



New early Paleocene (Danian) paguroids from deep-water coral/bryozoan mounds at Faxe, eastern Denmark

Novi zgodnjepaleocenski (danijski) raki samotarji iz globokovodnih koralno-briozojskih kop nahajališča Faxe na vzhodnem Danskem

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Ključne besede: Anomura, Paguroidea, paleogen, morfologija škarnikov, Danska

Abstract

During recent decades, decapod crustacean faunas from middle Danian (lower Paleocene) strata at Faxe (Sjælland, Denmark) have been studied in detail. However, paguroid anomurans have not yet been described formally. Two new species of hermit crab have lately been recognised in the collections of the Geomuseum Faxe. Percentages of total paguroid assemblages and feeding behaviour derived from the morphology of its chelae indicate that one of these, *Dardanus faxensis* sp. nov., as a generalist, was better adapted to inhabit the deep-water reefal environment of the Faxe carbonates than the more specialised, suspension-feeding *Paguristes frigoscopulus* sp. nov.

Izvleček

V zadnjih desetletjih so bile podrobno proučene združbe rakov deseteronožcev iz srednjedanijskih (spodnjepaleocenskih) plasti v Faxu (Sjælland, Danska), vendar raki samotarji do sedaj še niso bili opisani. Pri pregledu zbirk muzeja Geomuseum Faxe sta bili prepoznani dve novi vrsti rakov samotarjev, ki ju predstavljamo v tem prispevku. Zastopanost ostankov v celotni združbi in način prehranjevanja, ki ga kaže funkcionalna morfologija škarij, pričajo, da je bil eden od teh, to je vrsta *Dardanus faxensis* sp. nov., kot generalist bolj prilagojen za bivanje v globokomorskem grebenskem okolju od bolj specializiranega suspenziofaga *Paguristes frigoscopulus* sp. nov.

Introduction

In general, records of paguroid remains from Danian-aged rocks are scarce and hermit crab assemblages of this age remain largely understudied. Vega et al. (2007) recorded a right and an incomplete left chela of a diogenid from the Rancho Nuevo Formation at Coahuila (Mexico), while Armstrong et al. (2009) described a right paguroid palm, without systematic placement, from the Midway Group of Texas, USA. In addition, Cope et al. (2005) noted *Paguristes johnsoni* Rathbun, 1935, on the basis of a single, well-preserved propodus and an additional fragment of a carpus that were closely comparable to the type

material illustrated and described by Rathbun (1935) from the Sucarnoochee Formation of Alabama (USA).

Robin et al. (2017) mentioned an indeterminate species of *Paguristes* Dana, 1851 from a privately held collection of Danian decapod crustaceans from Vigny, France. It would appear that this locality was very rich in paguroids of earliest Paleocene age (Wallaard et al., 2020), but unfortunately this material is not currently accessible for scientific assessment and publication.

A brief visit to the collections of the Geomuseum Faxe (September 2019) has now resulted in the recognition of fourteen hermit crab speci-

mens along with the material from the collections at the Natural History Museum (Copenhagen), all partially complete chelae. The two new paguroid taxa erected to accommodate these forms from the middle Danian of Faxe present a valuable addition to the hermit crab faunas from this time interval.

Geological setting

A large, cool-water, subphotic coral/bryozoan mound complex at Faxe developed in the Danish Basin during the early Danian, shortly after the Cretaceous/Paleogene boundary event (e.g., Bjerager et al., 2018; Schröder & Surlyk, 2019). During the middle Danian, a low-diversity scleractinian coral fauna initiated the formation of extensive cold-water coral mound complexes that intercalated with bryozoan mounds (e.g., Lauridsen et al., 2012). The coral mounds started to grow below the photic zone over the easternmost part of the Ringkøbing-Fyn High, only 2 million years after the mass extinction at the K/Pg boundary (Lauridsen et al., 2012).

The middle Danian limestones exposed at Faxe quarry (Fig. 1) document the extraordinary preservation of a 63-myr-old, cold-water coral mound ecosystem. Bryozoan mounds dominate the stratigraphically lower parts and are overlain by interfingering coral and bryozoan mounds. The Faxe quarry exposes a large mound complex that includes individual coral mound bodies. The mound complex is dominated by the frame-building scleractinian coral species, *Dendrophyllia candelabrum* (Hennig, 1899), which is associated with common *Faksephyllia faxoensis* (Lyell, 1837) and minor numbers of *Oculina becki* (Brünnich Nielsen, 1922). A highly diverse fauna is found in middle Danian strata at Faxe quarry, including serpulid annelids, arthropods, brachiopods, bryozoans, coelenterates, echinoderms, sponges and molluscs (Lauridsen et al., 2012, table 1).

