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New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark

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Abstract

Two new genera and nine new species of crabs (Crustacea, Decapoda) from the Eocene Lillebælt Clay Formation (Ypresian/Lutetian) of Trelde Næs, SE Jutland, Denmark are described. They include the anomurans *Pagurus langei* sp. nov., and *Ctenocheles anderseni* sp. nov., and the brachyurans *Basinotopus tricornis* sp. nov., *Laeviranina treldenaesensis* sp. nov., *Goniochele madseni* sp. nov., *Panopeus bessmanni* sp. nov., *Glyphithyreus bituberculatus* sp. nov., *Fredericia barsoei gen.* et sp. nov. and *Falsiportunites longispinosus* gen. et sp. nov.

Key words: Crabs, new species, Lillebælt Clay Formation, Ypresian/Lutetian, SE Jutland, Denmark

Introduction

The earliest record of crabs from the Lillebælt Clay Formation appears to be that of *Plagiolophus wetherelli* Bell, 1858 (= *Glyphithyreus* Reuss, 1859), by Ravn (1903). The presence of *Glyphithyreus wetherelli*, in the Landenian, was subsequently quoted by Andersen (1944), Rasmussen (1966, 1969), Bonde (1968), Via (1969), Collins and Morris (1978), Heilmann-Clausen *et al.* (1985), Gravesen (1993) and most recently in a fieldtrip excursion program compiled by Bonde (1994). Another two species of crabs, *Dromilites* cfr. *lamarckii* (Desmarest, 1822) and *Coeloma* sp. were added by Bonde (1968, 1994). Mention of *Hoploparia* cfr. *gammaroides* Bell, 1858, by Bonde (1968 and 1994) remains the sole record for a macruran species in the Lillebælt Clay Formation. Bonde (1968) also mentioned the presence of two specimens of stomatopod "frontlimbs" and a unique hermit crab, a pagurid with a claw and pyritized body preserved within the shell of *Volutocorbis* sp.

New material now available as the result of recent intensive collecting by Steen B. Andersen, H. C. Bessmann Hansen, Mogens Madsen, Søren P. Andersen, Fredericia and Ole Barsøe Hansen, Kolding, not only provides the opportunity to eliminate anomalies in the above taxonomic records, but allows description of nine new species in as many genera, two of them new.

Previous Northern European records of *Ctenocheles* species appear to be limited to *Ctenocheles inaequidens* (Pelseneer, 1886), Maastrichtian, The Netherlands; two from the Oligocene, *Ctenocheles rupeliensis* (Beurlen, 1939), Hungary and *Ctenocheles* sp. (Polkowsky, pers comm.), Germany and three unnamed forms described by Rasmussen (1971), Lower Danian, Denmark; Philippe and Secretan (1971), Miocene, France; Förster and Mundlos (1982), Eocene, Germany. Thus the presence of *Ctenocheles* in the present assemblage marginally extends the Danish record for the genus.

Fossil hermit crab remains within domicile gastropods are rare in the fossil record and a right pagurid cheliped preserved *in situ* in the (peeled) body chamber of a *Volutocorbis* sp. allows the first description of such an occurrence in the European fossil record. Hitherto, fossil pagurid remains preserved *in situ* within domicile gastropod remains have been made known only from the Miocene of New Zealand (Hyden and Forest, 1980; Feldmann and Keyes, 1992; Walker and Ward, 1992). Mertin (1941) drew attention to a poorly preserved specimen from the Campanian of Germany and a pagurid/gastropod relationship was described by Aguirre Urreta and Olivero (1992) and Olivero and Aguirre Urreta (1994) from the Campanian of Antarctica. Karasawa (2002) described *Pagurus s.l.* sp. domiciled within a turritellid from the Oligocene of Japan, and reiterated reports of other pagurid/gastropod associations from the Upper Miocene and Holocene of Taiwan (Hu and Tao, 1996). A Lower Cretaceous ammonite containing *in situ* pagurid chelae was described by Fraaije (2003). *Petrochirus bouvieri* Rathbun,

1919, domiciled within several gastropod species has been recorded from the Gurabo Formation of Panama (Collins and Todd, in press). The New Zealand specimens were placed in *Pagurus*, a genus in which the major claw (when larger) is commonly on the right-hand side. The contrary applies to *Paguristes*. Without knowledge of the left cheliped it is considered unwise to speculate a more finite identification of the present specimen other than tentative placement in *Pagurus*.

A new dromiid, *Basinotopus tricornis* (formerly recorded as *Dromiopsis* cfr. *lamarckii*) is distinguished by a prominent rostrum flanked by rostral horns developed from the inner orbital margin. These features, seen also in well preserved specimens of the Lower Eocene London Clay (Ypresian) *Basinotopus lamarckii* (Desmarest, 1822), differ radically from the deeply sulcate, bifid appearance of the rostrum of *Dromilites bucklandii* (H. Milne Edwards, 1822), the type species of *Dromilites*, and other known fossil dromiid genera. Separation of *lamarckii* from *Dromilites* and its return to the hitherto regarded junior synonym, *Basinotopus* McCoy, 1849, was undertaken by Collins (2002). The new species has characters remotely in common, with the Recent genera *Hemispherodromia* Barnard, 1954 and *Speodromia* Barnard, 1947. The subspecies *Dromilites lamarckii humerosus* Quayle and Collins, 1981, was raised to full specific status and retained in *Dromilites* (Collins, 2002).

Represented by a single specimen, *Laeviranina treldenaesensis* sp. nov. retains elements of the sternites noted in only four of fifteen members of the genus (Tucker, 1996); the constriction at the base of the outer orbital spines distinguishes *L. treldenaesensis* from other known species in the genus. *Goniochele madseni* sp. nov. represents the second positively, known species of the genus, *Goniochele? armata* Rathbun, 1919 having been described only from a chela. The new species resembles, and is the obvious descendent of *Goniochele angulata* Bell, 1858, from the London Clay of England and Germany.

Comparison with carapaces of *Glyphithyreus wetherelli* (Bell, 1858) from the British London Clay and the Thanetian and Lower Eocene of Pakistan, Lillebælt Clay Formation carapaces of *Glyphithyreus bituberculatus* sp. nov. reveal differences in length/width ratios and lobation fully justifying specific separation. Carapaces of the new species attain a size more compatible with those of *Glyphithyreus wetherelli* from Pakistan than elsewhere. Also assigned to the Goneplacidae, *Fredericia barsoei* gen. et sp. nov. has characters in common with *Palaeograpsus loczyanus* Lőrenthey *in* Lőrenthey and Beurlen, 1929. Sternites of the new species show sexual dimorphism remarkably similar to those of *G. bituberculatus* sp. nov.

Falsiportunites longispinosus gen. et sp. nov. has morphological characters sufficiently distinct from *Portunites* to justify generic separation whilst implying sharing an ancestral stock form. The occurrence of two carapaces of *Falsiportunites longispinosus* (Pl. 8, Figs. 2a-b) in close contact one above the other, the upper

