

Barremian decapod crustaceans from Serre de Bleyton (Drôme, SE France)

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(With 10 figures)

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Abstract

Based on mostly small-sized isolated cheliped fingers, a new decapod crustacean assemblage is described from the Barremian of Serre de Bleyton (Drôme, SE France). The assemblage is composed mostly of representatives of the crab family Dynomenidae. In addition, remains of astacidean lobsters, axiidean shrimps, paguroid hermit crabs and brachyurous crabs of the families Necrocarcinidae and ?Cenomanocarcinidae occur in low numbers. *Graptocarcinus moosleitneri* (Dynomenidae) and ?*Paranecrocarcinus schloegli* (Necrocarcinidae) are introduced as new species. They both exhibit presence of multi-setal pores on dactyli that are interpreted as parts of a sieving mechanism used in feeding. The stratigraphic range of *Graptocarcinus* is extended herein to the Barremian.

Keywords: Decapoda, Astacidea, Axiidea, Anomura, Brachyura, Barremian, France

Introduction

Isolated decapod crustacean claws are virtually ubiquitous component of the Cenozoic benthic marine associations reported from all over the world. Due to strong calcification, especially claws of brachyurous crabs (Decapoda, Brachyura) have a large fossilization potential. However, as the evolutionary origins of the Brachyura can be traced as deep in the past as the Early and Middle Jurassic (SCHWEITZER & FELDMANN 2010), one would expect to find isolated cheliped fingers of brachyurans also in Mesozoic rocks. Indeed, during the Cretaceous brachyuran benthic associations appear to be well established (KLOMPMAKER *et al.* 2013) and isolated crab claws were sporadically reported from

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various Lower and Upper Cretaceous localities (e.g., BELL 1863; FORIR 1887; FRITSCH & KAFKA 1887; RATHBUN 1935; FRAAYE & COLLINS 1987; COLLINS & DIENI 1995; JAGT *et al.* 2010). However, only occasionally an entire assemblage including the decapod crustacean mesofauna has been described (for overview of selected Cretaceous decapod assemblages a reference is made to KLOMPMAKER 2013), as for instance that of Albian Glen Rose Limestone, Texas, published by BISHOP (1983). In general, chelae are of limited taxonomic utility and therefore they were largely neglected in recent re-evaluations of Cretaceous crab assemblages (e.g., SCHWEITZER *et al.* 2007, 2012; SCHWEITZER & FELDMANN 2011; KLOMPMAKER *et al.* 2011; KARASAWA *et al.* 2011, 2014). However, omission of isolated cheliped data causes an even more strongly biased fossil record; thus, making it difficult to interpret the published faunas in a wider context (e.g. comparison across lithostratigraphic units or selected time horizons) ignoring the chelae. Some efforts, however, have been made, and lately JAGT *et al.* (2010) provided a review of isolated claws of dynomenid crabs from Cretaceous strata and discussed the taxonomic issue of naming them.

This contribution focuses on the decapod association from the Barremian of Serre de Bleyton, France (KROH *et al.* 2010 and references therein). We tried to match chelipeds with taxa based on carapaces and so made an effort to extract as much information as possible. For the sake of better taxonomic identification we used a scanning electron microscope (SEM) to document the range of finger morphologies. It may be stressed that this method has rarely been adopted by researchers working with fossil decapods; in fact, so far the SEM has been used in greater extent only for examination of cuticle ultrastructure (FELDMANN & GAŹDZICKI 1998; WAUGH *et al.* 2006, 2009; MUTEL *et al.* 2008). Here we demonstrate that SEM photography can help to identify tiny (2–5 mm) cheliped elements in decapod assemblages and to evaluate the studied faunas more accurately.

Although erecting new taxa based on isolated brachyurous chelae is not common (JAGT *et al.* 2010), in our case new names are proposed for suitably well preserved material showing characters that allow distinction from other members of respective groups. Any undiagnostic material (*i.e.* most of the specimens) was kept in open nomenclature.

It is good to note that taxonomy of fossil decapod crustaceans is based on different body parts depending on the higher taxon studied. In brachyurans, for instance, features of dorsal carapace often are of prime interest (e.g., SCHWEITZER *et al.* 2007, 2012; SCHWEITZER & FELDMANN 2009; KLOMPMAKER *et al.* 2011) whereas it is a common practice to erect new callianassid or paguroid taxa based on chelipeds alone (e.g., BISHOP 1983; CRÔNIER & COURVILLE 2004; BRETON 2010, 2011; FRAAIJE *et al.* 2011). In paguroid hermit crabs, recently new genera and species were erected based on dorsal carapaces (VAN BAKEL *et al.* 2008; FRAAIJE *et al.* 2012a, b, 2013b, 2014) and the isolated 6th abdominal tergites (FRAAIJE *et al.* 2012c, 2013a). Regarding formal naming of isolated abdominal tergites, although claimed to represent parataxa (FRAAIJE *et al.* 2012c, 2013a), their newly proposed generic names are included in a Linnean system and are fully available.

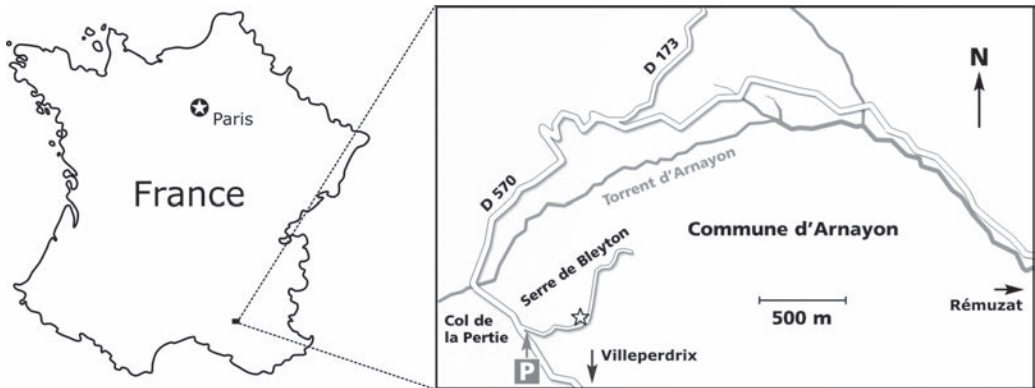


Fig. 1. Outline map of France indicating the position of the Serre de Bleyton area in the Département of Drôme, SE France (left) and detailed map of the study area (right). The position of the outcrops is marked by an asterisk (after KROH *et al.* 2010).

Study Area

The outcrops delivering the material studied here are located along a gravel road on the southern side of the Serre de Bleyton ridge in the Commune d'Aranyon (Drôme provençale), east of Col de Perty. The area lies about 20 km to the north-east of Nyons and 2 km south-east of Arnyon (Fig. 1). The strata exposed are of Barremian age and comprise light-grey intercalation of marls and turbiditic limestone beds of the pelagic “coulées boueuses” deposits (ARNAUD 2005). These represent channel and fan-structures terminating in the Vocontian Through (ADATTE *et al.* 2005; ARNAUD 2005). The site was chosen due to its high abundance of micro- and meso-scale bioclasts in several of the turbiditic beds, which is in contrast to other sites exposing the “coulées boueuses”. While the fossils are often difficult to extract from the sediment in most of the section, two beds were strongly affected by natural weathering, which enabled bulk sampling (Locality 1: N 44°28'55", E 05°18'00"; Locality 2: N 44°28'54", E 05°17'58"). For more detail on the study area see KROH *et al.* (2010).

Apart from the decapod material studied here these beds have delivered a wide range of other taxa, including dasycladales (BUCUR 2011), foraminifera, corals (LÖSER 2010), cephalopods [ammonites (LUKENEDER 2010), belemnites (JANSSEN 2010), and rhycolites (RIEGRAF & MOOSLEITNER 2010)], bivalves, gastropods (GRÜNDEL & KOLLMANN 2013), polychaetes (JÄGER 2011), brachiopods (GASPARD 2011), bryozoans (TAYLOR 2010), echinoderms [asteroids (VILLIER 2010), echinoids, crinoids (JÄGER 2010), ophiuroids (THUY & KROH 2011)], and ostracods (BABINOT & COLIN 2011). While some of these groups are exceptionally rich (*e.g.* ostracods and gastropods) there are few age-indicative forms. Cephalopod evidence (JANSSEN 2010; LUKENEDER 2010) indicates a Barremian, possibly Late Barremian age of fauna, which is supported by ostracod data (BABINOT & COLIN 2011).

Due to the turbiditic nature of the beds the assemblage contains a mixture of elements from a variety of habitats along the slope of the Vocontian Trough, ranging from terrestrial deposits (one land snail taxon), shallow tidal and subtidal habitats to outer platform deposits. In addition to being a mixture from different habitats the assemblage is also strongly size-sorted and thus represents a highly biased selection of taxa originally present in the area.

Material and methods

The studied material consists of approximately 100 isolated fragments of claws and dorsal carapaces. They were collected by Gero MOOSLEITNER (Salzburg) by surface picking on-site and from bulk-samples processed by wet-sieving.

