

The evolution of hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea) on the basis of carapace morphology: a state-of-the-art-report

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ABSTRACT

In our ongoing studies of both extinct and extant hermit crabs (Paguroidea Latreille, 1802), we have observed and recorded a number of morphological changes that have taken place between Early Jurassic times (*c.* 185 million years ago) and the present day. Species compositions of paguroid assemblages from

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 Branchial condensation,
 isochely,
 heterochely,
 Probeebeidae,
 Paguropsidae n. fam,
 new family.

marine Upper Jurassic and Lower Cretaceous rocks in Europe are here compared with those of modern marine settings. Basal paguroids with cylindrical carapaces predominated in reefal environments during the Late Jurassic, but were gradually replaced by hermit crabs with non-cylindrical carapaces. The most basal paguroids reveal a branchial groove, but branchial condensation towards a single (i.e., cervical) groove is here shown to have occurred early in their evolutionary history. In several extant genera remnants of a branchial groove, in combination with several other basal features, can be seen. For this reason, these are here considered to be the most primitive members amongst extant paguroids. In this study, we resurrect the family Probeebeidae and erect a new family, Paguropsidae n. fam, to accommodate extant basal hermit crabs such as *Paguropsis* Henderson, 1888, *Eopaguropsis* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012 and *Paguropsina* Lemaitre, Rahayu & Komai, 2018. Described are also one pair of Early Jurassic (Pliensbachian) and two pairs of Middle Jurassic (Callovian) isochelous paguroid chelae, all collected recently. A new specimen of *Schobertella* reveals some important morphological traits of the shield that had not been observed previously. The earliest known example to date of clearly heterochelous chelae in the fossil record of hermit crabs originates from upper Kimmeridgian/Tithonian strata in the Boulonnais (northwestern France). For the first time, a phylogenetic scheme of marine Paguroidea, as based on morphological data of carapaces, is presented.

RÉSUMÉ

L'évolution des bernard-l'hermite (Crustacea, Decapoda, Anomura, Paguroidea) à partir de la morphologie des carapaces: état des connaissances.

Dans nos études en cours sur les bernard-l'hermite fossiles et actuels (Paguroidea Latreille, 1802), nous avons observé et reconnu un certain nombre de changements morphologiques qui ont eu lieu entre le début du Jurassique (c. 185 millions d'années) et aujourd'hui. Les compositions d'espèces des assemblages de paguroïdes provenant de roches marines du Jurassique supérieur et du Crétacé inférieur d'Europe sont ici comparées à celles des environnements marins actuels. Les pagures basaux à carapaces cylindriques prédominaient dans les milieux récifaux du Jurassique supérieur, mais ont été progressivement remplacés par des bernard-l'hermite à carapaces non cylindriques. Les pagures les plus basaux révèlent un sillon branchial, mais la condensation branchiale vers un seul sillon (i.e., le cervical) est ici démontrée pour avoir eu lieu tôt dans leur histoire évolutive. Chez plusieurs genres modernes, les restes d'un sillon branchial sont visibles, en combinaison avec plusieurs autres caractères basaux. Pour cette raison, ceux-ci sont ici considérés comme les membres les plus primitifs parmi les pagures actuels. Dans la présente étude, nous rétablissons la famille Probeebeidae, et érigeons la nouvelle famille Paguropsidae n. fam, pour accueillir des bernard-l'hermite basaux actuels comme *Paguropsis* Henderson, 1888, *Eopaguropsis* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012 et *Paguropsina* Lemaitre, Rahayu & Komai, 2018. Sont également décrites une paire de pinces isochèles de pagure du Jurassique inférieur (Pliensbachien) et deux paires de pinces isochèles de pagures du Jurassique moyen (Callovien), toutes recueillies récemment. Un nouveau spécimen de *Schobertella* révèle certains traits morphologiques importants du bouclier qui n'avaient pas été observés auparavant. Le plus ancien exemple connu, à ce jour, de pinces clairement hétérochèles dans le registre fossile des bernard-l'hermite, provient des couches du Kimméridgien supérieur/Tithonien du Boulonnais (Nord-Ouest de la France). Pour la première fois, un schéma phylogénétique des Paguroidea marins, basé sur des données morphologiques de carapaces, est présenté.

MOTS CLÉS
 Condensation
 branchiale,
 isochélie,
 hétérochèlie,
 Probeebeidae,
 Paguropsidae n. fam,
 famille nouvelle.

INTRODUCTION

The classification of the superfamily Paguroidea Latreille, 1802, or hermit crabs, is by far the most convoluted amongst decapod crustaceans (McLaughlin *et al.* 2010) and fossil material has only rarely been considered in this respect. As a result of meticulous collecting from upper Mesozoic (Lower Jurassic–Upper Cretaceous) sedimentary rocks over the last twenty years, our insight into the diversity and evolutionary history of hermit crabs has greatly increased, despite the fact that details of paguroid evolution remain elusive. However, observations on morphological changes in (functional) hard parts can contribute in several ways to improving our understanding

of evolutionary patterns and processes amongst paguroids. The identification of morphological novelties during the course of their Mesozoic evolution adds important data in unravelling their history.

Following the landmark study by Van Bakel *et al.* (2008), over 55 carapace-based Mesozoic paguroid taxa have been recorded (Fraaije *et al.* 2019, 2020b) and assigned to eight families. Of these, the Gastrodoridae Van Bakel, Fraaije, Jagt & Artal, 2008, the Pilgrimchelidae Fraaije, 2014 and the Schobertellidae Schweigert, Fraaije, Havlik & Nützel, 2013 comprise exclusively Mesozoic representatives (Fraaije *et al.* 2019). With at least 18 species, in eight families, the Tithonian (Late Jurassic) paguroid fauna from Ernstbrunn (Austria) is the most diverse extinct

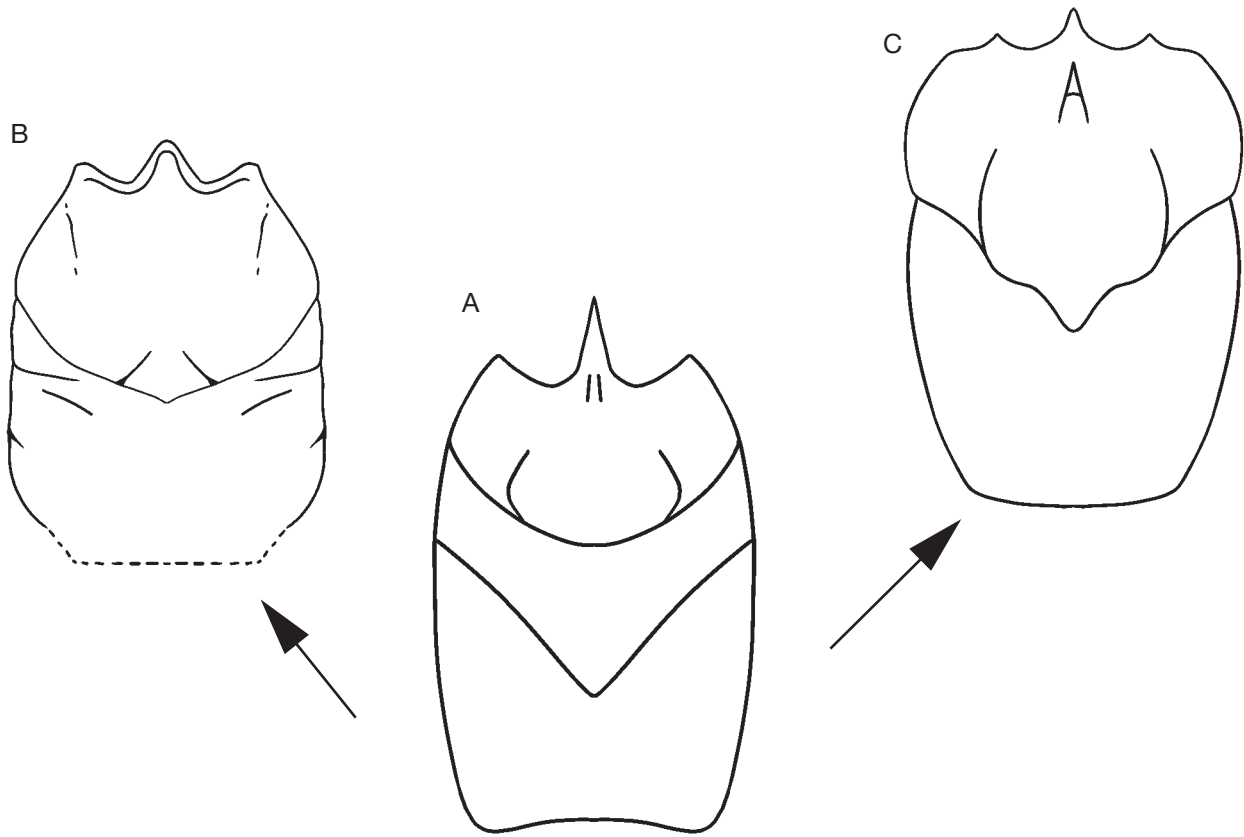


FIG. 1. — Branchial condensation in basal paguroid genera: **A**, *Platykotta* Chablais, Feldmann & Schweitzer, 2011; **B**, *Schobertella* Schweigert, Fraaije, Havlik & Nützel, 2013; **C**, *Eopaguropsis* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012.