The quarry at Faxe comprises the best-studied Danian decapod crustacean fauna worldwide (Jakobsen & Collins, 1997). Studies dealing with such taxa, in chronological order, are the follow-

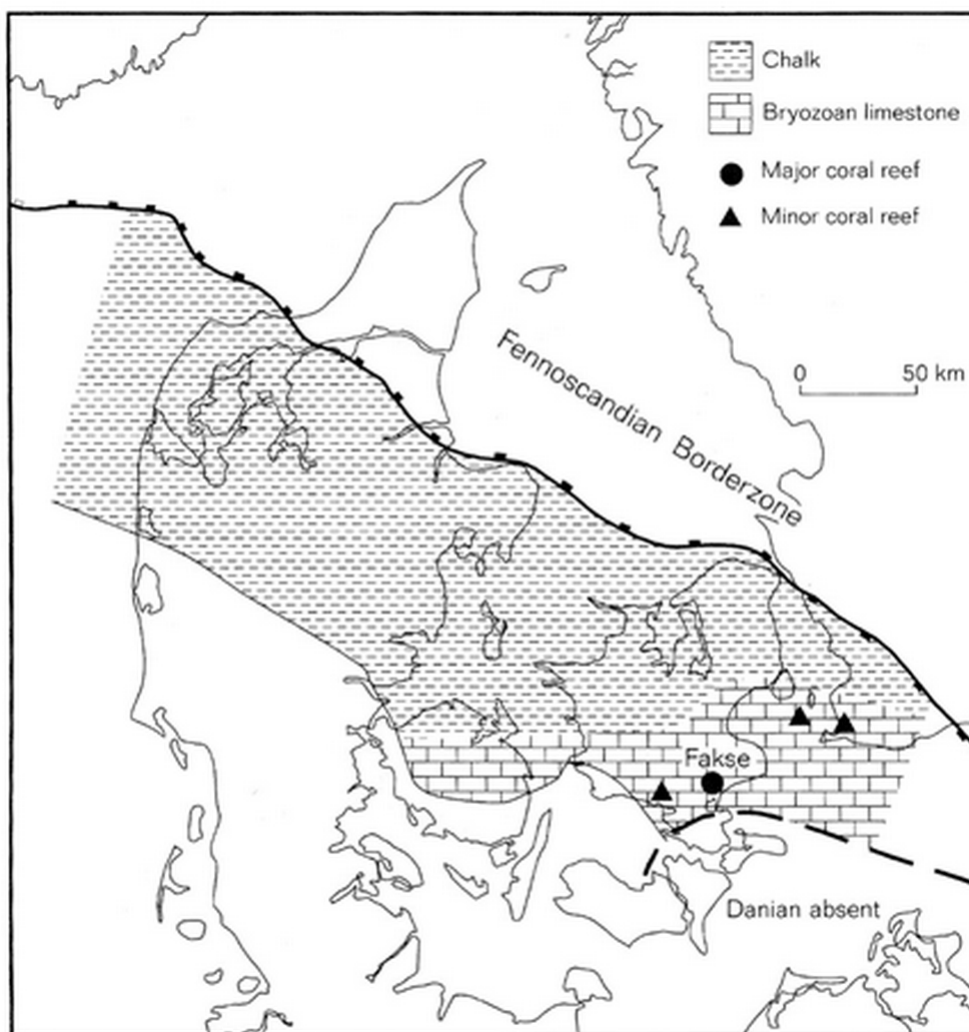


Fig. 1. Position of Faxe quarry and the main structure of the Danish area during the middle Danian (compilation by Dr Erik Thomsen, Geological Institute, Aarhus University, Denmark).

ing: von Schlotheim (1820), Reuss (1859), von Fischer-Benzon (1866), Segerberg (1900), Woodward (1901), Rasmussen (1973), Förster (1975), Jagt et al. (1993), Collins & Jakobsen (1994), Jakobsen & Collins (1997), Fraaije (2003), Jakobsen (2003), Jakobsen & Feldmann (2004), Collins (2010), Robin et al. (2015) and Klompmaker et al. (2015, 2016). However, in none of these are any paguroid remains recorded, so that our present note is the first formal description of middle Danian hermit crab taxa from Faxe.

Material and methods

The taxonomic descriptions are based on material stored at the Geological Museum (now Natural History Museum of Denmark) and Geomuseum Faxe. Our material comprises fourteen specimens belonging to two genera, represented by two new species. The material included in the present study was collected mainly by Curator Søren Bo Andersen and the late amateur palaeontologist, Alice Rasmussen, of Faxe. In 2012, the latter was awarded the prestigious Mary Anning Prize of the Palaeontological Association (London) in recognition of her outstanding work on fossils from the type locality of the Danian Stage at Faxe. The present material was collected in various parts of the quarry over many years.

The chelae are preserved mainly in the form of internal and external moulds in the coral limestone and therefore our descriptions are in part based on casts. However, that of the holotype of *Paguristes frigoscopulus* relied on the internal mould ('steinkern'). Preparation and photography of the material followed the procedures outlined in Jakobsen & Feldmann (2004).