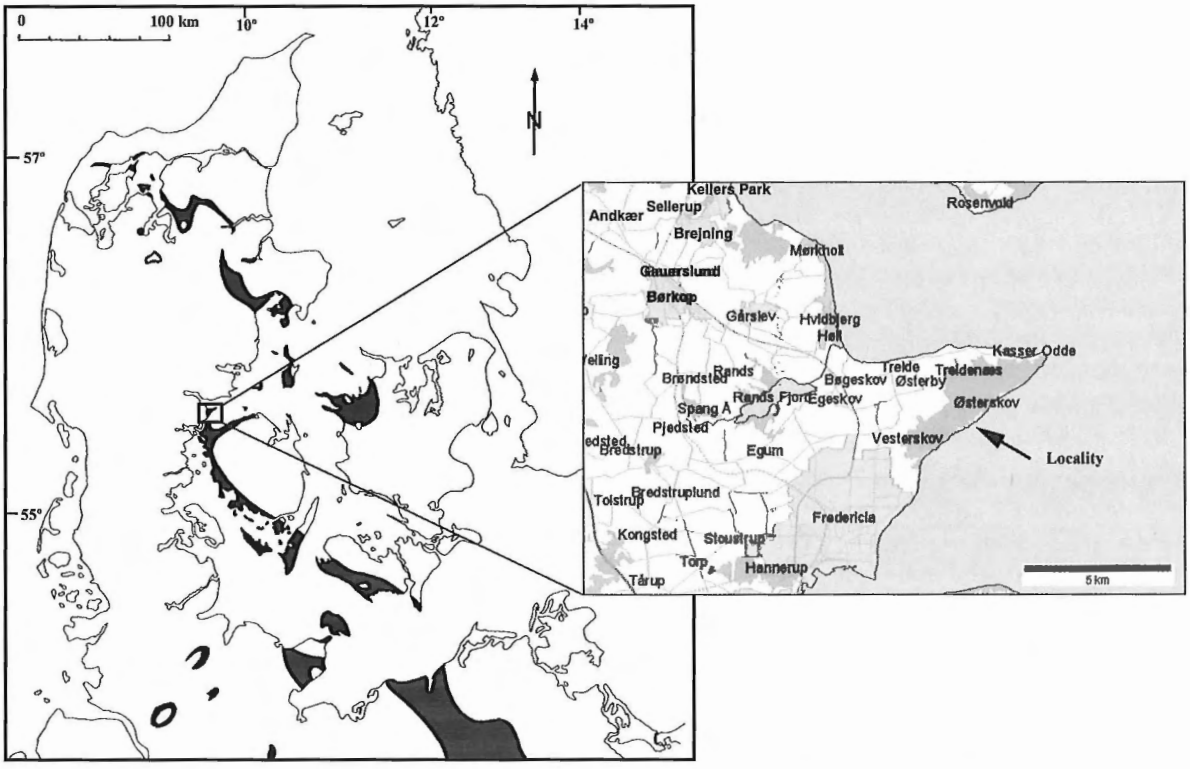


Fig. 1. Pre-Quarternary map showing the distribution of the Eocene deposits in Denmark with location map of Trelde Næs (after Gravesen, 1993).

the larger, could be interpreted as death of a recently moulted individual after a time interval sufficient to allow the new carapace to form.

Marginally increasing the geographical range of the genus, *Panopeus bessmanni* sp. nov. is distinguished from other European members of the genus by its well defined lobation and arrangement of ridges, in the former aspect it has a similarity to *Panopeus olearis* (Rathbun, 1926).

Judging from the prevalence of an undisturbed plural suture it would appear that, with the exception of *Basinotopus tricornis*, much of the material examined concerns dead crabs. Strangely, the majority of carapaces examined of *Basinotopus tricornis* consists only of carapaces of various growth stages, with no or little evidence of the underside. This is in sharp contrast with specimens of *Basinotopus lamarckii* from the London Clay of the Isle of Sheppey, England, where carapaces retaining undersides and/or chelae are not uncommon.

Stratigraphy

Most of the pre-Quarternary surface of Denmark consists of Paleogene and Neogene strata.Eocene sediments are present in scattered coastal cliffs, pits and quarries throughout the country distributed in NW to SE direction to contemporaneous deposits in northern Germany (Fig. 1), comprising the Røsnas, Lillebælt Clay and Søvind Marl Formations (Fig. 2). The study area for the Lillebælt Clay Formation is located along the southeast coast at Trelde Næs (Fig. 1). The fauna of the Lillebælt Clay Formation has been considered by the fish specialist Bonde (1968) who paid particular attention to the invertebrates. The stratigraphical and lithographical aspects of the formation (see Fig. 2) were more thoroughly considered by Heilmann-Clausen *et al.* (1985). The sections which were drawn up by those authors were formulated by data gathered from numerous exposures and/or boreholes which indicated the presence of six concretion-bearing beds within the Lillebælt Clay Formation. However, as noted below, since the crab-bearing nodules examined were obtained from randomly derived beach gleanings, it is, impossible to relate the material to any one particular bed.

Taphonomy

The general quality of preservation of fossil decapod material in the Lillebælt Clay Formation is excellent. Cuticle is most often preserved in such a fine detail that would allow potential examination of ultrastructure as demonstrated by Feldmann and Tshudy (1987) and Feldmann and Gazdzicki (1998).

The preservation, however, varies in many ways: often the shape of the concretion reflects that of the contained crab - a condition typical of most of the moulted specimens of *Basinotopus tricornis* which are usually covered only by a thin layer of matrix. Generally, carapaces and limb fragments exposed on the nodule are much beach-rolled and abraded. The carapaces may be filled with sediment, possibly faecal pellets consisting of short cylindrical rods (Pl. 8, Fig. 1), or may even be empty, a condition especially effecting the pereiopods. Some crab remains are little more than a crumbled mass, possibly as a result of death and internment occurring shortly after moulting.

Evidence of intensive burrowing activity is seen either as fine tubes immediately below the shell surface, although seldom breaking through the shell itself, or larger tubes ramifying at random. Judging from the prevalence of an undisturbed plural suture, it would appear that with the exception of *Basinotopus tricornis*, much of material examined concerns dead crabs. Strangely, the majority of carapaces examined of *B. tricornis* consists only of carapaces of various growth stages with little, or no evidence of the underside. This is in sharp contrast with specimens of *Basinotopus lamarckii* from the London Clay of the Isle of Sheppey, England, where carapaces retaining undersides and/or chelae are not uncommon. A sub-reniform area centred about the gastric region of *Laeviranina treldenaesensis* suggests evidence of decomposition of shell by gastric corruption which did not affect the stronger apodemes of the attractor epimeralis muscles. This condition, first recorded by Bishop (1986) in *Linuparus canadensis* (Whiteaves, 1885), is rarely observed among crabs. A small gastropod, *Limacina* sp. (Pl. 7, Fig. 3c) seen attached to the carapace surface also occurs both within and on the nodule surface. Pre-fossil fractures are common.

In some instances the formation of the enclosing concretion would appear to be related to infillings of burrow structures. Some elongated concretions clearly display evidence of burrowings typical of Recent stomatopods. This interpretation is supported by observations of numerous disarticulated remains of stomatopods not examined in this paper.

Burial of the decapod remains, and concretion formation seems to have occurred rapidly. The preservation of a hermit crab within its domicile and two previously mentioned concretions with presumed moultings of *Falsiportunites*, would form only under circumstances of extremely rapid burial. This is a very rare occurrence, especially in species of hermit crabs, because the cuticle of all but claws tends to be extremely thin and uncalcified. It is therefore highly unlikely that such a specimen would have been preserved in this fashion unless burial had been nearly instantaneous.

Materials and methods

The studied material comprises more than 3000 crab-bearing calcareous/phosphoritic/sideritic concretions, all of which the result of assiduous collecting by the above-named dedicated colleagues, at low tide exposed along the beach section at Trelde Næs, near Fredericia, Jutland (Fig. 1). Much of the material, including all type-specimens, was generously donated to the Geological Museum, Copenhagen (MGUH; GM). Other material is lodged in the Geological Museum, Fredericia. The concretions occur in various