assemblage so far (Fraaije *et al.* 2019). Other notable Mesozoic hermit crab faunules have been recorded from the Oxfordian (Upper Jurassic) of southern Poland (Fraaije *et al.* 2012b, c, 2014a, b), the Kimmeridgian (Upper Jurassic) of southern Germany (Van Bakel *et al.* 2008; Fraaije 2014; Fraaije *et al.* 2017), the Tithonian-Berriasian (Upper Jurassic-lowermost Cretaceous) of the Czech Republic (Fraaije *et al.* 2013c, 2020b), and the upper Albian (mid-Cretaceous) of northwest Spain (Fraaije *et al.* 2008, 2009, 2012a).

Our novel palaeontological data provide important additions to molecular analyses and morphological descriptions of internal organs published by biologists in order to unravel the phylogeny and taxonomy of paguroids, which were aptly referred to as the ‘paguroid puzzle’ by McLaughlin *et al.* (2010). The molecular study by Tsang *et al.* (2011) and our own work on fossil taxa (Fraaije *et al.* 2013b; Fraaije 2014; present paper) both demonstrate extant hermit crabs to have originated from symmetrically handed ancestors with cylindrical carapaces.

In order to gain a better insight into evolutionary processes amongst paguroids, we here present an overview of all currently available palaeontological data with regard to faunal compositions and notable changes in the morphology of both carapaces and first pereopods through geological time. Important basal morphological characters of carapaces observed in the fossil record are the following:

1. the presence of a branchial groove;

2. the presence of a long rostrum;
3. the possession of a well-ornamented carapace;
4. the presence of a mid-dorsal ridge on the shield;
5. the presence of a mesogastric process;
6. the possession of a well-calcified posterior carapace;
7. the presence of a calcified, delineated cardiac region.

In view of the above, it is highly unfortunate that, to our knowledge, there is not a single study of extant paguroids in which details of carapace morphology are considered (Fraaije *et al.* 2019). As a consequence, there is quite a lot of confusion in the literature regarding the nomenclature of carapaces regions (and their delineation) in hermit crabs (see e.g., Morgan & Forest 1991). On the basis of new data from the fossil record and, in particular, of the notion of ‘branchial condensation’, described here, carapace delineation can be understood much more easily and used in interpretation of both extinct and extant paguroids effectively. It is our hope that the data presented here will stimulate biologists to start using carapace morphology in order to achieve a more robust phylogeny for the superfamily Paguroidea.

BRANCHIAL CONDENSATION

Fraaije *et al.* (2012c) were the first to document an important trend seen in the carapace morphology of early (i.e., Late

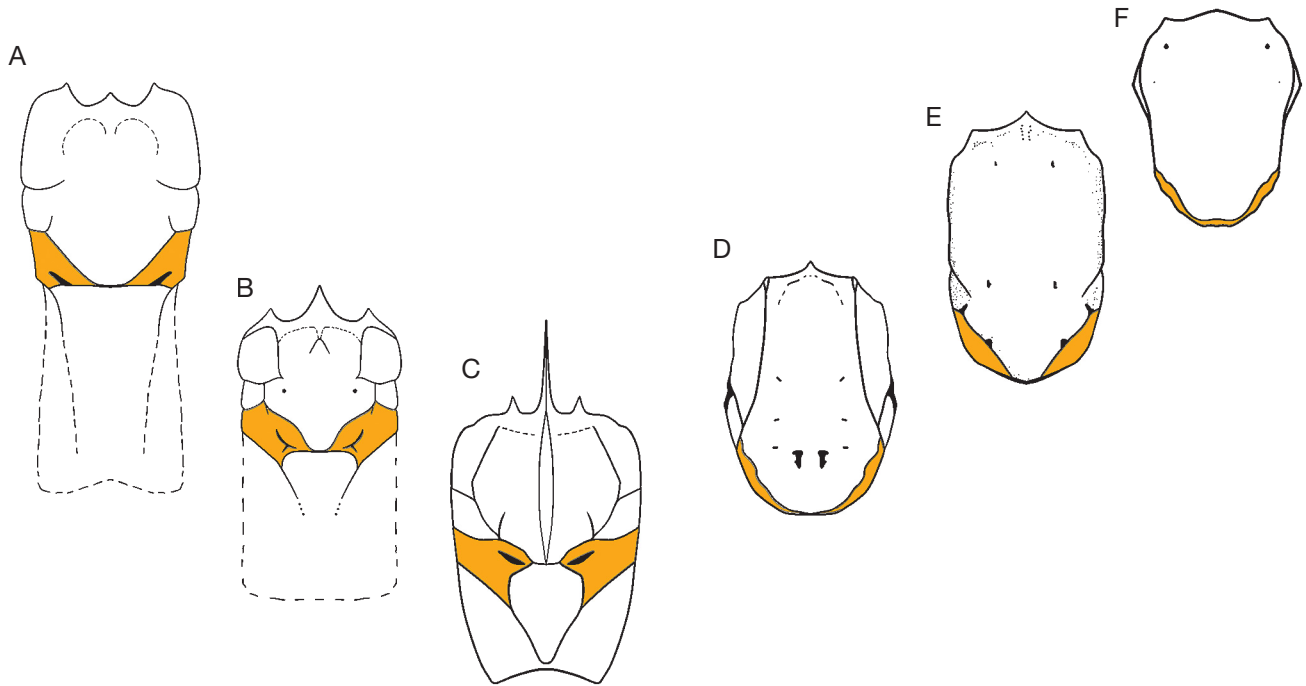


FIG. 2. — Branchial condensation in representatives of the families Parapylochelidae (A, B), Gastrodoridae (C), Xylopaguridae (D, E) and Pylojacquesidae (F).

Jurassic) paguroids. This concerns the fusion of the V-shaped branchial and subcircular cervical groove (as seen in, for instance, the genera *Platykotta* Chablais, Feldmann & Schweitzer, 2011, *Eogastrodorus* Van Bakel, Fraaije, Jagt & Artal, 2008 and *Gastrodorus* von Meyer, 1864, into a single, sinuous groove (cervical groove) in *Eopaguropsis* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012. This merger of two transverse carapace grooves into one, the cervical groove, is here referred to as ‘branchial condensation’ (Fig. 1); it occurs in all paguroid lineages. In some fossil and extant representatives, remnants of the branchial groove and/or small parts of the mesobranchial regions in between the cervical and branchial grooves can still be observed (see Figs 1B; 2). Traces of this double transverse groove system have been observed, amongst others, in the extant families Parapylochelidae Forest, 1987, Xylopaguridae Gašparič, Fraaije, Robin & De Angeli, 2016 and Pylojacquesidae McLaughlin & Lemaitre, 2001 (Fig. 2).

REDUCTION IN LENGTH OF (SPINOSE) ROSTRUM

One of the most basal paguroid genera known to date, *Gastrodorus* von Meyer, 1864, has a very long, spinose rostrum, with a midline crest that continues posteriorly towards the cervical groove. Amongst paguroid lineages in Mesozoic reefal settings, as inferred here, a rapid decrease in rostrum length has become apparent (Figs 2; 3).

Amongst extant paguroids only *Probeebei* Boone, 1926 (Boone 1926a), *Tylaspis* Henderson, 1885 and *Paguropsis* Henderson, 1888 have relatively long rostra with a midline crest. Apparently, a long spinose rostrum was advantageous only in certain deep-water habitats. Interestingly, but not unexpectedly, of the remaining extant groups, members of

the basal family Annuntidiogenidae Fraaije, 2014 (which includes the genus *Paguristes* Dana, 1851) have relatively long rostra as well (Fig. 4C).