Institutional abbreviations. MGUH, Natural History Museum of Denmark (Geological Museum), Copenhagen, Denmark; OESM, Geomuseum Faxe, Faxe, Denmark.

Systematic palaeontology

Order Decapoda Latreille, 1802
 Infraorder Anomura H. Milne Edwards, 1832
 Superfamily Paguroidea Latreille, 1802
 Family Annuntidiogenidae Fraaije, 2014
 Genus *Dardanus* Paul'son, 1875

***Dardanus faxensis* sp. nov.**
 (Figs. 2–5)

2005 Eremitkrebs 20 mm**; Damholt & Rasmussen, p. 22, unnumbered figures.

2005 Klo fra eremitkrebs 20 mm**; Damholt & Rasmussen, p. 38, unnumbered figure.

2010 Eremitkrebs 20 mm**; Damholt et al., p. 23, unnumbered figures.

2010 Klo fra eremitkrebs 20 mm***; Damholt et al., p. 42, unnumbered figure.

Diagnosis: Palm transversely oval; inner and outer sides longitudinally and transversely convex; outer side of palm covered with forwardly directed, largely spinose tubercles; proximal part of outer side of palm and distal part of inner side irregularly covered with capsulated setae arranged in a curved row; fixed finger elongated, with a horseshoe-shaped, spoon-like tip.

Etymology: In reference to the type locality.

Type material: The holotype, OESM 6811, is a near-complete right palm with fixed finger, measuring 10 mm in length and 6 mm in greatest width; both external and internal moulds are present (Fig. 2A–G). Paratypes are MGUH 33401, MGUH 33402, OESM 581, OESM 10178 OESM 10179 and OESM 10180, all representing incomplete right palms; MGUH 33403, MGUH 33404, MGUH 33405, MGUH 33406 and MGUH 33408 are incomplete left palms.

Locality and stratigraphy: The coral limestone assigned to the Faxe Formation has been known for centuries due to the extensive quarrying. The middle Danian levels exposed at Faxe quarry represents an extraordinary preservation of a 63-myr-old, cold-water coral mound complex. This coral limestone complex was formally described as a new formation by Lauridsen et al. (2012). The type locality of the Faxe Formation is a Danish GeoSite and is accessible to all members of the public. The formation was dated as middle Danian (calcareous nannoplankton zones D5–6 of Perch-Nielsen, 1979 and NNTp3–NNTp4a of Varol, 1998).

Description: Cross section of palm transversely oval; inner and outer sides longitudinally and transversely convex, curving slightly inwards; dorsal edge straight, ventral edge concave at central part; outer side of palm covered with forwardly directed, largely spinose tubercles, largest tubercles irregularly arranged along dorsal edge and outer distal half and proximal half of fixed finger, proximal part of outer side of palm irregularly covered with multiple capsulated setae arranged in circles or rows; inner side of palm smooth with on distalmost part few curved rows of multiple setae (Fig. 3B); fixed finger elongated, curved inwardly, with horseshoe-shaped, spoon-like tip, which is covered on outer side with a row of very large pits; the cutting edge is covered with about three variably sized, molar-like calcareous teeth.



Fig. 2. *Dardanus faxensis* sp. nov., holotype (OESM 6811). The top three - silicone rubber casts of external mould; the bottom four internal mould. Scale bar in millimetres.

Remarks: Normally, setal pits are situated around the bases of tubercles and/or on the adjacent integument, but usually not on the tubercles themselves. Multiple capsulated pits have previously been recorded for both fossil and extant species of paguroids (see Fraaije et al., 2011, 2015a; Hyžný et al., 2016). During the Paleogene, the genus *Dardanus* appears to have been highly successful and widely distributed (Fraaije & Polkowsky, 2016). In the case of *Dardanus faxensis* sp. nov. all tubercles on the outer side of the palm have large setal pits (Fig. 2A); this morphological trait differentiates it immediately from

all congeners. For a list of all known fossil species referred to the genus, reference is made to Fraaije et al. (2011) and to Fraaije & Polkowsky (2016). The shape of the chelae is indicative of a deposit feeder that was also capable of browsing, scavenging and suspension feeding. This type of paguroid fed by scraping material from corals or other solid surfaces using the tips of the spoon-like chelae (compare Schembri, 1982). One specimen, MGUH 33406, is totally covered with epibionts, mainly subcircular colonies of bryozoans (Fig. 4).