Usually distal parts of dactyli and fixed fingers are preserved because the calcification is strongest there (WAUGH *et al.* 2006; MUTEL *et al.* 2008). Several entire dactyli and fragments attributed to dorsal carapaces were found as well. The preservation of cuticle in claws is variable, presumably depending on the length of transport of isolated fingers prior to deposition. In a few cases the cuticle is relatively well preserved so the details of cuticular surface can be observed.

Specimens were cleaned in an ultrasonic bath and with the tenside Rewoquat (LIERL 1992). Selected specimens were coated with gold and photographed on a JEOL JSM 6610-LV system under high vacuum conditions. All specimens are deposited in the collection of the Department of Geology & Palaeontology at the Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria under the repository numbers NHMW 2014/0289/0001 to .../0049.

The higher classification used herein is a synthesis of works by KARASAWA *et al.* (2011, 2014), VAN BAKEL *et al.* (2012b), DWORSCHAK *et al.* (2012) and GUINOT *et al.* (2013).

Institutional abbreviations:

NHMW – Naturhistorisches Museum Wien, Austria

Systematic Palaeontology

Order Decapoda LATREILLE, 1802

Infraorder Astacidea LATREILLE, 1802

Discussion: Lobsters belong to the best known Mesozoic decapod remains (WAHLE *et al.* 2012; KARASAWA *et al.* 2013), although there is disagreement in classification of certain groups. Erymidae, for example, in some recent classifications are treated together with glypheids in the infraorder Glypheidea (DE GRAVE *et al.* 2009; SCHWEITZER *et al.*

2010; WAHLE *et al.* 2012; KARASAWA *et al.* 2013). Other papers, in contrast, treat them as astacideans (*e.g.* GLAESSNER 1969; CRÔNIER & COURVILLE 2004; GARASSINO & SCHWEIGERT 2006; SCHWEIGERT 2013). Most recent cladistic analysis by CHARBONNIER *et al.* (2014) places erymids outside the infraorder Glypheidea. Both infraorders, Astacidea and Glypheidea, can exhibit similar morphology in chelae, especially when dealing with incomplete material. For the sake of simplicity we treat the studied remains as astacideans.

Astacidea indet.

(Figs 2.1, 2.5–2.7)

Material examined: Isolated fragmentary dactyli (NHMW 2014/0289/0001, NHMW 2014/0289/0005 to .../0007). NHMW 2014/0289/0001 and .../0005 come from locality 1, the other specimens come from locality 2.

Description: The isolated finger fragments are long and narrow. Cross section is round or suboval. The occlusal surface forms a continuous ridge (presumably armed with teeth during life) or is finely serrated. The proximal part (where preserved) is distinctly higher than the rest of the finger which attains more-or-less the same height along its entire preserved length. No distinctive ornamentation is present in the material.

Discussion: The material is too fragmentary for reliable identification; however, it clearly shows that the fingers were long and slender. Their appearance is consistent with typical lobster claws; indeed, similar material has been reported from the Cretaceous of Japan (KARASAWA *et al.* 2008a: fig. 2.10) and New Jersey, USA (ROBERTS 1962: pl. 82, fig. 8). The specimens show also some similarities to crab chelae of the families Cenomanocarcinidae and Etyidae (Fig. 2.1). In the Cenomanocarcinidae the fingers are elongate and homodontous. The studied specimen (Fig. 2.5) is too short to make the comparison reliable. Members of the Etyidae have long and slender chelae, as far as can be deduced from the scarce published material (WRIGHT & COLLINS 1972: pl. 21, fig. 3; GUINOT & TAVARES 2001: fig. 4; FELDMANN *et al.* 2013: fig. 3). We consider the knowledge of the general morphology of the chelipeds in Etyidae as insufficient and the attribution of our material to this group as speculative. To conclude, the identification of the studied material as fingers of astacidean lobsters seems most likely.

Infraorder Axiidea DE SAINT LAURENT, 1979

Discussion: Following the arguments presented by POORE *et al.* (2014) we here use separate infraordinal taxa (Axiidea and Gebiidea) instead of Thalassinidea. Here we follow the concept of Axiidea as originally proposed by DE SAINT LAURENT (1979) and further supported by phylogenetic studies (see DWORSCHAK *et al.* 2012 for a review).

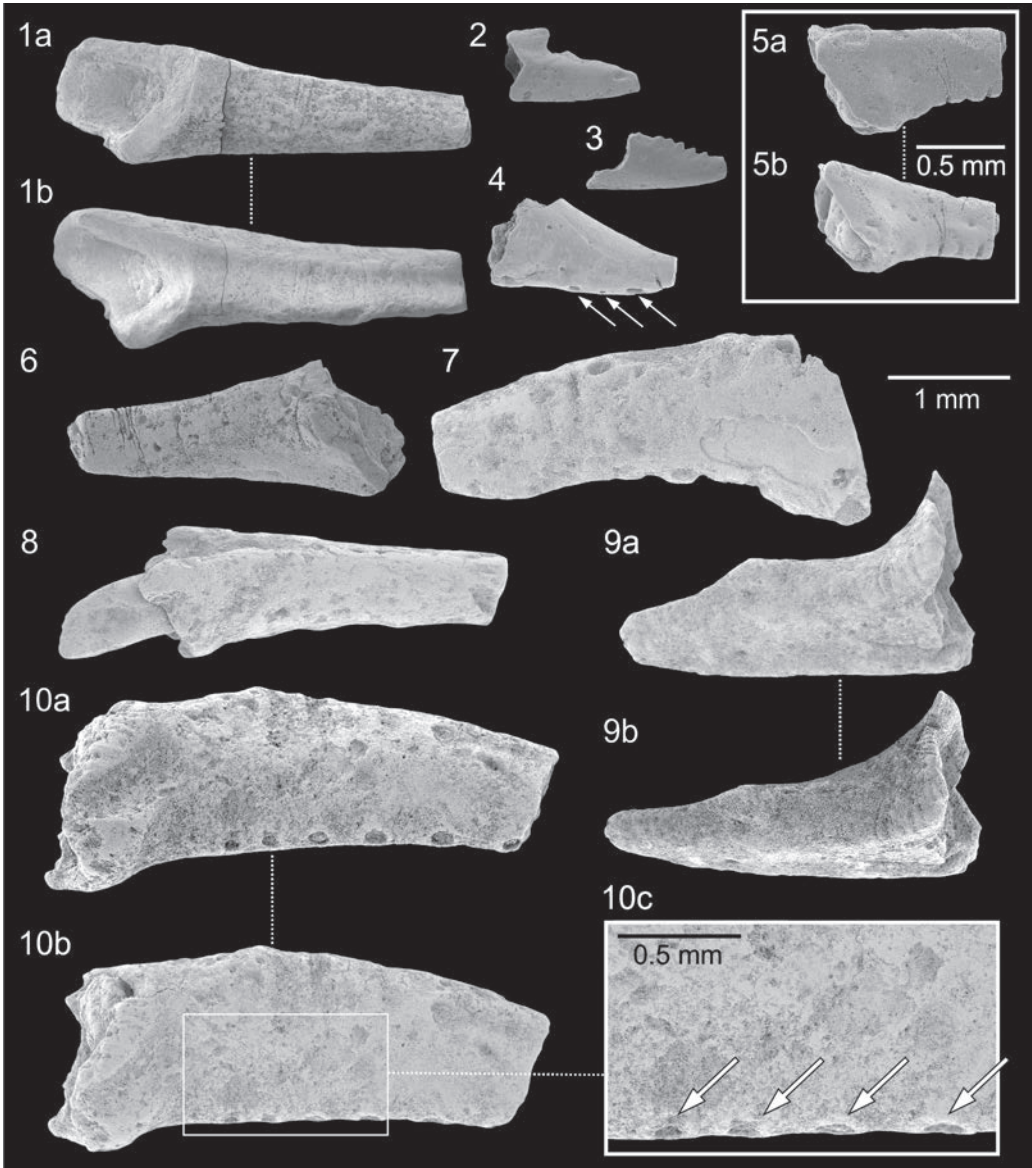


Fig. 2. Decapod crustaceans of Serre de Bleyton: isolated fingers of Astacidea and Axiidea. **1:** Astacidea indet., NHMW 2014/0289/0001, two views from different angles. **2:** Axiidea indet., morphotype 2, NHMW 2014/0289/0002. **3:** Axiidea indet., morphotype 3, NHMW 2014/0289/0003. **4:** Axiidea indet., morphotype 4, NHMW 2014/0289/0004, note setal pores (indicated with arrows). **5:** Astacidea indet., NHMW 2014/0289/0005, two views from different angles. **6:** Astacidea indet., NHMW 2014/0289/0006. **7:** Astacidea indet., NHMW 2014/0289/0007. **8:** ?*Ctenocheles* sp., NHMW 2014/0289/0008. **9:** Axiidea indet., morphotype 1, NHMW 2014/0289/0009, two views from different angles. **10:** ?*Ctenocheles* sp., NHMW 2014/0289/0010, 10a and 10b represent two views from different angles; note scars of broken teeth in 10c (indicated with arrows). All specimens (except 5 and 10c) are to scale.

