

New Decapoda (Brachyura) from the Paleocene Kambühel Formation, Austria

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(with 6 figures and 3 tables)

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Abstract

New brachyuran species from the ?Selandian to Thanetian units of the Kambühel Formation include *Dromiopsis bullamelga*, *Dromiopsis aedicula*, and *Braggicarpilius wanzenboeckii*. Four previously named brachyuran species are also present. Carpiliidae is both the only extant family present and the only family represented in the Kambühel Formation to originate after the end-Cretaceous. Half of the genera present in the Kambühel Formation (*Dromiopsis*, *Caloxanthus*, and *Titanocarcinus*) survived the end-Cretaceous mass extinction event, and all of the surviving genera originated during the Cretaceous. All of the identified species originated in the Paleocene. 87.5% of species and 95% of individual specimens found by two of us (RMF, CES) in one day of collecting at Fakse Quarry are podotrematous, while 80% of species and 46% of individual specimens found in the Kambühel Formation are podotrematous. The specimens from the Kambühel Formation suggest that by late Paleocene time, biomass of the heterotremes surpassed that of the podotremes.

Key words: Dromiacea, Carpilioidea, Etyoidea, crabs.

Introduction

The Kambühel Formation documents the recovery of decapods from the end-Cretaceous mass extinction (VERHOFF *et al.* 2009). Of 38 known Late Cretaceous decapod families, 79% survived into the Paleogene and 66% are extant (SCHWEITZER & FELDMANN

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2005). These surviving families were likely preadapted survivors, ecological generalists, refugium taxa, or taxa protected by their environments (HARRIES *et al.* 1996). Still, only 30% of the genera that originated before the end of the Cretaceous survived into the Paleocene, with entirely new genera within a surviving family appearing in the Paleocene or later (SCHWEITZER & FELDMANN 2005, 2015).

The record of Paleocene decapods is sparse. Notable occurrences include those at the Fakse Quarry of Zealand, Denmark, which is a stratotype of the middle late Danian that consists of unbedded limestone that was deposited as sub-tidal, deep-water (200–300 m) bryozoan and azooxanthellate coral mounds (COLLINS & JAKOBSEN 1994; JAKOBSEN & COLLINS 1997; BERNECKER & WEIDLICH 1990; JAKOBSEN & FELDMANN 2004; ROBIN *et al.* 2017). The presence of azooxanthellate corals suggests that the reef may have lived at or below the photic zone. With 20 identified species of decapods, it is one of the most diverse assemblages of both anomuran and brachyuran decapods of this interval (JAKOBSEN & FELDMANN 2004). Another well-known Paleocene occurrence of decapods is at Vigny Quarry of Val d’Oise, France. It consists of olistoliths of Danian reef limestone included within Cretaceous (Campanian) fluidized chalks (ROBIN *et al.* 2017). Unlike Fakse Quarry, this reef environment formed in normal marine salinity up to a depth of 90 m, and ROBIN *et al.* (2017) reported a decapod assemblage of multiple anomurans and brachyurans as well as axiideans. Their study also reported a diverse molluscan community typical of rocky substrates that includes both herbivorous gastropods that fed on calcareous algae as well as scavenger gastropods.

The more than forty brachyuran decapod fossils collected from the Kambüchel Formation have yielded important new findings. Previous to this study, only one of the brachyurans was identified, *Titanocarcinus kambuehelensis* VERHOFF, MÜLLER, FELDMANN & SCHWEITZER, 2009. The ?Selandian to Thanetian age of the Kambüchel Formation decapods helps to fill an important gap in our knowledge of the Paleocene record. A detailed discussion of the geology and sedimentology of the Kambüchel Formation appears in YOST *et al.* (2023, this volume: pp. 128–129).

Systematic Paleontology

Institutional abbreviations: KSU D, Kent State University Decapod Comparative Collection, Kent, Ohio, USA; NHMW, Naturhistorisches Museum Wien, Austria.

Molds and casts in this study: The late Pál Müller supplied specimens, plaster casts, and silicone molds of some specimens, as indicated herein. In some cases, the identity of the specimen that was cast is known and in others it is not. We have elected to use the molds and casts for descriptions of species, as there is some hope that they can be matched with specimens currently deposited in the NHMW or in the Hungarian Natural History Museum in Budapest. No holotypes were designated based upon casts, even though sometimes they appear to have been made from better preserved specimens.

Order Decapoda LATREILLE, 1802

Infraorder Brachyura LINNAEUS, 1758

Section Dromiacea DE HAAN, 1833

Superfamily Dromioidea DE HAAN, 1833

Family Dromiidae DE HAAN, 1833

Genus *Dromiopsis* REUSS, 1858 [imprint 1857]

Type Species: *Brachyurites rugosa* SCHLOTHEIM, 1820, by subsequent designation of BEURLEN (1928).

Included Species: *Dromiopsis aedicula* new species; *D. americana* ROBERTS, 1956; *D. bullamelga* new species; *D. ceratoi* BESCHIN, BUSULINI, TESSIER & ZORZIN, 2016; *D. depressa* SEGERBERG, 1900; *D. elegans* REUSS, 1858 [imprint 1857]; *D. gigas* FORIR, 1887; *D. granulata* COLLINS & RASMUSSEN, 1992; *D. laevior* REUSS, 1859; *D. longitudovata* BESCHIN, BUSULINI, TESSIER & ZORZIN, 2016; *D. marginospinosa* BESCHIN, BUSULINI & TESSIER in BESCHIN *et al.*, 2019; *D. mosae* COLLINS, FRAAYE & JAGT, 1995; *D. oscari* NYBORG, GARASSINO, VEGA & KOVALCHUK, 2019; *D. parvula* BESCHIN, BUSULINI, TESSIER & ZORZIN, 2016; *D. paucigranosa* BESCHIN, BUSULINI, DE ANGELI & TESSIER, 2007; *D. praelaevior* COLLINS, FRAAYE & JAGT, 1995; *D. rochetti* BESCHIN, BUSULINI & TESSIER in BESCHIN *et al.*, 2019; *D. rugosa* (SCHLOTHEIM, 1820); *D. ubaghsi* FORIR, 1889; *D. vicetinus* BESCHIN, DE ANGELI, CHECCHI & ZARANTONELLO, 2016.

Diagnosis: As in SCHWEITZER *et al.* (2012: p. 29).