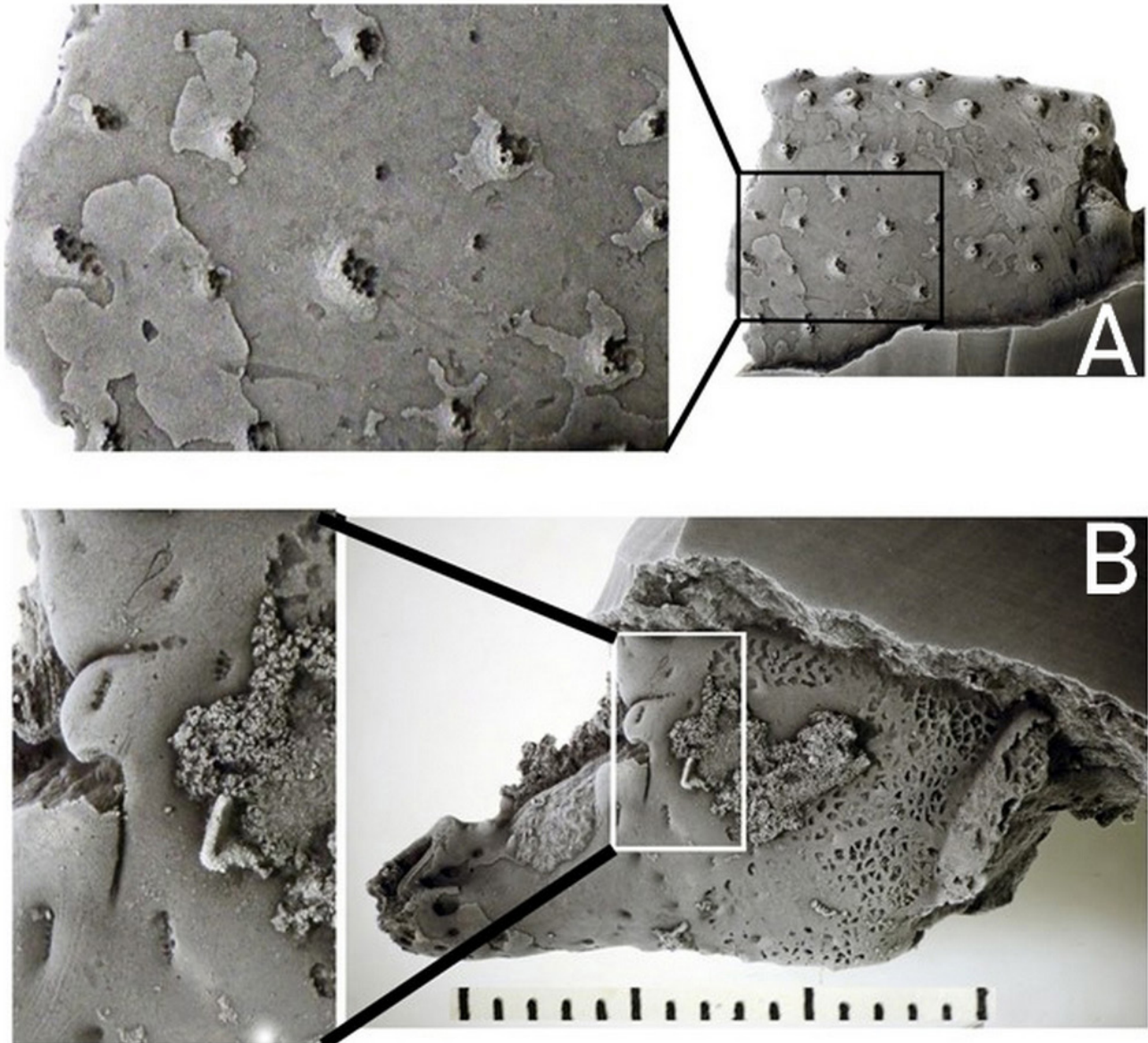


Fig. 3A. *Dardanus faxensis* sp. nov., silicone rubber cast of external mould of incomplete right palm, outer side (OESM 10178), showing setal pits and tubercles; B. Silicone rubber cast of external mould of incomplete right palm (MGUH 33401, GMF 2004-1802), showing rows of multiple setal pits. Scale bar in millimetres.

