

Paracapsulapagurus poponguinensis, a new hermit crab (Decapoda, Anomura, Paguroidea) from the Maastrichtian of Senegal

Matúš Hyžný,^{1,2} René H.B. Fraaije,³ Jeremy E. Martin,⁴ Vincent Perrier,⁴ and Raphaël Sarr⁵

¹Geological-Paleontological Department, Natural History Museum, Vienna, Burgring 7, A-1010 Vienna, Austria (matus.hyzny@nhm-wien.ac.at)

²Comenius University, Faculty of Natural Sciences, Department of Geology and Paleontology, Mlynská Dolina, Ilkovičova 6, SVK-842 15 Bratislava, Slovakia

³Oertijdmuseum De Groene Poort, Bosscheweg 80, 5283 WB Boxtel, The Netherlands (info@oertijdmuseum.nl)

⁴Laboratoire de Géologie de Lyon: Terre, Planète, Environnement, UMR CNRS 5276 (CNRS, ENS, Université Lyon 1), Ecole Normale Supérieure de Lyon, 69364 Lyon cedex 07, France (jeremy.martin@ens-lyon.fr), (vincent.perrier_at_univ-lyon1.fr)

⁵Laboratoire de Sédimentologie et Biostratigraphie, Département de Géologie, Université Cheikh Anta Diop de Dakar, Sénégal (rsarr@ucad.sn)

Abstract.—Based on a single right cheliped from the Cape de Naze Formation (middle–upper Maastrichtian), Senegal, a new genus and species of hermit crab with capsulated setae is described. *Paracapsulapagurus poponguinensis* n. gen. n. sp. is characterized by platy, scale-like, non-spinose tubercles with setae arranged in curved rows. This is only the third record of a fossil hermit crab with capsulated setae. These are documented in detail using SEM-imaging. For the first time, capsulated setae are also figured for the Early Jurassic hermit crab *Schobertella*.

Introduction

Although capsulated setae are not uncommon in paguroid hermit crabs, only recently were they reported in fossil forms. *Capsulapagurus christiaensi* Fraaije et al., 2011 from the lower Albian of the Pargny-sur-Saulx clay pit (Haute-Marne, northeastern France) was based on a single right chela. Recently, another paguroid with capsulated setae, *Capsulapagurus brocheti* Fraaije, Van Bakel, and Jagt, 2015, was reported from the lower Albian of Laneuville-au-Pont (Haute-Marne), again based only on a single right chela (Fraaije et al., 2015). According to Osawa (2012; see also Komai, 2003; Komai and Rahayu, 2014), eight extant species have close relationships, as established from the possession of capsulated setae on their chelipeds. Recently, Fraaije et al. (2015) transferred these eight species to *Capsulapagurus*. This short report adds another fossil paguroid with capsulated setae, *Paracapsulapagurus* n. gen., but this time from the Maastrichtian of Senegal.

Fossil decapods of Senegal are poorly known. Tessier (1952), Remy and Tessier (1954), and Gorodiski and Remy (1959) described several brachyuran species from Maastrichtian, Paleocene, and Eocene Senegalese deposits and reported on some unidentified callianassid claws. Recently, new decapod material from the middle to upper Maastrichtian of the Cap de Naze, Poponguine in Senegal (Fig. 1) has been reported, including a description of a new species of brachyuran genus *Costacopluma* Collins and Morris, 1975, by Hyžný et al. (2016).

Material and methods

The specimen was studied under binoculars Leica MZ6 and EZ4 and photographed using three different methods: 1) dry and

uncoated; 2) coated with ammonium chloride sublimate; and 3) using SEM (Philips XL30ESEM, University of Tartu, Estonia).

Repositories and institutional abbreviations.—BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; MAB: Oertijdmuseum De Groene Poort, Boxtel, The Netherlands; MNHN: Muséum National d'Histoire Naturelle, Département Histoire de la Terre, Paris, France; SENCN: Laboratoire de Géologie, Université Cheikh Anta Diop, Dakar, Senegal.