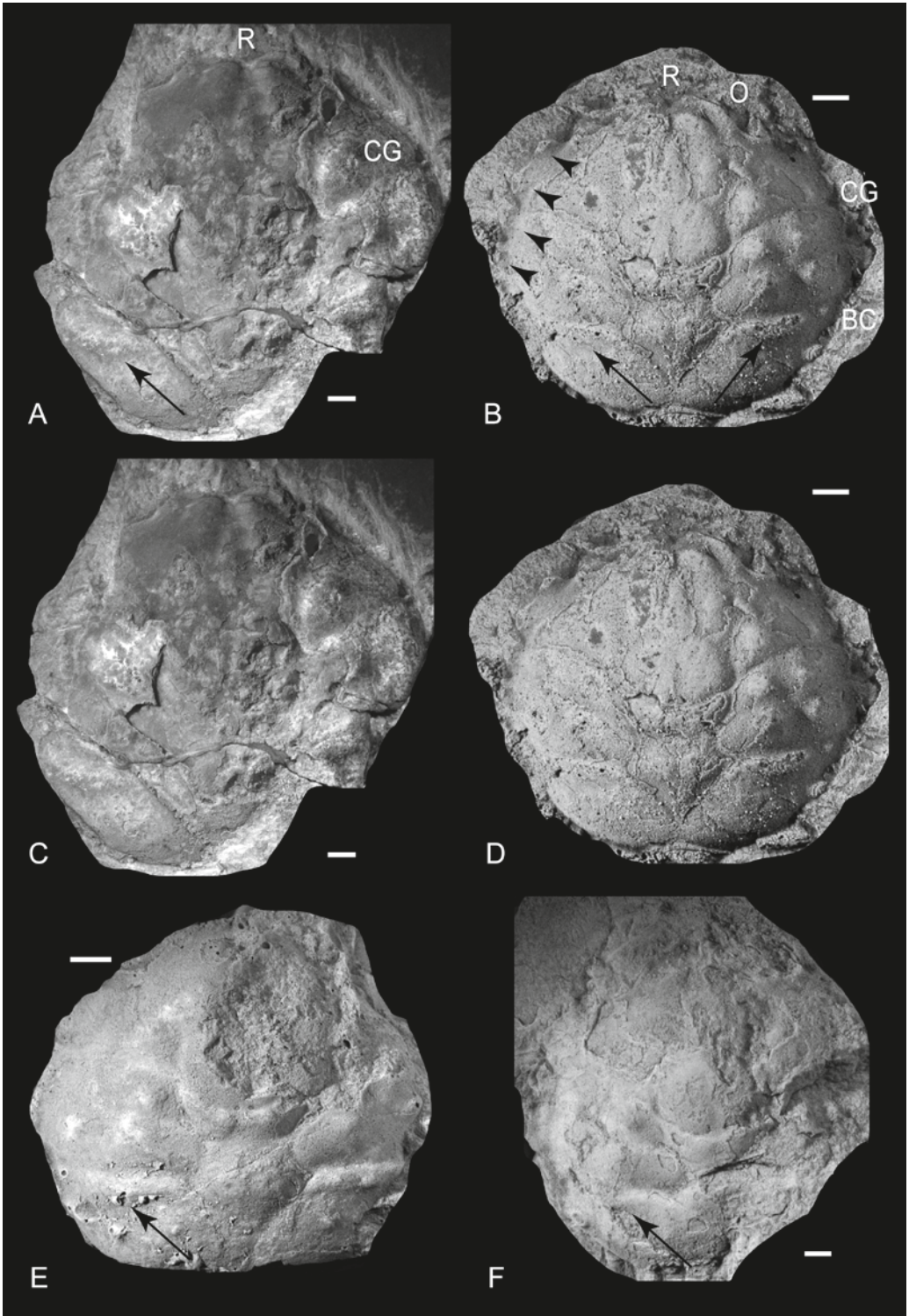
Discussion: The new species is referred to *Dromiopsis* in possessing a carapace about as wide as long, forward-directed orbits; spinose lateral margins; and deeply incised, distinct cervical and branchiocardiac grooves. The new species is similar to species of *Kromtitis* MÜLLER, 1984, of Dynomenidae ORTMANN, 1892, in possessing large swellings on the protogastric and epibranchial regions. However, the cervical and branchiocardiac grooves are not distinct in *Kromtitis*, and the various lobes and regions are granular and themselves lobate, not seen in the new species. Thus, we refer the new species to *Dromiopsis*.

***Dromiopsis bullamelga* new species**

(Fig. 1)

Diagnosis: Carapace circular, about as wide as long; rostrum triangular, rimmed; orbits directed forward; lateral margins spinose, deeply incised where intersected by cervical and branchiocardiac grooves; regions moderately defined; cervical, postcervical, and branchiocardiac grooves extending onto flanks.

Etymology: The species name, *bullamelga*, refers to the branchial swellings and ridges present on the new species that distinguish it from other species within the genus. From the Latin words “*bull*” (swelling) + “*amelga*” (ridge).



Types: Holotype NHMW-Geo 2022/0289/0001, 1 paratype NHMW-Geo 2022/0289/0004, 2 referred specimens NHMW-Geo 2022/0289/0002 and 2022/0289/0003.

Measurements: Dimensions (in mm) taken on the dorsal surface of *Dromiopsis bullamelga* new species are presented in Table 1.

Description: Carapace hexagonal, about as wide as long, length about 98% width, length to position of maximum width about two-thirds the distance posteriorly, moderately vaulted longitudinally and transversely. Rostrum blunt-triangular (Fig. 1A), bilobed, rimmed, axially sulcate, extending slightly beyond large, forward-facing orbits (Fig. 1B), rostral width about 35% carapace width; fronto-orbital width about 74% carapace width. Anterolateral margin anterior to cervical groove with two spines, not including large outer orbital spines; posterior to cervical groove, margin with 2 spines (Fig. 1B); posterolateral margins spinose with 1 or 2 large spines located just posterior to the branchiocardiac groove; spines broad and triangular. Posterior margin rimmed, concave. Margins incised by deep cervical and branchiocardiac grooves (Fig. 2A). Protogastric regions bilobed, one lobe parallel to mesogastric and one more equant lobe postolateral to it; hepatic regions flattened; mesogastric region with long anterior process, posteriorly rounded; metagastric region wide, with concave anterior margin and convex posterior margin; urogastric region narrow, depressed; cardiac region wide, narrowing posteriorly. Epibranchial region composed of four swellings; remainder of branchial regions undifferentiated, with pronounced, transverse ridges parallel to and just posterior to the branchiocardiac groove (Fig. 1A, B, E, F).

Discussion: *Dromiopsis bullamelga* new species most resembles *Dromiopsis rugosa*, due to their circular carapaces, triangular rostrums, well-defined regions, and deep cervical, postcervical, and branchiocardiac grooves, but with key differences in ornamentation. *Dromiopsis rugosa* has well-defined granules on the dorsal surface of its carapace, while *Dromiopsis bullamelga* is smoother overall, with branchial swellings and epibranchial ridges.

Specimens of the new species display spinose anterolateral margins, unlike *Dromiopsis americana*, *D. depressa*, *D. granulata*, *D. rochetti*, and *D. rugosa*. Additionally, only the lateral margins of *D. longitudovata* and the antero-lateral margins of *D. paucigranosa* are spinose. Spines in *Dromiopsis bullamelga* are broader than those of *D. ceratoi*, *D. paucigranosa*, or *D. vicetinus*. Regions are too well-defined to be referred to *D. americana*, *D. depressa*, *D. marginospinosa*, *D. mosae*, *D. paucigranosa*, or *D. praelaevior*, which have poorly defined regions. The gastro-hepatic regions of *D. granulata* as well

- ◀ Fig. 1. *Dromiopsis bullamelga* new species. **A, C**, holotype NHMW-Geo 2022/0289/0001, dorsal carapace; **B, D**, referred specimen NHMW-Geo 2022/0289/0003, cast of dorsal carapace; **E**, referred specimen NHMW-Geo 2022/0289/0002, cast of dorsal carapace; **F**, paratype NHMW-Geo 2022/0289/0004, dorsal carapace. Long arrows indicate ridge paralleling branchiocardiac groove; short arrows indicate anterolateral spines. BC, branchiocardiac groove; CG, cervical groove; O, orbit; R, rostrum. Scale bars equal 1 mm.

as the epigastric and mesogastric regions of *D. vicetinus* are not as well-defined as in *Dromiopsis bullamelga*. Carapace shape is sub-circular and slightly wider than long in *Dromiopsis bullamelga*, while *D. elegans* and *D. vicetinus* are ovate, *D. granulata* is pentagonal, *D. ceratoi* and *D. paucigranosa* are subpentagonal, and *D. ubaghshi* is hexagonal. Specimens of *Dromiopsis bullamelga* are narrower than those of *D. elegans* and are too short to be placed in *D. depressa*, *D. longitudovata*, *D. oscari*, or *D. vicetinus*. *Dromiopsis ceratoi*, *D. elegans*, *D. gigas*, *D. granulata*, *D. longitudovata*, *D. mosae*, *D. oscari*, *D. rugosa*, and *D. ubaghshi* are granular, whereas *Dromiopsis bullamelga* is smooth. The rostrum of *D. depressa* is more rounded than in *Dromiopsis bullamelga*, and the rostrum of *D. vicetinus* is not rimmed. While *D. laevior* may feature similar ridges, no currently listed species of *Dromiopsis* features both the branchial swellings and epibranchial ridges as seen in the Kambüchel specimens.