Family Ctenochelidae MANNING & FELDER, 1991

Genus *Ctenocheles* KISHINOUE, 1926

Discussion: *Ctenocheles* KISHINOUE, 1926 is a ghost shrimp genus with a relatively rich fossil record (HYŽNÝ & DULAI 2014: table 2). Although in the fossil state known mostly as chelipeds (HYŽNÝ *et al.* 2014; HYŽNÝ & DULAI 2014), their morphology is rather distinctive (bulbous propodus with long and slender pectinate claws with strongly hooked tips) and allows virtually immediate identification. It has to be stressed, however, that pectinate claws evolved in several independent lineages (TSHUDY & SORHANNUS 2000) and therefore we assign our material to *Ctenocheles* only tentatively. Misinterpretation of *Ctenocheles* claws for some other genus, such as the astacidean *Oncopareia* BOSQUET, 1854, has recently been discussed by HYŽNÝ *et al.* (2014).

?*Ctenocheles* sp.

(Figs 2.8, 2.10)

Material examined: Two fragmentary dactyli (NHMW 2014/0289/0008, NHMW 2014/0289/0010) from locality 2.

Description: The dactylus is long and slender with widened proximal part. The occlusal margin bears scars of broken teeth, spaced from each other in more-or-less regular intervals. Cross section of the teeth is circular.

Discussion: Dactylus NHMW 2014/0289/0008 (Fig. 2.8) shows a widened proximal part. Such widening, forked in the view from above, is quite typical for *Ctenocheles* (HYŽNÝ *et al.* 2014: fig. 5E). Another specimen NHMW 2014/0289/0010 (Fig. 2.10) exhibits an occlusal surface with scars of broken teeth. *Ctenocheles* characteristically possesses acicular teeth on both cheliped fingers (HYŽNÝ *et al.* 2014; HYŽNÝ & DULAI 2014; and references therein), which is consistent with the studied specimen. However, pectinate claws are present also in other taxa (TSHUDY & SORHANNUS 2000). The oldest fossil record of the genus has so far been *C. madagascariensis* SECRÉTAN, 1964 from Albian–Maastrichtian of Madagascar (SECRÉTAN 1964; CHARBONNIER *et al.* 2012). Thus, if the taxonomic attribution of the present specimens can be confirmed, it would constitute the oldest occurrence of the genus.

Axiidea indet.

(Figs 2.2–2.4, 2.9)

Material examined: Isolated fixed fingers of fragmentary nature (NHMW 2014/0289/0002 to .../0004, 2014/0289/0009) from locality 2.

Description: Axiidea indet., morphotype 1 (NHMW 2014/0289/0009): The fixed finger is slender and flattened laterally. It slightly converges distally and is connected to the manus laterally (when viewing from distal end). The cross section is triangular and the occlusal margin is armed with a blunt tooth.

Axiidea indet., morphotype 2 (NHMW 2014/0289/0002): The fixed finger is slender, slightly converging distally. Close to the tip there is a setal pore. Occlusal margin is armed with a sharp tooth directed distally and accompanied by a smaller one (positioned distally of the large one).

Axiidea indet., morphotype 3 (NHMW 2014/0289/0003): The fixed finger is slender, slightly converging distally. Occlusal margin is armed with a saw-like denticulation along the whole length of the studied fragment.

Axiidea indet., morphotype 4 (NHMW 2014/0289/0004): The fixed finger is robust, triangular in shape and converging distally. Occlusal margin has no teeth. Lateral surface and especially lower margin of the fixed finger show several setal pores arranged in a row.

Discussion: Although it is possible that the different morphotypes belong to several separate taxa, they are discussed together here due to their common characteristics. The fixed fingers are rather short (as far as it can be deduced from their fragmentary nature) and lack spatulate tips. The occlusal margin is often armed with one or several teeth. Although the combination of these characteristics can be found in numerous decapod taxa, we attribute them to axiidean shrimps. The cross section of the fingers points to laterally compressed chelipeds which are typical for axiideans. The armature of fixed fingers suggests they belong to adult or subadult specimens (juveniles usually have less pronounced armature, see *e.g.*, DWORSCHAK 2008: p. 82; HYŽNÝ & KARASAWA 2012: p. 62) and as such they fit the minute size of many axiidean shrimps, especially members of the families Axiidae and Callianassidae. Their chelae often possess one or more teeth (especially Axiidae) (*e.g.*, NGOC-HO 2003; POORE & COLLINS 2009; see DWORSCHAK *et al.* 2012 for a review) and normally numerous setae occur on the tips of chelae (*e.g.*, POORE & COLLINS 2009). Setal pores can be seen in the specimens retaining the cuticle (Fig. 2.4). Setal pores arranged in a row and positioned on the lower margin of the fixed finger as shown in morphotype 4 are typical for many axiideans, *e.g.* Callianassidae (BIFFAR 1971; NGOC-HO 2003; DWORSCHAK *et al.* 2012).

Many axiideans exhibit heterochely (DWORSCHAK *et al.* 2012) and often the armature of fingers differs significantly between the chelae of the same individual, thus, it is possible that some of the morphotypes described above belong to a single taxon. Due to the fragmentary nature of the material a more refined identification is impossible.

Infraorder Anomura MACLEAY, 1838

Superfamily Paguroidea LATREILLE, 1802

Discussion: Several major paguroid (hermit crab) lineages were already established in the Early Cretaceous (VAN BAKEL *et al.* 2008; FRAAIJE *et al.* 2012a, b, 2013b, 2014). Hermit crabs possess well calcified chelae, and thus they have relatively good fossilization potential. The attribution of the Serre de Bleyton material to paguroids is based on

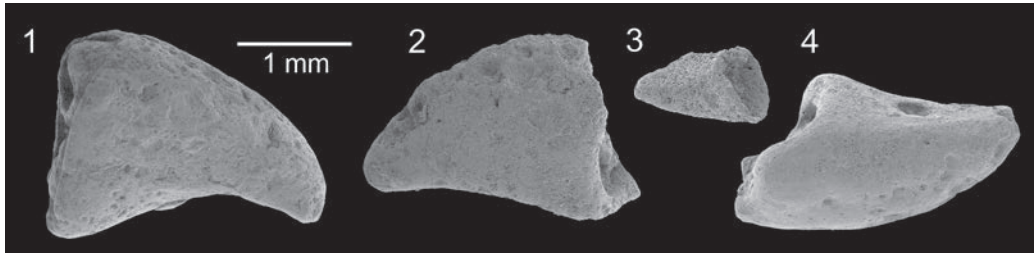


Fig. 3. Decapod crustaceans of Serre de Bleyton: isolated fingers of Paguroidea. 1: Paguroidea indet., morphotype 1, NHMW 2014/0289/0011. 2: Paguroidea indet., morphotype 1, NHMW 2014/0289/0012. 3: Paguroidea indet., morphotype 2, NHMW 2014/0289/0013. 4: Paguroidea indet., morphotype 2, NHMW 2014/0289/0014. All specimens are to scale.

rather short and stout finger tips typical for some hermit crabs and/or granular ornamentation which often is present in chelae of these taxa (McLAUGHLIN 2003: fig. 6).

Paguroidea indet.

(Figs 3.1–3.4, 4.1–4.6)

Material examined: Isolated dactyli and fixed fingers (NHMW 2014/0289/0011 to .../0020) from locality 2.

Description: Paguroidea indet., morphotype 1 (NHMW 2014/0289/0011, .../0012): Dactylus is short and stout, only slightly longer than high. Upper margin is arched; the tip is blunt and slightly hooked. External surface, including tip, is covered with setal pores. No apparent ornamentation is present.

Paguroidea indet., morphotype 2 (NHMW 2014/0289/0013, .../0014, NHMW 2014/0289/0018): Fixed finger (or dactylus) is short and stout, longer than high. Occlusal margin forms a cutting edge; it may possess a small tooth. The tip of the finger is blunt. External surface is smooth.

Paguroidea indet., morphotype 3 (NHMW 2014/0289/0015 to .../0017): Dactylus is triangular in outline, converging distally. Cross section at articulation with propodus is semiquadrant. Upper margin may have several tubercles proximally. Occlusal margin forms a continuous keel and is armed with a blunt tooth proximally. The tip is slightly hooked.

Paguroidea indet., morphotype 4 (NHMW 2014/0289/0019): The fixed finger is short and stout. Occlusal margin forms a cutting edge, becoming convex just at the tip. The tip of the finger is sharp and pointed forward.

Paguroidea indet., morphotype 5 (NHMW 2014/0289/0020): Dactylus is distinctly longer than high, upper margin is vaulted. Occlusal margin bears a blunt tooth proximally. External surface is covered with evenly spaced tubercles. The tip of the finger is blunt.

