyura). *Palaeontologia Electronica* 23, a32.
- Krobicki, M., Zatoń, M., 2008. Middle and Late Jurassic roots of brachyuran crabs: palaeoenvironmental distribution during their early evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 263, 30–43.
- Krobicki, M., Zatoń, M., 2016. A new homolodromioid crab (Brachyura: Dromiacea: Tanidromitidae) from the Bajocian of central Poland and a review of the stratigraphical distribution and paleoenvironments of the known Middle Jurassic homolodromioids. *Journal of Crustacean Biology* 36, 695–715.
- Kuhn, O., 1936. Neue Decapoden aus dem Fränkischen Jura. *Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B* 1936, 120–128.
- Latreille, P.A., 1802. *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes*, 3. F. Dufart, Paris, xii + 468 p.
- Leuprecht, M., Moshhammer, B., 2010. *Vilserkalk - Fakten und Überlegungen zu einer Neudefinition (Nördliche Kalkalpen, Austria)*. Eigenverlag Leuprecht und Moshhammer, Wien, November 2010.
- Lórenthey, E., Beurlen, K., 1929. Die fossilen Decapoden der Länder der Ungarischen Krone. *Geologica Hungarica (Palaeontologica)* 3, 1–421.
- Martin, J.W., 1990. Crabs of the family Homolodromiidae, II. *Dicranodromia felderi*, new species, from the western Atlantic, with notes on the type series of *D. ovata* A. Milne Edwards, 1880. *Journal of Crustacean Biology* 10, 708–720.
- Martin, J.W., Christiansen, J.C., Trautwein, S.E., 2001. Crabs of the family Homolodromiidae, VI. *Homolodromia monstrosa* new species (Decapoda, Brachyura) from the western North Atlantic with a redescription of the holotype of *Homolodromia paradoxa* A. Milne-Edwards, 1880 and comments on sexual dimorphism. *Bulletin of Marine Science* 68, 313–326.
- Milne Edwards, H., 1836–1844. *Les Crustacés*. In: Cuvier, G., *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Édition accompagnée de planches gravées [...] par une réunion des disciples de Cuvier [...]. Fortin, Masson et Cie, Paris, 17: pp. 1–278; 18 : pls. 1–80.
- Milne-Edwards, A., 1873–1880. *Cinquième Partie and Tome Premier*. In: *Études sur les Crustacés Podophthalmaires de la région mexicaine*. Mission scientifique au Mexique et dans l'Amérique centrale, ouvrage publié par ordre du Ministre de l'Instruction publique. Recherches zoologiques pour servir à l'histoire de la faune de l'Amérique centrale et du Mexique, publiées sous la direction de M. H. Milne Edwards, membre de l'Institut. Imprimerie nationale, Paris, pp. 45–368, pls. 13–63.
- Milne-Edwards, A. 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the United States Coast Survey Steamer "Blake," Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. VIII. *Études préliminaires sur les Crustacés*. *Bulletin of the Museum of Comparative Zoology* 8(1), 1–68.
- Moericke, W., 1897. Die Crustaceen der Stramberger Schichten. *Palaeontographica, Supplement 2* 6, 43–72.
- Morière, J., 1864. Note sur les crustacés fossiles des terrains jurassiques du Calvados. *Bulletin de la Société Linnéenne de Normandie* 8, 89–99.
- Moshhammer, B., Schlagintweit, F., 1999. The Ernstbrunn Limestone (Lower Austria): new data on biostratigraphy and applied geology. *Abhandlungen der Geologischen Bundesanstalt Wien* 56, 553–565.
- Müller, P., Krobicki, M., Wehner, G., 2000. Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) - their taxonomy, ecology and biogeography. *Annales Societatis Geologorum Poloniae* 70, 49–79.
- Ng, P.K.L., McClay, C.L., 2005. *Dicranodromia danielae*, a new species of homolodromioid crab from the Philippines (Crustacea: Decapoda: Brachyura). *Zootaxa* 1029, 39–46.
- Ng, P.K.L., Naruse, T., 2007. On two species of deep-sea homolodromioid crabs of the genus *Dicranodromia* (Crustacea: Decapoda: Brachyura: Homolodromiidae) from the Philippines, including one new species. *Raffles Bulletin of Zoology, Suppl.* 16, 47–53.