Specimens of *Dromiopsis bullamelga* are distinct from other species of *Dromiopsis* due to their pronounced, transverse ridges prominent on the epibranchial regions, parallel to and just posterior to the branchiocardiac groove; round swellings present on the branchial regions; and numerous, broad spines present on both the antero-lateral and

Table 1. Measurements (in mm) for specimens of *Dromiopsis* spp. Max W = maximum width, PW = posterior width, FOW = fronto-orbital width, FW = frontal width, L = maximum length, L to Max W = length to maximum width, L to Cervical Groove = length to the cervical groove.

| Specimen | Max W | PW | FOW | FW | L | L to Max W | L to Cervical Groove |
|--|-------|------|------|-----|------|------------|----------------------|
| <i>Dromiopsis bullamelga</i> n. sp. NHMW-Geo 2022/0289/0003 | 18.5 | 13.0 | 13.7 | 6.1 | 18.1 | 11.0 | 10.0 |
| <i>Dromiopsis bullamelga</i> n. sp. NHMW-Geo 2022/0289/0002 | 15.1 | 7.3 | 11.1 | 5.1 | 14.7 | 10.2 | 8.6 |
| <i>Dromiopsis bullamelga</i> n. sp. NHMW-Geo 2022/0289/0004 | 5.3 | – | 11.4 | 5.7 | – | – | – |
| <i>Dromiopsis bullamelga</i> n. sp. NHMW-Geo 2022/0289/0001 | – | 9.1 | 13.5 | 6.6 | 22.9 | – | – |
| <i>Dromiopsis aedicula</i> n. sp. NHMW-Geo 2022/0289/0007 | 7.7 | – | – | – | – | – | – |
| <i>Dromiopsis aedicula</i> n. sp. NHMW-Geo 2022/0289/0005 | 5.0 | 5.0 | 3.6 | 2.0 | 4.5 | 2.0 | – |
| <i>Dromiopsis aedicula</i> n. sp. NHMW-Geo 2022/0289/0008 | 4.3 | – | 3.5 | 1.8 | 4.0 | 2.7 | 2.4 |
| <i>Dromiopsis aedicula</i> n. sp. NHMW-Geo 2022/0289/0006 | 5.3 | 2.5 | 4.5 | 2.5 | 4.6 | 3.0 | 3.2 |
| ? <i>Dromiopsis rugosa</i> NHMW-Geo 2022/0289/0009 | 7.1 | 3.8 | 5.0 | 2.3 | 5.7 | 2.8 | 3.1 |

lateral margins. For these significant differences, these specimens belong to a new species of *Dromiopsis* that originated after the K/T boundary. Other species of *Dromiopsis* have been found in lower Cretaceous–Paleocene strata in Europe (Belgium, Denmark, France, Italy, the Netherlands, Sweden), Greenland, the United States (New Jersey, Oregon, South Dakota), and Madagascar (SCHWEITZER *et al.* 2012). The new specimens extend the range of the genus into the Austrian Alps.

***Dromiopsis aedicula* new species**

(Fig. 2)

Diagnosis: Sub-circular carapace; rimmed, triangular rostrum, obliquely directed orbits; spinose lateral margins; deeply incised cervical groove; cervical and branchiocardiac grooves extending onto the flanks. Dorsal surface covered in small pits; tuberculate branchial lobes; several small, triangular spines on lateral margins; poorly defined regions; moderately incised cervical groove; branchiocardiac groove more deeply incised than cervical groove.

Etymology: The species name, *aedicula*, is the Latin word “aedicula” (temple). The name refers to the triangular, steeple-like rostrum of the holotype, and to the collecting locality, near Neunkirchen, Austria. Neunkirchen is German for “nine churches”.

Types: Holotype NHMW-Geo 2022/0289/0005, 3 paratypes NHMW-Geo 2022/0289/0006 to 2022/0289/0008.

Measurements: Dimensions taken on dorsal surface of *Dromiopsis aedicula* new species are presented in Table 1.

Description: Carapace sub-circular to subpentagonal, slightly wider than long, length about 89% width. Rostrum rimmed, extending beyond wide orbits, with median sulcus, rostral width about 40% carapace width (Fig. 2C). Orbits obliquely directed, fronto-orbital width about 83% carapace width. Anterolateral margins spinose with up to five small, triangular spines (Fig. 2B); one small, triangular spine located on posterolateral margin, just posterior to intersection of branchiocardiac groove. Carapace surface covered with small pits, with small tubercles on hepatic and epibranchial regions near lateral margins. Regions not well-differentiated; mesogastric region with very long anterior process; mesogastric and urogastric regions not well differentiated from one another, cardiac region weakly inflated, triangular. Cervical and branchiocardiac grooves moderately defined, reaching lateral margins, branchiocardiac groove more deeply incised than cervical groove (Fig. 2A–C).

Discussion: *Dromiopsis aedicula* new species most closely resembles *Dromiopsis mosae*, due to similar dorsal tuberculation, carapace and rostrum shape, and poorly defined regions. However, *D. mosae* possesses larger, more bifid spines compared to the smaller, more triangular spines of the new species. *Dromiopsis aedicula* new species also resembles *Dromiopsis ceratoi* and *Dromiopsis paucigranosa*, due to similar spinose margins, spine size, well-defined cardiac and mesogastric regions, and cervical