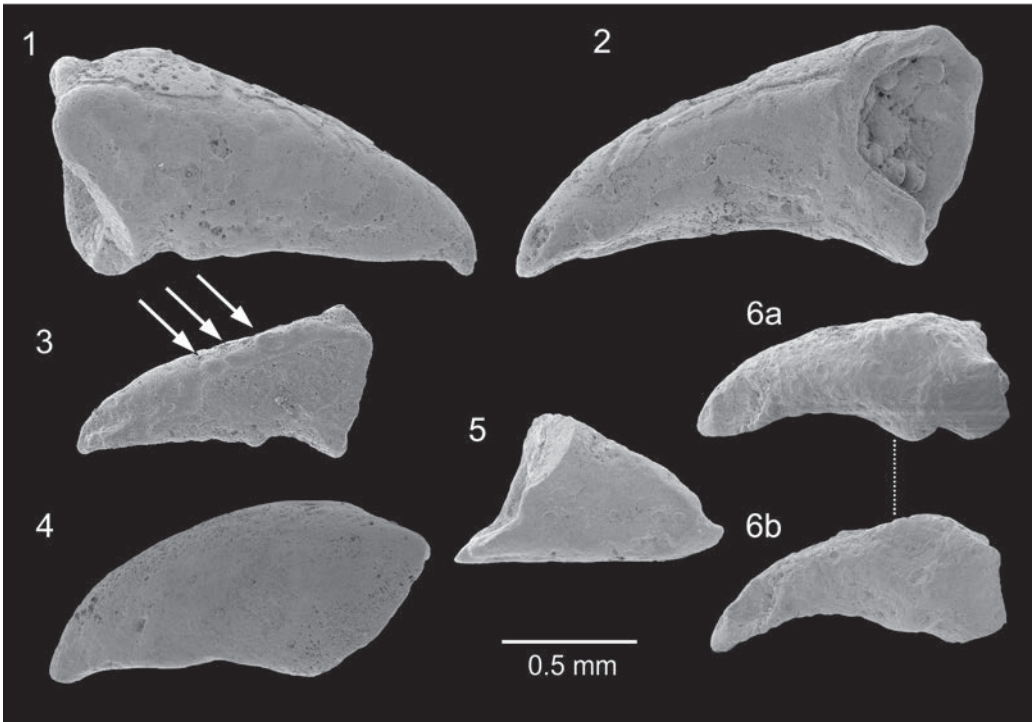


Fig. 4. Decapod crustaceans of Serre de Bleyton: isolated fingers of Paguroidea. **1:** Paguroidea indet., morphotype 3, NHMW 2014/0289/0015. **2:** Paguroidea indet., morphotype 3, NHMW 2014/0289/0016. **3:** Paguroidea indet., morphotype 3, NHMW 2014/0289/0017, note tubercles on the upper margin (indicated with arrows). **4:** Paguroidea indet., morphotype 2, NHMW 2014/0289/0018. **5:** Paguroidea indet., morphotype 4, NHMW 2014/0289/0019. **6:** Paguroidea indet., morphotype 5, NHMW 2014/0289/0020, two views from different angles; note tuberculation on the entire surface. All specimens are to scale.

Discussion: The different morphotypes apparently belong to several separate taxa, although some of them may represent fixed finger and dactyli of the same species (*e.g.* morphotypes 1, 2, 4). The fingers are rather short and stout or ornamented with tubercles in a manner differing from all other decapod morphotypes from Serre de Bleyton. Morphotype 4 (NHMW 2014/0289/0019; Fig. 4.5) is somewhat similar to *Pylojacquesia* MCLAUGHLIN & LEMAITRE, 2001 (family Pylojacquesidae; see MCLAUGHLIN & LEMAITRE 2001: fig. 4) or *Bathypaguropsis* MCLAUGHLIN, 1994 (family Paguridae; see MCLAUGHLIN 1994: fig. 3A). The dactylus of morphotype 2 (NHMW 2014/0289/0018; Fig. 4.4) seems to fit these taxa as well.

Infraorder Brachyura LATREILLE, 1802

Discussion: Numerous brachyuran families were already present in the Early Cretaceous; many of them are known only from dorsal carapaces and are extinct today [*e.g.*,

Diaulacidae, Etyidae, Goniopromitidae; see KARASAWA *et al.* (2011) for stratigraphic ranges and other details]. Thus, it is fairly possible that some of the material studied herein would be attributable to some of these extinct families if some data on chelae of these taxa were available. Therefore we tried to compare our material with either morphotypes present in extant taxa (Dynomenidae) or those known for extinct families (Cenomanocarcinidae, Necrocarcinidae).

Section Podotremata GUINOT, 1977

Subsection Dynomeniformia GUINOT, TAVARES & CASTRO, 2013

Superfamily Dromioidea DE HAAN, 1833

Family Dynomenidae ORTMANN, 1892

Discussion: JAGT *et al.* (2010) noted on the common association of “necrocarcinid” claws with dynomenid carapaces. The isolated finger material from Serre de Bleyton cannot be matched with any carapace fragments. Nevertheless after careful comparison with published material (see below) we classified it within taxa based on carapaces, and thus, avoid using parataxonomy.

Subfamily Graptocarcininae VAN BAKEL, GUINOT, CORRAL & ARTAL, 2012

Discussion: For members of the subfamily equal chelipeds with tumid propodus palm and short, stout, spoon-tipped fingers are typical (VAN BAKEL *et al.* 2012b).

Genus *Graptocarcinus* ROEMER, 1887

Discussion: According to JAGT *et al.* (2010), claws of the genus may be differentiated by the presence of a distinct articulating bulge. Moreover, *Graptocarcinus* (but also other closely related dynomenids) lack oval depression for setae in both fingers (JAGT *et al.* 2010; VAN BAKEL *et al.* 2012b). The carapace of this genus is characterized by distinctive uniform tuberculation (STENZEL 1944; COLLINS & DIENI 1995; FRAAYE 1996; VAN BAKEL *et al.* 2012b).

Apart from *Graptocarcinus* there is a second graptocarcinine taxon known from the Early Cretaceous, namely *Cyclothyreus* REMEŠ, 1895. Of that genus, however, no chelipeds are known so far and thus it is difficult to judge if the Serre de Bleyton material may or may not belong to this genus instead. Pending the discovery of chelipeds attached to *Cyclothyreus* carapaces the most parsimonious solution at present is to attribute the studied material to *Graptocarcinus* for which claws very similar to the studied ones have been recorded from the Cenomanian of France (JAGT *et al.* 2010) and Santonian to Maastrichtian of Spain (JAGT *et al.* 2010; VAN BAKEL *et al.* 2012b).

Graptocarcinus has so far been documented from the Aptian to Maastrichtian (ROEMER 1887; STENZEL 1944; COLLINS & DIENI 1995; FRAAYE 1996; VAN BAKEL *et al.* 2012b). The occurrence reported herein extends its stratigraphic range further back to the Barremian.

***Graptocarcinus moosleitneri* nov. spec.**

(Figs 5.1–5.2)

Diagnosis: Dactylus is short and stout, the tip is spoon-shaped. The upper margin bears three tubercles/spines positioned mesially. The occlusal margin has one blunt tooth positioned at the midpoint. Lateral surface and the tip of the finger are covered with circular depressions with multiple setal pores.

Etymology: Dedicated to Gero MOOSLEITNER who donated the studied material.

Holotype: Isolated left dactylus (NHMW 2014/0289/0021) with preserved cuticle from locality 2.

Paratype: Isolated left dactylus (NHMW 2014/0289/0022) from locality 2.