Systematic paleontology

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802

Remarks.—Of all known extant paguroid ingroups, only Parapaguridae Smith, 1882, and Pylojacquesidae McLaughlin and Lemaitre, 2001, have not yet been reported from the fossil record (De Grave et al., 2009). The Annuntidiogenidae Fraaije, 2014, Diogenidae Ortmann, 1892, Gastrodoridae Van Bakel et al., 2008, Parapylochelidae Fraaije et al., 2012, Pilgrimchelidae Fraaije, 2014, and Pylochelidae Bate, 1888, occur predominantly in reefal carbonates of the fossil record, whereas the Paguridae Latreille, 1802 seems to be confined to siliciclastic environments (Fraaije et al., 2011, 2015).

Family Paguridae Latreille, 1802
Genus *Paracapsulapagurus* new genus

Type species.—*Paracapsulapagurus poponguinensis* n. sp. by original designation and monotypy.

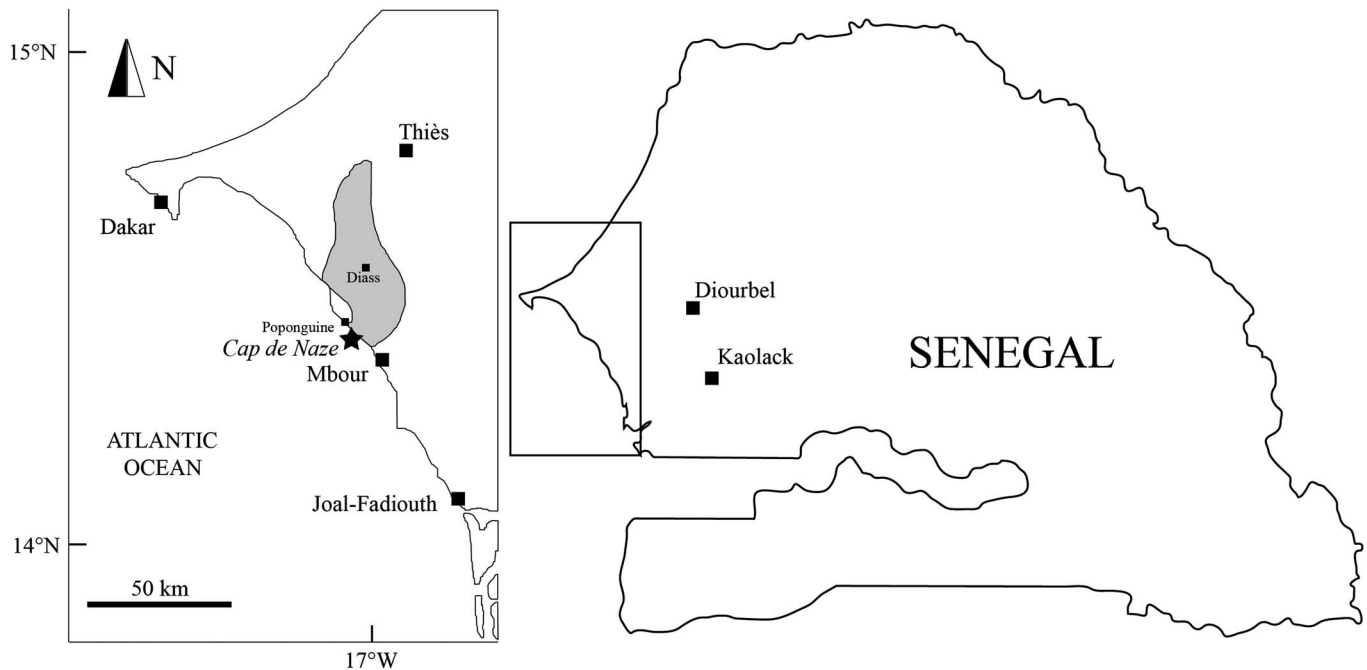


Figure 1. Studied area of Cape de Naze, Poponguine, Senegal. The area shaded in gray corresponds to the sediments of late Campanian–Maastrichtian age.

Diagnosis.—As for type species by monotypy.

Etymology.—From Greek παρά (pará = next to, near) and *Capsulapagurus*, alluding to the close relationship with *Capsulapagurus*.

Occurrence.—Known only from the middle–upper Maastrichtian of Cap de Naze, Senegal.