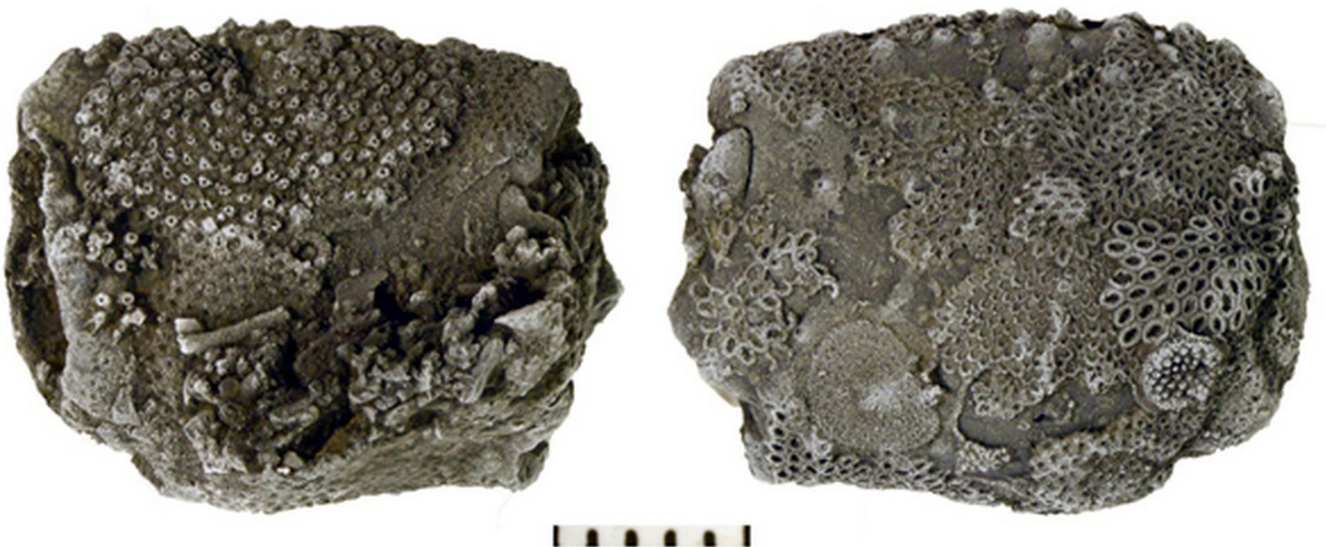


Fig. 4. *Dardanus faxensis* sp. nov., MGUH 33405, incomplete left palm covered with epibionts. Scale bar in millimetres.



Fig. 5. *Dardanus faxensis* sp. nov., specimens OESM 6811, OESM 10180 and OESM 10179, respectively, with remains of serpulid/spirorbid annelids (arrows) on the outer palm surface near the base of the fixed finger. Scale in millimetres.

Three specimens of *D. faxensis* sp. nov. bear remains of serpulid/spirorbid annelids on the outer palm surface at the base of the fixed finger (Fig. 5). This appears to have been a symbiotic relationship, rather than *post-mortem* serpulid attachment to moulted anomurans, as described by Jakobsen & Feldmann (2004).

Family Diogenidae Ortmann, 1892

Genus *Paguristes* Dana, 1851

***Paguristes frigoscopus* sp. nov.**

(Fig. 6A-E)

Diagnosis: Right cheliped transversely oval; outer, dorsal and ventral sides convex, inner side almost straight; outer side covered with regular, dense cover of fine, forwardly directed tubercles, fixed finger short, stout and triangular.

Etymology: From Latin, *frigus*, meaning cold, and *scopulus*, meaning reef.

Type material: The holotype, OESM 6705, is a near-complete right palm with fixed finger, measuring 8.5 mm in length and 5.5 mm in greatest width. The paratype, MGUH 33407, is an incomplete right palm, still embedded in coral-limestone.

