Ann. Naturhist. Mus. Wien, Serie A	124	149–166	Wien, 30 April 2023

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

Samantha L. YOST[1], Rodney M. FELDMANN[2] & Carrie E. SCHWEITZER[3]*

(with 5 figures and 1 table)

Manuscript submitted on August 2nd 2022,
the revised manuscript on November 12th 2022.

Abstract

New decapod crustaceans from ?Selandian to Thanetian strata of the Kambühel Formation, Austria, include the paguroid *Squamipelta insecta* new genus and species, and two new galatheoid species, *Protomunida kambuehelensis* and *Annieporcellana paleocenica*. The range of *Annieporcellana* is extended across the Cretaceous-Paleogene boundary. Selandian and Thanetian decapod occurrences are rare; thus, this report adds to the known decapod diversity in the recovery after the end-Cretaceous events.

Key words: Annuntidiogenidae, Munididae, Catillogalatheidae, Paguroidea, Selandian, Thanetian.

Introduction

The anomuran decapod fauna described here consists of Paleocene fossils from the Kambühel Formation in the Gosau Group, outside of Neunkirchen, Austria. These fossils are important because few decapods have been reported from the Selandian and Thanetian stages of the Paleocene, about 5–10 million years after the end-Cretaceous extinction. The anomuran material examined for this study includes 19 specimens: 14 fossils embedded in matrix and 5 casts, documenting one paguroid species, three indeterminate paguroids, two galatheoid species, and 1 indeterminate galatheoid. The Kambühel anomuran fauna includes taxa originating before and after the end-Cretaceous boundary.

[1] Canton City Health Department, Canton, OH 44702, USA.

[2] Department of Earth Sciences, Kent State University, 221 McGilvrey Hall, Kent, OH 44242, USA; e-mail: rfeldman@kent.edu

[3] Department of Earth Sciences, Kent State University at Stark, 6000 Frank Ave. NW, North Canton, OH 44720, USA; e-mail: cschweit@kent.edu

*Corresponding author

ZooBank LSID: urn:lsid:zoobank.org:pub:9BD7FB84-EE1F-4355-81F1-7857E1354520

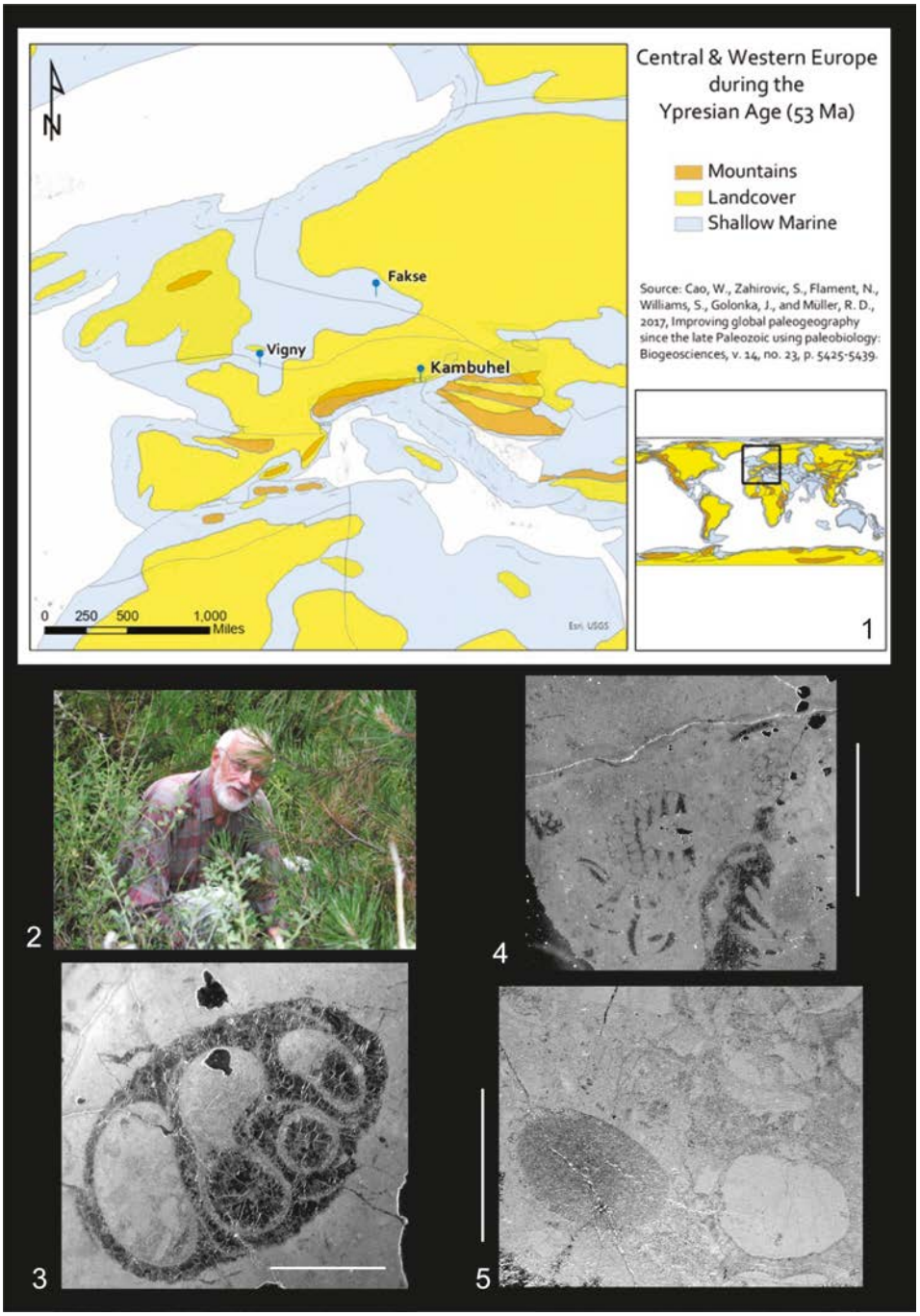

Fig. 1. 1, location map of the Kambühel Formation locality with respect to the Danian Fakse and Vigny localities; 2, Pál Müller in 2003, at the Kambühel Formation locality, showing the densely vegetated nature of the site; 3–5, thin sections of rock from which decapod specimens were collected. Scale bars = 2.5 cm.

Geologic Setting

The Kambühel Formation is a Cretaceous to Paleocene carbonate formation that is exposed southwest of Vienna, Austria. The sediment was deposited during the Maastrichtian (72.1–66 Ma) to Thanetian (59.2–56.0 Ma), and the crab-bearing part of the formation was deposited during the Paleocene (Schlagintweit *et al*. 2018; Sanders *et al*. 2020). The fossils were collected from the densely vegetated Kambühel Hill (N47°44.8′, E16°02′, Fig. 1), visited by two of us in the 2000's (RMF, CES). The age of the Kambühel Formation at this location is estimated as ?Selandian – Thanetian, close to section 3 of Sanders *et al*. (2020; Sanders 2021, personal communication).