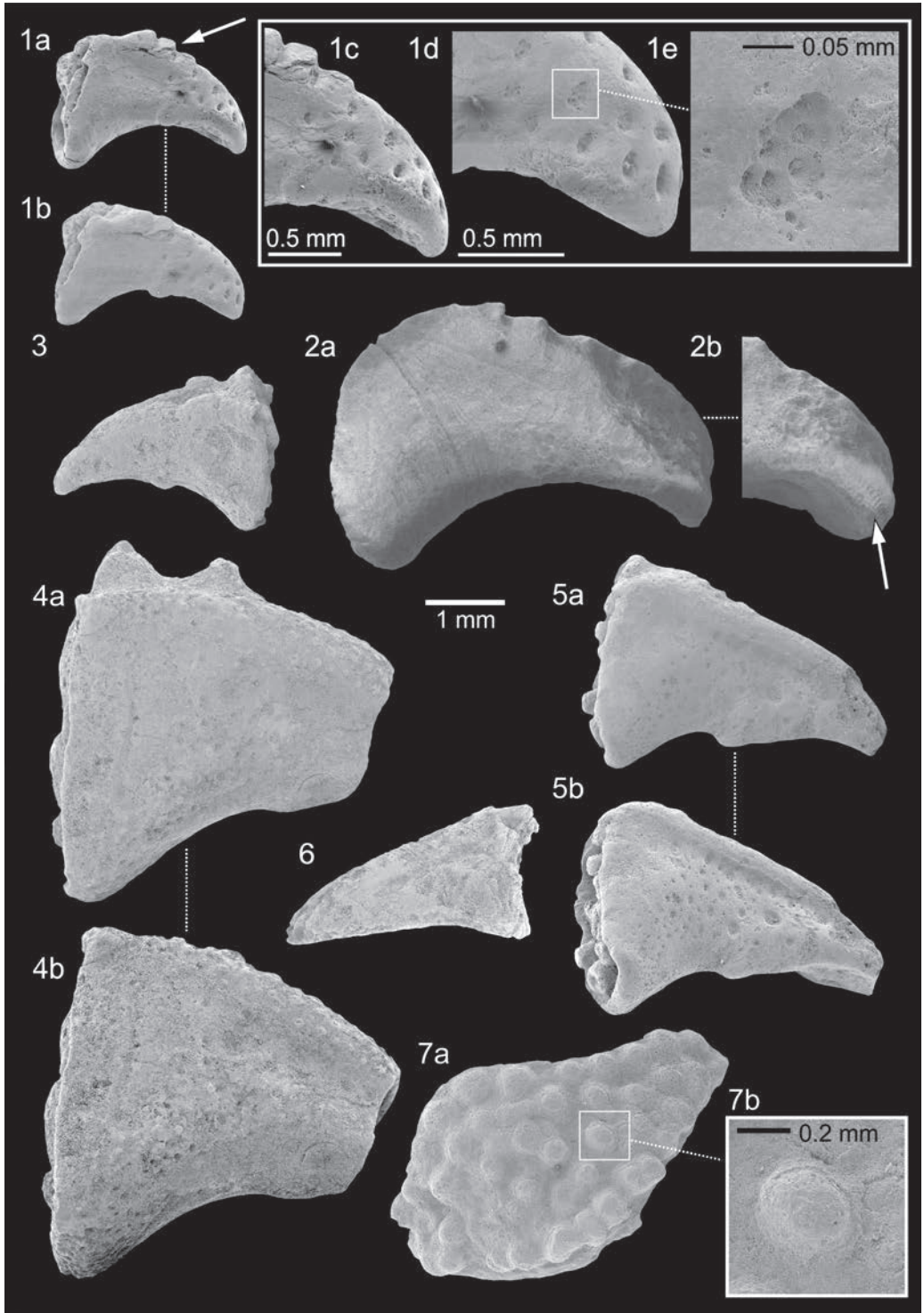
Type locality: Serre de Bleyton (Drôme, SE France), locality 2.

Type stratum: “Coulées boueuses”, Lower Cretaceous, Barremian.

Description: Dactylus is short and stout. The upper margin is adorned with three flat tubercles (or blunt spines) arranged in a row and positioned mesially. Approximately at the midpoint of the occlusal margin there is a single blunt tooth positioned mesially. Lateral surface and especially the tip of the finger are covered with circular depressions with multiple setal pores. The tip of the finger is broadly spoon-shaped.

Discussion: The arrangement of setal pores is unique for the genus and was not reported before, although the chelae of the genus are known (JAGT *et al.* 2010; VAN BAKEL *et al.* 2012b). The genus *Graptocarcinus* is based mostly on carapace material, however, it is clear that there are also differences in chelae, as it can be observed from published figures of chelipeds of *Graptocarcinus bellonii* COLLINS & DIENI, 1995 from the Cenomanian of Italy (COLLINS & DIENI 1995: fig. 2), *G. texanus* ROEMER, 1887 from the Maastrichtian of Spain (JAGT *et al.* 2010: fig. 3), *G. urbasaensis* VAN BAKEL, GUINOT, CORRAL & ARTAL, 2012 from the Santonian to Maastrichtian of Spain (VAN BAKEL *et*

Fig. 5. Decapod crustaceans of Serre de Bleyton: isolated fingers (1–6) and cuticular fragment (7) of *Graptocarcinus*. **1:** *Graptocarcinus moosleitneri* nov. spec., holotype NHMW 2014/0289/0021, 1a and 1b are two views from different angles; note the tubercles on the upper margin (in 1a indicated with arrows) and setal pores arranged in oval depressions (1c–1e). **2:** *Graptocarcinus moosleitneri* nov. spec., paratype NHMW 2014/0289/0022, note dentate margin of spoon-shaped tip (in 2b indicated with arrow). **3:** *Graptocarcinus* sp. 2, NHMW 2014/0289/0023. **4:** *Graptocarcinus* sp. 2, NHMW 2014/0289/0024, two views from different angles. **5:** *Graptocarcinus* cf. *urbasaensis*, NHMW 2014/0289/0026. **6:** *Graptocarcinus* sp. 1, NHMW 2014/0289/0027. **7:** ?*Graptocarcinus* sp., NHMW 2014/0289/0028, note regularly spherical tubercles (detail in 7b). All specimens (except 1c–1e and 7b) are to scale. ►



al. 2012b: figs 2F, 3B) and *Graptocarcinus* sp. from the Cenomanian of France (JAGT *et al.* 2010: fig. 4E–H). None of these species exhibits the setal pores arrangement of *G. moosleitneri* nov. spec., thus, the erection of the new species is warranted.

***Graptocarcinus* cf. *urbasaensis* VAN BAKEL, GUINOT, CORRAL & ARTAL, 2012**
(Fig. 5.5)

2012 *Graptocarcinus urbasaensis* VAN BAKEL, GUINOT, CORRAL & ARTAL, p. 47, figs 2–3.

Material examined: Isolated right dactylus (NHMW 2014/0289/0026) from locality 2.

Description: Dactylus is triangular, short and with a furrow parallel to upper margin. Upper margin is adorned proximally with several tubercles. Surface is tuberculated, lateral sides possess numerous setal pores. Occlusal surface armed with a blunt crushing tooth located approximately at the mid-length, the tip of the finger is spooned.

Discussion: The isolated dactylus is highly similar to those of *Graptocarcinus urbasaensis* from the Santonian and Maastrichtian of Spain (VAN BAKEL *et al.* 2012b: figs 2F, 3B), however, the sample studied herein is approximately 40 mya older. Because we do not have any carapace material, the direct comparison with diagnostic characters of *G. urbasaensis* is not possible.

Graptocarcinus cf. *urbasaensis* differs from *G. moosleitneri* nov. spec. in the arrangement of setal pores, less arched upper margin of dactylus and absence of a row of three blunt tubercles or spines on the upper margin.

***Graptocarcinus* sp. 1**
(Fig. 5.6)

Material examined: Isolated dactylus (NHMW 2014/0289/0027) from locality 2.

Description: Dactylus is distinctly longer than high. Probably due to poor preservation, the finger does not have any tuberculation on its surface. The tip of the finger is spoon-shaped.

Discussion: The outline of the studied finger is very similar to the dactylus of *Graptocarcinus* sp. from Lower Cenomanian of northern France as reported by JAGT *et al.* (2010: figs 4E–H). Upper layers of cuticle are not preserved in our material, therefore no ornamentation is visible. The chela of *Graptocarcinus* sp. from the Cenomanian of France is finely tuberculated.

***Graptocarcinus* sp. 2**
(Figs 5.3–5.4)

Material examined: Isolated dactyli (NHMW 2014/0289/0023, .../0024) from locality 2.

Description: The dactylus is triangular in outline, highest proximally. Upper margin has one or two large blunt spines, triangular in outline. Occlusal margin possesses crushing tooth proximally, close to midlength. External surface is densely covered with small tubercles.

Discussion: With the spines on the upper margin of dactylus, *Graptocarcinus* sp. 2 differs from other *Graptocarcinus* chelae from Serre de Bleyton. Morphologically, it is closest to *Graptocarcinus* cf. *urbasaensis*, which, however, has a lower profile and has no large spines on the upper margin of dactylus.

?*Graptocarcinus* sp.

(Figs 5.7)

Material examined: Cuticular fragment (presumably from dorsal carapace; NHMW 2014/0289/0028) from locality 2.

Discussion: The studied specimen is tentatively identified as a carapace fragment of *Graptocarcinus* on the basis of the well-developed and uniform tuberculation. The genus has also similarly tuberculated chelae (e.g., JAGT *et al.* 2010: fig. 3; VAN BAKEL *et al.* 2012b: figs 2F, 3B), but the tubercles on chelipeds are not so densely packed. In our specimen, the tubercles are densely packed and no predominant association of tubercles is distinguishable. In this respect, the fragment is similar to *G. muiri* STENZEL, 1944 from the Aptian of Mexico (STENZEL 1944: pl. 93 fig. 2) and *G. bellonii* from the Cenomanian of Italy (COLLINS & DIENI 1995: figs 1–2).