Remarks.—*Paracapsulapagurus* n. gen. differs from *Capsulapagurus* in having platy, scale-like, non-spinose tubercles, in the absence of spines on the dactylus, and in the absence of large embedded setal areas on both fingers. Multiple setal pits of *Paracapsulapagurus* n. gen. are typically arranged in a curved row, whereas the multiple setal pits of *Capsulapagurus* spp. are concentrically arranged.

Paracapsulapagurus poponguinensis new species
Figures 2.1–2.3, 3.1–3.9, 4.1

Holotype.—Right chela consisting of articulated dactylus, propodus, carpus, and merus (Collection n° SENCN-054) (Fig. 2.1–2.3) from the middle to upper Maastrichtian of the Unit 3 of the Cap de Naze Formation, Poponguine, Senegal.

Diagnosis.—Right cheliped propodus with concave lower margin at the base of the fixed finger; fixed finger with longitudinal keel extending onto manus; outer surface covered with platy non-spinose tubercles; capsulated setae arranged mostly in a curved row.

Occurrence.—Material was collected from the middle to upper Maastrichtian marine sandstones of the Unit 3 of the Cap de Naze Formation outcropping at Cap de Naze, Poponguine, Senegal.

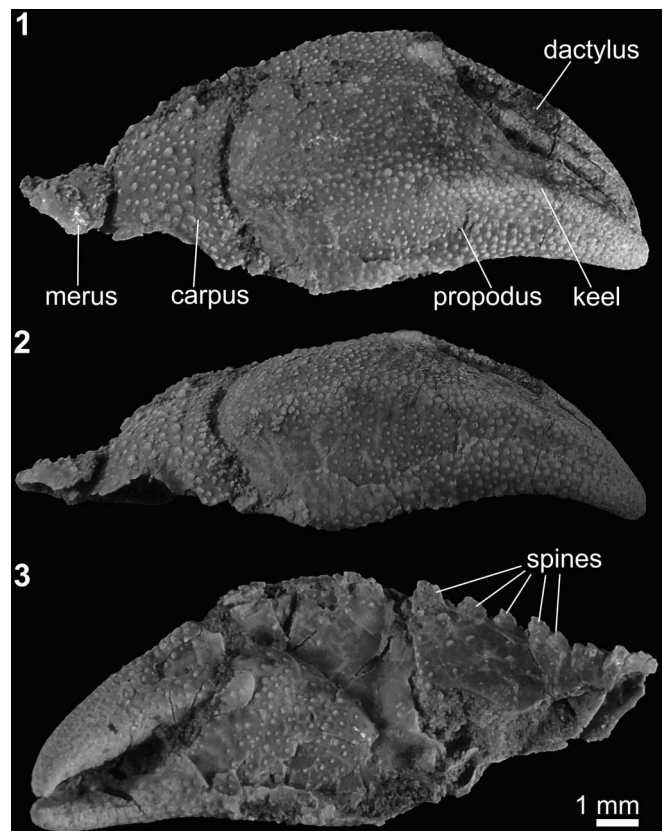


Figure 2. *Paracapsulapagurus poponguinensis* n. gen. n. sp. (holotype SENCN-054); middle–upper Maastrichtian of the Cap de Naze Formation, Poponguine, Senegal: (1), outer lateral view; (2), angled view showing the keel on the fixed finger and manus; (3), inner lateral view. Specimen coated with ammonium chloride.