UNIFORM CARAPACE ORNAMENTATION

When considering overall carapace morphology and, in particular, the presence of large, rimmed orbital cavities, the Triassic genus *Platykotta* may be interpreted as the most ancient paguroid known. This, as well as the Early Jurassic genera *Schobertella* Schweigert, Fraaije, Havlik & Nützel, 2013 and *Eogastrodorus* and the Late Jurassic to mid-Cretaceous *Gastrodorus*, all have uniformly granular to tuberculate shields and posterior carapaces (see e.g., Krzemińska *et al.* 2020). Amongst extant paguroids only *Labidochirus* Benedict, 1892, *Probeebei*, *Tisea* Morgan & Forest, 1991 and *Tylaspis* have completely ornamented carapaces. In none of the other hermit crab families recognised currently has uniform ornamentation been observed.

CARAPACE MIDLINE CREST

In many Mesozoic paguroid families, a midline crest on the carapace has been documented, for instance, in the Gastrodoridae (stratigraphical range: Bajocian [Middle Jurassic] to Albian; see Van Bakel *et al.* 2008; Klompaker *et al.* 2011; Krzemińska *et al.* 2016). As far as the family Parapylochelidae is concerned, there are examples of such crests in Kimmeridgian (Fraaije 2014: fig. 9d) and Albian members (Fraaije *et al.* 2012a: fig. 5b), while there are also Kimmeridgian taxa assigned to the families Pilgrimchelidae and Pylochelidae (Fraaije 2014: figs 7a; 9e), as well as diogenids of Oxfordian (Fraaije *et al.* 2012c: fig. 2b, e), Tithonian (Fraaije *et al.* 2019: fig. 2c-f) and Albian

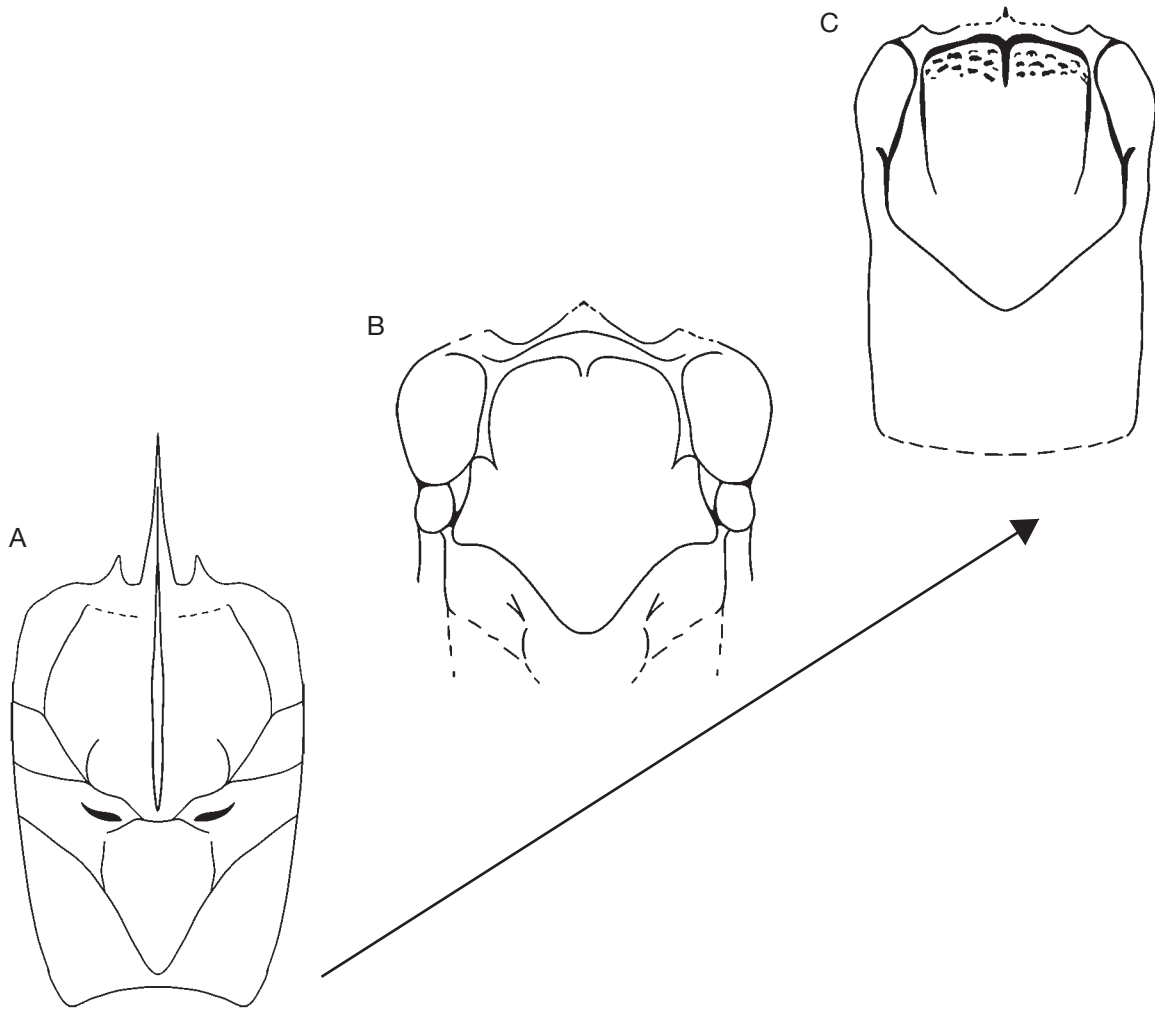


FIG. 3. — Reduction of rostral length during the Late Jurassic in representatives of the families Gastrodoridae (A), Parapylochelidae (B) and Pylochelidae (C).

age (Fraaije *et al.* 2012a: fig. 5a). The oldest members of the Paguridae known to date, of Tithonian age, also reveal a midline crest on the shield (Fraaije *et al.* 2019: figs 4a-c; 5b).

In modern hermit crabs, only *Probeebei*, *Tylaspis* and *Paguroopsis* show a midline crest on the rostrum that continues, to a greater or lesser extent, onto the shield.

MESOGASTRIC ANTERIOR PROCESS

In the Jurassic families Gastrodoridae, Schobertellidae, Diogenidae Ortmann, 1892, Paguropsidae n. fam (see below) and Parapylochelidae, a mesogastric anterior process is often present (see e.g., Fraaije *et al.* 2019: figs 2g-i; 3a-e; 4d). In modern paguroids, we have not been able to document any mesogastric anterior processes.

WELL-CALCIFIED POSTERIOR CARAPACE

In general, members of the families Gastrodoridae, Paguropsidae n. fam (see below), Parapylochelidae, Probeebeidae, Pylochelidae and Schobertellidae have relatively well-calcified posterior carapaces. Generally speaking, such are absent in all other families.

CALCIFIED AND DELINEATED CARDIAC REGION

Gastrodorids have a well-calcified and well-delineated cardiac region, while this region is in part well delineated in parapylochelids, probeebeids and paguropsids. Members of all other hermit crab families lack this character.

TRENDS WITHIN PAGUROID FAMILIES

Within the various families we have observed changes in a range of morphological features over geological time. For instance, in annuntidiogenids, a widening of the frontal shield has been observed in a number of species. In addition, the massetic region becomes bulkier and changes shape, from an elongated strip towards a more rectangular, globose part of the shield (Fig. 4).

Another trend is seen in the formation of, and a change in shape in, an intragastric Y-linea within the Calcinidae Fraaije, van Bakel & Jagt, 2017 (Fraaije *et al.* 2017: fig. 2, 2020a). Unfortunately, the fossil record of paguroid carapaces of Paleogene and Neogene age is extremely scanty, with only a handful of specimens having been described to date. Needless to say, this hampers our understanding of paguroid