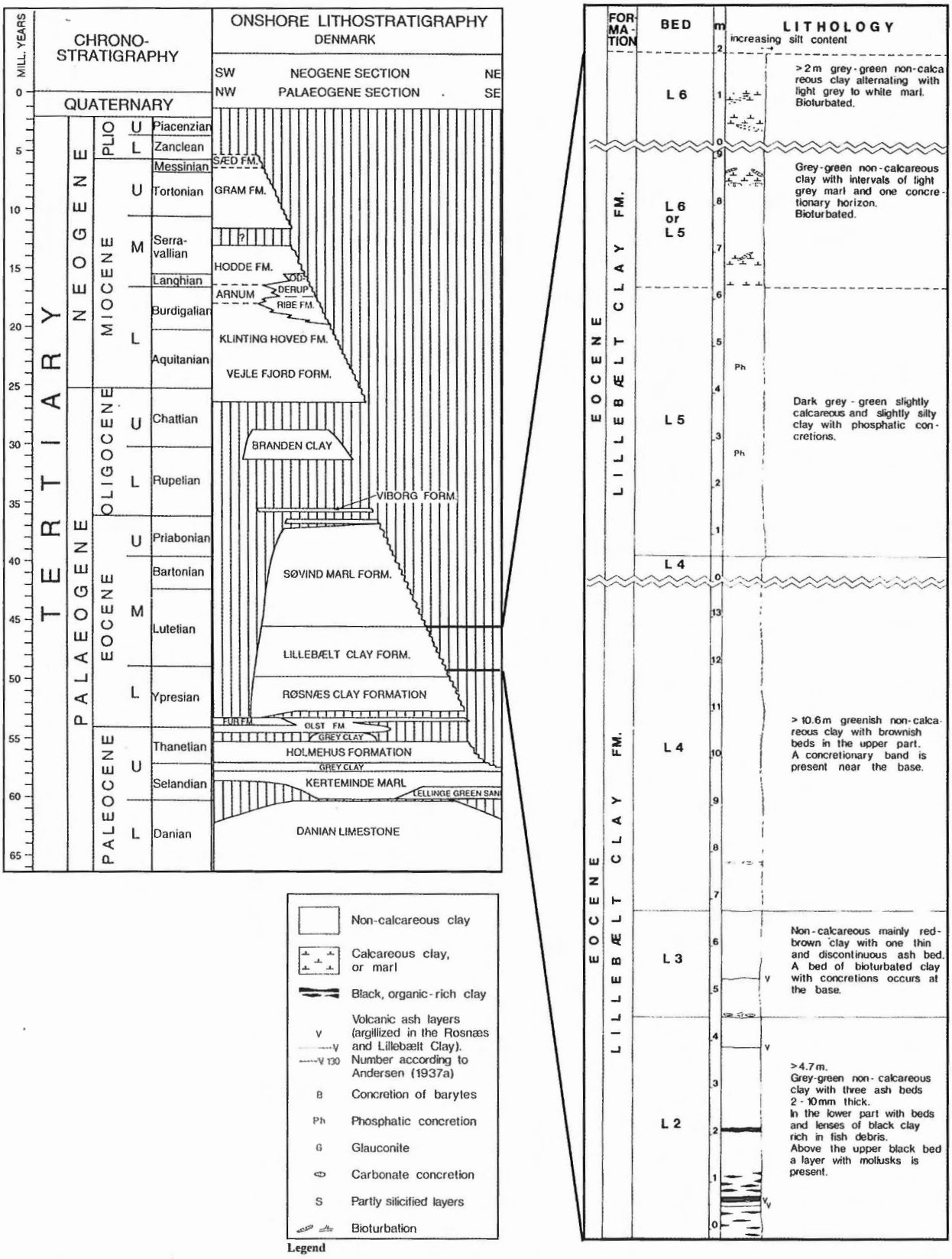


Fig. 2. Composite stratigraphic section (right) of Lillebælt Clay Formation at Trelde Næs (after Heilmann-Clausen *et al.*, 1985).

shapes and sizes ranging from c. 150mm × 80 mm to the more frequent c. 50 × 40 mm. Because of the relatively small size of these concretions, distal parts of the walking legs are rarely preserved.

Preparation techniques

Some collectors prefer to split a typical crab-bearing nodule immediately in order to verify its content, while others reserve it for later examination and preparation. The former method is not recommended as fragments can be lost in the process. Most collectors are content to leave their specimens as preserved - a wise precaution in the absence of sophisticated preparation techniques. However, in this condition the amount of retrievable scientific data is limited. Important features such as sternites, mouth parts, abdominal somites etc., may be obscured in the concretions. Also difficulties arise with regard obtaining accurate measurements.

Considering the large amount of the material available, maximum effort has been made to find the most convenient method to prepare the specimens for study. The techniques adopted here are not beyond the scope of many amateurs, but involve the use of laboratory facilities and chemicals that may not be readily available. The enthusiast may be able to adopt these techniques on a limited scale, but should be warned of the many potential pitfalls that could result in irreversible damage to specimens.

The preparation follows basically two different kinds of treatment. The first is a cleaning process whereby the surrounding matrix is removed; the second involves removal of the entire crab remains (a so called negative preparation) leaving an external mould from which a cast can be made. Since each type of fossil preservation may require its own special preparation techniques, the first step is to consider the most advantageous method. Specimens with good potential for entire preservation still entombed in the nodule were selected for cleaning with tools such as pneumatic air scribes (Desoutter Pen and pneumatic air scribe W 224). For preliminary exposure the Desoutter Pen is recommended since it quickly removes thicker portions of surrounding matrix. Air scribe W224 is more adapted for carefully cleaning of the finest structures of the crab's exoskeleton.

In instances where the exposed legs were not sediment filled they have been reinforced (injected) with appropriate consolidant, like polyvinyl acetate, to strengthen them prior to preparation. Ignoring that step will result in the limbs collapsing under vibration from the reciprocating impact caused by the cleaning processes. Great care was taken not to touch the fragile cuticle, and areas of newly exposed parts were protected by coating with a thin layer of diluted consolidant (polyvinyl butyral). All in all, a preparation method that often requires many hours of time consuming work.

Negative preparation

In some instances when the concretion exhibits an exposed, abraded specimen, normally discarded by most collectors, a negative preparation has proved to be the most convenient, fastest and profitable treatment. Most of the enclosed crab remains were removed by the Desoutter Pen followed by cleaning with a watergun (Wagner paint sprayer W 400 SE). This gun generates a fine, highly powered jet stream of water (adjustable up to 180 bar) capable of blowing off most of the shell debris without harming the surface details. In such cases where shell debris remained, it was painstakingly removed by Ultra Sonic Scaler, as used in the dental practices. Since the water rinse used in dentistry to flush loosened debris is not favourable in some fossils, the water supply can simply be disconnected. Such work should be carried out under a binocular microscope.

Experiments with some very dense nodules, especially those impregnated with manganese and iron salts, were successfully treated by using the heating and quenching method described by Pojeta and Balanc (1989, 1997). A heating burner was pointed directly to the surface for about 20-30 seconds for rapid locally heating and the specimen quickly immersed in ice cold water, thus causing the cuticle debris to be wholly or partly loosened without harming the surface details of the imprints. This procedure is repeated as many times as necessary.

In some cases, concerning isolated cuticle remains can subsequently be glued back to the opposite part of the fossils, preferably by using a slow evaporating adhesive (polyvinyl butyral diluted with toluene). Prepared nodules were then ready for casting with either ordinary latex rubber (black tone colour incorporated) or silicone rubber (Wacker silicone 4400 or Dow Corning Silastic 9161). For rapid determination of sexes exhibited by imprints of sternites/abdominal somites in the mould, a fast curing vinyl polyxilosane impression material like Exaflex Putty was made. Exaflex Putty is a dental material composed of a base and catalyst component which, when thoroughly mixed, applied to the imprints and allowed to set, can be removed from the external mould after a couple of minutes.

In a few instances some nodules of very complex nature, a vacuum impregnated silicone rubber cast (Silastic 9161) was made, and after polymerisation (24 hours) the surrounding matrix was removed completely by soaking in a bath of 15 percent hydrochloric acid. Such acid prepared specimens often exhibit unexpected bioerosional activity like micro-burrowings, trace fossils etc. (Pl. 8, Fig. 3) not normally captured in latex casts or Exaflex impression compound. The choice of this method reduced the preparation time to a fraction of that required by other methods - with even better results.

Photography

In order to create a uniform photographic appearance, all material was blackened either with black ink airbrushed to the fossils, or by using dry colour powder dusted to the silicone rubber casts, with excessive powder blown away by compressed air, thus creating a fine black coating. Removal of the ink was achieved by simply soaking in household bleaching agent, followed by a freshwater rinse. This pre-treatment makes a superb background colour prior to a light coating with ammonium chloride which further enhances the contrast

in the final images. Digital images were made of individuals exhibiting the best preserved morphological features, some were mirror reversed, others had elements filled in by use of an image-editing program (e.g. Adobe Photoshop version 6) to create a near complete reconstruction. Drawings were likewise made by using the same program, changing the images with the filter "poster edges" in the tool bar which converts the images to a drawing-like picture. Subsequent minor retouching and correction of the appropriate contrast is needed to accomplish the final drawing.

Systematic Descriptions

Order Decapoda Latreille, 1802
Infraorder Thalassinidea Latreille, 1831
Family Thalassinidae Latreille, 1831
Genus *Ctenocheles* Kishinouye, 1926

Type species: *Ctenocheles balssi* Kishinouye, 1926, by monotypy.
Range: Upper Cretaceous - Recent.

Ctenocheles anderseni sp. nov.