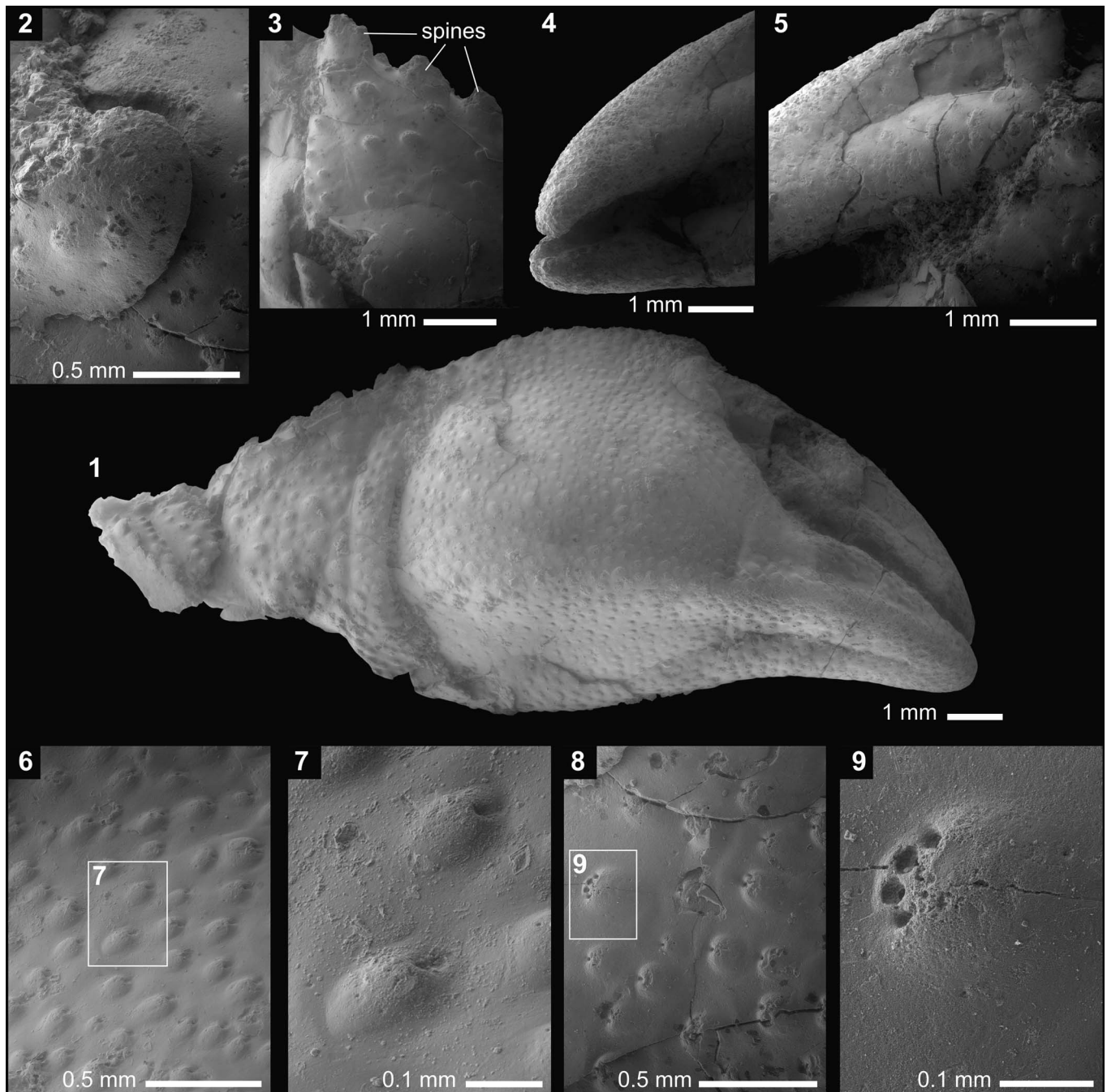


Figure 3. *Paracapsulapagurus poponguinensis* n. gen. n. sp. (holotype SENCN-054); middle–upper Maastrichtian of the Cap de Naze Formation, Poponguine, Senegal: (1), lateral view of the right cheliped; (2), capsulated setae on the inner lateral surface of merus; (3), inner lateral surface of carpus; note well-developed spines; (4), finger tips in inner lateral view; (5), basal portion of dactylus in inner lateral view; (6, 7), capsulated setal pores on the inner lateral surface of propodus; (8, 9), capsulated setal pores on the outer lateral surface of propodus. All figures are SEM images.

The age is based on foraminifers and ammonites from the units 2 and 4, as discussed in detail by Hyžný et al. (2016). More details about the geology and subdivisions of the deposits were given by Tessier (1952), Castelain et al. (1965), Khatib et al. (1990), Sarr (1995), and Cuny et al. (2011).