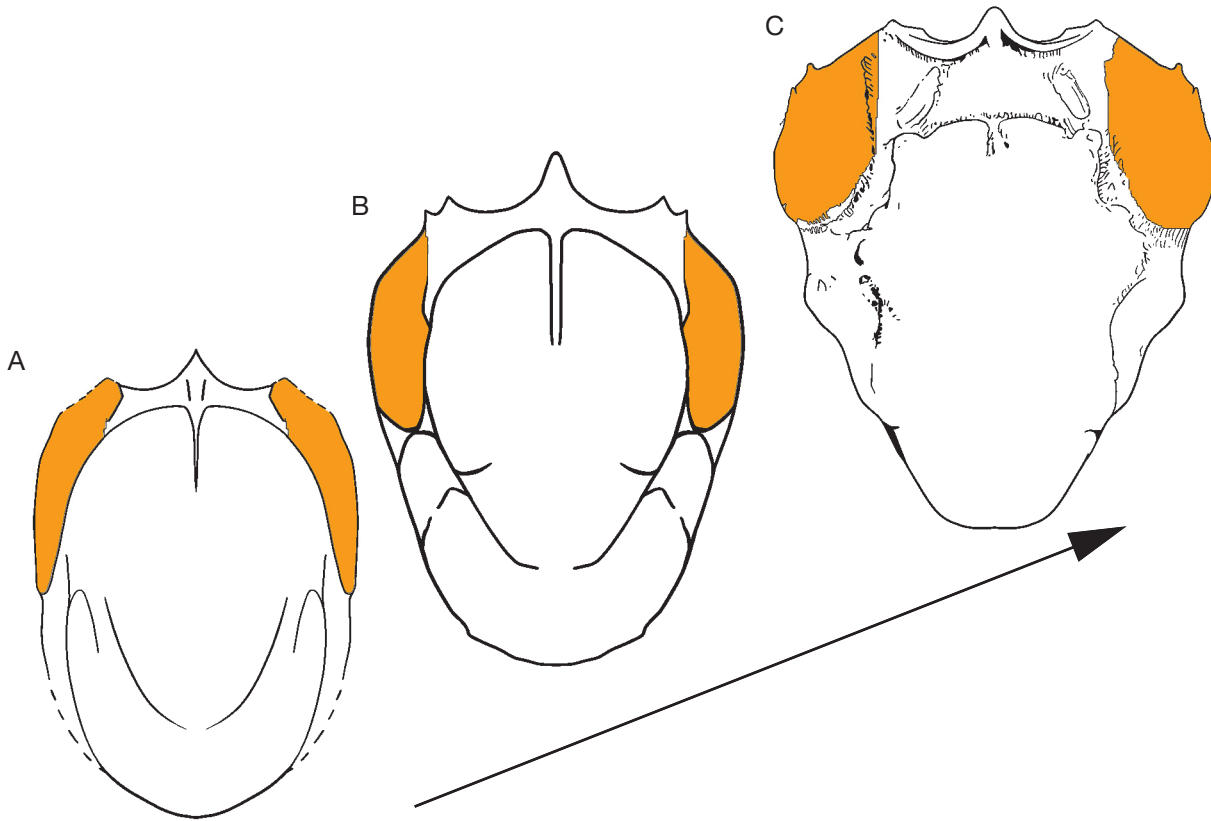


FIG. 4. — Changes in the mastic regions through time; from the Late Jurassic *Annuntidiogenes jurassicus* Fraaije, 2014 (A) to the mid-Cretaceous (late Albian) *Annuntidiogenes worfi* Fraaije, van Bakel, Jagt, Klompmaker & Artal, 2009 (B) and extant *Paguristes* sp. (C).

evolution during the Cenozoic (e.g., Beschin *et al.* 2016; Fraaije *et al.* 2020a; Wallaard *et al.* 2020).

PAGUROID ISOCHELY AND HETEROCHELY IN THE FOSSIL RECORD

To date, we are aware of only five examples of paired (isochelous) hermit crab chelae of Early and Middle Jurassic age, as follows:

- The holotype of *Schobertella simonsenetlangi* Schweigert, Fraaije, Havlik & Nützel, 2013, and another specimen of the same species (Fig. 5) described herein (see below), both from the upper Pliensbachian of southern Germany;
- *Orhomalus spinosus* Schweitzer, Feldmann & Lazăr, 2009, from the lower Callovian of Romania, and two newly collected specimens from the middle Callovian of France (Fig. 6). These individuals all reveal isochelous or near-isochelous chelae; they were collected during field work along the high-speed railway line LGV SEA (Ligne à Grande Vitesse Sud Europe Atlantique) by X. Valentin's team, from the Gratte-Loup limestones near Chasseneuil-du-Poitou (Vienne, France). These levels are dated as middle Callovian (*Coronatum* ammonite Zone; see Cariou 1980) and are situated near the historical quarries of Grand Pont, Bonnillet and Lourdines (Mathieu 1968). These specimens were associated with abundant bivalves, remains of marine crocodyliforms, plesiosaurs, sharks and bony fish, as well as terrestrial plants. These two pairs of chelae will be the subject of a forthcoming taxonomic study.

The first example of a hermit crab with a clear pair of heterochelous chelae (Fig. 7) is now contained in a private collection; it has been collected from the upper Kimmeridgian-lower Tithonian of the Atlantic Coast near Wimereux (Pas-de-Calais, northwest France). On the basis of a few photographs of this particular specimen that we have received from the collector, we have been able to document that the major right chela is about 1.5 to 2 times larger than the left one.

There is a match, in geological time, between this presence of heterochelous chelae in a Late Jurassic paguroid and the first occurrences of carapaces of members of the 'asymmetrically handed' Annuntidiogenidae, Diogenidae and Paguridae. Interestingly, the majority of extant primitive genera (e.g., *Labidochirus*, *Paguroopsis*, *Paguropsina* Lemaitre, Rahayu & Komai, 2018, *Probeebei* and *Tisea*) also have equal or subequal chelae. As a matter of fact, cheliped morphology in *Labidochirus*, *Probeebei* and *Tisea* resembles that of *Cryptopagurus* (see Schweigert *et al.* 2013: fig. 10a), whereas that of *Paguroopsis* and *Paguropsina* is close to that in *Schobertella* (see Schweigert *et al.* 2013: figs 3-5; 9).

The chelae of *Schobertella simonsenetlangi* were described in detail by Schweigert *et al.* (2013). They are convex both externally and internally and covered with about 20 irregular longitudinal rows of variably sized, forwardly directed tubercles on either side. The fixed fingers and dactyli are

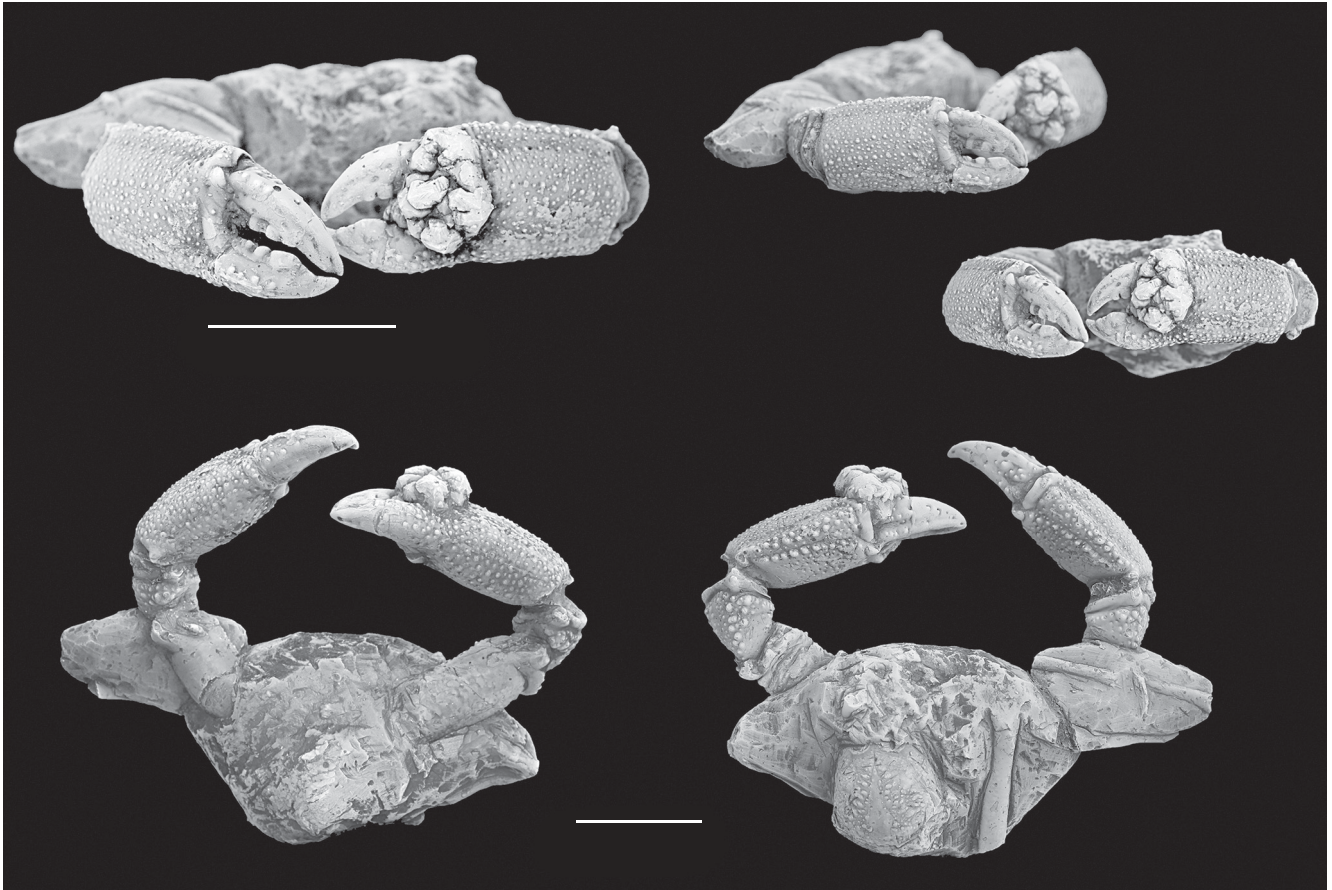


FIG. 5. — Isochelous chelae of *Schobertella simonsenetlangi* Schweigert, Fraaije, Havlik & Nützel, 2013 (SMNS 70555, Staatliches Museum für Naturkunde Stuttgart, Germany, from the Lower Jurassic (upper Pliensbachian) Amaltheenton Formation of Iggingen near Aalen, southwestern Germany. Scale bars: 5 mm.