Sanders *et al*. (2020) provided a very detailed study of the tectonic setting, lithology, age, and depositional environment for the Kambühel Formation. The ?Selandian to Thanetian part of the formation is composed of packstones, grainstones, and rudstones deposited in a shallow open marine system (Sanders *et al*. 2020). The fossils in the unit include many fragmented corals and red algae as well as gastropods, brachiopods, crustaceans, and foraminifera (Schlagintweit *et al.* 2003; Müller 2004; Schlagintweit 2005; Dulai *et al.* 2008; Krische *et al.* 2012; Schlagintweit *et al.* 2018; Sanders *et al*. 2020).

Preliminary investigation of the Kambühel decapod fauna suggested that it was not very diverse, although the number of specimens was considered to be rather high (Müller 2004). It appears that Müller's original supposition of low diversity holds, especially in comparison with the Danian Fakse localities in Denmark. One decapod species was previously described from the Kambühel Formation, *Titanocarcinus kambuhelensis* Verhoff, Müller, Feldmann & Schweitzer, 2009. In this work and Miller *et al*. (2023), we complete the work initiated by Pál Müller in the early 2000's.

Abbreviations

NHMW – Naturhistorisches Museum Wien, Austria

USNM – United States Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Systematic Paleontology

Infraorder Anomura MacLeay, 1838

Superfamily Paguroidea Latreille, 1802

Family Annuntidiogenidae Fraaije, 2014

Included genera: *Annuntidiogenes* Fraaije, van Bakel, Jagt & Artal, 2008; *Squamipelta* new genus.

Diagnosis: Shield of carapace longer than wide, with central gastric furrow; massetic region elongate; postrostral ridge usually present; Y-linea parallel to posterior-most groove of shield (adapted from Fraaije 2014).

Discussion: Several extant genera were included in Annuntidiogenidae when it was originally proposed (Fraaije 2014). As this placement has not been adopted by the wider carcinological community (Worms 2022), for now we recognize only the type genus and the new genus as members of the family.

Placement of the new genus within Annuntidiogenidae is based upon its similarity with *A. ruizdegaonai* Fraaije, van Bakel, Jagt & Artal, 2008, the type species, from the Albian-Cenomanian of Spain. Because the new taxon possesses a post-frontal ridge, a scabrous area posterior to the post-frontal ridge, and a central gastric groove similar to those of *A. ruizdegaoni*, and a very weak axial expression of the Y-linea, as in other species of *Annuntidiogenes*, we refer it to Annuntidiogenidae. The massetic region of the new taxon differs from all of the taxa discussed here in being short, only extending slightly posterior to the axial furrow. In the other species it is longer or positioned well posterior to that furrow. Further, the massetic region extends quite far anteriorly from the post-frontal ridge, not seen in any other species discussed here. Thus, the new specimen is referred to a new genus. Of note is that the *linea anomurica* is very clear on the new taxon, which seems to differentiate it from all of the current species of *Annuntidiogenes* as well.

Comparison of the new species to other species of *Annuntidiogenes* and thus determination of its generic placement is problematic, as the sole specimen of the type species of *Annuntidiogenes* is only the anterior half of the shield. It retains a post-frontal ridge, a central gastric groove, and a very weakly convex massetic region that is about twice as long as wide and not subdivided. The posterior morphology of the type species is unknown. The situation is further complicated by the very broad range of morphologies exhibited by the various species referred to *Annuntidiogenes*. *Annuntidiogenes sunuciorum* Fraaije, van Bakel, Jagt & Artal, 2008, has a scabrous frontal area on the shield and a central gastric groove as in the type species, but the massetic regions on that species are much more inflated than those of the type species. *Annuntidiogenes sagittula* Fraaije, van Bakel, Jagt & Skupien, 2020, has a massetic region subdivided into two or three regions. *Annuntidiogenes massetispinosus* Fraaije, van Bakel & Jagt, 2017, is much shorter overall than other species and has a bilobed massetic region and a lobate anterior branchial area. *Annuntidiogenes worfi* Fraaije, van Bakel, Jagt, Klompmkaer & Artal, 2009, is similar to the type species in its scabrous area posterior to the post-frontal ridge, but the massestic region is much reduced, only developed posteriorly, posterior to the central gastric groove. The Jurassic *Annuntidiogenes hoelderi* Fraaije, Robins, van Bakel, Jagt & Bachmayer, 2019, has a very wide massetic region that is bilobed, whereas the shield of *A. elongatus* Fraaije, Robins, van Bakel, Jagt & Bachmayer, 2019, is ovoid and lacks the massetic swelling altogether. Thus, it is difficult to develop a diagnosis that fits all of the species of *Annuntidiogenes*; examination of type material will be necessary to address these issues. In this circumstance it was considered most prudent to place the new material in a new genus as it differs from all of the species currently referred to *Annuntidiogenes*.

Genus *Squamipelta* new genus

Type and sole species: *Squamipelta insecta* new species, by original designation.

Diagnosis: Shield elongate, irregularly pitted, divided into regions by grooves. Postrostral ridge biconvex, central gastric groove extending posteriorly; pitted ornamentation in anterior gastric region; massetic region moderately inflated laterally, extending posteriorly to just posterior to the position of the end of the axial furrow; anterior branchial area elongate, much longer than wide, tapering posteriorly; short groove extending anteriorly and axially from lateral margin at position about 60 % the distance posteriorly, possibly linea-D; posterior margin incised by short, deep groove, possibly posterior part of Y-linea; *linea anomurica* very strong.

Etymology: The genus name is a combination of the Latin words "squama", meaning scale, and "pelta", meaning small shield, in reference to the scaly appearance of the shield of this animal. The gender is feminine.

***Squamipelta insecta* new species**
(Fig. 2)

Diagnosis: as for genus.

Etymology: The species name, *insecta*, refers to the overall appearance of the specimen, which superficially looks like a beetle (Coleoptera).

Measurements: Measurements (in mm) taken on the dorsal carapace, mostly the dorsal oval, of NHMW-Geo 2019/0042/0018: carapace length (front broken), 12.7; carapace width, 8.8.

Types: The holotype is a dorsal carapace, NHMW-Geo 2019/0042/0018.

Additional material: a cast of a dorsal carapace NHMW-Geo 2019/0042/0019.