Description.—Merus of right chela presumably subquadrate in outline (as far as it can be inferred from the broken margin) with several transverse rows of tubercles. Carpus with subtrapezoidal outline in lateral view, dorsal margin with distinct spines

(Fig. 3.3); distal margin concave, enveloping proximal margin of propodus; outer surface coarsely granular proximally and finely granular distally. Propodus oval in outline (Fig. 3.1), upper margin convex, lower margin initially converging distally and concave at the base of the fixed finger; fixed finger robust, curving inward, with lateral keel running continuously onto the manus (Figs. 2.1, 3.1). Dactylus curving inward, blunt-tipped (Fig. 3.4). Occlusal margins of the fingers armed with subequal molariform denticles. Inner and outer lateral surfaces of all preserved elements more-or-less evenly

covered with densely packed platy, scale-like tubercles (Fig. 3.6, 3.8), forming distinct spines on merus and carpus (Fig. 2.3); outer surfaces covered more densely than inner ones. Capsulated setal structures preserved in most tubercles, directed distally; tubercles on the outer lateral surface usually bearing 1–2 setal pits (Fig. 3.6, 3.7), tubercles on the inner lateral surface usually bearing 3–4 setal pits (Fig. 3.8, 3.9).

Etymology.—The species epithet refers to the type locality at Poponguine, Senegal.

Remarks.—*Paracapsulapagurus poponguinensis* n. gen. n. sp. differs from *Capsulapagurus* spp. in several major aspects. The new species possesses a concavity on the lower margin of the propodus, just at the base of the fixed finger. The upper margin of the propodus is strongly convex (Fig. 2). Neither *Capsulapagurus christiaensi* nor *C. brocheti* has such a concavity (Fraaije et al., 2011, fig. 1B, 1C; Fraaije et al., 2015, figs. 1B, 1C; respectively), and the upper margin of the latter species is straight (Fraaije et al., 2015, fig. 1B, 1C). The holotype of *C. christiaensi* is fragmentary and the upper propodal margin cannot be sufficiently described (Fraaije et al., 2011, fig. 1). Both Albian taxa have large tubercles on the upper margin of the propodus, occasionally forming spines. The new material from Senegal has the upper margin of the propodus without such large tubercles, although a few broken spines are present on the proximal-most part of the upper margin; much larger spines are present on the carpus and merus (Figs. 2.3, 3.3). The propodus outline of *Paracapsulapagurus poponguinensis* n. gen. n. sp. differs strikingly from *C. brocheti*, which has a more elongated propodus (Fraaije et al., 2015, fig. 1).

Discussion

Although SEM imaging has been used for documentation of the cuticular surfaces of numerous fossil decapod taxa (in lobsters:

e.g., Simpson and Middleton, 1985; Feldmann and Tshudy, 1987; in brachyurans: e.g., Vega et al., 1994; Feldmann and Gaździcki, 1998; Haj and Feldmann, 2002; Waugh et al., 2009; Hyžný and Kroh, 2015; Hyžný et al., 2016), it has only rarely been used to document the morphology of extinct paguroid hermit crabs. Müller (1984, pl. 11, figs. 7–9) used the SEM technique for imaging *Anapagurus miocenicus* Müller, 1984, from the middle Miocene of Hungary. Van Bakel et al. (2003) provided a detailed description of *Ciliopagurus obesus* Van Bakel, Jagt, and Fraaije, 2003 from the Oligocene (Rupelian) of Belgium based on SEM images. This technique proved invaluable in documenting the stridulatory apparatus of this species (Van Bakel et al., 2003, figs. 1.1, 2.1).

In this report, SEM imaging provided detailed documentation of capsulated setae of a new paguroid species and helped to identify crucial differences in their development from all hermit crabs with capsulated setae known to date (for a review, see Fraaije et al., 2015). The setal pores in *Paracapsulapagurus poponguinensis* n. gen. n. sp. are arranged in curved rows (Fig. 4.1), whereas in representatives of *Capsulapagurus* they are arranged in more-or-less circular clusters (Fig. 4.2, 4.3). The rows of setal pores in *P. poponguinensis* n. sp., are best developed on the inner lateral surface of the propodus. Interestingly, some comparable capsulated setal pits are reported here to occur also on the representative of *Schobertella simonsenetlangi* Schweigert et al., 2013 (Fig. 4.4) from the Early Jurassic (Pliensbachian) of France and Germany, indicating that Schobertellidae Schweigert et al., 2013, possibly are close to, or even ancestral to Paguridae.