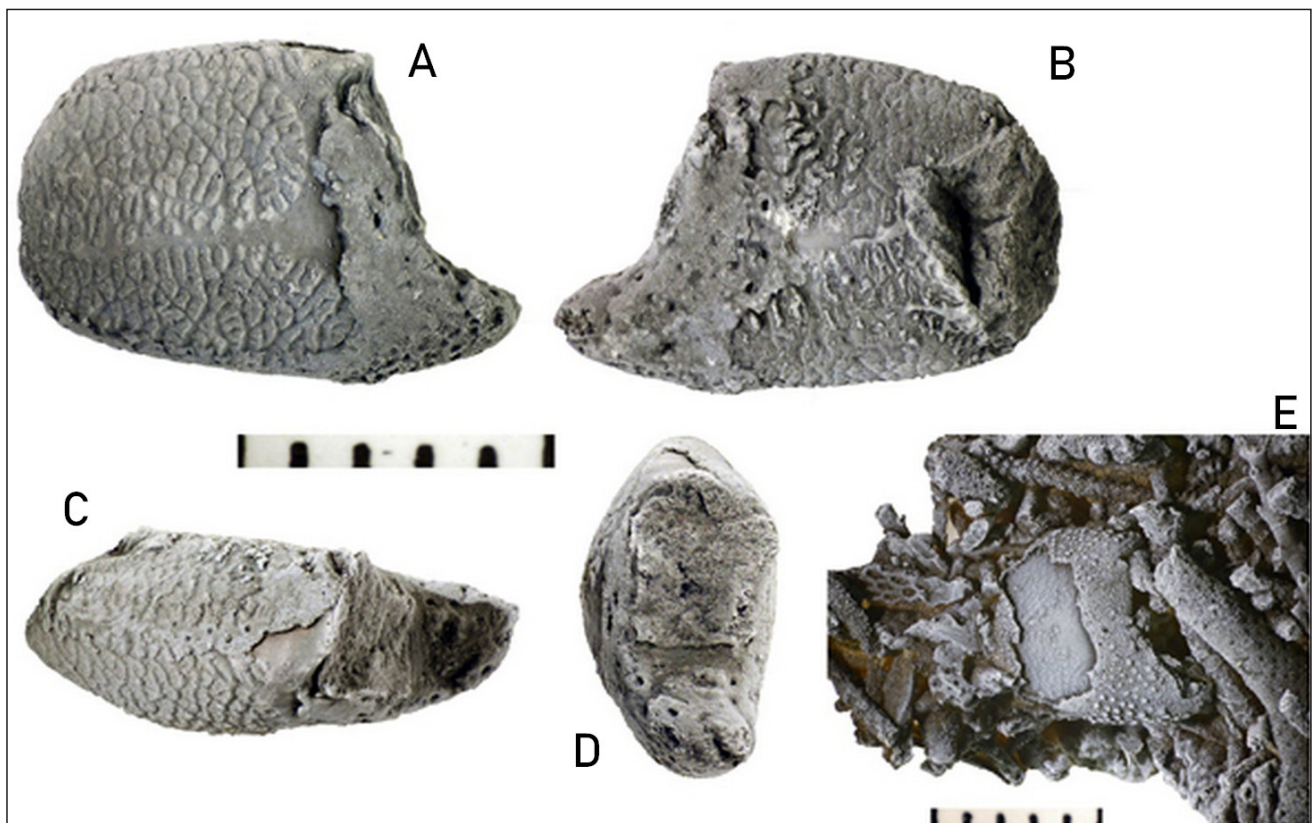


Fig. 6A-E. *Paguristes frigoscopus* sp. nov., A-D. Holotype (OESM 6705), a near-complete right palm in internal mould preservation; E. Paratype (MGUH 33407), an incomplete right palm, still embedded in coral limestone. Scale bar in millimetres.

Locality and stratigraphy: The same as for *Dardanus faxensis* sp. nov. (see above).

Description: Cross section of right palm transversely oval; outer, dorsal and ventral sides convex, inner side almost straight; outer side with regular, dense cover of fine, forwardly directed tubercles; fixed finger short, stout and triangular; occlusal margin straight without teeth, surrounded by few large pores; interdigital margin oblique; length of fixed finger about one quarter of total length.

Remarks: Fraaije et al. (2015b) listed all extinct species of *Paguristes* known at that time. With a convex dorsal and ventral edge and a short, convex triangular fixed finger, *P. frigoscopulus* sp. nov. is morphologically closest to the late Albian *P. liwinskii* Fraaije, van Bakel, Jagt & Machalski, 2015 from east-central Poland and *P. santamartaensis* Feldmann, Tshudy & Thomson, 1993, from the Campanian of Antarctica. It differs in having a less dense, more forwardly directed, tuberculate ornamentation.

Conclusions

In total, fourteen specimens were available for the present study. Of these, about 86 % (12 specimens) are attributed to *D. faxensis* sp. nov. and only c. 14 % (2 specimens) to *P. frigoscopulus* sp. nov. Unfortunately, there are no detailed studies yet that relate cheliped morphology to feeding strategy. Schembri (1982) is one of the few studies that documented a close relationship between cheliped morphology and types of feeding. If we extrapolate his data to *Dardanus faxensis* sp. nov., that species may be considered to have been a generalist and better adapted to the Danian deep-water reefal environment of Faxø than *P. frigoscopulus* sp. nov., which probably was mainly a filter feeder.

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References

- Armstrong, A., Nyborg, T., Bishop, G.A., Ossó-Morales À. & Vega, F.J. 2009: Decapod crustaceans from the Paleocene of central Texas, USA. *Revista Mexicana de Ciencias Geológicas*, 26/3: 745-763.
- Bjerager, M., Sheldon, E. & Lauridsen, B.W. 2018: Mound-forming cold-water corals and bryozoans in the Early Paleocene of Denmark. *Sedimentology*, 65/4: 1331-1353. <https://doi.org/10.1111/sed.12424>
- Brünnich Nielsen, K. 1922: Zoantharia from Senon and Paleocene deposits in Denmark and Skåne. *Det Kongelige Danske Videnskabernes Selskabs Skrifter, naturvidenskabelig og matematisk, Afdeling 3*: 199-233.
- Collins, J.S.H. 2010: New species of crabs (Crustacea, Decapoda), one from the Middle Danian of Denmark, and three new species from the Upper Cretaceous of Nigeria. *Bulletin of the Mizunami Fossil Museum*, 36: 13-19.
- 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.
- Cope, K.H., Utgaard, J.E., Masters, J.M. & Feldmann, R.M. 2005: The fauna of the Clayton Formation (Paleocene, Danian) of southern Illinois: a case of K/P survivorship and Danian recovery. *Bulletin of the Mizunami Fossil Museum*, 32: 97-108.
- Damholt, T. & Rasmussen, A. 2005: Fossiler fra Faxø Kalkbrud. *Geomuseum Faxø*: 44 p.
- Damholt, T., Rasmussen, A. & Rasmussen, L. 2010: Fossiler fra Faxø Kalkbrud. *Revideret og udvidet udgave. Geomuseum Faxø*: 48 p.
- Dana, J.D. 1851: Paguridae. *Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe reipublicae foederatae duce, lexit et descripsit. Proceedings of the Academy of Natural Sciences of Philadelphia*, 5: 267-272.
- Feldmann, R.M., Tshudy, D. & Thomson, M. 1993: Late Cretaceous and Paleocene decapod crustaceans from James Ross Basin, Antarctic Peninsula. *The Paleontological Society Memoir*, 67/S28: 1-41. <https://doi.org/10.1017/S0022336000062077>
- Fischer-Benzoni, R. von. 1866: Über das relative Alter des Faxø-Kalkes und über die in demselben vorkommenden Anomuren und Brachyuren. *Schweis'sche Buchhandlung, Kiel*: 30 p.