Description: Shield elongate, irregularly pitted, most densely pitted anteriorly, divided into regions by grooves. Postrostral ridge biconvex, central gastric groove extending posteriorly; pitted ornamentation in anterior gastric region; massetic region moderately inflated laterally, extending posteriorly to just posterior to the position

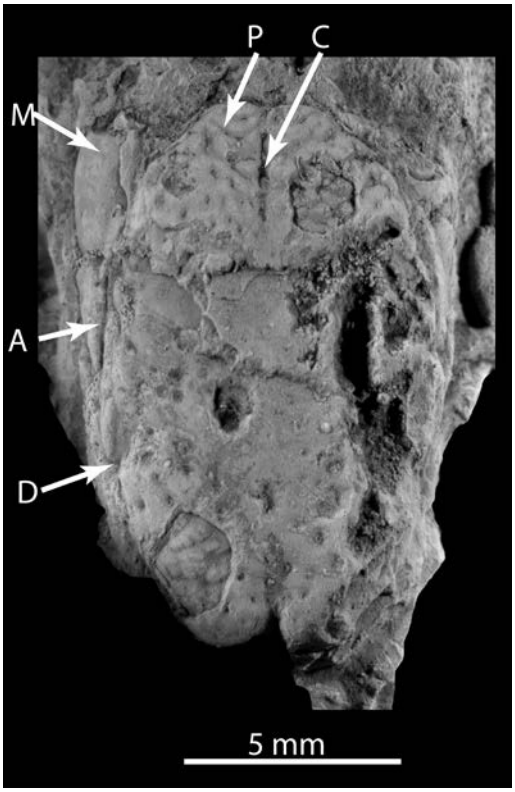

Fig. 2. *Squamipelta insecta* new genus, new species, holotype NHMW-Geo 2019/0042/0018. A, anterior branchial area; C, central gastric groove; D, linea-D; M, massetic region; P, post-frontal ridge.

of the end of the axial furrow; anterior branchial area elongate, much longer than wide, tapering posteriorly; short groove extending anteriorly and axially from lateral margin at position about 60% the distance posteriorly, possibly linea-D; posterior margin incised by short, deep groove, possibly posterior part of Y-linea; *linea anomurica* very strong.

Discussion: The holotype of the new species exhibits exfoliation of cuticle layers, exposing three layers and a mold of the interior at posterior left. The shield is not associated with chelae.

Paguroidea indeterminate A
(Fig. 3A)

Material examined: One cast of right propodus, NHMW-Geo 2019/0042/0017.

Description: Cast of right propodus with partial fixed finger; dactylus unknown; length/height ratio of 3.9 (17.8 mm / 4.5 mm). Manus (hand) slightly longer (11.4 mm) than high (10.1 mm); outer surface gently convex with few low, small (<1 mm) nodes widely arranged somewhat transversely, perpendicular to upper/lower surfaces; nodes with distally-directed pits, possibly evidence of setal pores. Slight concavity present near upper surface with very fine, stippled ornamentation. Upper surface with straight ridge ornamented with low nodes; remainder of upper surface smooth with slight downward angle toward inner surface. Smooth rim present where dactylus articulates. Inner surface not visible on cast. Fixed finger longer (6.8 mm) than wide (3.0 mm), tapers distally; distal end indistinct; nodes are more concentrated along outer surface compared to the manus. Lower distal surface of finger curves slightly upward. Lower surface with small, low nodes more concentrated distally; lower margin straight proximally becoming slightly convex distally along lower surface of fixed finger. Occlusal surface mostly smooth with three distinct, raised denticles; remainder of surface indistinct.

Discussion: The cast of an isolated right chela of a paguroid preserves the right outer surface of the propodus. Paguroidea indeterminate A has similar ornamentation with distinctly dentate occlusal surfaces and nodes along the upper/lower surfaces to many paguroids. More material is necessary to place the specimen within a family or genus.

Paguroidea indeterminate B
(Fig. 3B)

Material examined: One left propodus, NHMW-Geo 2019/0042/0016.

Description: Left propodus with fixed finger imbedded in matrix; dactylus unknown; length/height ratio of 2.8 (10.4 mm / 3.7 mm). Manus (hand) slightly longer (5.9 mm) than high (5.2 mm). Outer surface convex, covered with small (<1 mm), low nodes densely packed and arranged somewhat transversely, parallel to upper/lower surfaces. Articulation for carpus attachment present at base of manus; surface slightly pitted. Upper surface with four distinct, medium (<1 mm), raised nodes along margin with smaller nodes intercalated between them; nodes grade slightly onto inner surface. Inner

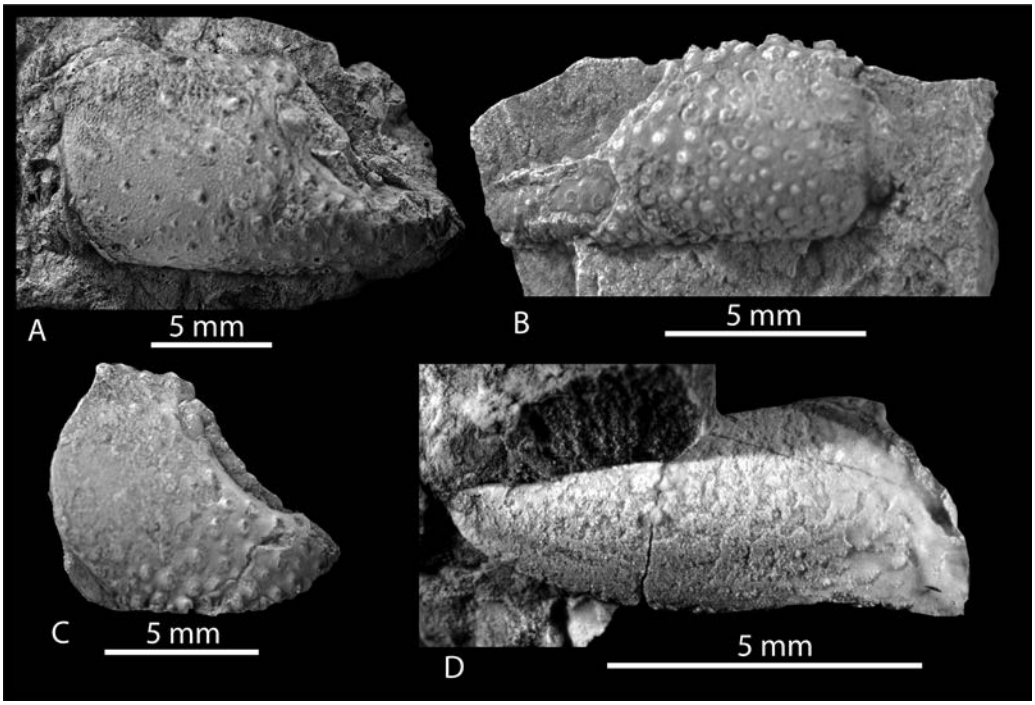

Fig. 3. Paguroidea and Galatheoidea indeterminate. **A**, Paguroidea indeterminate A, right propodus, NHMW-Geo 2019/0042/0017; **B**, Paguroidea indeterminate B, left propodus, NHMW-Geo 2019/0042/0016; **C**, Paguroidea indeterminate C, right propodus, NHMW-Geo 2019/0042/0015; **D**, Galatheoidea indeterminate, Porcellanidae, outer surface of right propodus, NHMW-Geo 2019/0042/0003.

surface convex, partly obscured, imbedded in matrix; surface relatively smooth with few large nodes near upper margin; smooth rim present where dactylus attaches. Fixed finger long (4.2 mm), slender (1.4 mm wide), and appears to taper but distal termination is indistinct; outer surface ornamented with small, low nodes; missing portions of replaced cuticle show similar ornamentation present on different layers. Lower surface imbedded in matrix; small low nodes present along margin. Occlusal surface obscured by matrix.