For the possible function of the setae, McLaughlin and Lane (1975) suggested that they may act both to detect and repel predators. To our knowledge, no further physiological, behavioral, or prey-predator studies of hermit crabs with capsulated setae have been conducted to date. In this respect, the fossil record of taxa with capsulated setae does not offer enough data to analyze.

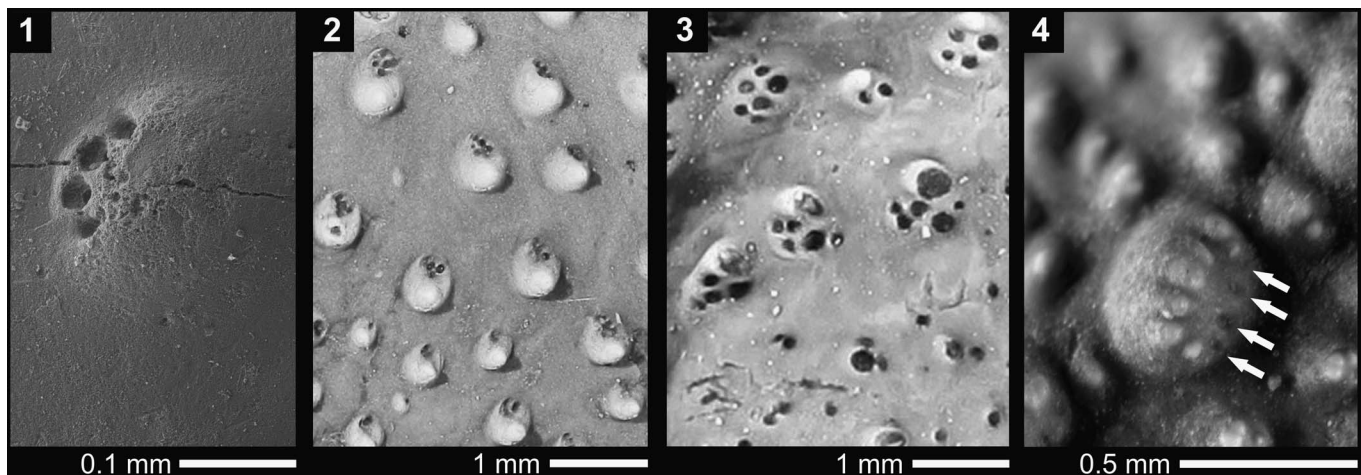


Figure 4. Arrangement of setal pores in all fossil species with capsulated setae known to date: (1), inner lateral surface of the propodus of *Paracapsulapagurus poponguinensis* n. gen. n. sp. (holotype SENCN-054); middle–upper Maastrichtian of the Cap de Naze Formation, Poponguine, Senegal; (2), outer lateral surface of the propodus of *Capsulapagurus christiaensi* Fraaije et al., 2011 (holotype MAB k. 3158); lower Albian of the Pargny-sur-Saulx clay pit, Département Marne, northeast France; (3), upper portion of the outer lateral surface of the propodus of *Capsulapagurus brocheti* Fraaije et al., 2015 (holotype MNHN.F.A52940); lower Albian of the Pargny-sur-Saulx clay pit, Marne, northeast France; (4), upper margin of the propodus of *Schobertella simonsenetlangi* Schweigert et al., 2013 (BSPG 2011 XI 62); lower Pliensbachian of the Amaltheenton Formation, Buttenheim/Franconia. (1) Is a SEM image; (2, 3) are light pictures of specimens coated with ammonium chloride; (4) is a light picture of a specimen without ammonium chloride coating.

Acknowledgments

G. Schweigert (Staatliches Museum für Naturkunde, Stuttgart) provided photo of the capsulated setae of *Schobertella simonsenellangi*. JEM and RS warmly thank the members of the PaleoSen team for help in the field: L. Hautier, M. Thiam, B. Sambou, S. Adnet, F. Lihoreau, R. Lebrun, and R. Tabuce. Reviewers R. Feldmann and G. Schweigert and associate editor J. Haug are thanked for constructive criticism. This research is part of the PaleoSen project (www.paleosen.com). JEM and RS were supported in the field by ANR PALASIAFRICA (ANR-08-JCJC-0017), PICS-CNRS, the international Exchange Scheme of the Royal Society and the National Geographic Society's Global Exploration Fund (Northern Europe). The research of MH has been supported by the Slovak Research and Development Agency under contracts no. APVV-0644-10 and APVV-0436-12.