(Pl. 1, Figs. 2-4)

Diagnosis: Length of right manus about three times distal height, upper and lower margins convex, lower depressed at base of fixed finger; fingers about one third longer than manus. Upper and lower margin of left manus subparallel, tapering distally, fingers about as long as manus.

Material: Holotype. Internal view of right chela, MGUH 26772 associated with paratype, an inner view of a left chela MGUH 26773; paratypes, MGUH 26774-26775.

Derivation of name: In recognition of the cooperation of Steen B. Andersen, Fredericia, in gathering and making available some of the material and for providing facilities for its early preparation.

Description: Right chela, inner surface, distal height of manus is about one fourth the length, subovate in transverse section: upper margin gently convex, lower margin strongly convex, becoming concave at junction with deflexed fixed finger. A low ridge leads from the articulation of the dactylus, becoming suppressed, it divides to embrace a widening depression. Carpal margin damaged. Fingers about one third longer than the manus, the dactylus is flattened, incurved and sharply downturned at the tip; spinules lining the occludent margin are regularly arranged 1 3 2 3 1 in height. Occludent margin of fixed finger not preserved.

Left chela, inner surface, incurved, the upper and lower margins are subparallel and gently convex, distal height one third the length; the upper edge is narrowly rounded and lined with minute setae pores; the lower edge leading from the fixed finger is subcarinate and lined with setae pores to midlength of the manus. A weak groove lines an almost vertical interdigital margin. Length of subovate fingers about equal to that of manus. The tip of the fixed finger is slightly upturned; the occludent margin is weakly convex and minutely granulated. Distal height of dactylus about equal to that of the fixed finger, but narrows rapidly. Occludent surface obscured.

Discussion: With but one exception, all other known northern European species of *Ctenocheles* differ from *C. anderseni* in the arrangement of the denticles lining the dactyl occludent margin. The exception, *Ctenocheles* sp. Philippe and Secretan (1971) has a more or less similar arrangement of denticles, but they are more numerous than those of *C. anderseni*. Other species listed in Tshudy and Sorhannus (2000) differ accordingly, or are insufficiently preserved to permit comparison.

Remarks: A nodule exposing a right propodus conforming with the holotype, also contains a dactylus (Pl.1, Fig. 3b) corresponding to paratype MGUH 26775, and two fragmentary left propodi (Pl. 1, Fig. 3) somewhat larger and shorter in relation to width than the holotype/associated paratype. With the limited material on hand, we prefer to regard these propodi as *insertae sedis*.

Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family Paguridae Latreille, 1802
Subfamily Pagurinae Latreille, 1802
Genus *Pagurus* Fabricius, 1775

Type species: *Cancer bernhardus* Linnaeus, 1758 (on Official List ICZN) by subsequent designation of Latreille, 1810.
Range: Lower Cretaceous - Recent.

Pagurus? langei sp. nov.

(Pl. 1, Fig. 1)

Diagnosis: Right (minor) propodus robust; a median depression along upper surface and a groove along lower margin of outer surface.

Holotype: The right cheliped, carpus and merus of left cheliped domiciled within a gastropod, *Volutocorbis* sp. MGUH 26771, from the Lillebælt Clay Formation of Trelde Næs, SE Jutland.

Derivation of name: The species is named for the late Henning Lange, collector.

Description: Right, minor cheliped: distal height of a partly exposed merus is about half the length, transverse section ovate; the lower edge thin and lined with a few blunt spines. Carpus, about one third longer than the merus, distal height twice length of lower margin; upper margin straight along its distal part, rounded proximally and narrowly ridged. Lower margin gently concave and sharp; outer surface nearly flat. Propodus robust, as long as carpus, proximal height a little longer than carpal margin and nearly twice that of carpus. As viewed, the upper margin is slightly concave before the fixed finger and there is a broad furrow along the straight lower margin of the outer surface. The interdigital margin very oblique. Fingers broken; estimated length of fixed finger equals that of manus, it is depressed and slightly ovoid in section. Dactylus narrowly ovate with a line of granules bordering lower margin, a granular ridge bordering the occludent margin extends to interdigital margin. Occludent margins of both fingers sharp, outer sur-

face granulated to finely reticulated. Pyritised remains of the left merus indicates it was almost twice the size of the right.

The peeled loss of shell extends for about a complete whorl; the claw follows the shell's spiral beyond the columella lip.

Discussion: Eocene *Pagurus* species are comparatively rare in the European fossil record: Via (1969) listed four valid named species, and one was described by Müller & Collins (1991), from the Szépvölgy Formation of Hungary.

Length/width proportions of the right propodus of *Pagurus latidactylus* Müller & Collins (1991) agree with *P.? langei*; the outer surface is densely granulated in contrast to the smooth (? worn) surface of *P.? langei* which is granulated on the surviving part of the dactylus, not preserved with *P. latidactylus*. *Pagurus marceti* Via, 1959 has serrated upper and lower margins; little remains of the right propodus of *Pagurus marini*, but a sinuous lower margin distinguishes it from *P.? langei*.

Infraorder Brachyura Latreille, 1802
Section Dromiacea de Haan, 1833
Family Dromiidae de Haan, 1833
Genus *Basinotopus* McCoy, 1849

Type species: *Inachus lamarckii* Desmarest, 1822 by monotypy.

Diagnosis: Carapace subovate, longer than wide; rostrum unidentate and produced; inner orbital spines well developed as rostral horns; lateral margins with four pairs of spines; gastric region weakly tumid, epi- and mesobranchial lobes partially bisected by postcervical furrow; metabranchial lobes scabrous.

Range: Lower Eocene - Middle Eocene.

***Basinotopus tricornis* sp. nov.**
(Fig. 3; Pl. 2, Figs. 1-7)

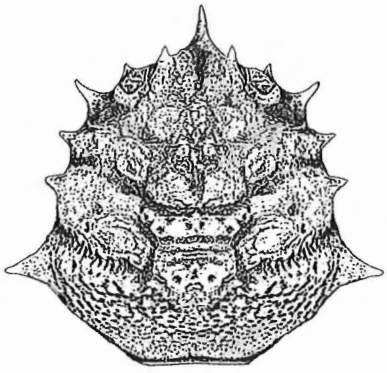


Fig. 3. *Basinotopus tricornis* sp. nov., carapace reconstruction, line drawing.

1968. *Dromilites* cfr. *lamarckii* (Desmarest): Bonde, 149.

Diagnosis: Rostrum slender, a line of four tubercles extending from slender rostral horns behind upper orbital margin; protogastric lobes more or less united with epigastric lobes.

Material: 336 specimens. Holotype, An external mould, MGUH 26778, Paratypes MGUH 26776-26777, MGUH 26779-26782, GM 2003.2-293, GM 2003.1347-1391, from the Lillebælt Clay Formation of Trelde Næs, SE Jutland.

Derivation of name: With reference to the three 'horned' front.

Description: Carapace subovate, slightly longer (from base of rostrum) than wide, widest about two thirds distant from the front; moderately convex in both sections. The produced front occupies the median half of the orbitofrontal width which takes up 63 percent of the carapace width. From a triangular base the well produced rostrum becomes circular in section and tapers rapidly to a point. At its base, slender and slightly diverging inner orbital spines rise directly from the upper orbital margin. Broadly ovate orbits are obliquely directed; the upper orbital margin is entire and weakly rimmed to a stout outer orbital spine. Stout orbital peduncles, curving into deep sockets, obscure all but the tip of a strong spine at the lower orbital angle. The lateral margin has four sharp, upwardly directed triangular, circular-sectioned spines, increasing in size posteriorly; the first pair, separated by a broad cervical notch from a spine on the rounded epibranchial margin and another at the lateral angle, the posterior pair are more widely separated from one another than the anterior pair. The posterior margin is a little wider than the front, straight to gently convex, bounded by a thickened rim and shallow groove. From a pair of gastric pits, the cervical furrow is almost straight across the midline to the outer mesogastric angles, becoming fainter, it runs in two shallow loops to the margin. The branchiocardiac furrow, bounded by a weak ridge, curves gently to the cardiac region where it divides; the forward (postcervical) branch defines the urogastric lobe and partially bisects the meso- and epibranchial lobes. The hinder branch curves back, separating the cardiac region and metabranchial lobes. A weak median sulcus extending from the base of the rostrum divides at the base of low, ovate epigastric lobes to embrace the short anteromesogastric process. There are two granules (fused on internal moulds) on the hepatic regions and two pairs of rounded nodes on the weakly tumid protogastric lobes. The subtriangular mesogastric lobe has an anterior pair of granules close to the midline and trapezoidal (rounded in internal moulds) basal nodes. A narrow, subrectangular, urogastric lobe has obliquely directed lateral angles; on it, six pairs of pits are evenly dispersed laterally and there is a minute pit median and posterior to them. The broad, shield-shaped cardiac region has a pair of cratered nodes midlength. Four granules diverge lineally from the upper orbital margins; the gastric and epi-metabranchial regions are smooth in contrast to the densely scabrous metabranchial and basal part of the cardiac regions.