Discussion: Isolated chela can be difficult to assign taxonomically, especially for paguroids. This specimen in particular has partially obscured inner and occlusal surfaces. Paguroidea indeterminate B has a carpus articulation and surface ornamentation that is relatively common among paguroids, especially the minor chelae. More material is necessary to place the specimen within a family or genus.

Paguroidea indeterminate C
(Fig. 3C)

Material examined: One left propodus, NHMW-Geo 2019/0042/0015.

Description: Left propodus with fixed finger; dactylus unknown; length/height ratio of 1.7 (11.3 mm / 6.5 mm). Manus (hand) short, squat, and higher (9.1 mm) than long (6.2 mm); outer surface convex, covered with large, low nodes, densely spaced, arranged somewhat transversely and perpendicular to upper/lower margins; nodes with gentle slope directed proximally and steep slope directed distally; nodes becoming smaller distally. Outer surface slightly concave before reaching upper surface; small nodes on upper surface. Inner surface gently convex, weakly concave where fixed finger attaches to palm; surface with small (>1 mm), densely spaced nodes arranged somewhat transversely (most noticeable proximally). Fixed finger short, squat, and slightly longer (4.9 mm) than high (4.2 mm); finger tapers to blunt point, slightly curved toward the inner surface. Lower surface nodose; nodes grade onto both inner and outer surfaces. Occlusal surface mostly obscured by matrix, although there are two blunt denticles (slightly >1 mm) arranged along margins near distal end; one slightly larger, blunt denticle near base of occlusal surface.

Discussion: Paguroid fossils commonly consist of chelae as isolated remains. Because handedness is important in taxonomic classification, preservation of only one claw makes the organism difficult to identify. The variation in ornamentation and morphology of paguroid claws can also make taxonomic assignment difficult. Schweitzer *et al.* (2005) provided detailed examples of the broad variation in morphology and ornamentation of claws, especially when comparing recent and fossil specimens of the same genus. They also noted that some chelae in one taxon can resemble chelae in more than one genus or even family. Thus, we leave the specimen in open nomenclature.

Superfamily Galatheoidea Samouelle, 1819

Family Munididae Ahyong, Baba, Macpherson & Poore, 2010

Genus *Protomunida* Beurlen, 1930

Type species: *Galathea munidoides* Segerberg, 1900, by original designation.

Included species: *Protomunida bennickei* Klompmaker, Robins, Jakobsen & Sheldon, 2022; *P. eurekantha* Klompmaker, Robins, Jakobsen & Sheldon, 2022; *P. kambuehelensis* new species; *P. munidoides*; *P.*? *pentaspinosa* Beschin, Busulini, Tessier & Zorzin, 2016; *P. primaeva* (Segerberg, 1900); *P. spitzbergica* (Gripp, 1927).

Diagnosis: as in Klompmaker, Robins, Jakobsen & Sheldon (2022: p. 11).

Discussion: All previously known species of *Protomunida* are Paleocene in age, except the questionably referred *P. pentaspinosa* from the Ypresian (early Eocene) of Italy (Klompmaker *et al*. 2022). Thus, the new species does not extend the geographic or geologic range but is the only known species specifically reported from ?Selandian to Thanetian aged rocks. *Protomunida* appeared in the Paleocene and radiated rather quickly, only to become extinct by the Eocene, based on current records (Segerberg 1900; Beschin *et al*. 2016; Hryniewicz *et al*. 2019; Klompmaker *et al*. 2022).

***Protomunida kambuehelensis* new species**

(Fig. 4)

Diagnosis: Rostrum with pair of short spines at about 80% the length distance distally; accessory spines at base of rostrum very short, blunt; epigastric region with between three and four spines; transverse ridges on carapace of varying lengths, scabrous, discontinuous.

Etymology: The species name is derived from the formation from which the specimens were collected.

Types: Holotype, NHMW-Geo 2019/0042/0008. Paratypes, NHMW-Geo 2019/0042/0006, 2019/0042/0007, 2019/0042/0022, 2019/0042/0023, 2019/0042/0025 to 2019/0042/0029, 2023/0078/0002 to 2023/0078/0003.

Additional material: two casts NHMW-Geo 2019/0042/0002, 2019/0042/0010, and 2019/0042/0024.

Measurements: Measurements (in mm) taken on specimens of *Protomunida kambuehelensis* new species are presented in Table 1.

Description: Carapace longer than wide excluding rostrum, width about 86% length excluding rostrum; regions well-defined; moderately vaulted transversely; ornamented with strong transverse, terraced ridges. Lateral margins nearly parallel, rounded at posterior edge, with lateral spines extending entire length to posterior margin. Rostrum narrow, long triangular, wider at base, base about 30% carapace width, with very short, blunt, accessory spines, axially sulcate, with axial keel basally, extending about 30% the distance distally; lateral margins of rostrum entire except for one lateral spine on each side about 80% the distance distally. At least two small orbital spines.

Epigastric regions moderately inflated, transversely ovoid, with three or four short spines arranged transversely and decreasing in size toward margin. Triangular projection of mesogastric region separates epigastric regions, extending anteriorly toward frontal region and slightly onto rostrum. Triangular projection has three distinct transverse ridges. Hepatic regions have numerous small nodes and spines. Remainder of gastric regions weakly distinguishable. Protogastric and mesogastric regions confluent with discontinuous, imbricate transverse ridges.

Table 1. Measurements (in mm) taken on the specimens of *Protomunida kambuehelensis* new species.

Specimen	Length Excluding Rostrum	Length Including Rostrum	Maximum Carapace Width	Width at Base of Rostrum	Length to Position of Maximum Width
Holotype NHMW-Geo 2019/0042/0008	7.1	10.5	6.3	1.9	2.8
Paratype NHMW-Geo 2023/0078/0003	4.6	6.2	4.0	1.4	2.4
Paratype NHMW-Geo 2019/0042/0007	5.5	7.6	4.5	1.3	–