- Ng, P.K.L., Yang, C.-H., 2021. On two new species of deep-sea carrier crabs (Crustacea: Brachyura: Homolodromiidae: *Dicranodromia*) from Taiwan and the Philippines, with notes on other Indo-Pacific species. *ZooKeys* 1072, 129–165.
- Patrullius, D., 1959. Contributions à la systématique des décapodes néojurassiques. *Revue de Géologie et de Géographie* 3, 249–257.
- Pezy, J.-P., Gendry, D., 2016. Re-examination of the decapod fauna from the Upper Bathonian of Ranville (Calvados, France). 6th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Villers-sur-mer 14–18 June 2016.
- Rioul, M., 1964. Victor VAN STRAELEN (1889–1964). *Bulletin de la Société Linnéenne de Normandie, série 10* (5), 12–19.
- Robin, N., Van Bakel, B.W.M., d'Hondt, J., Charbonnier, S., 2015. A new early brachyuran (Crustacea, Decapoda) from the Middle Jurassic of northwest France, epibionts and ecological considerations. *Contributions to Zoology* 84, 179–191.
- Robins, C.M., Feldmann, R.M., Schweitzer, C.E., 2012. The oldest Munididae (Decapoda: Anomura: Galatheaidea) from Ernstbrunn, Austria (Tithonian). *Annalen des Naturhistorischen Museums in Wien, Serie A* 114, 289–300.
- Robins, C.M., Feldmann, R.M., Schweitzer, C.E., 2013. Nine new genera and 24 new species of the Munidopsidae (Decapoda: Anomura: Galatheaidea) from the Jurassic Ernstbrunn Limestone of Austria, and notes on fossil munidopsid classification. *Annalen des Naturhistorischen Museums in Wien, Serie A* 115, 167–251.
- Robins, C.M., Feldmann, R.M., Schweitzer, C.E., Bonde, A., 2016. New families Paragalatheaidea and Catillogalatheaidea (Decapoda: Anomura: Galatheaidea) from the Mesozoic, restriction of the genus *Paragalathea*, and establishment of 6 new genera and 20 new species. *Annalen des Naturhistorischen Museums in Wien, Serie A* 118, 65–131.
- Samouelle, G., 1819. *The Entomologist's Useful Compendium; or an Introduction to the Knowledge of British Insects, Comprising the Best Means of Obtaining and Preserving them, and a Description of the Apparatus Generally Used; Together with the Genera of Linné, and the Modern Method of Arranging the Classes Crustacea, Myriapoda, Spiders, Mites and Insects, from their Affinities and Structure, According to the Views of Dr. Leach*. Thomas Boys, London, 496 p.
- Schmid, D.U., Leinfelder, R.R., Schweigert, G., 2005. Stratigraphy and Palaeoenvironments of the Upper Jurassic of Southern Germany – A Review. *Zitteliana* B26, 31–41.
- Schweigert, G., Kuschel, H., Scherzinger, A., 2016. Following the steps of Hermann v. Meyer: a newly collected brachyuran fauna from Late Jurassic sponge-microbial limestones near Geislingen an der Steige, SW Germany. 6th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Villers-sur-mer, p. 63–64.
- Schweigert, G., Koppka, J., 2011. Decapods (Crustacea: Brachyura) from the Jurassic of Germany and Lithuania, with descriptions of new species of *Planoprosopon* and *Tanidromites*. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 260, 221–235.
- Schweigert, G., Kuschel, H., 2018. Schwäbische und Fränkische Alb – ein Paradies für Jura-Krabben. *Fossilien* 2018 (4), 14–23.
- Schweitzer, C.E., Feldmann, R.M., Karasawa, H., 2012. Part R, Revised, Volume 1, Chapter 8M: Systematic descriptions: Infraorder Brachyura, Section Dromiacea. *Treatise Online* 51, 1–43.
- Schweitzer, C.E., Feldmann, R.M., Lazăr, I., 2007. Decapods from Jurassic (Oxfordian) sponge megafacies of Dobrogea, Romania and reconsideration of *Nodoprosopon* Beurlen, 1928. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 244, 99–113.