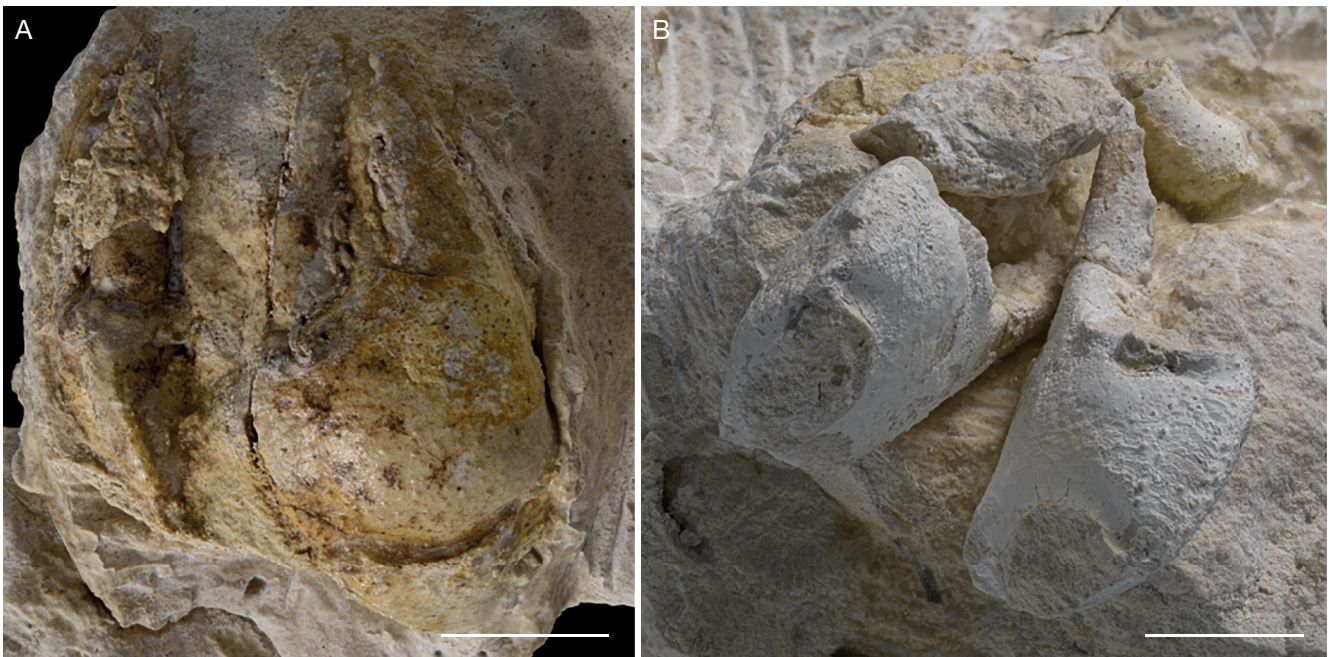


FIG. 6. — Isochelous chelae of paguroids from the middle Callovian of Poitou, France: **A**, specimen UP/CGL.12.10 (UP = Université de Poitiers, CGL = Calcaires de Gratte-Loup). **B**, specimen UP/CGL.12.11. Photographs: Philippe Loubry. Scale bars: 10 mm.



FIG. 7. — The oldest example of heterochelous paguroid claws from the Upper Jurassic of the Wimereux area (Boulonnais, northwestern France); an individual preserved *in situ* in the internal mould of a Vetigastropoda (private collection of Mr Gilles Dron). The maximum diameter of the gastropod is about 7 cm.

stout and compact with inwardly curved tips. The dentition, especially with extremely strong, elongate teeth close to the distal end of the fingers, points to a shell-cracking function. A recently collected new specimen of *Schobertella simonsenlangi* reveals well-preserved details of the frontal part of the shield (Fig. 8A): a triangular rostrum with large subcircular orbital rim ending in blunt outer orbital

spine; a prominent central gastric process ending in a deep incision at the base of the rostrum, a tapered and rounded anterolateral border and tuberculate ornamentation. This new specimen hints at a close relationship with the early paguropsid *Eopaguropsis nidiaquilae* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012, from the Oxfordian of Poland (Fig. 8B).

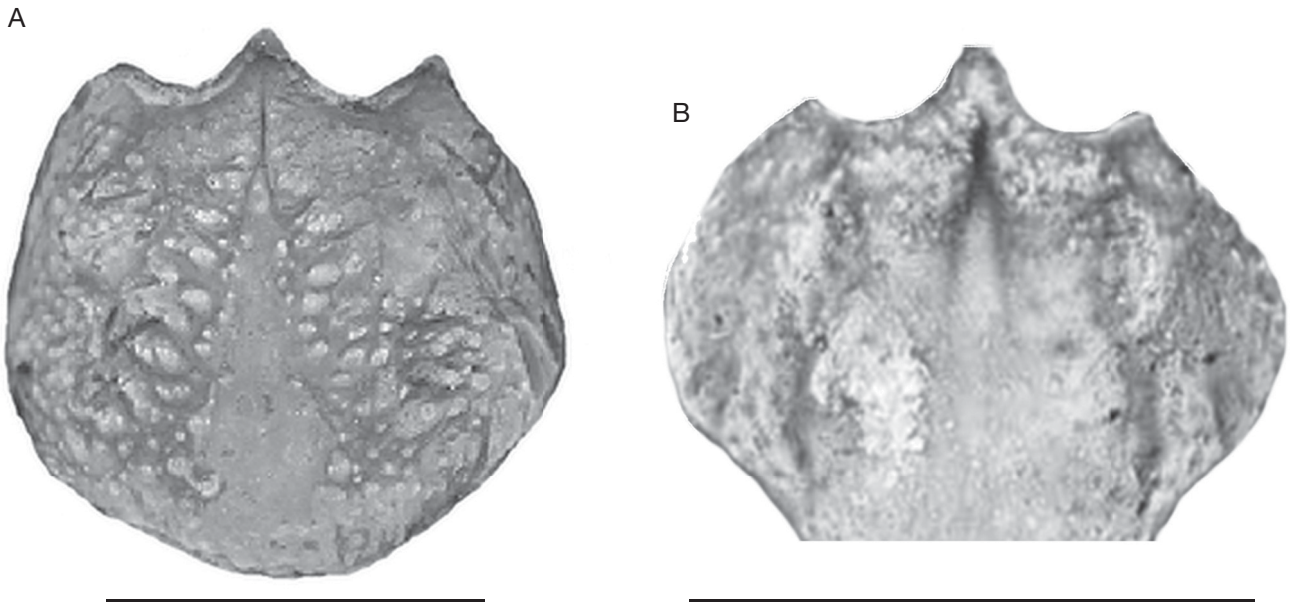


FIG. 8. — *Schobertella simonsenlangi* Schweigert, Fraaije, Havlik & Nützel, 2013 (SMNS 70555; see also Fig. 5), from the Lower Jurassic (upper Pliensbachian) Amaltheenton Formation of Iggingen near Aalen, southwestern Germany: (A) showing new details of shield morphology, compared to *Eopaguropsis nidiaquillae* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012 (B) (see Fraaije *et al.* 2012c: fig. 2d). Scale bars: 10 mm.

PAGUROID FAUNAL COMPOSITION THROUGH TIME

In order to document changes in paguroid faunal composition through time we have used three groups, namely the family Gastrodoridae, paguroids with ‘cylindrical carapace’ (i.e., all families depicted in Figure 12, to the left of the Gastrodoridae) and other (‘non-cylindrical’) hermit crabs (i.e., those to the right of the Gastrodoridae).