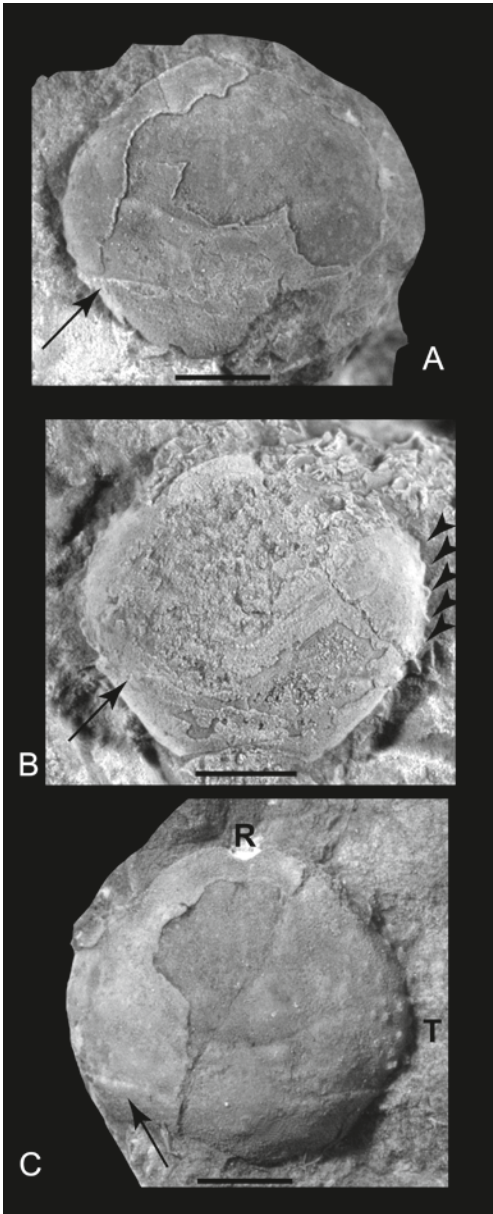


Fig. 2. *Dromiopsis aedicula* new species. **A**, paratype NHMW-Geo 2022/0289/0008, dorsal carapace; **B**, holotype NHMW-Geo 2022/0289/0005, dorsal carapace; **C**, paratype NHMW-Geo 2022/0289/0006, dorsal carapace. Long arrows indicate branchiocardiac groove; short arrow heads indicate lateral spines. R, rostrum; T, tubercles on carapace just left of the letter. Scale bars equal 1 mm.

and branchiocardiac grooves reaching the lateral margins close to each other. However, both *D. ceratoi* and *D. paucigranosa* are subpentagonal. There are also some differences regarding ornamentation. *Dromiopsis ceratoi* does not have the large granules seen in *Dromiopsis aedicula*, and its granules are only more apparent on the posterior branchial lobes, whereas *Dromiopsis aedicula* also possesses large granules on the metagastric regions. *Dromiopsis paucigranosa* is almost smooth and lacks the granules more apparent on *Dromiopsis aedicula*. Additionally, *D. mosae*, *D. ceratoi*, and *D. paucigranosa* are all Eocene (Ypresian) species.

Specimens of *Dromiopsis aedicula* new species have spinose anterolateral margins, unlike *D. americana*, *D. depressa*, *D. granulata*, *D. rochetti*, and *D. rugosa*. Carapace shape is near circular and wider than long, while *D. americana* is sub-circular, *D. laevior*, *D. elegans*, and *D. vicetinus* are ovate, *D. granulata* is pentagonal, and *D. ubaghshi* is hexagonal. *Dromiopsis*

aedicula is narrower than *D. elegans* and is too short to be placed in *D. depressa*, *D. longitudovata*, *D. oscari*, and *D. vicetinus*. *Dromiopsis americana* and *D. laevior* are smooth, whereas *Dromiopsis aedicula* features fine pores. While the dorsal surface of *D. granulata* is also covered with small pores, it is not tuberculate. The rostrum of *D. depressa* is more rounded than *Dromiopsis aedicula*, and the rostrum of *D. vicetinus* is not rimmed. For these significant differences, these specimens belong to a new species of *Dromiopsis*.

?*Dromiopsis rugosa* (SCHLOTHEIM, 1820)
(Fig. 3A)

- 1820 *Brachyurites rugosus* – SCHLOTHEIM: 36.
 1858 *Dromiopsis rugosa* (SCHLOTHEIM) – REUSS: 10.
 1859 *Dromiopsis rugosa* (SCHLOTHEIM) – REUSS: 10, pl. 3, figs 2, 3, pl. 5, fig. 6.
 1866 *Dromia rugosa* (SCHLOTHEIM) – FISCHER-BENZON: 24, pl. 3, figs 1–3.
 1900 *Dromiopsis rugosa* (SCHLOTHEIM) – SEGERBERG: 358, pl. 7, figs 8, 9.
 1928 *Dromiopsis rugosa* (SCHLOTHEIM) – BEURLIN: 157.
 1994 *Dromiopsis rugosa* (SCHLOTHEIM) – COLLINS & JAKOBSEN: 38, pl. 10, fig. 8.
 1997 *Dromiopsis rugosa* (SCHLOTHEIM) – JAKOBSEN & COLLINS: pl. 3, fig. 7.
 2004 *Dromiopsis rugosa* (SCHLOTHEIM) – JAKOBSEN & FELDMANN: figs 5, 7.
 2010 *Dromiopsis rugosus* (SCHLOTHEIM) – SCHWEITZER *et al.*: 65.
 2012 *Dromiopsis rugosa* (SCHLOTHEIM) – SCHWEITZER *et al.*: 29, fig. 19a–c.

Material Examined: NHMW-Geo 2022/0289/0009.

Description of material: Carapace sub-ovate to sub-circular, wider than long. Frontal width about one third of the maximum width; fronto-orbital width slightly over two thirds of maximum width. Maximum width located anterior to the cervical groove, at about half of the length moving posteriorly. Entire dorsal surface with large granules. Rostrum straight, bilobed, extends slightly beyond forward-facing orbits (Fig. 3A). Well-developed cervical, postcervical, and branchiocardiac grooves (Fig. 3A). Unclear if regions are moderately- or well-defined due to the condition of the specimen cast. Margins entire and crispate.

Measurements: Dimensions (in mm) were taken on the dorsal surface of specimen NHMW-Geo 2022/0289/0009 (Table 1).

Discussion: Specimen NHMW-Geo 2022/0289/0009 is a cast that most closely resembles *Dromiopsis rugosa* due to its carapace shape, granular dorsal surface, well-developed grooves, and lack of spinose margins. Due to the poor condition of the cast, it is difficult to discern details about the carapace regions. Therefore, this specimen is tentatively placed within *D. rugosa*. If the identification is confirmed, the range for the species would be extended into the ?Selandian to Thanetian.

Family Sphaerodromiidae GUINOT & TAVARES, 2003

Genus *Dromilites* H. MILNE EDWARDS, 1837

Type species: *Dromia bucklandi* H. MILNE EDWARDS, 1837 [in 1834–1840], by subsequent designation of GLAESSNER (1929b).

Included Species: *Dromilites alpina* (GLAESSNER, 1929a); *D. belli* VAN BAKEL, ROBIN, CHARBONNIER & SAWARD, 2017; *D. bucklandi*; *D.?* *cardwelli* (ARMSTRONG, NYBORG, BISHOP, OSSÓ-MORALES & VEGA, 2009); *D. montenati* ROBIN, VAN BAKEL, PACAUD & CHARBONNIER, 2017; *D. simplex* QUAYLE & COLLINS, 1981; *D. vicensis* BARNOLAS CORTINAS, 1973.

Diagnosis: As in SCHWEITZER *et al.* (2012: p. 33).

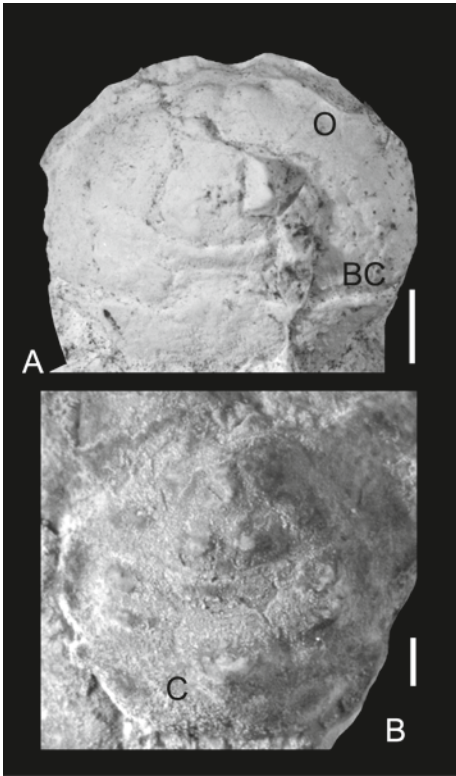


Fig. 3. **A**, ?*Dromiopsis rugosa* (SCHLOTHEIM, 1822), NHMW-Geo 2022/0289/0009, cast of dorsal carapace; **B**, *Dromilites* sp., NHMW-Geo 2022/0289/0010, cast of dorsal carapace. BC, branchiocardiac groove; C, cardiac region to the right of the letter; O, orbit. Scale bars equal 1 mm.