- Förster, R. 1975: Ein Krebs aus dem oberen Campan von Misburg. *Berichte der Naturhistorischen Gesellschaft zu Hannover*, 119: 285-294.
- Fraaije, R.H.B. 2003: Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. *Contributions to Zoology*, 72/2-3: 119-130. <https://doi.org/10.1163/18759866-0720203010>
- 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. <https://dx.doi.org/10.1127/0077-7749/2014/0419>
- Fraaije, R.H.B. & Polkowsky, S. 2016: *Dardanus colosseus*, a new paguroid from the Eocene of Austria preserved in its host gastropod shell. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 279/1: 157-162.
- Fraaije, R.H.B., Van Bakel, B.W.M., Iserbyt, A. & Jagt, J.W.M. 2011: New extinct Paguroidea (Crustacea, Decapoda, Anomura), with the first example of capsulated setae from the fossil record. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 262: 247-255.
- Fraaije, R.H.B., Van Bakel, B.W.M. & Jagt, J.W.M. 2015a: A new Albian hermit crab (Anomura, Paguroidea) from France - another example of capsulated setae in an extinct form. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 277/3: 353-359. <https://doi.org/10.1127/njgpa/2015/0511>
- Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M. & Machalski, M. 2015b: A new hermit crab (Anomura, Paguroidea) from the upper Albian (Cretaceous) of Annapol, Poland. *Zootaxa*, 3955/4: 588-594. <https://doi.org/10.11646/zootaxa.3955.4.9>
- Hennig, A. 1899: Studier öfver den baltiska Yngre kritans bildningshistoria. *Geologiska Förening i Stockholms Förhandlingar*, 21: 133-188.
- Hyžný, M., Fraaije, R.H.B., Martin, J.E., Perrier, V. & Sarr, R. 2016: *Paracapsulapagurus popouguinensis*, a new hermit crab (Decapoda, Anomura, Paguroidea) from the Maastrichtian of Senegal. *Journal of Paleontology*, 90/6: 1133-1137. <https://doi.org/10.1017/jpa.2016.65>
- Jagt, J.W.M., Collins, J.S.H. & Fraaye, R.H.B. 1993: A new early Palaeocene genus of raninid crab (Crustacea, Decapoda) from Denmark, southern Sweden and The Netherlands. *Contributions to Tertiary and Quaternary Geology*, 30/3-4: 177-182.
- Jakobsen, S.L. 2003: A new preparatory approach of decapod and thoracican crustaceans from the Middle Danian at Fakse, Denmark. *Contributions to Zoology*, 72: 141-145. <https://doi.org/10.1163/18759866-0720203015>
- Jakobsen, S.L. & Collins, J.S.H. 1997: New middle Danian species of anomurans and brachyuran crabs from Fakse, Denmark. *Bulletin of the Geological Society of Denmark*, 44: 89-100.
- Jakobsen, S. L. & Feldmann, R.M. 2004: Epibionts on *Dromiopsis rugosa* (Decapoda: Brachyura) from the late Middle Danian limestones at Fakse Quarry, Denmark: novel preparation techniques yield amazing results. *Journal of Paleontology*, 78: 953-960.
- Klompaker, A.A., Hyžný, M. & Jakobsen, S. L. 2015: Taphonomy of decapod crustacean cuticle and its effect on the appearance as exemplified by new and known taxa from the Cretaceous-Danian crab *Caloxanthus*. *Cretaceous Research*, 55: 141-151. <https://doi.org/10.1016/j.cretres.2014.11.011>
- Klompaker, A.A., Jakobsen, S. L. & Lauridsen, B. W. 2016: Evolution of body size, vision, and biodiversity of coral-associated organisms: evidence from fossil crustaceans in cold-water coral and tropical coral ecosystems. *BMC Evolutionary Biology*, 16: 132. <https://doi.org/10.1186/s12862-016-0694-0>
- Latreille, P.A. 1802-1803: *Histoire naturelle, générale et particulière, des Crustacés et des Insectes* 3. Dufart, Paris: 467 p.
- Lauridsen, B.W., Bjerager, M. & Surlyk, F. 2012: The middle Danian Faxe Formation - new lithostratigraphic unit and a rare taphonomic window into the Danian of Denmark. *Bulletin of the Geological Society of Denmark*, 60: 47-60.
- Lyell, C. 1837: On the Cretaceous and Tertiary strata of the Danish islands of Seeland and Moen. *Transactions of the Geological Society of London*, 6: 243-257.
- Milne Edwards, H. 1832: Extrait d'une lettre sur les caractères des crustacés anomures, adressée à M. Audouin. *Annales des Sciences naturelles, Zoologie et Biologie animale*, 26: 255-256.
- Ortmann, A. 1892: Die Dekapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen,