References

- Bate, C.S., 1888, Report on the Crustacea Macrura dredged by H.M.S. Challenger during the years 1872–76, in Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76: *Zoology*, v. 24, 942 p.
- Castelain, J., Jardiné, S., and Monciardini, C., 1965, Excursions géologiques dans le Sénégal occidental: Mémoire du Bureau de Recherches Géologiques et Minières, v. 32, p. 357–365.
- Collins, J.S.H., and Morris, S.F., 1975, A new crab, *Costacopluma concava* from the Upper Cretaceous of Nigeria: *Palaeontology*, v. 18, p. 823–829.
- Cuny, G., Martin, J.E., and Sarr, R., 2011, A neoselachian shark fauna from the Late Cretaceous of Senegal: *Cretaceous Research*, v. 34, p. 107–115.
- De Grave, S., and 17 others 2009, A classification of living and fossil genera of decapod crustaceans: *The Raffles Bulletin of Zoology*, Supplement No. 21, p. 1–109.
- Feldmann, R.M., and Gaździcki, A., 1998, Cuticular ultrastructure of fossil and living homolodromiid crabs (Decapoda: Brachyura): *Acta Palaeontologica Polonica*, v. 43, p. 1–19.
- Feldmann, R.M., and Tshudy, D., 1987, Ultrastructure in cuticle from *Hoplopatria stokesi* (Decapoda: Nephropidae) from the Lopez de Bartolano Formation (Late Cretaceous–Paleocene) of Seymour Island, Antarctica: *Journal of Paleontology*, v. 61, p. 1194–1203.
- 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*, v. 273, p. 121–145.
- Fraaije, R.H.B., Van Bakel, B.W.M., Iserbyt, A., and 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*, v. 262, p. 247–255.
- Fraaije, R.H.B., Klompmaker, A.A., and Artañal, P., 2012, New species, genera and a family of hermit crabs (Crustacea, Anomura, Paguroidea) from a mid-Cretaceous reef of Navarra, northern Spain: *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, v. 263, p. 85–92.
- Fraaije, R.H.B., Van Bakel, B.W.M., and Jagt, J.W.M., 2015, 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*, v. 277, p. 353–359.
- Gorodiski, A., and Remy, J.-M., 1959, Sur les Décapodes éocènes du Sénégal occidental: *Bulletin de la Société Géologique de France 7^e série*, v. 1, p. 315–319. pl. 19a.
- Haj, A.E., and Feldmann, R.M., 2002, Functional morphology and taxonomic significance of a novel cuticular structure in Cretaceous raninid crabs (Decapoda: Brachyura: Raninidae): *Journal of Paleontology*, v. 76, p. 472–485.
- Hyžný, M., and Kroh, A., 2015, Barremian decapod crustaceans from Serre de Bleyton (Drôme, SE France): *Annalen des Naturhistorischen Museums in Wien, Serie A*, v. 117, p. 121–152.
- Hyžný, M., Perrier, V., Robin, N., Martin, J.M., and Sarr, R., 2016, *Costacopluma* (Decapoda: Brachyura: Retroplumidae) from the Maastrichtian and Paleocene of Senegal: a survivor of K/Pg events: *Cretaceous Research*, v. 57, p. 142–156.
- Khatib, R., Ly, A., Sow, E., and Sarr, R., 1990, Rythmes sédimentaires liés aux variations eustatiques globales au Campanien et Maastrichtien du Sénégal. Révision stratigraphique de la série du Crétacé terminal du Cap de Naz: *Comptes Rendus de l'Académie des Sciences, Paris*, v. 311, Série 2, p. 1089–1095.
- Komai, T., 2003, Identities of *Pagurus japonicus* (Stimpson, 1858) and *P. similis* (Ortmann, 1892), with description of a new species of *Pagurus*: *Zoosystema*, v. 25, p. 377–411.
- Komai, T., and Rahayu, D.L., 2014, New records and new species of the hermit crab genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Philippines: *Raffles Bulletin of Zoology*, v. 62, 620–646.
- Latreille, P.A., 1802–1803, *Histoire Naturelle, Générale et Particulière, des Crustacés et des Insectes*, 3: Paris, F. Dufart, 408 p.