The endostome forms an isosceles triangle with ridged lateral margins and a median notch has a strongly ridged basal margin; green gland openings are prominent above the basal angles. The endognath of (partly) preserved 3rd maxillipedes is almost twice the width of the exognath.

Female abdomen broad, somites with two low median granules; anterolateral angles of 2nd somite deeply excavated, there are two median spinules on the anterior margin and the lateral margin is spinose. Length of possible male 4th sternites about twice distal width with a concave, weakly sulcate anterior margin; coxal margin slightly concave, widening abruptly into a strong triangular process between 1st and 2nd pereiopods. 5th sternites defined by an anteriorly inclined lateral sinus.

Right cheliped: merus subtriangular in section with weakly carinate upper margin terminating in long, slender spine; basal margin lined with six small spines; carpus, subquadrate, about half length of merus, with strong upper, median and basal spines overhanging the propodus. Propodus as long as merus, distal height about half length, tapering to one third proximally; a weak depression before the fixed finger; interdigital margin concave and slightly inclined.

Left propodus (Pl. 2, Fig. 6): subovate in transverse section, distal height of manus almost equals the length, with a vague depression along the upper margin, which forms a weak concavity, is straight distally and down-curved proximally. The lower margin is gently convex to a shallow depression before the fixed finger. The fixed finger is a little more than half length of manus, ovate in section, the boldly convex lower margin is on a lower plane than that of the manus; occludent margin obscured, the tip weakly spooned. Dactylus robust, almost as long as manus, occludent margin thin and weakly sinuous. The interdigital margin, bounded by a shallow depression, is straight and slightly inclined basally and straight and vertical along the dactyl margin.

Discussion: Bell (1858) in his description of *Dromilites lamarckii*, referred to, "front with short, triangular rostrum somewhat inflected and channelled with a small tooth above each side [no indication on figures] and a tubercle forming the inner angle of the orbit [Pl. 5, Fig. 2]". A carapace (C19324) in the Sedgwick Museum, Cambridge (Pl. 8, Fig. 6) from the London Clay of the Isle of Sheppey, retains an exceptionally well preserved front which shows the rostrum to be moderately downturned, broadly triangular with rounded apex and with pronounced rounded tubercles rising from the upper orbital margin.

A recently developed carapace (In 48212) in the Department of Palaeontology, The Natural History Museum, London, retains more typical preservation of both the rostrum and 'rostral horns'. The overall robustness of these characters contrasts sharply with, yet fully foreshadows, the delicate development of the front of *B. tricornis*. *Basinotopus lamarckii* differs further in having much reduced to obsolete tubercles on the upper orbital margin and the urogastric lobe is isolated from epibranchial lobes. A carapace fragment MGUH 26783, also from the London Clay of the Isle of Sheppey, in the Geological Museum, Copenhagen has an eroded rostrum misleadingly similar to that of *B. tricornis*. This same specimen retains a left chela (Pl. 2, Fig. 8c) which differs in having a deeper, pitted, depressed area lining a straighter upper margin; a slightly deflexed fixed finger, one third the manus length and flattened in transverse section, with a convex median portion of the occludent margin.

These, and other characters clearly separate the two species of *Basinotopus*, yet indicate a relationship between that genus and *Dromilites bucklandii* Milne Edwards which has a simple downturned, deeply sulcate rostrum appearing bifid in upper view.

In his review of Recent dromiid genera McLay (1993) referred to those with unidentate, bidentate and tridentate fronts. The last condition prevails among the 28 genera recognised by McLay and, in almost every instance, the tridentate form consists of a rostrum supported by rostral spines (or horns) isolated from the inner orbital spines, no matter how weakly developed any of these characters may be. In only two cited genera, *Hemispherodromia* Barnard, 1954 and *Speodromia* Barnard, 1947, do the spines rise directly from the upper orbital margin similar to those of *Basinotopus*. However, neither *Hemispherodromia* nor *Speodromia* have other diagnostic characters in common with *Basinotopus* and, as in the other tridentate genera cited by McLay, there is a tendency for the bases of flattened-triangular rostral horns to unite directly at midline or be separated only by a narrow, U-shaped sulcus above the rostrum.

Glaessner (1929) drew attention to the close similarity of *Dromilites alpina* Glaessner, 1929b (Lutetian, Saltzburg) to *Dromilites lamarckii*, drawing particular attention to the strong spines each side of the distinct rostrum and *D. alpina* was included in *Basinotopus* by Collins (2002). However, as observed by Glaessner (1919) that species differs from *B. lamarckii* in having a well developed 3rd lateral spine as opposed to the 4th spine as in *B. lamarckii*. In this, *B. alpina* differs from *B. tricornis*.

Immediately distinguished from *Basinotopus* by having a tridentate front of the broadly triangular type isolated from inner orbital spines, *Epidromia* McLay, 1993 contains species with gastric areolation in common with *Basinotopus tricornis* and *Dromilites* spp. - particularly to *D. bucklandii* - but close, coarse granulation replaces the scabrous ornament on the metabranchial region.

Camouflage carried by Recent genera considered above is reported to be generally sponges and/or ascidians (McLay, 1993).

Unfortunately, the Dromiidae is sparsely recorded in the fossil record, but it is evident that from presumed, as yet unknown Cretaceous ancestors, *Basinotopus* has characters in common with Lower Eocene *Dromilites* species, and, more remotely, with members of Recent genera such as *Hemispherodromia* and *Speleodromia*.

The erstwhile subspecies *Dromilites lamarckii humorosus* Quayle and Collins (1981) was raised to specific rank and retained in *Dromilites* by Collins (2002).

Section Eubrachyura Saint Laurent, 1980
Subsection Raninoida de Haan, 1839
Superfamily Raninoidea de Haan, 1839
Family Raninidae de Haan, 1839
Genus *Laeviranina* Lőrenthey *in* Lőrenthey and Beurlen, 1929
Type species: *Ranina* (*Laeviranina*) *budapestinensis* Lőrenthey,

1897 by subsequent designation of Glaessner (1929a).

Range: Paleocene - late Eocene.

***Laeviranina treldenaesensis* sp. nov.**

(Fig. 4; Pl. 3, Fig. 5)



Fig. 4. *Laeviranina treldenaesensis* sp. nov., carapace reconstruction, line drawing.

Diagnosis: Carapace width about 61 percent of length from base of rostrum, with a weak transverse postfrontal ridge and a slight constriction at base of outer orbital spines; anterolateral spines weakly developed.

Material: Holotype, Carapace preserving sternites MGUH 26786.

Derivation of name: From Trelde Næs, Jutland, the type locality.

Description: Carapace width about 61 percent of length from base of rostrum, widest about one fourth distant from the front; smoothly rounded transversely, longitudinally depressed anteriorly and posteriorly. The poorly preserved orbitofrontal margin occupies 0.7 percent of the carapace width: the base of the rostrum is weakly sulcate, the sides converging to short, sinuous upper orbital margins to a (damage exaggerated) inner notch, the outer notch just indents the margin before the base of (possibly) weak outer orbital spines, the sides of which are noticeably constricted to a shallow transverse ridge. Very short, weakly concave anterolateral margins terminate in small spines inclined at c. 30 degrees to the midline. Smoothly convex posterolateral margins converge to rounded posterior angles. Shallow lateral concavities in the posterior margin accommodate nodes on the proximal margin of the 1st abdominal somite.

Dorsal surface sparsely and minutely granulated posteriorly, a subsurface shell layer reveals a few pits either side of the midline and a circular group posterior to a pair of gastric pits. There are three insipient nodes at the base of the cardiac region.