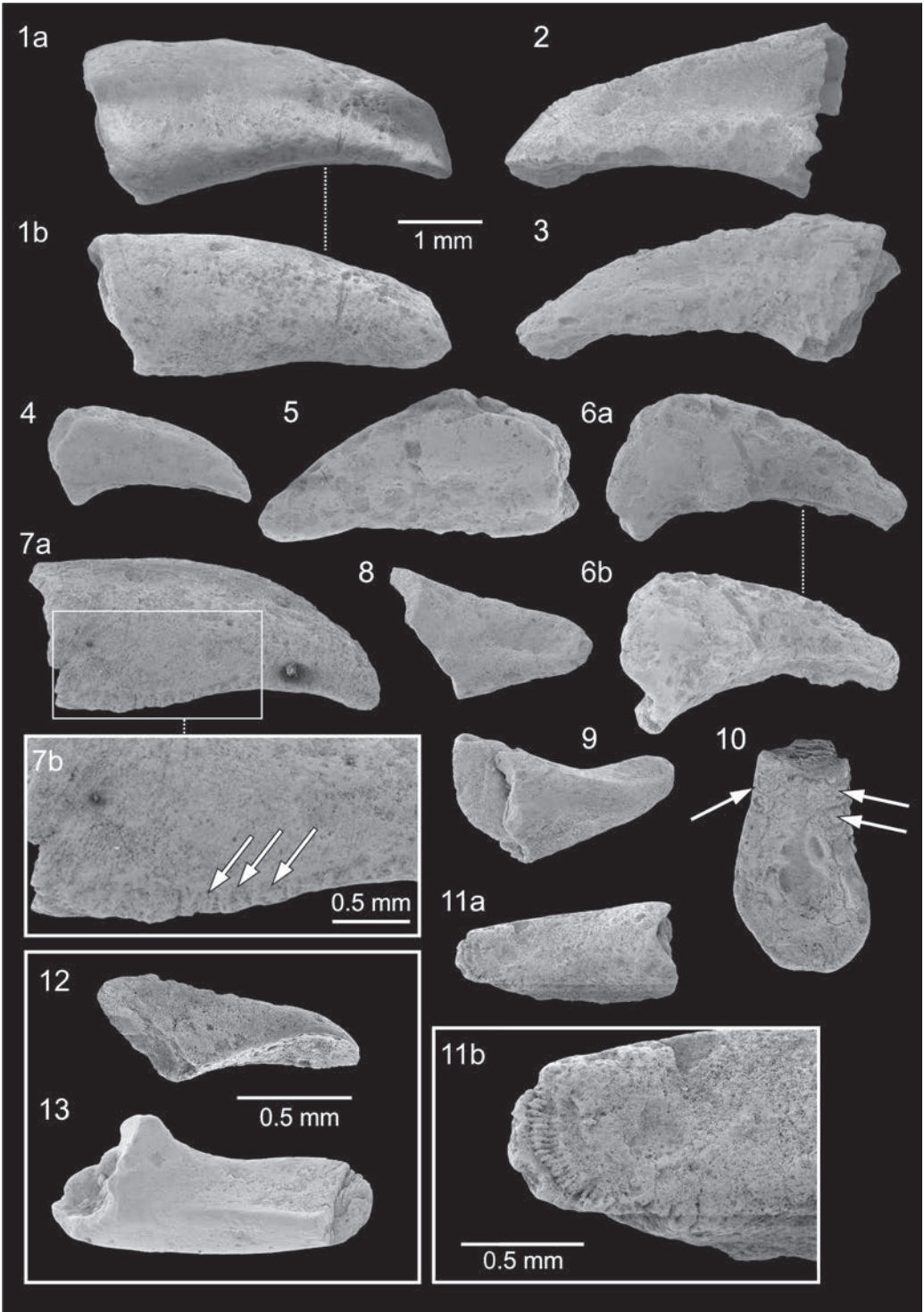
Dynomenidae indet.

(Figs 6.1–6.13)

Material examined: Isolated dactyli (NHMW 2014/0289/0029 to .../0035; NHMW 2014/0289/0038 to .../0040) and fixed fingers (NHMW 2014/0289/0036, .../0037, .../0041). Specimens 2014/0289/0029 and 2014/0289/0034 are from locality 1; the other specimens are from locality 2.

Description: Dactylus is slender; upper margin is smooth or without any apparent ornamentation forming faint keel. Occlusal margin in some specimens possesses a blunt crushing tooth positioned proximally close to the articulation with propodus. Fixed finger is short and high in profile. Both fingers exhibit spooned tips which may be dentate.

Discussion: Spoon-shaped finger tips are present in many extant crabs, however, most of their lineages evolved later during the Cenozoic. Within Cretaceous brachyurous crabs known up-to-date, dynomenids are the best candidates for the studied material. Isolated fingers possessing spooned finger tips are typical for dynomenid crabs (MCLAY 1999). Dynomenids usually have blunt teeth on the occlusal margins of the cheliped fingers (MCLAY 1999), these, however, are not discernible in the material from Serre de Bleyton, possibly because of degradation of the uppermost cuticle layers. MCLAY (1999) reported that the tips are dentate; this character is visible in the studied material (Figs 6.7, 6.10).



Subsection *Gymnopleura* BOURNE, 1922Superfamily *Palaeocorystoidea* LÖRENTHEY in LÖRENTHEY & BEURLEN, 1929Family *Cenomanocarcinidae* GUINOT, VEGA & VAN BAKEL, 2008

Discussion: *Cenomanocarcinidae* was erected by GUINOT *et al.* (2008) and revised by VAN BAKEL *et al.* (2012a). The chelipeds are known only for its type genus *Cenomanocarcinus* VAN STRAELEN, 1936: they are robust, long, homodontous with elongated fingers (BRETON & COLLINS 2007: fig. 4; GUINOT *et al.* 2008: figs 5E, 6A).

?*Cenomanocarcinidae* indet.

(Figs 7.1–7.3)

Material examined: Isolated dactyli (NHMW 2014/0289/0042, .../0043) and fixed finger (2014/0289/0044) from locality 2.

Description: The fragments show relatively long and slender fingers. Along the entire length of the occlusal margin there are teeth of the same size. One examined dactylus (Fig. 7.2) seems to possess a keeled upper margin.

Discussion: With rounded teeth present on the occlusal margins, the studied specimens differ significantly from all other specimens in the studied sample. Their attribution to *Cenomanocarcinidae* is only tentative, however, since homodontous chelae are unknown in other Cretaceous crabs.

Family *Necrocarcinidae* FÖRSTER, 1968Subfamily *Paranecrocarcininae* FRAAIJE, VAN BAKEL, JAGT & ARTAL, 2008Genus *Paranecrocarcinus* VAN STRAELEN, 1936

Discussion: Chelae of *Paranecrocarcinus* VAN STRAELEN, 1936 are typified by possessing an upper margin with flattened triangular tubercles and tumid, tubercular outer surface (VAN BAKEL *et al.* 2012a).

- ◀ Fig. 6. Decapod crustaceans of Serre de Bleyton: isolated fingers of *Dynomenidae* indet. **1:** NHMW 2014/0289/0029, two views from different angles. **2:** NHMW 2014/0289/0030. **3:** NHMW 2014/0289/0031. **4:** NHMW 2014/0289/0032. **5:** NHMW 2014/0289/0033. **6:** NHMW 2014/0289/0034, two views from different angles. **7:** NHMW 2014/0289/0035, note denticulation of occlusal margin in 7b (indicated with arrows). **8:** NHMW 2014/0289/0036. **9:** NHMW 2014/0289/0037. **10:** NHMW 2014/0289/0038, spoon-shaped tip; note the denticulation on the margin (indicated with arrows). **11:** NHMW 2014/0289/0039, note denticulation on the spoon-shaped tip (11b). **12:** NHMW 2014/0289/0040. **13:** NHMW 2014/0289/0041. All specimens (except 7b, 11b, 12 and 13) are to scale.

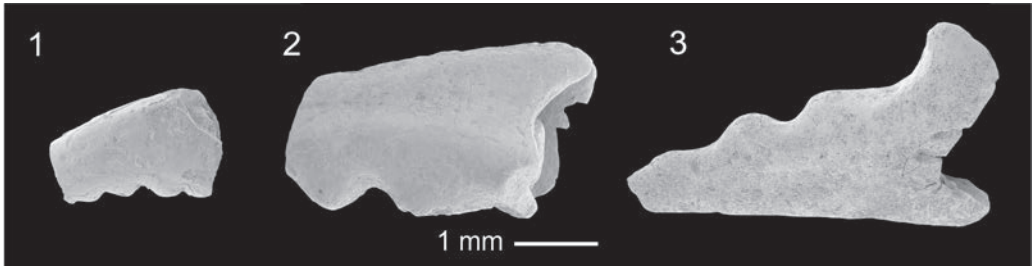


Fig. 7. Decapod crustaceans of Serre de Bleyton: isolated fingers of ?Cenomanocarcinidae indet. 1: NHMW 2014/0289/0042. 2: NHMW 2014/0289/0043. 3: NHMW 2014/0289/0044. All specimens are to scale.

?*Paranecrocarcinus schloegli* nov. spec.

(Fig. 8.2)

Diagnosis: Dactylus is short with triangular outline and cross section. Upper margin has rounded tubercles proximally and a longitudinal keel along the whole length. Occlusal margin has two blunt teeth proximally. Upper and lateral surface possess longitudinal ridges and setal pores forming clusters in larger depressions arranged in rows.

Etymology: Dedicated to Ján SCHLÖGL (Comenius University, Bratislava), an enthusiastic palaeontologist and former supervisor during the Ph.D. studies of the first author.

Holotype: Isolated right dactylus (NHMW 2014/0289/0046) from locality 1.