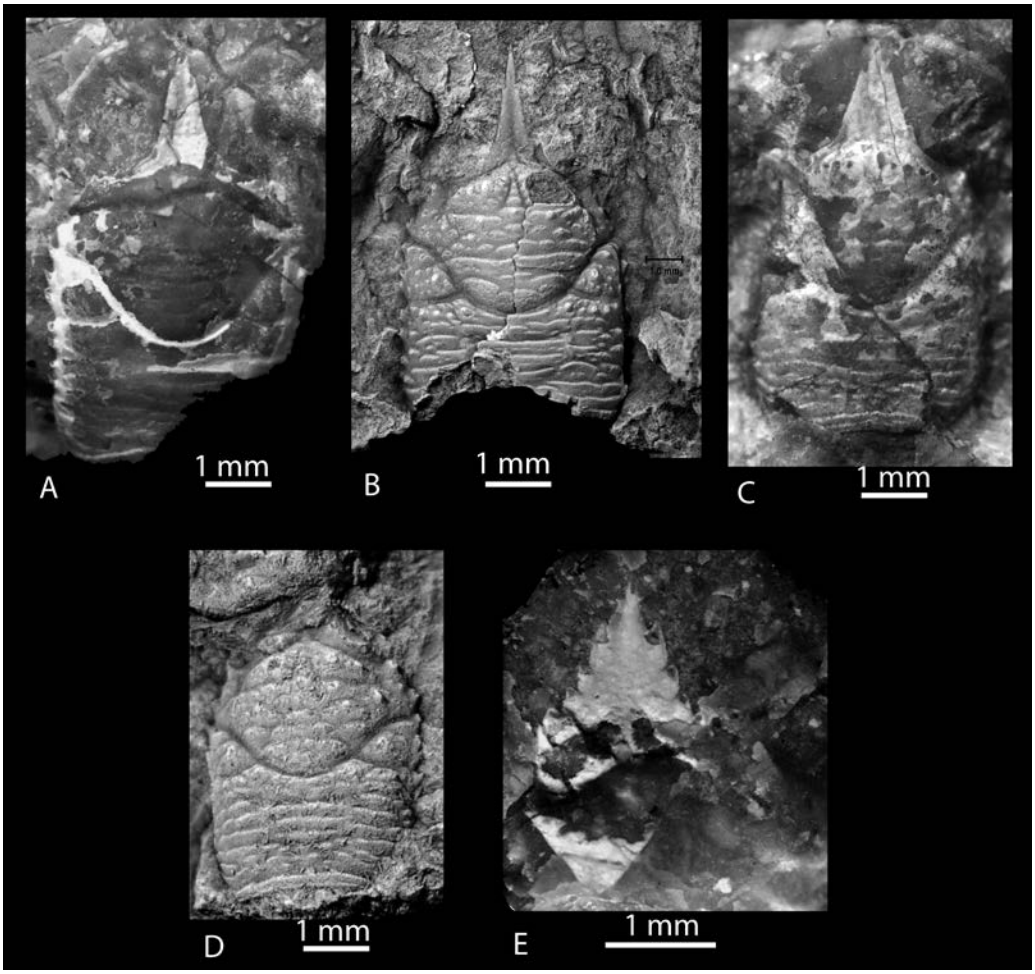

Fig. 4. **A–D**, *Protomunida kambuehelensis* new species. **A**, paratype NHMW-Geo 2019/0042/0007; **B**, holotype NHMW-Geo 2019/0042/0008; **C**, paratype NHMW-Geo 2023/0078/0003; **D**, paratype NHMW-Geo 2019/0042/0022; **E**, Galatheoidea indeterminate, distal portion of rostrum, NHMW-Geo 2019/0042/0001.

Cervical groove and anterior and posterior branches of cervical groove deeply incised and well-defined. Anterior branch of cervical groove parabolic in shape, posterior branch transverse; row of tubercles parallel and posterior to posterior branch. Epibranchial regions have nodes and two prominent epibranchial dorsal spines. Urogastric transverse ridges mostly continuous and slightly imbricate; cardiac region weakly defined with continuous transverse ridges that grade into discontinuous transverse ridges to nodes in branchial regions. Branchial transverse ridges become more continuous near posterior margin. Cardiac region poorly defined, slightly raised, with transverse ridges. Cardiac region narrows posteriorly toward intestinal region, forming triangular shape. Narrowing portion of cardiac with discontinuous ridges. Discontinuous ridges of cardiac and

intestinal regions stippled with small granules. Small portion of posterior margin preserved. Remainder of carapace and appendages unknown.

Discussion: *Protomunida kambuehelensis* new species differs from *P. munidoides*, *P. primaeva*, *P. eurekantha*, *P.*? *pentaspinosa*, and *P. bennickei* in having short, scabrous, discontinuous carapace ridges, whereas the latter four species have long, continuous ridges. The new species is more similar to *P. spitzbergica* in this regard, which has short, discontinuous ridges. However, the rostrum of *P. spitzbergica* is wider and shorter than that of *P. kambuehelensis* and lacks the tiny spines near the tip as seen in the new species.

The specimens referred to *Protomunida kambuehelensis* new species exhibit a range of morphological variation, some of which may be attributable to preservation. Most notable is the width of the rostrum. In the holotype (Fig. 4B) and paratype NHMW-Geo 2019/0042/0007 (Fig. 4A), the rostrum is narrow, with a pair of tiny spines near the tip. The rostrum of paratype NHMW-Geo 2023/0078/0003 is distinctly wider. However, the spines, transverse ridges, and development of regions and grooves is nearly identical in all of the specimens referred to the new species. Because each specimen is missing part of the carapace and cuticle, it seems plausible that the differences are due to preservation. Thus, for now we refer all of the specimens to the same species until more complete material can be used to verify whether paratype NHMW-Geo 2023/0078/0003 should be referred to a different taxon (Fig. 4C).

Galatheoidea family, genus and species indeterminate
(Fig. 4E)

Material examined: NHMW-Geo 2019/0042/0001.

Discussion: The specimen is composed of the distal portion of a rostrum. It has at least three spines on each side. This is reminiscent of the distal end of the rostrum of *Faxegalathea platyspinosa* JAKOBSEN & COLLINS, 1997, or the rostrum of *Galathea strigifera* FISCHER-BENZON, 1866, both of which are known from the Danian of Denmark. Not enough of the specimen at hand is preserved to identify it, but it is different from the rostra of specimens of *Protomunida kambuehelensis*.

Family Catillogalatheidae ROBINS, FELDMANN, SCHWEITZER & BONDE, 2016

Genus *Annieporcellana* FRAAIJE, VAN BAKEL, JAGT & ARTAL, 2008

Type species: *Annieporcellana dhondtae* FRAAIJE, VAN BAKEL, JAGT & ARTAL, 2008, by original designation.

Other species: *Annieporcellana paleocenica* new species.

Diagnosis: Carapace ovate; rostrum long, axially sulcate; epigastric regions inflated; lateral margins serrate; cervical and branchiocardiac grooves moderately deep; mesogastric region well-defined; branchial regions with short transverse ridges laterally.

Discussion: The new species bears striking similarities with the type species of both *Annieporcellana* and *Hispanigalathea*. The new species has similarities and differences with each. The key difference between the new species and the type species of *Annieporcellana* is that the latter appears to be widest at about the midlength, whereas in the new species, the widest part is in the branchial regions on some specimens and is uniformly wide throughout the lateral margins in others. Both *Annieporcellana* and the type species of *Hispanigalathea* have similar ornamentation and similar groove development, but the anterior and lateral branches of the cervical groove and the definition of the mesogastric region are stronger in *Annieporcellana*.

The new species from the Paleocene of Austria bears many similarities with the type species of *Annieporcellana*; thus, we place it in that genus. In the new species, these grooves are weaker than in either *Annieporcellana* or *Hispanigalathea*. *Annieporcellana dhondtae* has a flared, rimmed orbital margin similar to that seen in the new species. The weak, transverse to scabrous ornamentation, the deep cervical groove with weaker anterior and lateral branches, and the sulcate and apparently wide rostrum are all reminiscent of the sole species of the genus. This extends the geologic range of *Annieporcellana* from the Albian-Cenomanian into the ?Selandian-Thanetian, across the end-Cretaceous boundary, and the geographic range from Spain to Austria.