Dromilites sp.

(Fig. 3.B)

Material Examined: NHMW-Geo 2022/0289/0010.

Description of material: Carapace granular, subovate, slightly wider than long length about 98% width. Rostrum straight, bi-lobed, extends beyond large, obliquely directed orbits, fronto-orbital width about 92% carapace width. Margins do not appear spinose. Margins well-defined, incised by deep cervical, postcervical, and branchiocardiac grooves; branchiocardiac groove extends into flanks. Large tubercules present

on well-defined hepatic, posterior mesogastric, and epibranchial regions. Cardiac region inflated (Fig. 3B). Posterior margin broad, slightly over half of the maximum width.

Measurements: Dimensions (in mm) taken on dorsal carapace of specimen NHMW-Geo 2022/0289/0010: maximum width, 7.9 mm; posterior width, 4.2 mm; fronto-orbital width, 7.3 mm; frontal width, 2.9 mm; maximum length, 7.7 mm; length to maximum width, 4.8 mm; length to cervical, 4.0 mm.

Discussion: The Kambübel specimen exhibits some of the characteristics of *Dromilites montenati*, as described by ROBIN *et al.* (2017). There are striking similarities between the carapace size and shape, the well-defined tuberculate regions, and cervical grooves. Additionally, *D. montenati* has been found in coral limestone from the Danian Vigny Quarry in France. The specimen referred to *Dromilites* sp. here has a very inflated cardiac region that differentiates it from other species of *Dromilites* and *Dromiopsis*. The lateral margins and front are poorly preserved in the new specimen; thus, we opt not to place it within a species. *Dromilites? cardwelli* was recovered from Danian clay in Texas. The rest of the described species of *Dromilites* have only been found in Eocene (Ypresian, Lutetian, and Priabonian) strata. The regions of the new specimen are too well-defined to be placed in *D. simplex*, in which they are poorly defined. The Kambübel specimen is sub-ovate, while *D. bucklandi* and *D. vicensis* are sub-circular, *D. simplex* is sub-pentagonal, and *D. vicensis* is pentagonal. The Kambübel specimen seems to lack

spines, whereas *D. alpina* and *D. simplex* are spinose. Placement of the specimen in *Dromilites* does not extend the generic range, as it was already known from the Paleocene through Eocene of Europe.

Section Etyoida GUINOT & TAVARES, 2001

Superfamily Etyoidea GUINOT & TAVARES, 2001

Family Feldmanniidae GUINOT & TAVARES, 2001

Genus *Caloxanthus* A. MILNE-EDWARDS, 1864

Type species: *Caloxanthus formosus* A. MILNE-EDWARDS, 1864, by monotypy.

Included Species: *Caloxanthus americanus* RATHBUN, 1935; *C. brittanicus* COLLINS, 2015; *C. kuypersi* FRAAYE, 1996; *C. formosus*; *C. kavanaughii* COLLINS, GARVIE & MELLISH, 2019; *C. ornatus* (FISCHER-BENZON, 1866); *C. paraornatus* KLOMPMAKER, ARTAL, VAN BAKEL, FRAAIJE & JAGT, 2011; *C. purleyensis* (WITHERS, 1928); *C. simplex* (SECRETAN, 1964); *C. thompsonorum* KLOMPMAKER, HYŽNÝ & JAKOBSEN, 2015; *C. vignyensis* KLOMPMAKER, HYZNY & JAKOBSEN, 2015; *C. wrightii* COLLINS & BRETON, 2011.

Diagnosis: As in SCHWEITZER *et al.* (2017: p. 8).

***Caloxanthus ornatus* (FISCHER-BENZON, 1866)**

(Fig. 4)

- 1866 *Carpiliopsis ornatus* – FISCHER-BENZON: 28, pl. 2, figs 1–3, pl. 5, fig. 2.
- 1900 *Carpiliopsis ornatus* FISCHER-BENZON – SEGERBERG: 28, pl. 3, figs 15–17.
- 1994 *Caloxanthus ornatus* (FISCHER-BENZON) – COLLINS & JAKOBSEN: 41, pl. 10, fig. 16.
- 1997 *Caloxanthus ornatus* (FISCHER-BENZON) – JAKOBSEN & COLLINS: pl. 3, fig. 9.
- 2010 *Caloxanthus ornata* (FISCHER-BENZON) – SCHWEITZER *et al.*: 67.
- 2016 *Caloxanthus ornatus* (FISCHER-BENZON) – KLOMPMAKER *et al.*: fig. 3e, f.
- 2017 *Caloxanthus ornatus* (FISCHER-BENZON) – SCHWEITZER *et al.*: 8, fig. 3.2a.

Material Examined: NHMW-Geo 2022/0289/0011 to 2022/0289/0015.

Description of material: Carapace wider than long, ovoid, length about 75% carapace width. Dorsal surface granular, regions mostly undefined on cuticle surface, subtly expressed on molds of interior of carapace. Orbits large, facing obliquely, fronto-orbital width about 84% carapace width. Frontal region bi-lobed, each lobe with a small swelling located posterior of center, about 44% carapace width. Three small tubercles arranged in a triangle located on hepatic region, of which two lateral-most are arranged vertically parallel to axis, and third tubercle located along axis. Mesogastric region poorly defined, narrow process and pits along posterior margin of region observable widest anteriorly, extends to cervical groove. Cardiac region triangular, with three small tubercles arranged in a triangle, of which anterior-most two are set one on each side of axis, third tubercle is located on axis near posterior-most part. Branchiocardiac grooves developed as arcuate

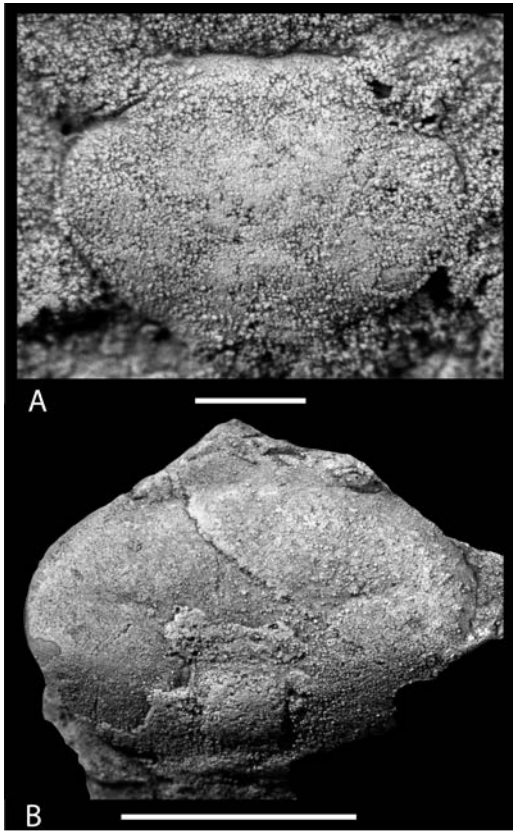


Fig. 4. *Caloxanthus ornatus* (FISCHER–BENZON, 1866). **A**, NHMW-Geo 2022/0289/0011, cast; **B**, NHMW-Geo 2022/0289/0012, cast. Scale bars equal 1 mm.

grooves laterally on either side of cardiac region. Margins not spinose. Posterior margin weakly concave and smooth.