Small, tectate 3rd sternites are minutely beaded; the convex anterior margin of the 4th sternites is as wide as the base of the coxal margin. The anterior margin of the 5th elements is broadly angular, the lateral margins converge almost straight to, and just overlap tip of subtriangular 6th elements. A median sulcus, deep along 6th elements, forms a pit at the base of the 5th elements, becomes shallow and extends to 4th/5th junction.

Discussion: As far as preservation allows comparison, the constriction in carapace width before the transverse ridge distinguishes *L. treldenaesensis* from all known members of *Laeviranina*. Little is known about the sternites in this genus, but of the four, out of fifteen species, recorded by Tucker (1998) there is, by and large, similarity between the sternites of *Laeviranina fabiani* Lőrenthey *in* Lőrenthey and Beurlen, 1929.

Subsection Heterotremata Guinot, 1977

Superfamily Calappoidea de Haan, 1841

Family Necrocarcinidae Főrster, 1968

Genus *Goniochele* Bell, 1858

Type species: *Goniochele angulata* Bell, 1868 by monotypy.

Range: Lower Eocene - Middle Eocene.

***Goniochele madseni* sp. nov.**

(Pl. 3, Figs. 1-3)

Diagnosis: Carapace subquadrate, anterolateral margins with three small irregular sized nodes and an enlarged posterolateral spine, fixed finger much deflexed.

Material: 5 specimens. Holotype, a carapace, MGUH 26784, paratypes MGUH 26785, GM 2003.688-690.

Derivation of name: In honour of the collector Mogens Madsen, Fredericia.

Description: Carapace subquadrate, frontal region not well preserved, two inframedian orbital spines, the inner, broadly triangular, extend beyond the smaller, more conical outer orbital spine. Short, rounded anterolateral margins become almost straight laterally and have three small irregular sized spines and there is a prominent triangular posterolateral spine rather more than two thirds distant from the front. The posterolateral margins curve broadly round the posterior angle. Crossing the midline about carapace midlength, the cervical furrow curves sharply round the mesogastric lobe, recurves in an acute angle, becomes very shallow and runs almost straight to the margin. Broadly V-shaped branchiocardiac furrows either side of the urogastric lobe curve broadly to the margin. On either side of a basal node on the anteromesogastric process, three nodes, weakening laterally, form a curving row. A node on each mesobranchial lobe is sometimes developed. A tumid epi-mesobranchial ridge is weakly developed. Granules of several diameters, many of the lateral ones medially divided, crowd the dorsal surface.

Female sternites: elements 1 and 2 are fused, triangular and divided laterally by a groove from subcrescentic 3rd elements which are excavated round the 3rd maxilliped ischiognath, notching into a noticeable recess, and concave round prominent nodes on the subtrapezoidal 4th elements, behind which are triangular-based mammillate nodes; the posterior nodes are granulated. The 5th/6th ele-

ments are triangular with a low, granulate basi-lateral ridge.

Right chela: (exposing inner surface) strong with the fingers abruptly deflexed, almost subchelate; distal height of manus almost equals its length; the rounded lower margin is deeply excavated before the fixed finger which is almost as long as the manus and circular in section, sharp denticles alternating in size, line the occludent margin. The dactylus is also rounded in section; the occludent margin is obscured; at least 6 strong spines line the upper margin and there is a small spine on the lower margin of the fixed finger.

Discussion: By and large, there is marked agreement in distribution of gastric nodes with those of *G. angulata*, although the epi/mesobranchial lobe tends to be smoother. There is also agreement in the deflexed nature of the chela and, particularly, with the structure of the female sternites. The 3rd sternites of *G. angulata* (not available to Bell, 1858) have weak nodes either side of the midline and the posterior nodes on the 4th sternites abut the lateral margin rather than isolated as in *G. madseni*. *Goniochele madseni* differs further in having tumid metabranchial lobes less inclined to form vertical 'ridges' of *G. angulata*, Better preserved specimens show that the posterolateral spine of *G. angulata* is more attenuated, or as possessed by *G. madseni*, and generally forms a more pronounced angle with the margin than depicted by Bell (1858, pl. 4, fig. 3) - more nearly approaching that of *G. madseni*.

A left chela of *G. angulata* figured by Bell 1858, pl. 4, fig. 6) is similarly deflexed and has a triangular propodus with a much reduced fixed finger, also the dactylus upper margin of *G. madseni* is spinose in contrast to the smooth upper margin of *G. madseni*.

As remarked by Rathbun (1919) the dactylus - the sole component of *Goniochele armata* Rathbun, 1919 strongly resembles that of *G. angulata*, which is straighter along the upper margin and more spinose than *G. madseni*.

The female sternites of *Silvacarcinus laurae* Collins and Smith, 1993 also show remarkable similarity to those of *G. madseni* sp. nov. the principle difference being the more posterior position of the hinder pair of nodes on the 4th sternal elements - in which respect they more closely resemble *G. angulata*.

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polybiinae Ortmann, 1893
Genus *Falsiportunites* gen. nov.

Diagnosis: Carapace subhexagonal in outline, wider than long with 4 pairs of anterolateral spines, 4th pair anterior to midlength, elongated; basal widths of spines alternately narrow and wide; front 4-lobed (including inner orbital spines); epibranchial ridge more or less straight to weakly arcuate; one tubercle on each hepatic and mesobranchial lobe; metabranchial ridge weakly developed, oblique to midline, with two tubercles.

Type species: *Falsiportunites longispinosus* sp. nov. by monotypy.

Range: Middle Eocene.

Derivation of name: From the Latin *falsus* - false - and *Portunites*.

***Falsiportunites longispinosus* sp. nov.**
(Fig. 5; Pl. 4, Figs. 1-6)

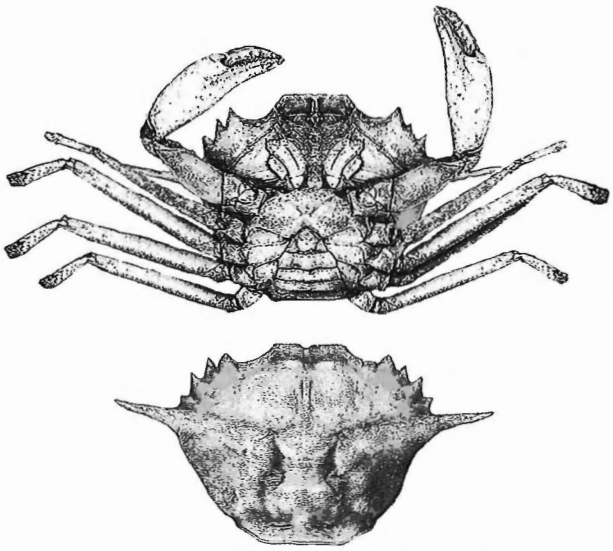


Fig. 5. *Falsiportunites longispinosus* n. gen., n. sp., carapace and near complete reconstruction of a female specimen.

1968. *Coeloma* sp.: Bonde, 149.

Diagnosis: As for genus

Material: 462 specimens. Holotype, an external mould of a carapace, MGUH 26787, paratypes MGUH 26788-26792, GM 2003.295-677, GM 2003.1483-1562 from the Lillebælt Clay Formation, Trelde Næs, SE Jutland.

Derivation of name: Alluding to the elongate anterolateral spines.

Description: Carapace subhexagonal in outline, length about five sixths of carapace width (88 percent) widest a little anterior to midlength; moderately arched transversely and steeply arched longitudinally, highest near widest carapace width. The orbitofrontal margin, slightly in advance of the outer orbital spine, occupies about 80 percent of the carapace width; deep more or less circular orbits take up rather less than the outer thirds (31.0 percent). A shallow frontal notch separates small, rounded median nodes suppressed between broadly rounded outer nodes. Of two notches in the thin, slightly oblique upper orbital margin, the inner occurs about midlength and the outer is midway towards a prominent, blunt, triangular outer orbital spine. There are three triangular, flattened spines on the rounded anterolateral margins, the 4th spine at the lateral angle is robust, circular in section and directed upwards and forwards. Including the outer orbital spine, the spines are alternately wide and narrow based. Almost straight posterolateral margins converge to shallow coxigeal incisions (more noticeable in internal casts) and well rounded posterior angles lead to a ridged posterior margin bounded by a thin groove. Regions and lobes are well de-

fined, The cervical furrow curves broadly across the base of the small rounded-pentagonal mesogastric lobe posterior to midlength, turns sharply forwards to join the broader hepatic furrow, weakens, then runs straight to the margin. The 4th spine leads back to a broad, almost transverse ridge forming the epibranchial lobe, barely differentiated from an almost circular, tuberculate mesobranchial lobe. The ridge is sinuous along the anterior margin with a row of three (sometimes fused) granules at its base, and excavated posteriorly. The tip of the anteromesogastric process extends to the base of transversely ovate, steep-fronted epigastric lobes. The protogastric lobes are rounded, and depressed hepatic regions have a low tubercle behind the 2nd lateral spine. A depression separates a small, subtriangular urogastric lobe from the lingulate cardiac region which has three low tubercles in an inverted triangle (the upper two fused on the shell surface). A tubercle on each mesobranchial lobe, together with two on each metabranchial lobe form a row diverging towards the coxigeal incision. Lateral to the tubercles, the metabranchial lobes are steeply inclined to the margin. (This depression is fully occupied by the 4th and 5th pereiopods in resting position.) A smaller node is inserted between the urogastric and cardiac lobes.