The oldest known paguroid faunule based on carapace remains is that from the Oxfordian of southern Poland (Van Bakel *et al.* 2008; Fraaije *et al.* 2012b, c, 2014a; Krzemińska *et al.* 2016). This comprises a single species of gastrodorid, three pilgrimchelids, two pylochelids and a single paguropsid.

The Kimmeridgian assemblage from Nusplingen (southern Germany) has also been documented in detail in recent years (Fraaije 2014) and comprises at least two gastrodorids, three parapylochelids, two pilgrimchelids, three pylochelids, as well as one annuntidiogenid and one diogenid each.

Tithonian faunules from Ernstbrunn (Austria) are the most diverse extinct assemblage recorded to date (Fraaije *et al.* 2019), with two gastrodorids, three pylochelids, two pilgrimchelids, two parapylochelids, one schobertellid, two annuntidiogenids, four diogenids, one pagurid and two paguropsids.

From Tithonian-Berriasian strata in Moravia (Czech Republic), Fraaije *et al.* (2013c, 2020a) have described an assemblage that includes a single gastrodorid, two parapylochelids, one pilgrimchelid, two pylochelids, one diogenid, one paguropsid and two pagurids.

So far, only a single mid-Cretaceous faunule is on record from the upper Albian of northwest Spain (Fraaije *et al.* 2008, 2009, 2012a), comprising one gastrodorid, one parapylochelid, one pylochelid and two annuntidiogenids.

When percentages for these three groups are plotted (see Fig. 9), a significant decline in cylindrical paguroids, coupled with an increase in the numbers of non-cylindrical ones, can be noted. In modern reefal settings, there are no basal paguroids; instead, a predominance of asymmetrically handed paguroids is apparent. The most basal taxa amongst extant paguroids, such as parapylochelids, pylochelids, paguropsids and probeebeids, survived only in a few bathyal habitats and, in this way, are comparable to ‘Lazarus’ lobster taxa from such settings, such as *Neoglyphea inopinata* Forest & de Saint Laurent, 1975, *Laurentaeglyphea neocaledonica* Forest, 2006 and polychelids (Polychelida).

RESURRECTION OF THE FAMILY PROBEEBEIDAE BOONE, 1926

The monotypic genus *Probeebeei*, and its type species, *P. mirabilis*, were originally described as a primitive macruran by Boone (1926a). In the same year, Boone (1926b) erected a new family, the Probeebeidae, to accommodate this enigmatic crustacean. Much later, Wolff (1961) provided a detailed redescription of *Probeebeei* and demonstrated that it was a hermit crab, which he assigned to the family Paguridae Latreille, 1802. The genus *Probeebeei* was later transferred to the Parapaguridae Smith, 1882, by de Saint Laurent (1972). However, that author barely considered the carapace morphology of this genus, yet based her assignment to the Parapaguridae on features such as the presence of a labral spine, the absence of an exopodal flagellum on the first maxilliped, the presence of undivided abdominal tergites and an unpaired left gonopore in females and the lack of a median constriction on the telson (compare Lemaitre 1998). None of these characters was used in the descriptions of *Probeebeei* and *Tylaspis* by de Saint Laurent (1972) and are not found either in any

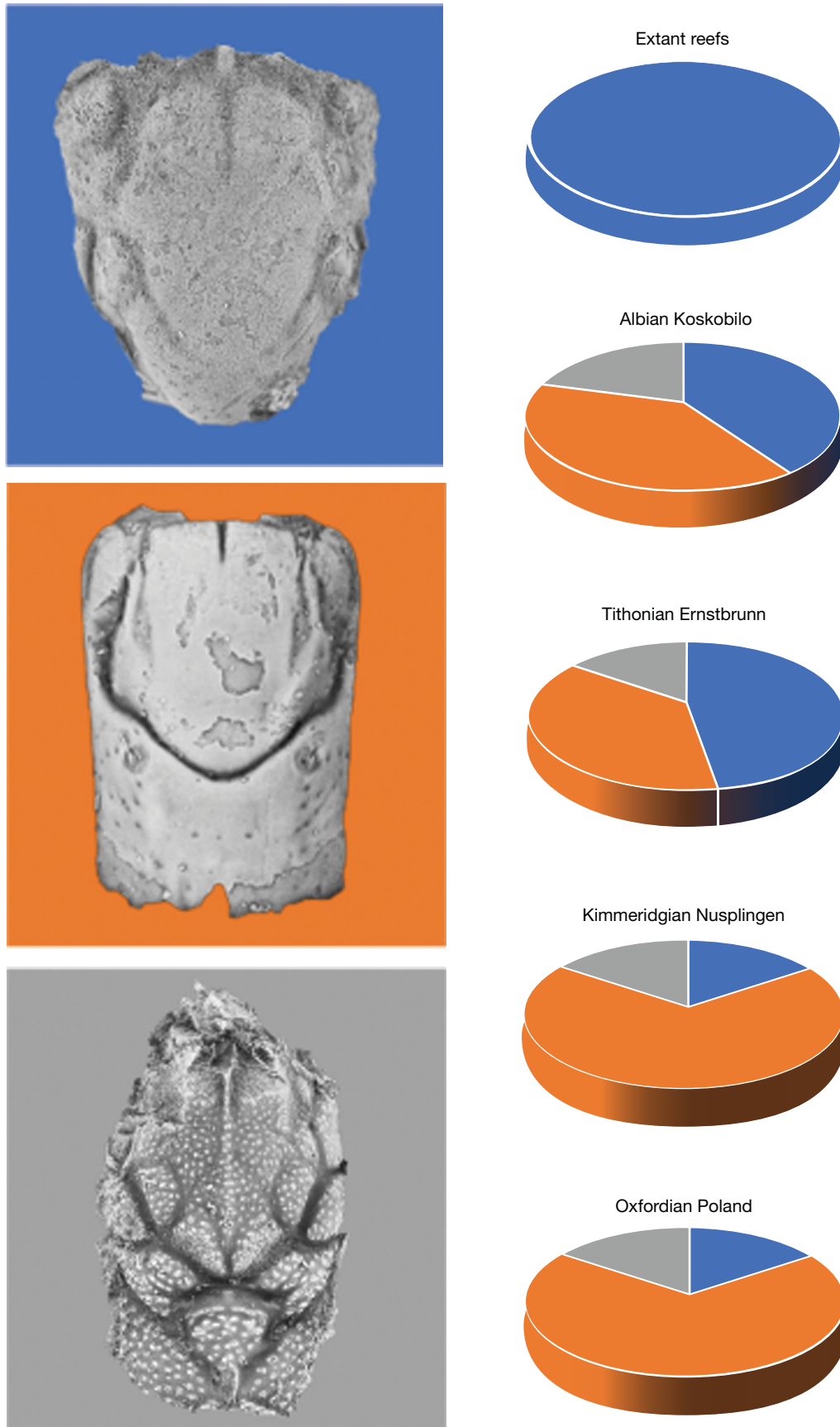


FIG. 9. — Changes in taxonomic composition amongst paguroid assemblages within reefal settings during the Late Jurassic (Oxfordian, Kimmeridgian and Tithonian) and mid-Cretaceous (Albian) compared to modern faunas. **Grey**, Gastrodoridae; **orange**, cylindrical carapace; **blue**, non-cylindrical carapace.