Measurements: Measurements (in mm) taken on dorsal surface of specimens of *Caloxanthus ornatus* are presented in Table 2.

Discussion: The Kambüchel specimens are referred to *Caloxanthus ornatus* due to their similar carapace shape, granular dorsal surface with groups of small tubercles oriented in triangular patterns, obliquely-facing orbits, thin mesogastric process, triangular cardiac region, curved ridges lateral to the cardiac region, spineless margins, and weakly convex posterior margin. All of these features are also present in *C.*

paraornatus. However, *C. paraornatus* was originally found in upper Albian strata (Albeniz Unit, Equino Formation) of the Koskobilo quarry in Navarra, Spain (KLOMPMAKER *et al.* 2011), whereas *C. ornatus* was originally found in the Danian Fakse quarry in Denmark (FISCHER–BENZON 1866). KLOMPMAKER *et al.* (2011) postulated that *C. paraornatus* was the precursor of *C. ornatus* by 36 million years. If that is correct, then the Kambüchel specimens indicate that the evolutionary descendants of *C. paraornatus* had spread to both Denmark and the Austrian Alps. The new specimens of *C. ornatus* also expand the geologic range of the species to the ?Selandian and Thanetian.

Table 2. Measurements (in mm) for specimens of *Caloxanthus ornatus* (FISCHER–BENZON, 1866). Max W = maximum width, PW = posterior width, FOW = fronto-orbital width, FW = frontal width, L = maximum length, L to Max W = length to maximum width, L to Cervical Groove = length to the cervical groove.

| Specimen | Max W | PW | FOW | FW | L | L to Max W | L to Cervical Groove |
|-------------------------|-------|----|-----|-----|-----|------------|----------------------|
| NHMW-Geo 2022/0289/0012 | – | – | 2.5 | 1.4 | 2.2 | 1.1 | – |
| NHMW-Geo 2022/0289/0013 | – | – | – | – | 5.4 | 2.7 | – |

Section Eubrachyura DE SAINT LAURENT, 1980

Superfamily Carpilioidea ORTMANN, 1893

Family Palaeoxanthopsidae SCHWEITZER, 2003

Genus *Jakobsenius* SCHWEITZER, 2005

Type and sole species: *Xanthilites cretaceus* SEGERBERG, 1900, by original designation.

Diagnosis: As in SCHWEITZER *et al.* (2018: p. 8).

***Jakobsenius cretaceus* (SEGERBERG, 1900)**

(Fig. 5)

- 1900 *Xanthilites? cretacea* – SEGERBERG: 29, pl. 3, figs 19, 20.
 1994 *Xanthilites cretacea* SEGERBERG – COLLINS & JAKOBSEN: 41, pl. 10, fig. 12.
 1997 *Xanthilites cretaceus* SEGERBERG – JAKOBSEN & COLLINS: pl. 3, fig. 12.
 2005 *Jakobsenius cretaceus* (Segeberg) – SCHWEITZER: 289, fig. 4.4.
 2010 *Jakobsenius cretaceus* (Segeberg) – SCHWEITZER *et al.*: 115.
 2018 *Jakobsenius cretaceus* (Segeberg) – SCHWEITZER *et al.*: 8, fig. 6.1.

Material Examined: NHMW-Geo 2022/0289/0016 to 2022/0289/0025 and NHMW-Geo 2022/0289/0029 to 2022/0289/0030.

Description of material: Carapace wider than long, finely granular, slightly vaulted anteriorly, with front downturned. Measured maximum length about three-quarters of maximum width. Maximum width located about three-fifths of length posteriorly. Regions moderately well-defined, separated by deep grooves. Orbits rimmed, forward-facing, fronto-orbital width about 58% carapace width. Front poorly preserved, with swellings located posterior to orbits, frontal width about 28% carapace width. Anterolateral margins spinose with 4 spines with rectangular bases and triangular tips separated by fissures. Swellings located on epigastric regions. Protogastric regions elevated above mesogastric region. Hepatic and epibranchial regions moderately inflated.

Measurements: Dimensions (in mm) taken on dorsal carapace of specimens of *Jakobsenius cretaceus* are presented in Table 3.

Discussion: Like other specimens of *Jakobsenius cretaceus*, the carapace is vaulted longitudinally in the anterior third. The front is downturned, and the frontal width is 28.3% of the estimated maximum width. Anterolateral regions have four spines with rectangular bases and triangular tips separated by fissures. *Jakobsenius* generally has a fronto-orbital width of about 50% of the maximum width. One specimen (NHMW-Geo 2022/0289/0019) may be a juvenile based upon its relatively small size and because the frontal-orbital width is over 50% of the maximum width as previously suggested (WRIGHT & COLLINS 1972). *Jakobsenius* has been found in Danian coral limestone

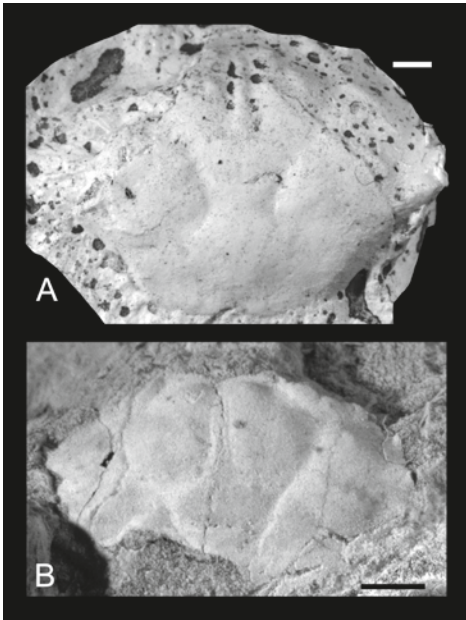


Fig. 5. *Jakobsenius cretaceus* (SEGERBERG, 1900). A, NHMW-Geo 2022/0289/0016, cast of dorsal carapace; B, NHMW-Geo 2022/0289/0023, partial dorsal carapace. Scale bars equal 1 mm.

localities in Denmark and France (SEGERBERG 1900; ROBIN *et al.* 2017). Due to their overall resemblance to *J. cretaceus*, the Kambühel specimens should be placed within that species. The presence of *Jakobsenius* in the Kambühel Formation expands the geographic range of the genus from France and Denmark to Austria and the geologic range from the Danian through the ?Selandian and Thanetian.

Family Tumidocarcinidae SCHWEITZER, 2005

Genus *Titanocarcinus* A. MILNE-EDWARDS, 1863

Type species: *Titanocarcinus serratifrons* A. MILNE-EDWARDS, 1863, by subsequent designation of GLAESSNER (1929b).

Other species: *Titanocarcinus briarti* (FORIR, 1887); *T. decor* SCHWEITZER, ARTAL, VAN BAKEL, JAGT & KARASAWA, 2007; *T. faxeensis* (FISCHER-BENZON, 1866); *T. kambuehelensis* VERHOFF, MÜLLER, FELDMANN & SCHWEITZER, 2009; *T. mammilatus* SECRETAN, 1964; *T. raulinianus* A. MILNE-EDWARDS, 1863; *T. schweitzerae* ROBIN, VAN BAKEL, PACAUD & CHARBONNIER, 2017; *T. serratifrons*; *T. subellipticus* (SEGERBERG, 1900).