- 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; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835 and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa"*: London, Smith, Elder, and Co., p. 53–71, 2 pl.
- McLaughlin, P.A., and Lane, C.E., 1975, The morphology of unique structures on the spines of a deep-water Hawaiian hermit crab (Crustacea: Decapoda: Paguridae): *Journal of Zoology*, London, v. 176, p. 519–526.
- McLaughlin, P.A., and Lemaitre, R., 2001, A new family for a new genus and new species of hermit crab of the superfamily Paguroidea (Decapoda: Anomura) and its phylogenetic implications: *Journal of Crustacean Biology*, v. 21, p. 1062–1076.
- Müller, P., 1984, Decapod Crustacea of the Badenian: *Geologica Hungarica, Series Palaeontologica*, v. 42, p. 3–317.
- Ortmann, A.E., 1892, Die Decapoden-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. Die Abtheilungen Galatheidea und Paguridea: *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Thiere*, v. 6, p. 241–326.
- Osawa, M., 2012, A new species of the genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Ryukyu Islands, southwestern Japan, in Naruse, T., Chan, T.Y., Tan, H.H., Ah Yong, S.T., and Reimer, J.D., eds., *Scientific Results of the Marine Biodiversity Expedition—KUMEJIMA 2009: Zootaxa*, v. 3367, p. 155–164.
- Remy, J.-M., and Tessier, F., 1954, Décapodes nouveaux de la partie ouest du Sénégal: *Bulletin de la Société Géologique de France, Série 6*, v. 4, p. 185–192.
- Sarr, R., 1995, Etude biostratigraphique et paléoenvironnementale des séries d'âge Crétacé terminal à Eocène moyen du Sénégal occidental. Systématique et migration des ostracodes. Thèse doctorat d'Etat Sciences [Ph.D. dissertation]: Université Cheikh Anta Diop de Dakar, 335 p.
- Schweigert, G., Fraaije, R., Havlik, P., and Nützel, A., 2013, New Early Jurassic hermit crabs from Germany and France: *Journal of Crustacean Biology*, v. 33, p. 802–817.
- Simpson, M., and Middleton, R., 1985, Gross morphology and the mode of life of two species of lobster from the Lower Cretaceous of England: *Meyeria ornata* (Phillips) and *Meyerella magna* (M'Coy): *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 76, p. 203–215.
- Smith, S. I., 1882, Reports on the results of dredging, under the supervision of Alexander Agassiz, on the East Coast of the United States, during the summer of 1880, by the U. S. Coast Survey Steamer "Blake," Commander J.R. Bartlett, U.S.N., Commanding. 18. Report on the Crustacea. Part I. Decapoda: *Bulletin of the Museum of Comparative Zoology at Harvard College*, v. 10, p. 1–104, pls. 1–14.
- Tessier, F., 1952, Contribution à la stratigraphie et à la paléontologie de la partie ouest du Sénégal (Crétacé et Tertiaire): *Bulletin de la Direction des Mines de l'AOF*, v. 14, 570 p.
- Van Bakel, B.W.M., Jagt, J.W.M., and Fraaije, R.H.B., 2003, *Ciliopagurus obesus*, a new species of Oligocene hermit crab from northwest Belgium: *Cainozoic Research*, v. 2, p. 109–116.
- Van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M., and Artañal, P., 2008, An unexpected diversity of Late Jurassic hermit crabs (Crustacea, Decapoda, Anomura) in Central Europe: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 250, p. 137–156.
- Vega, F.J., Feldmann, R.M., and Davila-Alcocer, V., 1994, Cuticular structure in *Costacopluma mexicana* Vega and Perrilliat, from the Difunta Group (Maastrichtian) of northeastern Mexico, and its paleoenvironmental implications: *Journal of Paleontology*, v. 68, p. 1074–1081.
- Waugh, D.A., Feldmann, R.M., and Schweitzer, C.E., 2009, Systematic evaluation of raninid cuticle microstructure: *Bulletin of the Mizunami Fossil Museum*, v. 35, p. 15–41.

Accepted 16 February 2016