It should be noted that the morphological range of variation in *Hispanigalathea* has been greatly expanded since it was first recognized, making diagnosis of the genus and therefore referral of species to it difficult. In addition, the type species and some other species are superficially similar to some species in genera within Porcellanidae in terms of the reduced ornamentation and groove patterns and the spatulate rostra. *Hispanigalathea tithonia* Robins, Feldmann, Schweitzer & Bonde, 2016 is quite different in ornamentation and carapace ratios from those of the type species, most notably bearing a much deeper branchiocardiac groove and a much shorter urogastric, cardiac, and intestinal regions than those of the new species. *Hispanigalathea raymondcaseyi* van Bakel, Fraaije, Jagt & Simpson, 2020 has much more well-developed and diverse carapace regions and grooves than galatheoids in general and is reminiscent of *Withersella* Wright & Collins, 1972 a brachyuran from the same formation as *H. raymondcaseyi*, in the United Kingdom.

***Annieporcellana paleocenica* new species**

(Fig. 5)

Diagnosis: Carapace not much longer than wide excluding rostrum; widest along posterior branchial region; ornamented with low, transverse, discontinuous ridges; cervical groove well-developed, anterior branch well developed, and posterior branch of cervical groove weakly developed.

Etymology: The species name reflects the age of the specimen of the species.

Types: The holotype is NHMW-Geo 2019/0042/0014. Paratypes include NHMW-Geo 2019/0042/0005, 2019/0042/0009, 2019/0042/0011 to 2019/0042/0013, and 2019/0042/0030.

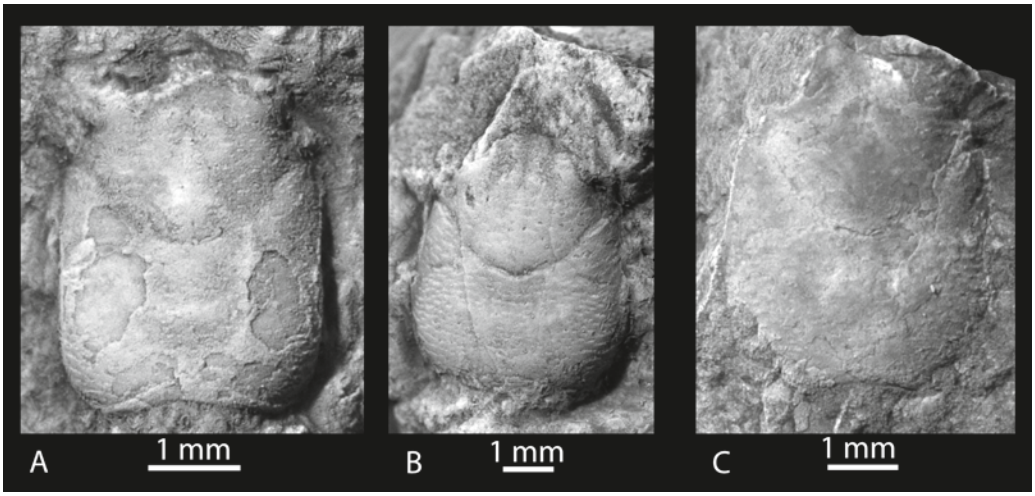

Fig. 5. *Annieporcellana paleocenica* new species. **A**, paratype NHMW-Geo 2019/0042/0005; **B**, holotype NHMW-Geo 2019/0042/0014; **C**, paratype NHMW-Geo 2019/0042/0009

Measurements: Measurements (in mm) taken on the carapace of *Annieporcellana paleocenica* new species: Holotype NHMW-Geo 2019/0042/0014: carapace length excluding rostrum, 3.6; carapace width, 3.5; width at base of rostrum, 1.3; length to position of maximum width, 2.2. Paratype NHMW-Geo 2019/0042/0005: carapace length excluding rostrum, 3.6; carapace width, 3.3; width at base of rostrum, 1.6; length to position of maximum width, 2.4.

Description: Carapace subrectangular with rounded posterior, slightly longer than wide, width about 95% length excluding rostrum, widest along posterior branchial region though difference is slight; weakly vaulted longitudinally; moderately vaulted transversely; surface marked by subtle, low, discontinuous, transverse ridges most apparent in anterior regions and posterior branchial margins. Flanks poorly exposed, appear to be short, slightly higher along posterior branchial margins.

Frontal margin incomplete and wide; base of rostrum sulcate, rather wide, about 42% carapace width, remainder of rostrum unknown. Orbits circular, rimmed, slightly anterolaterally directed and raised, with small, forward-directed, outer-orbital spine; fronto-orbital width about 70% maximum carapace width. Lateral margins parallel to weakly convex posteriorly. Slight notch in lateral margin at weak posterior cervical groove intersection, followed by blunt lateral branchial spine. Margin rimmed posterior to epibranchial region, posterior margin rounded at lateral edges, concave axially, rimmed. Posterior rim widest axially.

Cervical groove well defined, most deeply incised axially; anterior cervical groove well defined, posterior cervical groove very weakly defined, most prominent where it intersects cervical groove. Regions weakly to poorly defined. Frontal margin and hepatic region ornamented with small granules. Epigastric regions ovate, weakly inflated,

separated from frontal margin by shallow grooves; mesogastric region raised with long anterior process forming triangular shape where it meets epigastric regions; shallow groove separates epigastric regions; protogastric regions with scabrous transverse ridges. Epibranchial region with small nodes, epibranchial spine just posterior to anterior cervical groove near lateral margin, extending axially into ridge parallel to anterior cervical groove; cardiac region weakly defined, circular, slightly raised; branchial regions with transverse ridges. Venter and appendages unknown.

Discussion: Specimens assigned to *Annieporcellana paleocenica* new species exhibit some range in morphological variation, some of which may be attributable to preservation. The holotype (Fig. 5B) appears to exhibit slightly more convex lateral margins than those of paratype NHMW-Geo 2019/0042/0005 (Fig. 5A) and may have a slightly deeper cervical groove. However, in all other regards the specimens are similar, and as all are missing part of the carapace and cuticle, it is most prudent at this time to refer them to the same taxon.

Galatheoidea incertae sedis

Galatheoidea indeterminate
(Fig. 3D)

Material examined: Isolated propodi, NHMW-Geo 2019/0042/0003, 2019/0042/0004, 2019/0042/0020, and 2019/0042/0021.

Description of material: Right propodus with fixed finger, dactylus unknown. Manus elongate, flattened, ovoid in cross-section; longer (6.4 mm) than high (2.9 mm), tapers toward carpus articulation. Manus outer surface finely textured, convex with scabrous transverse ridges; ridges prominent in slight concavity where fixed finger meets manus, less developed on outer surface of fixed finger. Manus lower surface with strong ridge that thins along length of fixed finger; upper surface with ridge but not as strongly developed as lower surface.

Inner surface convex with weakly developed granular texture, most prominent near ridge along lower surface and proximal to fixed finger. Slight concavity where fixed finger meets manus, most prominent on inner surface. Fixed finger long, slender, tapering to sharp point, inclined away from long axis of propodus. Occlusal surface smooth with sharp, granulated ridge along upper, inner surface of fixed finger.