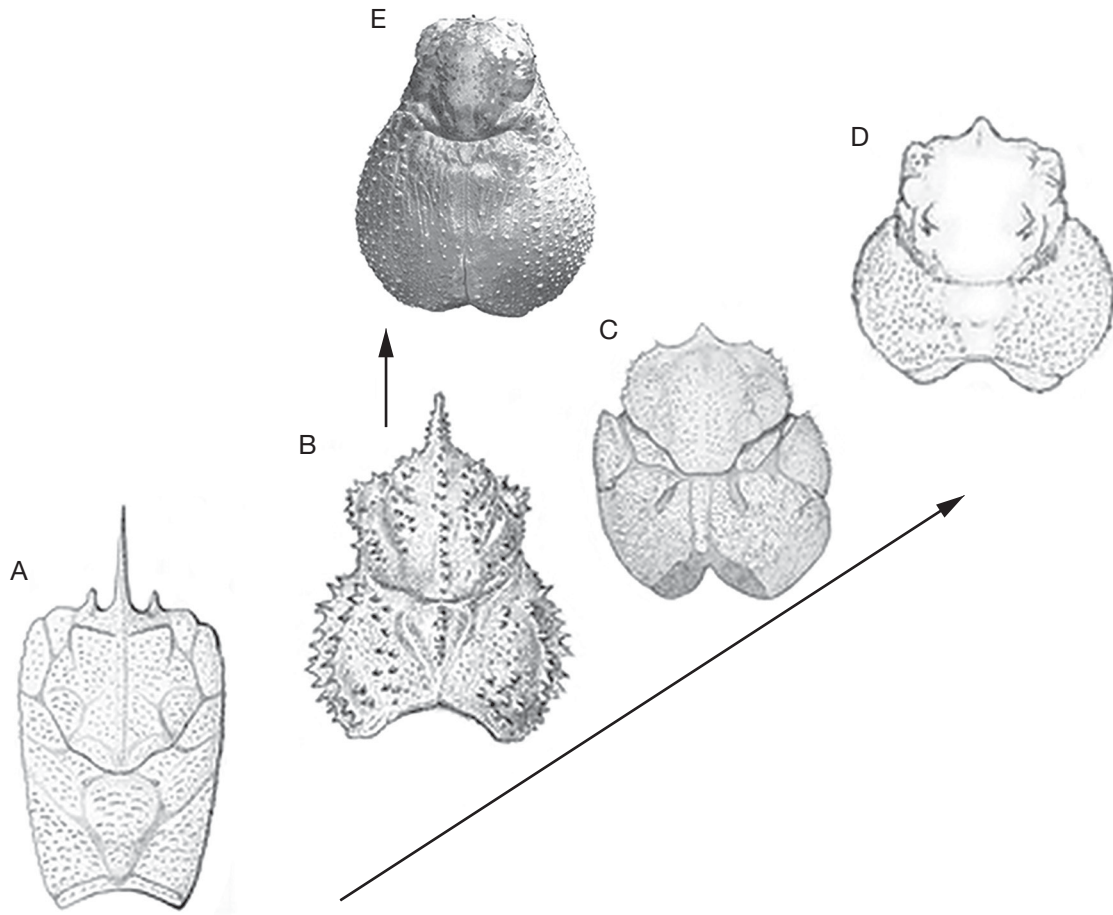


FIG. 10. — Transition from the Gastrodoridae to the Probeebeiidae, featuring branchial condensation, reduction of rostrum, reduction of ornament on shield, inflation of posterior carapace, reduction of delineation of cardiac and reduction of midline carapace crest: A, *Gastrodorus*; B, *Probeebei*; C, *Labidochirus*; D, *Tylaspis*; E, *Tisea*.

of the more recent accounts on parapagurid taxa (see e.g., Lemaitre 2013, 2014). An unpaired left gonopore is also a common trait in the Paguridae (e.g., Lemaitre 2003).

The monotypic genera *Probeebei* and *Tylaspis* were restudied and redescribed in detail by Lemaitre (1998), who noted that de Saint Laurent (1972) had erroneously indicated that she had examined specimens of *Tylaspis anomala* Henderson, 1885 from the Indian Ocean. In actual fact, this material had originated from the Pacific Ocean. Lemaitre (1998) also stated that several important morphological features of *T. anomala* had been inaccurately or insufficiently recorded in previous studies and found additional discrepancies or inaccuracies in published accounts of *Probeebei* and *Tylaspis*. He also observed a similar mode of life and identical morphological characters of the carapace (different from those of other parapagurids) for these two crab-like genera and assumed these two paguroids to be advanced forms. Our data show these two taxa retain almost all of the ‘remnant’ basal carapace characteristics mentioned above. For this reason, we consider them to be the most basal ones amongst extant paguroids. In fact, together with *Parapylocheles* Alcock, 1901, they are amongst the most primitivex of modern-day hermit crabs.

Family PROBEEBEIDAE Boone, 1926, emended herein

Probeebeiidae Boone, 1926b: 73.

TYPE GENUS. — *Probeebei* (Boone, 1926) by monotypy.

OTHER GENERA INCLUDED. — *Labidochirus* Benedict, 1892, *Tisea* Morgan & Forest, 1991 and *Tylaspis* Henderson, 1885.

DIAGNOSIS. — Shield (excluding rostrum) strongly convex, well calcified, width equal to length or width exceeding length, with distinct bulges (i.e., keraial and massetic regions) laterally, strong to weaker spinose ornament. Rostrum well developed, exceeding lateral projections. Cervical and branchial grooves subparallel, encompassing small branchial regions. Posterolateral margins spinose. Posterior carapace well calcified, broadly inflated, with dense spinose ornamentation. Well-developed cardiac grooves encompassing cardiac region.

REMARKS. — The bulges on the shield of extant probeebeiids (Fig. 10) are quite similar to those of the most basal paguropsid, *Eopaguropsis nidiacquilae* (see Fraaije *et al.* 2012c: figs 2c; 3), which also has a spinose ornamentation on the gastric and lateral parts of the shield.

ERECTION OF A NEW FAMILY, PAGUROPSIDAE N. FAM.

Paguropsis Henderson, 1888 has remained a monotypic genus ever since its original description. In spite of the uniqueness

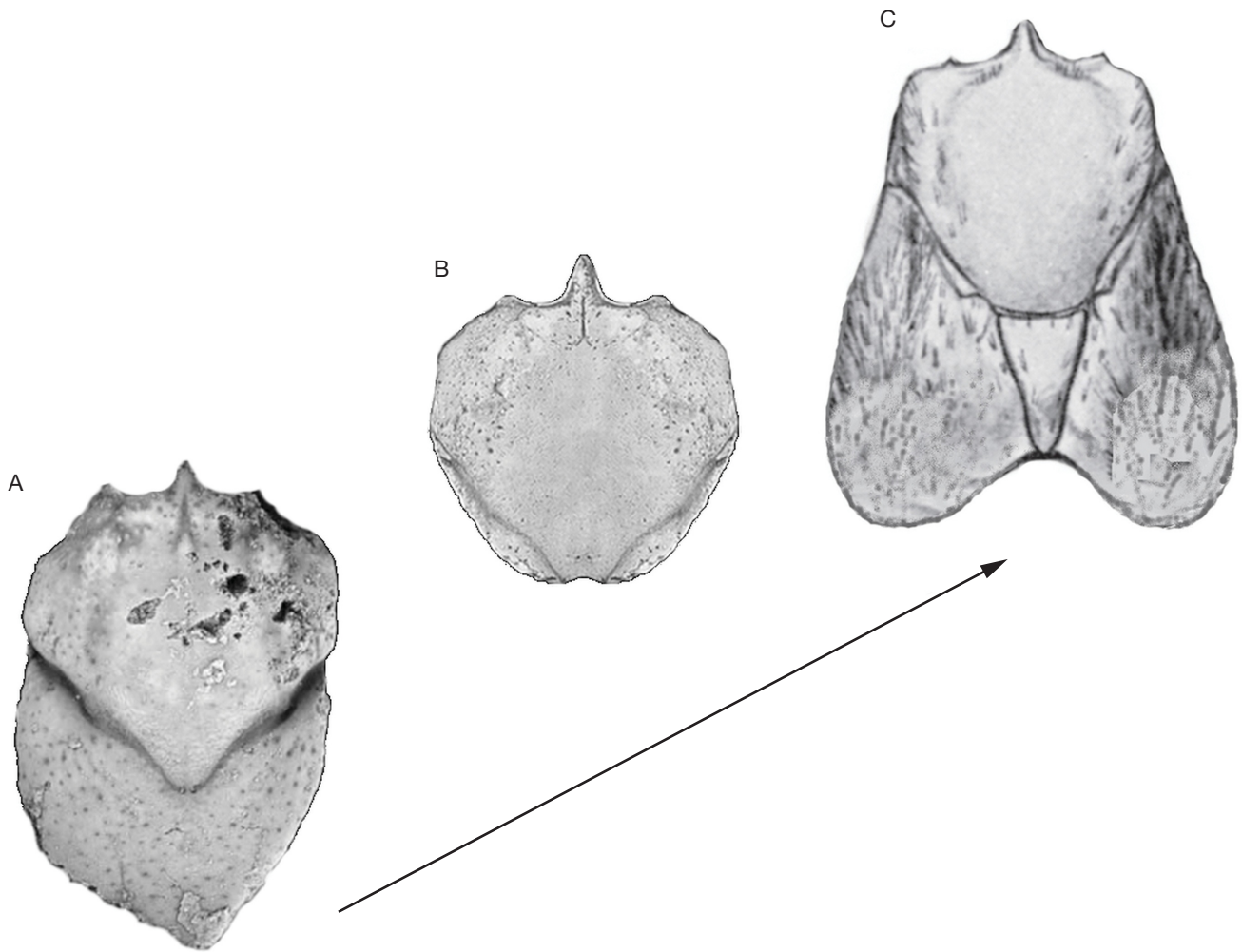


FIG. 11. — Paguropsids (Paguropsidae n. fam) through time, from the Oxfordian *Eopaguropsis* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012 (A), via the Tithonian *Eopaguropsis* (B) to extant *Paguropsis* Lemaitre, Rahayu & Komai, 2018 (C).