Type locality: Serre de Bleyton (Drôme, SE France), locality 1.

Type stratum: “Coulées boueuses”, Lower Cretaceous, Barremian.

Description: Dactylus is short and triangular in outline. Cross section is triangular, tip is broken. Upper margin is adorned with several rounded tubercles proximally and a keel running along the whole length. Occlusal margin has two blunt teeth proximally. Upper and lateral surface have longitudinal ridges and are covered with setal pores arranged in rows. Setal pores tend to form clusters situated in larger depressions.

Discussion: The fragmented finger shows similarities to the dactylus of *Pseudomicippe granulosa* PELSENEER, 1886 (based on isolated chelae) from the Maastrichtian type area, considered to be conspecific with the carapace-based taxon *Paranecrocarcinus quadriscissus* (NOETLING, 1881) by JAGT *et al.* (2010), specifically the presence of tubercles on the upper margin and two teeth on the occlusal surface positioned proximally (JAGT *et al.* 2010: figs 2E–G). However, the setal pores seem to be unique for the morphotype from Serre de Bleyton. Their arrangement is somewhat similar to that seen in *Graptocarcinus moosleitneri* nov. spec. discussed above and the tufts of setae that protruded from the pores might have had a similar function (see discussion below). Chelae of paranecrocarcinines are known only from well illustrated chelae (e.g. JAGT *et al.* 2010), therefore, the comparison of our material is difficult. Its distinct

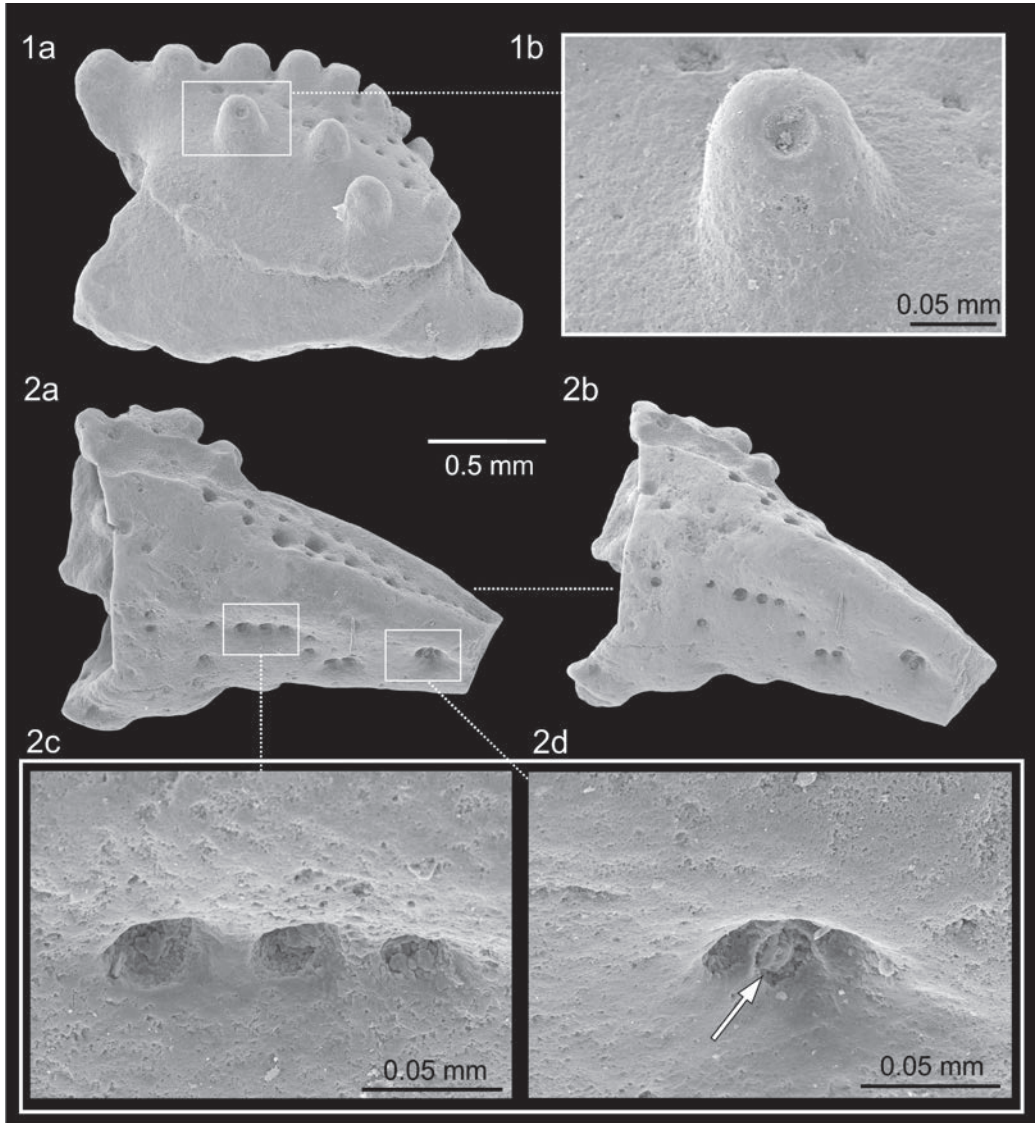


Fig. 8. Decapod crustaceans of Serre de Bleyton: cuticle fragment (1) and dactylus (2) of *?Paranecrocarcinus*. 1: *?Paranecrocarcinus*, NHMW 2014/0289/0045, note the supposed setal pore on the top of the tubercle (1b). 2: *?Paranecrocarcinus schloegli* nov. spec., holotype NHMW 2014/0289/0046; 2c and 2d show the specimens from different angles; note the details of setal pores in 2c and 2d. Specimens in 1a, 2a and 2b are to scale.

morphology and presence of peculiar setal pores, however, does not have any analogue in the published record. Thus, the erection of a new species is warranted, although its generic placement is not secured. In this respect it is worth mentioning that within a single genus differently shaped chelae may be present, for instance in dynomenid

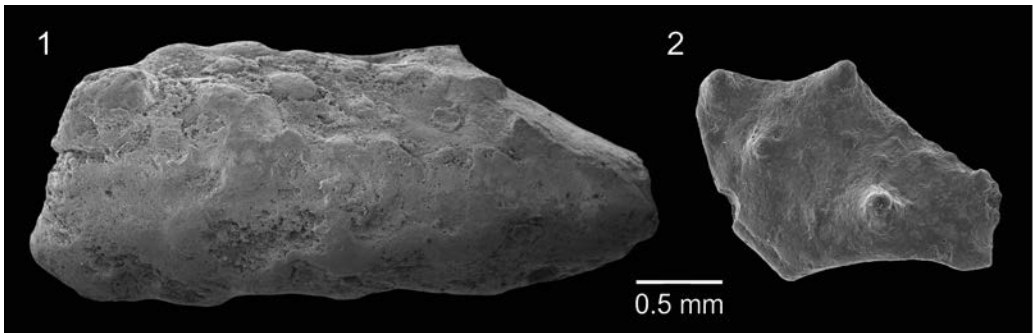


Fig. 9. Decapod crustaceans of Serre de Bleyton: indeterminate cuticular fragments. 1: NHMW 2014/0289/0047. 2: NHMW 2014/0289/0048. Both specimens are to scale.

crabs of the genus *Dynomene* DESMAREST, 1823 (MCLAY 1999). It is fairly possible that similar variation was present also in other basal brachyuran families, for instance Necrocarcinidae.

?*Paranecrocarcinus* sp.

(Fig. 8.1)

Material examined: Cuticular fragment (NHMW 2014/0289/0045) from locality 2.

Description: The cuticle fragment possesses rows of rounded tubercles and pores. One of the tubercles has a depression (pore?) on its top.

Discussion: The cuticle fragment is associated to the dactylus here based on the similarities in sculpture. It is interpreted to represent a fragment of the dorsal carapace, presumably belonging to *Paranecrocarcinus* or a related taxon. In fact, the fragment is very similar to a part of dorsal carapace of *P. quadriscissus* (JAGT *et al.* 2010: fig. 2B; see also FRAAIJE 2002: fig 3) and may represent a portion with preserved anterolateral or posterolateral margin.

The supposed setal pore positioned on a tubercle is somewhat similar to so called capsulated setae known mostly in paguroid hermit crabs. FRAAIJE *et al.* (2011) reported the first fossil example of a paguroid with capsulated setae from the Albian of France and also provided an overview of extant paguroid species possessing this feature.

Decapoda indet.

(Figs 9.1–9.2)

Material examined: Approximately 50 isolated fingers of fragmentary nature (under collective numbers NHMW 2014/0289/0025 and 2014/0289/0049) and cuticular fragments (2014/0289/0047, .../0048) from localities 1 and 2.

Discussion: The material is too fragmentary for identification. The preservation of these specimens precludes attribution to any of the taxa discussed above, but they

illustrate that the original diversity of decapods at Serre de Bleyton might be even higher than the number of taxa we were able refer to specific decapod groups.

A fragment NHMW 2014/0289/0047 (Fig. 9.1) is rather elongated and covered with tubercles, thus, it may represent a portion of cheliped, maybe of some paguroid hermit crab.