Measurements: NHMW-Geo 2019/0042/0003: length of manus, 3.0 mm, height of manus, 1.1 mm. NHMW-Geo 2019/0042/0004: length of fixed finger, 0.7 mm, height of fixed finger, 0.4 mm.

Discussion: Disarticulated appendages are difficult to identify. The morphology of these chelae is most similar to those of members of Porcellanidae, which generally have a convex lower margin of the manus, which is notably higher distally, and slender fingers (Chan 2010).

Discussion

Anomuran decapods from the Kambühel Formation include two galatheoid species, one paguroid species, and four indeterminate taxa. This fauna is notable for its ?Selandian to Thanetian age and coral-associated environment, making direct comparisons with other Paleocene faunas difficult. For example, the well-known Danian (Paleocene) decapod fauna studied from Fakse, Denmark (Collins & Jakobsen 1994; Jakobsen & Collins 1997; Klompmaker *et al*. 2022) differs from the Kambühel fauna not only in being older but also in having been deposited in a deeper and colder environment with a bryozoan-coral mound complex (200–300 m) (Bernecker & Weidlich 1990), compared to the shallow-water, coralgal reef complex of the Kambühel Formation (Krische *et al*. 2012). Among anomurans, the faunas of Fakse and Kambühel only share the genus *Protomunida*. The Danian reefal deposits at Vigny, France, have yielded four anomuran taxa, one genus of which is shared with Kambühel, *Protomunida* (Robin *et al*. 2017). The paleoenvironment of the Vigny area has been interpreted as shallow marine, up to 90 m, with colonial hermatypic corals (Robin *et al*. 2017), similar to that of the Kambühel Formation. An older fauna, the Cretaceous (Albian-Cenomanian) decapod assemblage from Northern Spain has yielded a diverse decapod fauna including nine anomuran taxa (see Klompmaker 2013, for a summary), deposited in a reefal environment. Only one genus, *Annieporcellana*, is shared with the Kambühel Formation.

Fossil localities from the Eocene of Europe can also be compared to the coral-associated decapod fauna of the Kambühel. One such comparable fauna comes from the late Eocene of Hungary, but it does not share any anomuran genera with the Kambühel fauna (Müller & Collins 1991). De Angeli & Garassino (2002) reported a rich collection of anomurans from Northern Italy (Vicenza) spanning the early Eocene, late Eocene, and early Oligocene. Despite the diverse sample and familial associations, these faunas share no genera with the Paleocene Kambühel fauna. An additional decapod fauna was reported from the northeast of Italy (Bolca area, Verona and Vicenza) and is early Eocene in age (Beschin *et al.* 2016). This diverse assemblage was collected from small outcrops of coralgal domes and shares only the genus *Protomunida* (Munididae) with the Paleocene Kambühel fauna.

Thus, the Kambühel anomuran fauna contains genera that originated in the Late Cretaceous as well as some that originated in the Paleocene, contributing to the rather scarce fossil record of Selandian and Thanetian decapods. With the additional new taxa described, one anomuran genus is reported to cross the Cretaceous boundary into the Paleocene, *Annieporcellana.* The new genus, *Squamipelta*, is known only from the Paleocene, and *Protomunida* ranges from the Paleocene into the Eocene.

Acknowledgements

Diethard Sanders (University of Innsbruck, Austria) provided an interpretation of the position of our collecting locality in the Kambühel section. Karen Reed (USNM, Washington, DC) facilitated our visit to Crustacea at USNM to examine extant axiidean specimens.

Rafael Lemaitre (USNM, Washington, DC) offered advice on interpreting some of the specimens. Cristina Robins (University of Alabama, Tuscaloosa) provided much needed clarity on identification of the galatheoid specimens. Holly Grimmett (KSU) assisted with photography. Constructive reviews by Matúš Hyžný (Comenius University, Bratislava, Slovakia) and Cristina Robins greatly improved the manuscript. We gratefully thank Gerhard Wanzenböck (Bad Vöslau) for the donation of some of the specimens studied herein. Alfréd Dulai (Hungarian Natural History Museum) is acknowledged for assisting in enciphering the provenance of the specimens and returning the specimens to Austria.

Supplementary material

Detailed specimen lists of the material studied herein (Yost *et al*. 2023) are available for download from the NHMW Data Repository (https://doi.org/10.57756/jps7q5)

References

Ahyong, S.T., Baba, K., Macpherson, E. & Poore, G.C.B. (2010): A new classification of the Galatheoidea (Crustacea: Decapoda: Anomura). – Zootaxa, **2676**: 57–68.

Bernecker, M. & Weidlich, O. (1990): The Danian (Paleocene) coral limestone of Fakse, Denmark: a model for ancient aphotic, azooxanthellate coral mounds. – Facies, **22**: 103–138.

Beschin, C., Busulini, A., Tessier, G. & Zorzin, R. (2016): I crostacei associati a coralli nell'Eocene inferiore dell'area di Bolca (Verona e Vicenza, Italia nordorientale). – Memorie del Museo Civico di Storia Naturale di Verona, 2. serie, Sezione Scienze della Terra, **9**: 1–190.

Beurlen, K. (1930): Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. – Fortschritte in der Geologie und Paläontologie, **8**: 317–586.

Chan, T.-Y. (2010): Crustacean fauna of Taiwan: crab-like anomurans (Hippoidea, Lithodoidea and Porcellanidae). – 197 pp., Keelung (National Taiwan Ocean University).

Collins, J.S.H. & Jakobsen, S.L. (1994): A Synopsis of the Biostratigraphic Distribution of the Crab Genera (Crustacea, Decapoda) of the Danian (Palaeocene) of Denmark and Sweden. – Bulletin of the Mizunami Fossil Museum, **21**: 35–46.

De Angeli, A. & Garassino, A. (2002): Galatheid, chirostylid and porcellanid decapods (Crustacea, Decapoda, Anomura) from the Eocene and Oligocene of Vicenza (N Italy). – Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, **30**: 1–40.

Dulai, A., Bitner, M.A. & Müller P. (2008): A monospecific assemblage of a new rhynchonellide brachiopod from the Paleocene of Austria. – Fossils and Strata, **54**: 193–201.

Fischer-Benzon, R. von (1866): Über das relative Alter des Faxe-Kalkes und über die in demselben vorkommenden Anomuren und Brachyuren. – 30 pp., 6 plates, Kiel (Schwers'sche Buchhandlung).

Fraaije, R.H.B. (2014): Diverse Late Jurassic anomuran assemblages from the Swabian Alb and evolutionary history of paguroids based on carapace morphology. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **273**: 121–145.

Fraaije, R.H.B., van Bakel, B.W.M. & Jagt, J.W.M. (2017): A new paguroid from the type Maastrichtian (upper Cretaceous, the Netherlands) and erection of a new family. – BSGF Earth Sciences Bulletin, **188**/17: 4.

Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M. & Artal, P. (2008): New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. – Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (Sciences de la Terre), **78**: 193–208.

Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M. & Skupien, P. (2020): Paguroid anomurans from the upper Tithonian–lower Berriasian of Štramberk, Moravia (Czech Republic). – Geologija (Llubjana), **63**: 7–16.