Diagnosis: As in SCHWEITZER *et al.* (2018: p. 15).

Table 3. Measurements (in mm) for specimens of *Jakobsenius cretaceus* (SEGERBERG, 1900) given in mm. Max W = maximum width, PW = posterior width, FOW = fronto-orbital width, FW = frontal width, L = maximum length, L to Max W = length to maximum width.

| Specimen | Max W | PW | FOW | FW | L | L to Max W |
|-------------------------|-------|-----|-----|-----|-----|------------|
| NHMW-Geo 2022/0289/0024 | 17.2 | – | – | – | – | – |
| NHMW-Geo 2022/0289/0022 | 10.3 | – | – | – | – | 4.0 |
| NHMW-Geo 2022/0289/0016 | 11.9 | 6.7 | 8.5 | 3.7 | 9.2 | 5.4 |

***Titanocarcinus kambuehelensis* VERHOFF, MÜLLER, FELDMANN & SCHWEITZER, 2009**

2009 *Titanocarcinus kambuehelensis* – VERHOFF, MÜLLER, FELDMANN & SCHWEITZER: 227, figs 2, 3.

Material Examined: NHMW-Geo 2022/0289/0028 and NHMW-Geo 2007z0166/0001 to 2007z0166/0013

Description: as in VERHOFF *et al.* (2009).

Discussion: The Kambühel specimens are referred to *Titanocarcinus kambuehelensis* due to their carapace size and shape, grooves separating well-defined regions, and shallow groove between metagastric and cardiac regions. The specimens include fragmentary material not originally included in VERHOFF *et al.* (2009) and do not add to the original description.

Family Carpiliidae ORTMANN, 1893

Included genera: *Braggicarpilius* BESCHIN, BUSULINI & TESSIER, 2015; *Bryocarpilius* FELDMANN, SCHWEITZER, BENNETT, FRANȚESCU, RESAR & TRUDEAU, 2011; *Carpilius* DESMAREST, 1823; *Corallicarpilius* DE ANGELI & CECCON, 2015; *Eocarpilius* BLOW & MANNING, 1996; *Holcocarcinus* WITHERS, 1924; *Laticarpilius* FELDMANN, SCHWEITZER, BENNETT, FRANȚESCU, RESAR & TRUDEAU, 2011; *Liopsalis* VON MEYER, 1862; *Lovarcarpilius* BESCHIN, DE ANGELI, CHECCHI & ZARONTONELLO, 2016; *Maurocarpilius* OSSÓ, GAGNAISON & BAILLEUL, 2020; *Montemagralia* DE ANGELI & CECCON, 2016; *Ocalina* RATHBUN, 1929; *Oscacarpilius* ARTAL & VAN BAKEL, 2018; *Palaeocarpilius* A. MILNE-EDWARDS, 1862; *Paraocalina* BESCHIN, BUSULINI, DE ANGELI & TESSIER, 2007; *Proxicarpilius* COLLINS & MORRIS, 1978; *Tethyscarpilius* DE ANGELI & ALBERTI, 2016.

Diagnosis: As in SCHWEITZER *et al.* (2018, p. 2).

Genus *Braggicarpilius* BESCHIN, BUSULINI & TESSIER, 2015

Type species: *Braggicarpilius marginatus* BESCHIN, BUSULINI & TESSIER, 2015, by original designation.

Included Species: *Braggicarpilius wanzenboeckii* new species; *B. marginatus*.

Diagnosis: As in SCHWEITZER *et al.* (2018: p. 3).

Discussion: The new species most closely resembles *Braggicarpilius marginatus* due to its smooth, unmarked carapace; obliquely-directed orbits; convex, entire anterolateral margins; and weakly concave posterolateral margin. However, the carapace of *B. marginatus* is ovate, with smaller length to width and frontal width to maximum width ratios, is only moderately vaulted, and possesses a sinuous frontal margin. Due to the condition of the two specimens, it is indeterminate if they possessed deep branchio-cardiac grooves as in *B. marginatus*. While the specimens lack enough distinguishable

features to justify the description of a new genus, they are sufficiently similar for *B. marginatus* to be placed within *Braggicarpilius*. *Braggicarpilius* has been found in Ypresian coral limestone deposits in Italy, which minimally extends its geographic range to the Austrian Alps, and it extends its geologic range to the ?Selandian and Thanetian, making it one of the oldest genera in Carpiliidae.

The margins of the new species are entire, unlike species of *Bryocarpilius*, *Lovaracarpilius*, *Maurocarpilius*, *Palaeocarpilius*, *Proxicarpilius*, and *Tethyscarpilius*. Carapace regions are too undefined to be *Bryocarpilius* or *Lovaracarpilius*, and grooves are not incised enough to be referable to *Carpilius* or *Lovaracarpilius*. While the new species is wider than long, it is not transversely ovate enough to be placed in *Bryocarpilius*, *Corallicarpilius* or *Montemagralia*. Additionally, the new species is not transversely vaulted enough to be placed in *Montemagralia*. The frontal region of the new species is not observably bi- or quadri-lobed, as seen in species of *Carpilius*, *Bryocarpilius*, *Corallicarpilius*, and *Paraocalina*. The frontal margin of the new species is entire and not triangular as in species of *Bryocarpilius*, *Holcocarcinus*, *Laticarpilius*, *Liopsalis*, *Lovaracarpilius*, *Palaeocarpilius*, or *Tethyscarpilius*. The carapace of the new species is too smooth and un-ornamented to be placed in *Carpilius*, *Bryocarpilius*, *Corallicarpilius*, *Eocarpilius*, *Holcocarcinus*, *Lovaracarpilius*, *Ocalina*, *Proxicarpilius*, or *Tethyscarpilius*.

***Braggicarpilius wanzenboeckii* new species**

(Fig. 6)

Diagnosis: Carapace smooth, unornamented; anterolateral margins entire; fronto-orbital width about 82% carapace width, frontal margin arcuate, weakly convex.

Etymology: The species name, *wanzenboeckii*, refers the Austrian fossil collector Gerhard Wanzenböck, who collected and donated the holotype specimen.

Types: Holotype NHMW-Geo 2023/0078/0001 (casts: NHMW-Geo 2022/0289/0026), 1 paratype NHMW-Geo 2022/0289/0027

Measurements: Dimensions taken on dorsal surfaces of specimens NHMW-Geo 2022/0289/0026 and NHMW-Geo 2022/0289/0027. Average maximum carapace width 12.6 mm; frontal width 7.1 mm for both specimens; average fronto-orbital width 10.4 mm; average posterior width 4.8 mm. Average maximum length 11.1 mm; average length to maximum width 6.9 mm posteriorly.