Another cuticular fragment NHMW 2014/0289/0048 (Fig. 9.2) with sparsely set tubercles or spines is similar to *Necrocarcinus* BELL, 1863, as figured by JAGT *et al.* (2010: fig. 4A–D). No other features, however, are visible in the studied fragment.

Discussion

Due to its poor preservational state the Serre de Bleyton decapod assemblage appears rather unimportant at a first glance. Despite that usage of scanning electron microscopy allowed enough features to be documented to describe a rich Early Cretaceous decapod fauna. The main significance of the assemblage, however, lies in the fact that the current status on Early Cretaceous decapod faunas is very scarce compared to Late Cretaceous assemblages. Therefore, even this relatively poor material reveals some new insights on decapod assemblages from that period, which are discussed below.

Early Cretaceous decapod faunas of France

There are only few reports on Early Cretaceous decapod assemblages from France. Older records comprise ROBINEAU-DESVOIDY (1849), DE TRIBOLET (1875, 1876) and VAN STRAELEN (1936); newer ones include the contributions evaluating the decapod fauna of the Albian stratotype by BRETON (2010, 2011) and new descriptions by GARASSINO & BRETON (2010), FRAAIJE *et al.* (2011) and VAN BAKEL *et al.* (2012a). KLONPMAKER (2013: appendix A) provided an overview of decapod taxa from Early Hauterivian of the Calcaires à Spatangues Formation and the Lower-Middle Albian Formation des Argiles tégulines de Courcelles. Secrétan (1988) reported nephropid lobster from the Aptian of France. Regarding Barremian strata of France, in brief report DELANOY *et al.* (2012) mentioned crustaceans (supposedly decapods) from Gard Department, SE France. Otherwise, the present contribution is the first reported decapod assemblage from the Barremian of France.

Differential diversity

The majority of studied cheliped fragments from Serre de Bleyton belong to brachyurans. This might imply that the studied association was dominated by brachyurans, specifically dynomenid crabs. Alternatively, a preservational bias might be responsible for this pattern.

The studied association is remarkably diverse. Recently, KLONPMAKER (2013) compared the differential diversities of 17 Cretaceous localities with at least 10 recorded species.

The decapod fauna of Serre de Bleyton contains representatives of presumably four infraorders (Astacidea, Axiidea, Anomura, Brachyura) and at least eleven taxa. This is comparable with other Lower Cretaceous decapod assemblages from France (KLOMPMAKER 2013: appendix A). Some of the cheliped taxa named in open nomenclature likely include more than one biological species, but insufficient preservation and/or lack of diagnostic characters prevent further subdivision into smaller groups. Carapace material would allow a more refined subdivision of these groupings, so the original diversity at Serre de Bleyton might have been higher. However, the implication is clear: if macrofaunal elements were preserved, the studied assemblage would be even more species-rich. The same applies to already reported assemblages: if mesofaunal elements would have been studied, the number of recognized species would be undoubtedly higher. Anyway, as expected the decapod families recognized in Serre de Bleyton herein, have already been reported from either the Early or Late Cretaceous of France (BRETON & COLLINS 2007, 2011; BRETON 2010, 2011; KLOMPMAKER 2013: appendix A)

Stratigraphic ranges of primitive brachyurans

Although the family Dynomenidae is considered one of the most ancient families (GUINOT 2008; VAN BAKEL *et al.* 2012b) its fossil record is younger than that of the oldest brachyurans (SCHWEITZER & FELDMANN 2010). GLAESSNER (1960, 1969) reported stratigraphic range of the family as the Late Jurassic to Recent. Since then the familial placement of the Late Jurassic genus *Cyclothyreus* has been contentious. SCHWEITZER & FELDMANN (2009) classified it in Dynomenidae *sensu lato*, but later removed it and placed in Goniidromitidae (DE GRAVE *et al.* 2009; SCHWEITZER *et al.* 2010). KARASAWA *et al.* (2011) considered *Graptocarcinus* as the oldest confirmed member of the Dynomenidae. This genus has predominantly been documented from the Late Cretaceous of Europe (COLLINS & DIENI 1995; FRAAYE 1996; VESELSKÁ 2011; VAN BAKEL *et al.* 2012b). The oldest species of *Graptocarcinus*, *G. muiri*, was reported from the Albian of Mexico, but VEGA & FELDMANN (1992: p. 134) regarded its age as Aptian. The occurrence from Serre de Bleyton reported herein is slightly older, coming from the Barremian strata. Thus, the stratigraphic span of *Graptocarcinus* is extended herein. Recently, VAN BAKEL *et al.* (2012b) classified *Cyclothyreus* within a newly erected subfamily Graptocarcininae of the family Dynomenidae, being the oldest member of the family.

The oldest occurrence of Cenomanocarcinidae is from the Upper Albian of Colombia (GUINOT *et al.* 2008). If the attribution of the Serre de Bleyton material to this family can be confirmed, the stratigraphic range of the family would be extended by approximately 20 million years.

Feeding habits in primitive brachyurans

Because of their limited taxonomic utility and unattractive appearance in comparison with dorsal carapaces and small size, the isolated cheliped fingers of brachyurans were

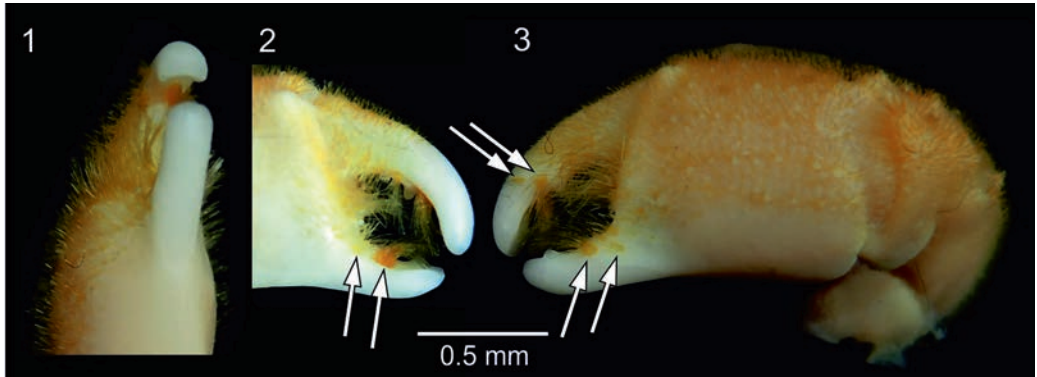


Fig. 10. Cheliped of *Dynomena hispida* (LATREILLE, 1812), NHMW 1816. **1**: ventral view showing spoon-shaped finger tips. **2**: inner side. **3**: outer side. Note clusters of setae (indicated with arrows).

and still are often omitted in both scientific studies and private collections. Although their use in taxonomy is limited they offer an insight into the ecological niches the crabs were occupying. Because decapod chelipeds are in fact tools used for manipulating or obtaining food (as well as for other functions as attack and defence or courtship behaviour; see WARNER 1977 and MARIAPPAN *et al.* 2000 for reviews), they are under strong selection pressure, and thus, prone to convergence (TSHUDY & SORHANNUS 2000).

The presence of particular finger types in particular stratigraphic horizons can add data for interpreting prevalent feeding strategies among decapods. For instance, based on the assemblage studied herein, large setal pores at the tip of the fingers are present not only in dynomenids but also in necrocarcinids – suggesting similar way of feeding for both families (or at least some of their members). The presence of numerous setae arranged in clusters on the fingertips points to the presence of a sieving mechanism in these crabs, which is analogous to present day Dynomenidae (MCLAY 1999; Fig. 10).

The studied decapod assemblage of Serre de Bleyton includes also supposed predatory brachyurans. According to GUINOT *et al.* (2008: p. 688), cenomanocarcinid chelae exhibit the morphology “perfectly suited to catch and crush (swimming) molluscs such as ammonites”. Today, several brachyuran groups are specialized for active hunt, *i.e.* members of the family Portunidae. These groups have robust fossil record; however, virtually all lineages of portunoid crabs have a Late Cretaceous origin (KARASAWA *et al.* 2008b).

Conclusions

The studied decapod association of Serre de Bleyton composed of isolated cheliped fingers (mostly of fragmentary nature) exhibits relatively high diversity comparable to assemblages of similar age (based on macrofossil remains) known so far. Most of the specimens show spatulate tip of the fingers pointing to specific ecological niche of the

animals, *i.e.* algae grazers. The presence of multi-setal pores point to the presence of sieving mechanism in the claws of some of the studied crabs. Therefore it can be concluded that this feeding strategy, so common in extant relatives (MCLAY 1999), was established in dynomenid crabs already in the Barremian.

As cheliped fingers of brachyurans have a much higher fossilization potential than dorsal carapaces, there is a good chance that the spatial and temporal ranges of numerous crab families could be considerably extended if isolated chelipeds were regularly included in faunal analyses. Of course, specific care has to be taken when working with cheliped fragments; for many groups more detailed comparative studies are needed to convincingly match carapace-based taxa with isolated fingers.

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