Fraaije, R.H.B., Robins, C., 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 Museum in Wien, Serie A, **121**: 257–289.

Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M., Klompmaker, A.A. & Artal, P. (2009): A new hermit crab (Crustacea, Anomura, Paguroidea) from the mid-Cretaceous of Navarra, northern Spain. – Boletín de la Sociedad Geológica Mexicana, **61**: 13–16.

Gripp, K. (1927): Beiträge zur Geologie von Spitzbergen. – Abhandlungen aus dem Gebiete der Naturwissenschaften, herausgegeben vom Naturwissenschaftlichen Verein Hamburg, **21**/3–4: 1–38, pls 1–7.

Hryniewicz, K., Amano, K., Bitner, M.A., Hagström, J., Kiel, S., Klompmaker, A.A., Mörs, T., Robins, C.M. & Kaim, A. (2019): A late Paleocene fauna from shallow-water chemosynthesis-based ecosystems, Spitsbergen, Svalbard. – Acta Palaeontologica Polonica, **64**: 101–141.

Jakobsen, S.L. & Collins, J.S.H. (1997): New middle Danian species of anomuran and brachyuran crabs from Fakse, Denmark. – Bulletin of the Geological Society of Denmark, **44**: 89–100.

Klompmaker, A.A. (2013): Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. – Cretaceous Research, **41**: 150–185.

Klompmaker, A.A., Robins, C.M., Jakobsen, S.L. & Sheldon, E. (2022): Systematics of 12 Jurassic, Cretaceous, and Paleogene squat lobster taxa (Galatheoidea). – Journal of Paleontology, **96**: 1087–1110. https://doi.org/doi:10.1017/jpa.2022.32

Krische, O., Gawlick, H.J. & Schlagintweit, F. (2012): Resedimented upper Paleocene shallow-water clasts (Kambühel Formation) in the Zwieselalm Formation of the Weitenau area and their tectonic implications (Northern Calcareous Alps, Austria). – Austrian Journal of Earth Sciences, **105**/3: 38–47.

Latreille, P.A. (1802–1803): Histoire naturelle, générale et particuliére, des crustacés et des insectes, Volume 3. – 468 pp., Paris (F. Dufart).

MacLeay, W.S. (1838): On the Brachyurous Decapod Crustacea brought from the Cape by Dr. Smith. – In: Smith, A. (ed.): Illustrations of the Annulosa of South Africa; consisting chiefly of Figures and Descriptions of the Objects of Natural History Collected during an Expedition into the Interior of South Africa, in the Years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa." – pp. 53–71, 2 pls., London (Smith, Elder & Company).

Miller, J.B., Schweitzer, C.E. & Feldmann, R.M. (2023): New Decapoda (Brachyura) from the Paleocene Kambühel Formation, Austria. – Annalen des Naturhistorischen Museums in Wien, Serie A, **124** (2022): 125–148. [this volume]

Müller, P.M. (2004): History of reef-dwelling decapod crustaceans from the Palaeocene to the Miocene with comments about Mesozoic occurrences. – Földtani Közlöny, **134**/2: 237–255.

Müller, P. & Collins, J.S.H. (1991): Late Eocene coral-associated decapods (Crustacea) from Hungary. – Contributions to Tertiary and Quaternary Geology, **28**: 47–92.

Robin, N., van Bakel, B.W.M., Pacaud, J.-M. & Charbonnier, S. (2017): Decapod crustaceans from the Paleocene (Danian) of the Paris Basin (Vigny stratotype and allied localities) and a limpet palaeoassociation. – Journal of Systematic Palaeontology, **15**: 257–273.

Robins, C.M., Feldmann, R.M., Schweitzer, C.E. & Bonde, A. (2016): New families Paragalatheidae and Catillogalatheidae (Decapoda: Anomura: Galatheoidea) 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. – 496 pp., London (T. Boys).

Sanders, D., Keller, G., Schlagintweit, F. & Studeny, M. (2020): Cretaceous-Paleocene transition along a rocky carbonate shore: implications for the Cretaceous-Paleocene boundary event in shallow platform environments and correlation to the deep sea. – In: Adatte, T., Bond, D.P.G. & Keller, G. (eds): Mass Extinctions, Volcanism, and Impacts: New Developments. – Geological Society of America Special Paper, **544**: 137–163.

Schlagintweit, F. (2005): Cryptobiotic foraminifera from the Paleocene Kambühel Formation (northern calcareous Alps, Austria). – Studia UBB Geologia, **50**/1: 13–17.

Schlagintweit, F., Švábenická, L. & Lobitzer, H. (2003): An occurrence of Paleocene Reefal Limestone in the Zwieselalm Formation of Gosau (Upper Austria). – In: Weidinger, J.T., Lobitzer, H. & Spitzbart, I. (eds): Beiträge zur Geologie des Salzkammergutes. – pp. 173–180, Gmunden (Gmundner Geo-Studien).

Schlagintweit, F., Sanders, D. & Studeny, M. (2018): The nepionic stage of *Solenomeris* Douville, 1924 (Acervulinidae, Foraminiferida): New observations from the uppermost Maastrichtian–early Danian of Austria (Kambuhel Formation, Northern Calcareous Alps). – Facies, **64**: 27. https://doi.org/10.1007/s10347-018-0540-5

Schweitzer, C.E., Gonzalez Barba, G., Feldmann, R.M. & Waugh, D.A. (2005): Decapoda (Thalassinidea and Paguroidea) from the Eocene Bateque and Tepetate formations, Baja California Sur, México: Systematics, cuticle microstructure, and paleoecology. – Annals of Carnegie Museum, **74**: 275–293.

Segerberg, K.O. (1900): De Anomura och Brachyura dekapoderna inom Skandinaviens Yngre krita. – Geologiska Föreningens i Stockholm Förhandlingar, **22**/5: 347–388, pls 7–9.

van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M. & Simpson, M.I. (2020): *Hispanigalathea raymondcaseyi*, a new squat lobster (Crustacea, Decapoda, Galatheoidea) from the Gault (Albian) of Folkestone, England. – Proceedings of the Geologists' Association, **131**: 383–385.

Verhoff, J., Müller, P., Feldmann, R.M. & Schweitzer, C.E. (2009): A new species of Tumidocarcinidae (Decapoda, Carpilioidea) from the Kambühel Formation (Paleocene) of Austria. – Annalen des Naturhistorischen Museums in Wien, Serie A, **111**: 225–232.

WoRMS – World Register of Marine Species (2022): Annuntidiogenidae Fraaije, 2014. Available from https://www.marinespecies.org/aphia.php?p=taxdetails&id=1580766. Accessed 2022-09-22.

Wright, C.W. & Collins, J.S.H. (1972): British Cretaceous crabs. – Palaeontographical Society Monographs, **126**/533: 1–113.

Yost, S., Feldmann, R.M. & Schweitzer, C.E. (2023): Dataset to: Yost *et al.* (2023): "New Decapoda (Anomura) from the Paleocene Kambühel Formation, Austria". NHMW Data Repository. https://doi.org/10.57756/jps7q5