- IV. Theil. Die Abtheilungen Galattheidea und Paguridea. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere, 6: 241-326.
- Paul'son, O. 1875: Issledovaniya rakoobraznykh krasnago morya s zametkami otnositel'no rakoobraznykh drugikh morei. Chast' 1. Podophthalmata i Edriophthalmata (Cumacea), xiv. S.V. Kul'zhenk, Kiev: 144 p.
- Perch-Nielsen, K. 1979: Calcareous nannofossil zonation at the Cretaceous-Tertiary boundary in Denmark. In: Birkelund, T. & Bromley, R.G. (eds): Cretaceous-Tertiary Boundary Events Symposium, 1. The Maastrichtian and Danian of Denmark: 115-135. Copenhagen, University of Copenhagen.
- Rasmussen, H.W. 1973: En lyssky hulefauna fra Fakse som vidnesbyrd om koralkalkens dannelse i lyszonen. Dansk Geologisk Forening, Årsskrift, (1972): 87-91.
- Rathbun, M.J. 1935: Fossil Crustacea of the Atlantic and Gulf Coastal Plain. Geological Society of America, Special Paper 2: 1-160.
- Reuss, A.E. 1859: Zur Kenntniss fossiler Krabben. I. Die Kurzschwänzer der Kreideformation. Denkschriften der kaiserlichen Akademie der Wissenschaften in Wien, 7: 1-90.
- Robin, N., Van Bakel, B.W.M., d'Hondt, J.-L. & Charbonnier, S. 2015: A new early brachyuran (Crustacea, Decapoda) from the Middle Jurassic of northwest France, epibionts and ecological considerations. Contributions to Zoology, 84/3: 179-191. <https://doi.org/10.1163/18759866-08403001>
- 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, 15/4: 257-273. <https://doi.org/10.1080/14772019.2016.1182950>
- Schembri, P.J. 1982: Feeding behavior of fifteen species of hermit crabs (Crustacea: Decapoda: Anomura) from the Otago region, southeastern New Zealand. Journal of Natural History, 16: 859-878.
- Schlotheim, E.F. von. 1820: Die Petrefaktenkunde, auf ihrem jetzigen Standpunkte, durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreiches der Vorwelt erläutert, Becker, Gotha: lxii + 437 p.
- Schröder, A.M. & Surlyk, F. 2019: Adaptive morphologies of the brachiopod fauna from Danian coral mounds at Faxe, Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology, 534: 109332. <https://doi.org/10.1016/j.palaeo.2019.109332>
- Segerberg, K. O. 1900: De Anomura och Brachyura Decapoderna inom Scandinaviens Yngra Krita. Geologiska Förening i Stockholm Förhandlingar, 22: 347-390.
- Varol, O. 1998: Palaeogene. In: Bown, P.R. (ed.): Calcareous nannofossil biostratigraphy [British Micropalaeontological Society Series], Chapman & Hall/Kluwer Academic, Cambridge: 200-224.
- Vega, F.J., Nyborg, T.G., Fraaije, R.H.B. & Espinosa, B. 2007: Paleocene decapod Crustacea from the Rancho Nuevo Formation (Parras Basin - Difunta Group), northeastern Mexico. Journal of Paleontology, 81/6: 1432-1441. <https://doi.org/10.1666/06-018R.1>
- Wallaard, J.J.W., Fraaije, R.H.B., Jagt, J.W.M., Klompmaker, A.A. & Van Bakel, B.W.M. 2020: The first record of a paguroid shield (Anomura, Annuntidiogenidae) from the Miocene of Cyprus. Geologija, 63/1: 37-43. <https://doi.org/10.5474/geologija.2020.004> (present issue).
- Woodward, H. 1901: On some Crustacea collected by Miss Caroline Birley and Miss L. Copland from the Upper Cretaceous of Faxe, Denmark. Geological Magazine, new series, 4/8: 486-501.