Description: Carapace hexagonal, slightly ovate, wider than long, length about 88% carapace width, smooth, with undefined regions. Carapace extremely vaulted toward the anterior, maximum height located slightly anterior to maximum width. Vaulting is asymmetrical toward the right side of paratype. Frontal margin entire, slightly convex, frontal width about 56% carapace width. Orbits small, facing obliquely anterolaterally (Fig. 6B, C), fronto-orbital width about 82% carapace width. All margins entire; anterolateral margins rimmed. Cardiac region ornamented with three nodes arranged in a triangle, of

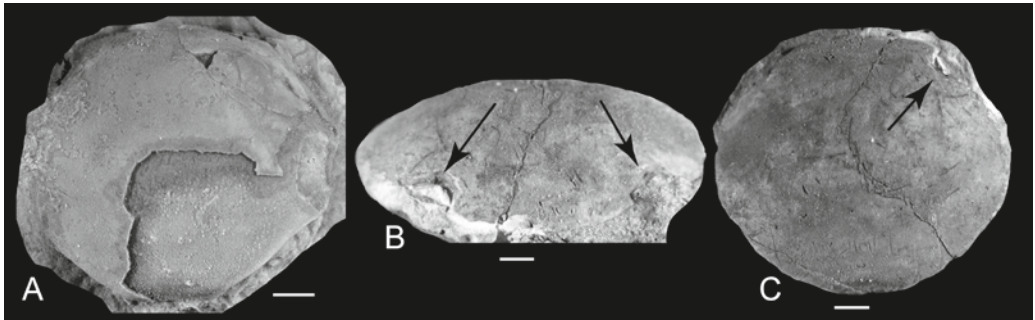


Fig. 6. *Braggiarpilius wanzenboecki* new species. **A**, paratype NHMW-Geo 2022/0289/0027, dorsal carapace; **B**, cast (NHMW-Geo 2022/0289/0026) of the holotype, anterior view of front and orbits; **C**, cast (NHMW-Geo 2022/0289/0026) of the holotype, dorsal view. Arrows indicate orbits. Scale bars equal 1 mm.

which anterior-most two parallel each other horizontally, situated somewhat anterior of center, and third node located on axis near posterior-most part. Cuticle of right posterior portion of paratype missing, obscuring definition of much of the metagastric, cardiac, and intestinal regions, as well as posterolateral margins.

Discussion: The carapace of NHMW-Geo 2022/0289/0027 is extremely vaulted towards the anterior and asymmetrical toward the right side of the specimen. The swelling does not appear to be the result of parasites. One of the best preserved and easily recognizable examples of parasitism in the fossil record are isopod-induced swellings in the branchial chamber of marine decapod crustaceans (KLOMPMAKER *et al.* 2014). However, these swellings are clearly separate from other carapace swellings, and bopyrid isopods favor anomurans over eubrachyurans (KLOMPMAKER *et al.* 2014). Since NHMW-Geo 2022/0289/0027 is only a carapace, and the deformation simply manifests in one side being larger than the other, the specimen may have been a molted exoskeleton that was deformed after the crab had shed it. The holotype specimen exhibits no such swelling.

Discussion

Six families, six genera, and eight species of brachyurans are recognized from the Kambüchel Formation. While there are no new genera described in this study, one third of the described species are new. *Dromiopsis* is the only genus with multiple species represented in this collection, two of which are new. *Dromilites* is the least numerous taxon represented in this collection, with only one specimen. *Titanocarcinus kambuehelensis* is the most abundant species with fourteen specimens in this collection, followed by *Jakobsenius cretaceus* with nine.

Carpiliidae is both the only extant family present and the only one to originate after the end of the Cretaceous. Five families present in this collection originated during the Cretaceous, Dromiidae, Sphaerodromiidae, Feldmanniidae, Tumidocarcinidae, and

Palaeoxanthopsidae. The Kambühel specimens extend Feldmanniidae from the Alban-Danian to the ?Selandian to Thanetian, and they extend Carpiliidae from the Thanetian-Recent to the ?Selandian to Thanetian. Dromiidae, Sphaerodromiidae, and Tumidocarcinidae already contained genera that lived during the Paleocene. Half of the genera present in the Kambühel Formation (*Dromiopsis*, *Caloxanthus*, and *Titanocarcinus*) survived the end-Cretaceous mass extinction event, and all of these surviving genera originated during the Cretaceous period. This study extends the range of *Caloxanthus* from the Danian to the ?Selandian and Thanetian. The stratigraphic range of *Braggicarpilius* is extended from the Eocene to the ?Selandian and Thanetian. All of the identified species originated in the Paleocene. The Kambühel Formation and older Fakse Quarry share several species, including *Dromiopsis rugosa*, *Caloxanthus ornatus*, and *Jakobsenius cretaceus*. Species of *Titanocarcinus* also occur in both localities. The occurrence of *Braggicarpilius* marks one of the oldest for the Carpiliidae, extending the range from the Eocene into the Paleocene. Thus, as might be expected, the middle-late Paleocene Kambühel Formation documents both Cretaceous survivors and newly appearing taxa.

Three of the six families present are podotrematous, and all of them originated during the Mesozoic. Three of the families and genera present are heterotrematous. Two of us (RMF, CES) collected specimens from the Fakse Quarry in Denmark over a period of one day. In that day's collection, housed at KSU and numbered KSU D 110–116, 87.5% of species and 95% of individual specimens are podotrematous. Of the specimens collected from the Kambühel Formation, 80% of species and 47% of individual specimens are podotrematous. Because this comparison is between one day of collecting at Fakse versus several collecting sessions at Kambühel, the results are not directly comparable. However, the stark difference in ratios between podotrematous and heterotrematous individuals among the two localities is notable and should be further investigated.

The difference in heterotreme to podotreme ratios in each collection may be due to the age and depositional environments of the sample locations. Podotreme populations declined from the Maastrichtian to the Thanetian, while heterotreme populations increased from the Danian to the Selandian before declining slightly in the Thanetian (SCHWEITZER & FELDMANN 2015). While both groups are found in Danian coral limestone deposits, heterotremes are more abundant in Thanetian carbonate deposits than podotremes. Additionally, heterotremes possess well-calcified carapaces and a propensity to live in a multitude of environments, many of which are fossilizable (SCHWEITZER & FELDMANN 2015). Podotremes and heterotremes reproduce differently, wherein heterotremes have internal fertilization, their seminal receptacles have a direct connection to the ovaries via the oviducts, and the gonopores are sternal (MCLAY & BECKER 2015). In contrast, podotremes store sperm in the spermathecae, with no internal connection to the ovaries, and the gonopores are coxal (MCLAY & BECKER 2015). This may have allowed the heterotremes to reproduce more often or more successfully than the podotremes, thus increasing the chances of their offspring surviving to sexual maturity.

These findings are in line with preexisting decapod faunal turnover data (SCHWEITZER & FELDMANN 2015). Heterotremes and podotremes compose 24% and 30–40% of late

Cretaceous decapod fauna respectively (SCHWEITZER & FELDMANN 2015). After the end-Cretaceous mass extinction event, the podotremes steadily declined, while the heterotremes composed 50% or more of the decapod fossil record by the end of the Paleocene (SCHWEITZER & FELDMANN 2015). Thus, the brachyurans from the Kambühel Formation may document the beginning of the domination of heterotremes rather than the podotremes.

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Specimens were collected primarily by the late Pál M. Müller as well as Gerhard Wanzenböck (Bad Vöslau, Austria) and James Verhoff (then a KSU student). We gratefully thank Gerhard Wanzenböck for the donation of one of the specimens studied herein. Alfréd Dulai (Hungarian Natural History Museum, Budapest) is acknowledged for assisting in deciphering the provenance of the specimens and returning the specimens to Austria. Neil Wells (KSU) aided with identifying fossils in thin section. Holly Grimmett assisted with photography. Constructive reviews by Hiroaki Karasawa (Mizunami Fossil Museum, Japan), Àlex Ósso (Tarragona, Spain), and editor Andreas Kroh (NHMW) greatly improved the manuscript.

Supplementary material

Detailed specimen lists of the material studied herein (MILLER *et al.* 2023) are available for download from the NHMW Data Repository (<https://doi.org/10.57756/38b3hd>)

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