- Schweitzer, C.E., Feldmann, R.M., 2008. Revision of the genus *Laeviprosopon* Glaessner, 1933 (Decapoda: Brachyura: Homolodromiidae: Prosopidae) including two new species. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 250, 273–285.
- Schweitzer, C.E., Feldmann, R.M., 2009. Revision of the Prosopinae *sensu* Glaessner, 1969 (Crustacea: Decapoda: Brachyura) including four new families, four new genera, and five new species. *Annalen des Naturhistorischen Museums in Wien* A110, 55–121.
- Schweitzer, C.E., Feldmann, R.M., 2010. The oldest Brachyura (Decapoda: Homolodromiidae: Glaessneropsoidea) known to date (Jurassic). *Journal of Crustacean Biology* 30, 251–256.
- Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H., Schweigert, G., 2010. Systematic list of fossil decapod crustacean species. *Crustaceana Monographs* 10, 1–221.
- Schweitzer, C.E., Feldmann, R.M., Lazăr, I., Schweigert, G., Franțescu, O.D., 2018. Decapoda (Anomura: Brachyura) from the Late Jurassic of the Carpathians, Romania. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 288, 307–341.
- Stolley, E., 1914. Über einige Brachyuren aus der Trias und dem Dogger der Alpen. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 64, 675–682.
- Tavares, M., Lemaitre, R., 2014. New morphological and distributional information on Homolodromiidae and Homolidae (Decapoda: Brachyura) from the Americas, with description of a new species and comments on western Pacific species. *Journal of Crustacean Biology* 34, 504–524.
- Van Bakel, B.W.M., Mychko, E.V., Spiridonov, A., Jagt, J.W.M., Fraaije, R.H.B., 2020. New Cretaceous crabs (Crustacea, Brachyura) from Moscow Oblast and Dagestan (Russia): patterns in phylogeny and morphospace of the oldest eubrachyurans (Dorippoidea). *Cretaceous Research* 119, 104675.
- Van Bakel, B.W.M., Maerten, L., Jagt, J.W.M., Fraaije, R.H.B., van Bakel et al. 2021. *Bajoprosopon piardi* n. gen. and sp. from the Middle Jurassic of France, with a revised diagnosis of the family Prosopidae from Meyer, 1860 (Brachyura, Podotremata) and notes on the availability of names introduced by Hermann von Meyer (1835, 1857). *Palaeontologia Electronica* 24 (2), a26.
- Van Straelen, V., 1925. Contribution à l'étude des Crustacés décapodes de la période Jurassique. *Mémoires de l'Académie royale de Belgique, Classe des Sciences* (27) (misdated 1924), 1–462.
- von Meyer, H., 1840. Neue Gattungen fossiler Krebse aus Gebilden vom Bunten Sandsteine bis in die Kreide. E. Schweizerbart, Stuttgart.
- von Meyer, H., 1842. Ueber die in dem dichten gelben Jurakalk von Aalen in Württemberg vorkommenden Species des Crustaceen genus *Prosopon*. *Beiträge zur Petrefaktenkunde* 5, 70–75.
- von Meyer, H., 1857. Briefliche Mittheilungen an Professor H. Bronn. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* 1857, 554–557.

- von Meyer, H., 1860. Die Prosoptoniden oder die Familie der Maskenkrebse. *Palaeontographica* 7, 183–222, 305, pl. 23.
- von Siebold, C.T., 1848. Lehrbuch der vergleichenden Anatomie. Teil 1. Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere: Berlin, Veit, 679 p.
- Wehner, G., 1988. *Über die Prosoptoniden (Crustacea, Decapoda) des Jura*. Ph.D. Thesis, Ludwig-Maximilians-Universität, München, 154 p., 8 pls. (published by the author).
- Woodward, H., 1866. On the oldest known British Crab (*Palaeinachus longipes*) from the Forest Marble of Malmesbury, Wilts. *Quarterly Journal of the Geological Society* 22, 493–494.
- Woodward, H., Salter, J.W., 1865. Chart of fossil Crustacea, with descriptive catalogue. Stanford, London.
- Zeiss, A., 2001. Die Ammonitenfauna der Tithonklippen von Ernstbrunn, Niederösterreich. *Neue Denkschriften des Naturhistorischen Museums in Wien* 6, 1–116.