A double row of fine granules lines the upper orbital margin and granules of several diameters crowding the dorsal surface are larger on the tumid areas. The third male sternites are separated by an inclination of the margin from triangular 1st/2nd sternites and by a weak notch from the 4th. Rounded anterior angles of the 4th sternites turn abruptly backward to form long episternites, the straight basal margin is directed medio-posteriorly; semicircular, tumid areas anteriorly are duplicated on the 3rd sternites. The fifth to seventh sternites are subrectangular, all with rounded anterolateral angles leading to long episternites. The first female sternites are distinguished from 2nd by expansion of lateral margin and weak transverse groove. A concave groove separates 3rd sternites, convex anterior margins of which are much extended to pointed lateral angles notched from trapezoidal 4th sternites. These have a concave coxigeal margin terminating in an articulating notch before a short episternite. The 5th - 7th sternites are chordate, each with short episternites. The 3rd sternites and proximal areas of 4th are finely granulated. Telson of semielliptic abdomen broadly rounded with a tumid median portion; 6th somite half as long again as 5th and 4th, both of which have a weak proximal ridge.

The anterior margin of the male sternites is straighter than that of the female; the cleft between the 3rd and 4th is shallower and the anterolateral depression straighter, otherwise there is little difference between the other sternites. The abdomen is angulate, the length of the triangular telson is a little more than half the width. The basal width of the 6th somite is three times the median height; the base of the 5th is one fifth longer than that of the 6th. The 5th/4th somites are separated by short lateral fissures and a median groove; the lateral margin of the 4th is angularly directed towards the 3rd somite, the anterior margin of which is almost one third longer than that of the 4th, while the lateral margins are directed a little towards the midline. Weak ridges are developed on the anteromedian margin of the 6th somite, across the junction of the 5th/6th somites and, more prominently, on the anterolateral portions of the 4th and 3rd somites. Lateral tumidities are present on the 6th and 4th somites (3rd obscured). There is a median tumidity on the 5th, but on the 4th somite it is ridged and unites with the lateral tumidities. Ischiognath of 3rd maxillipeds subtrapezoidal, lateral margin of exopodite weakly concave and ridged; endopodite half width of exopodite.

Discussion: The diagnostic characters of *Portunites* Bell, 1858 according to Schweitzer and Feldman (2000) require the carapace to be wider than long (0.61- 0.76 percent), an orbitofrontal margin width/carapace width of 50-71 percent, a 6-lobed front (including the inner orbital spines), an arcuate epibranchial ridge and metabranchial ridges parallel to the carapace midline. While superficially resembling *Portunites*, the carapace of *Falsiportunites* is relatively wider in relation to length (86.7 percent) and the orbitofrontal margin is wider in proportion to carapace width (80.7 percent); the epibranchial ridge is more or less transverse to weakly arcuate and the metabranchial ridges are oblique to the midline. Furthermore, The robust, elongate 4th anterolateral spines separate *Falsiportunites longispinosus* sp. nov. from known species of *Portunites*. Species recently excluded (Schweitzer and Feldmann, 2000) from *Portunites* and assigned to other genera include *Imaizumila arucana* (Phillippi, 1887), *Minohellenus triangulum* (Rathbun, 1926), *Megokkus alaskensis* (Rathbun, 1926), *Megokkus hexagonalis* (Nagao, 1932), *Megokkus macrospinus* (Schweitzer and Feldmann, 2000) *Stintonius subovatus* (Quayle and Collins, 1981). The status of one of the above genera underwent revision by Schweitzer and Feldmann (2002) when *Imaizumila* was relegated to junior synonomy of *Minohellenus*. At the same time (2002) *Meandricampus* was introduced to contain the erstwhile *Minohellenus triangulum* and *Portunites granuliferus* (Glaessner, 1960).

Falsiportunites approaches *Meandricampus triangulum*, the latter has prominent 4th lateral spines, but these lead to a curved epibranchial ridge, there is a small mesobranchial tubercle, another lateral to it and a transverse pair between the urogastric and cardiac lobes. However, only one tubercle occurs on each metabranchial lobe anterior to a weak, slightly diverging metabranchial ridge.

Imaizumila species are distinguished among other characters, in having a frontal margin with six well developed spines, an orbitofrontal margin/carapace width ratio of about 0.48, and an arcuate, smooth epibranchial ridge. Species of *Megokkus* have been described only from the North Pacific Rim (Schweitzer, 2000b). As a whole the genus differs immediately from *Falsiportunites* in being shorter in relation to width (67.0-74.0 percent), in having comparatively wider orbits, an arcuate epibranchial ridge, hepatic and protogastric ridges and in lacking the branchial tubercles and longitudinal ridges. The Bartonian species *Stintonius subovatus*, from Christchurch Bay, England, is now considered to have characters

more closely related to *Montezumella* Rathbun, 1930 (Collins, 2002).

Superfamily Xanthoidea MacLeay, 1838
Family Goneplacidae MacLeay, 1838
Genus *Glyphithyreus* Reuss, 1859

Type species: By monotypy *Plagiolophus wetherelli* Bell, 1858 (*non* Pommel, 1847).

Range: ? Cenomanian - Middle Eocene.

***Glyphithyreus bituberculatus* sp. nov.**
(Fig. 6; Pl. 5, Figs. 1-5)

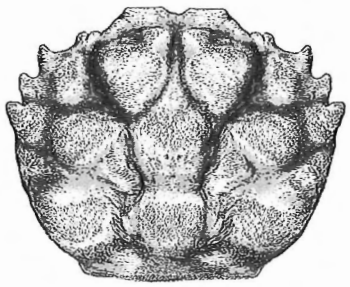


Fig. 6. *Glyphithyreus bituberculatus* sp. nov., carapace reconstruction, line drawing.

1968. *Plagiolophus wetherelli* Bell: Bonde, 149.
1969. *Glyphithyreus wetherelli* (Bell): Via, 302.
1978. *Glyphithyreus wetherelli* (Bell): Collins and Morris, 1980.
1985. *Glyphithyreus wetherelli* (Bell): Heilmann-Clausen, 289.

Diagnosis: Carapace subquadrate, hepatic and epibranchial lobes strongly tumid; a tubercle lateral to each epigastric lobe.

Derivation of name: With reference to the tubercle on either side of the epigastric lobes.

Material: 219 specimens. Holotype. An external mould of a carapace MGUH 26794, paratypes, MGUH 26793 and MGUH 26795-26797, GM 203.1132-1346.

Description: Carapace subquadrate in outline, the width slightly exceeding the length, transversely and longitudinally moderately convex. Deep, broadly ovate orbits take up the outer thirds of the broadly rounded orbitofrontal margin which occupies about 65 percent of the carapace width. The slightly produced, straight front has a broadly V-shaped median sulcus and is separated by a notch from thickened and granulated upper orbital margins; of two marginal notches, the second is stronger. The orbits are slightly oblique to a weak outer orbital spine. There are four sharply upturned spines on the anterolateral margin, the 3rd spine the largest. From the 4th spine a strong, rounded ridge bounds the branchiocardiac furrow along the branchiostegite. Weakly rounded posterolateral margins converge to the posterior margin which is narrower than the orbitofrontal margin, upturned and bounded by a granulated ridge.