of this genus amongst the Paguroidea, the taxonomy and morphology of *Paguropsis typica* have not been studied in any detail that would meet the requirements of modern paguroid studies (Lemaitre *et al.* 2018). Lemaitre *et al.* (2018) noted that *Paguropsis* was not monotypic any longer, and that in addition to *P. typica*, there was an additional genus and six species. The striking symmetry of the carapace, pereopods (including chelipeds), uropods and telson, are unique amongst the so-called “asymmetrically handed” paguroids. In illustrations provided by Lemaitre *et al.* (2018: figs 2a-d and 18d, in particular), important, yet hitherto unobserved and/or unrecorded paguroid carapace features are shown for *Paguropsis* and *Paguropsina*. These features are: deep slits along the postfrontal ridges centrally posterior to the orbital cavity and centrally directed incisions near the cervical groove between the posterior margin and branchial area in the central part of the narrow lateral carapace lobe. These features are also seen in an Eocene paguroid from Italy (Beschin *et al.* 2021). A decalcified longitudinal fissure on the ventral face of the coxae of the chelipeds occurs in all species of *Paguropsis* and *Paguropsina*. A similar, and presumably homologous, fissure

on cheliped coxae has also been documented in species of *Paguristes* (Lemaitre *et al.* 2018). Alcock (1905) had already indicated that *Paguropsis* was closely related to *Paguristes*. Species of *Paguropsis* and *Paguropsina* are all symbionts of acontiate anemones (Actiniaria) (Lemaitre *et al.* 2018). This type of association and habitat can potentially be postulated for Mesozoic counterparts (*Eopaguropsis* spp.) as well.

Family PAGUROPSIDAE n. fam.

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TYPE GENUS. — *Paguropsis* Henderson, 1888.

OTHER GENERA INCLUDED. — *Eopaguropsis* Fraaije, Krzemiński, Van Bakel, Krzemińska & Jagt, 2012 and *Paguropsina* Lemaitre, Rahayu & Komai, 2018 (Fig. 11).

ETYMOLOGY. — The name is derived from the type genus.

DIAGNOSIS. — Prominent subtriangular rostrum, considerably exceeding lateral projections. Cervical and branchial grooves subparallel,

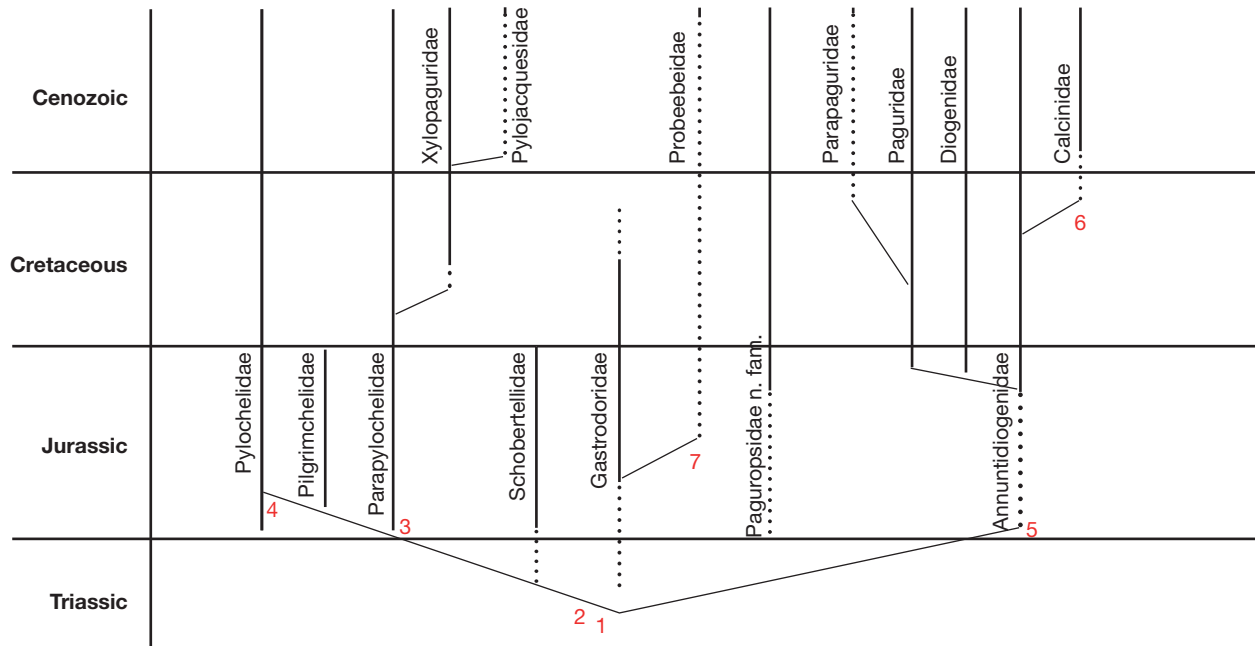


FIG. 12. — Intuitive phylogenetic tree based on carapace morphologies as outlined in the present study and on data from McLaughlin *et al.* (2007) and Fraaije *et al.* (2019). Important synapomorphies include the following: 1, cylindrical carapace; 2, cervical and branchial grooves widely separated; 3, arrow-shaped gastric region; 4, cervical groove not extending to lateral border; 5, intragastric grooves; 6, Y-linea; 7, spinose posterolateral borders.

encompassing small branchial regions (= lateral lobes) or forming broad, sinuous groove. Shield well calcified, subtriangular or subrectangular; dorsal surface slightly vaulted with incomplete midline crest; well-delineated massetic region covered with numerous setal pits; posterior carapace less calcified, delineated cardiac region; uropods and telson symmetrical. Chelipeds subequal, similar in armature and setation.

PHYLOGENY OF THE PAGUROIDEA BASED ON CARAPACE MORPHOLOGY

Based on the data presented above and the stratigraphical ranges of extinct paguroid taxa based on carapaces, a phylogeny of all marine paguroids is here proposed (Fig. 12).

Overall, it can be concluded that branchial condensation within the Paguroidea appeared early in the Jurassic; it has also been recognised (and used for taxonomic purposes) in a wide array of Mesozoic brachyurans (Van Bakel *et al.* comm. pers.). Recognition and documentation of this phenomenon facilitate our understanding of paguroid carapace delineation. Together with other carapace characters, cheliped size and trends through time, as outlined above, the fossil data have contributed to the family tree of marine hermit crabs presented here. The occurrence of paired isochelous chelae and symmetrical calcified tergites in extinct paguroids (Fraaije *et al.* 2012d, 2013c, 2014b) provides strong support for the symmetrical ancestry of the Paguroidea.

Major Mesozoic evolutionary and radiation events amongst marine phyto- and zooplanktonic microbiota led, both directly and indirectly, to a rise of new ecological niches and, concomitantly, development of various marine benthic and nektonic groups (Fraaije *et al.* 2018). Linked to the occupation of these

novel niches through time, shifts in carapace and cheliped morphologies occurred. A better-adapted metabolism and changes of food source also had an impact on gill structure and internal musculature and consequently led to internal rearrangement (e.g. Van Bakel *et al.* 2012). Additional material and more in-depth studies are needed to document the increased diversity in morphology, physiology and behaviour within the Paguroidea during deep time.

Acknowledgements

Our late colleague Patsy McLaughlin opened our eyes when, around 2007, we embarked on our studies of extinct hermit crabs, by hinting at the close relationships of our Late Jurassic material with the genera *Paguropsis* and *Tylaspis* and members of the family Pylochelidae; her assistance was instrumental in producing our 2008 paper. Dr Charles Fransen (Naturalis Biodiversity Center, Leiden, the Netherlands) supplied several items of literature for which we are grateful. G. G. and X. V. are appreciative to the municipality of Chasseneuil-du-Poitou (Mr C. Eidelstein) and to Mrs E. Blandin, P. Ferchaud and J. M. Terrason for field assistance. Their work is supported in part by the Lisea Fondation Biodiversité (research grant 97 to Palaios association with the project “Past of Biodiversity from Vienne”). Hemke Dekkers, Shjalina Lentink, Mila van Loon, Lars Rongen, all students from SintLucas Vakschool voor creatief talent, Eindhoven, assisted in finishing all figures. Finally, comments made by Rok Gašparič (Kamnik/Ljubljana, Slovenia) and an anonymous reviewer on an earlier version of the typescript are much appreciated.

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