Lobes are well differentiated and tumid. From just below a pair of gastric pits, the cervical furrow is faint and broadly V-shaped to the mesogastric angles then sinuous to the margin. The mesogastric lobe is onion-shaped; its slender anterior process extends to the base of small, ovate epigastric lobes. Flattened subtriangular protogastric lobes contrast with markedly nodose, circular hepatic regions. Equally nodose, ovate epibranchial lobes are well separated from small, subtriangular mesobranchial lobes. The urogastric lobe anteriorly forms a narrow ridge embracing the mesogastric lobe and is depressed posteriorly. The internal mould of the cardiac region has three weak tubercles in an inverted triangle, but on the shell surface they are represented by pits, the basal one on a slight prominence. There is a small, but distinct tubercle lateral to each epigastric lobe; minute granules crowd the tops of the lobes, the furrows are smooth.

Male sternites are wider in proportion to length than those of female. Length (from 3rd/4th suture)/width (across 6th sternites) of male, 94.5 percent; of female, 77 percent; surface features remain basically similar in both sexes. The first and second sternites are small and equitriangular with weakly biconcave base; 3rd sternites with median trough expanding proximally, are biconvex distally with sharp lateral angles and well rounded basally; 4th sternites subquadrate, a groove from distal margin, rather more than half distance from midline, curves towards a small articulating notch from which a comparatively large episternite is directed straight along the 5th sternite margin. Sternites 5-7 subtriangular with the well rounded anterolateral angle curving to broad episternites. The male abdomen reaches just beyond midlength of 4th sternites; telson subtriangular. Somites not fused - or if so, strongly sutured; 6th slightly longer than 5th; 4th somites slightly wider than 5th; 3rd twice width of 6th. Abdomen of female reaches the 3rd/4th suture; telson almost semicircular; basal width of 6th somite twice that of the male, otherwise relative length/width proportions of somites agree. A broadly rounded median ridge is more prominent in the female.

Chelae are markedly heterochelate by allometric progression in the male, less so in the female. Male right (major) chela: merus about one third carapace width, transversely ovate, distal height about half the length, with a prominent spine before constriction bounding the carpal margin and a blunt spine at the base of the constriction; Carpus about half length of merus, outer surface obscured, there is a sharp distal spine on the upper margin. Propodus longer than the combined merus and carpus; upper and lower margins almost straight and parallel, outer surface convex, inner surface flattened; there is a marked depression before the convex, slightly depressed fixed finger which is about as long as the manus, with the angular corner continuing as an obscure ridge along the manus. The occludent margin has two small proximal cusps and another one third distant from the tip. In closed position the dactylus forms a continuous arc with the upper margin of the manus.

The left chela is about half the size of the right, the upper margin

is more convex, the fixed finger more in line with the basal margin. Carapace MGUH 26795 is peculiar in having the above distinctive chelae on opposite sides, additionally, the smaller chela, retains 'right-hand' features. Possible female associated chelae are somewhat more delicate.

Discussion: *Glyphithyreus bituberculatus* sp. nov. has much in common with *Glyphithyreus wetherelli* with which it has been confused on several occasions; it differs in having a tubercle either side of relatively smaller epigastric lobes, distinctly separated epi- and mesobranchial lobes and in lacking a ridge extending across the metabranchial and cardiac lobes (which in worn carapaces of *G. wetherelli* appears continuous); in addition, the hepatic and epibranchial lobes of *G. bituberculatus* are markedly tumid and the cardiac tubercles are poorly developed. There is also a disparity in the carapace length/width ratios. Length/width (between 2nd and 3rd lateral spines) percentages taken by Collins and Morris (1978) of British and Pakistani carapaces of *G. wetherelli* (which in Pakistan ranges in age from Thanetian Upper Ranikot Formation to Lower Eocene Ghazi Formation) ranged between 74.5-83.4 and were shown to fall into two groups 74-77 and 79-83 which difference was attributed to possible sexual dimorphism. The L/W percentage of *Glyphithyreus formosus* Reuss, 1859 (Cenomanian) is a distinctive 64.0 percent (Collins and Morris, 1978). Percentages calculated from the Lillebælt carapaces range between 84.1-90.8. These, likewise fall into two groups, 84.1-86.7 and 88.0-90.8.

The presence of only three pairs of lateral spines immediately distinguishes both the North American species, *Glyphithyreus weaveri* (Rathbun, 1926) and *Glyphithyreus vancouverensis* Woodward (1896) both of which species were considered by Feldmann *et al.* (1998) to be better placed elsewhere. Characters distinguishing ? *Glyphithyreus wickmanni* Feldmann *et al.*, 1995 (Danian, Argentina) from *G. wetherelli* serve to differentiate that species from *G. bituberculatus*. The lobes of *Glyphithyreus sturgeoni* Feldmann *et al.*, 1998, Middle Eocene, North Carolina, considered by those authors to be "most closely related to the type species" are less well defined, the protogastric lobes are smooth and the extra frontal tubercles are wanting.

The dorsal surface of *G. bituberculatus* has characters in common with *Lobonotus* spp., particularly in the isolated nature of the cardiac/metabranchial lobes (which, nonetheless, have a tendency to become conjoined by inserted tubercles). Associated chelipeds are rare in *Lobonotus*, but as exemplified by *Lobonotus lobulatus* Feldmann *et al.*, 1995, a right (? major) chela is much stouter then the (left hand) major claw of *G. bidentatus*; the occludent margins of both fingers of *L. lobulatus* have a typical xanthid arrangement of several coarse proximal tubercles, developing, on the fixed finger, to small, tricuspid tubercles distally. In sharp contrast, as remarked above, in *G. bituberculatus* the occludent margin carries only three small cusps; a similar number of opposing cusps lines the fixed finger.

Genus *Fredericia* gen. nov.

Type species: *Fredericia barsoei* sp. nov. by monotypy.

Diagnosis: Carapace circular in outline, a miniscule spine at lateral angle, subglobose; a bilobed front with median nodes slightly in advance of inner orbital angles; orbitofrontal margin about 57 percent carapace width; orbits circular; regions ill-defined, an inconspicuous cervical notch; a broad transverse depression posterior to midlength; 3rd/5th male abdominal somites fused.

Range: Middle Eocene.

Derivation of name: Fredericia - a principle town near to Trelde Næs.

***Fredericia barsoei* sp. nov.**
(Fig. 7; Pl. 6, Figs. 1-7)



Fig. 7. *Fredericia barsoei* sp. nov., carapace reconstruction, line drawing.

Diagnosis: As for genus.

Derivation of name: In recognition of the cooperation of Ole Barsøe Hansen, Kolding.

Material: 482 specimens. Holotype, a carapace with chelipeds MGUH 26798, paratypes, MGUH 26799-26804, GM2003.741-1126; 2003.1392-1482.

Description: Carapace subcircular in outline, a little wider than long, longitudinally steeply arched, reaching its highest point one third distant from the front, weakly arched transversely. The orbitofrontal margin occupies rather more than two thirds of the carapace width; of this the front, taking up the median 60 percent, extends beyond bluntly rounded inner orbital spines; a wide U-shaped notch separates a pair of bluntly rounded frontal lobes; thickened, concave sides terminate at rounded inner orbital nodes. The orbital margin is entire and the outer angle is sharp, to bluntly rounded. Orbits are circular and deep. The epistome is narrow and triangular. Isosceles-triangular basal antennule segments occupy the basal half of the antennary fossae, while small subtriangular basal antenna segments are lodged below the inner orbital angles. Short anterolateral margins have a sharp edge terminating in an inconspicuous cervical notch; and become rounded behind an incipient spine at the lateral angle, anterior to a broad, transverse depression. Weak coxigeal incisions are almost in line with the posterior margin which is as wide as the front and bounded by a ridge and deep groove.

Regions weakly defined. A faint cervical furrow, curving broadly

across the midline anterior to midlength, unites with a more conspicuous hepatic furrow and, turning outwards becomes obsolete before reaching the margin or, on internal casts, seen as a depression behind the triangular hepatic region. The hepatic furrow extends towards the outer orbital angle. Internal casts also indicate a sulcus extending from the frontal notch bifurcating round the tip of a parallel sided anteromesogastric process of a small, triangular mesogastric lobe. Short cardiac furrows delineate a rectangular urogastric lobe and distal part of a long shield-shaped cardiac region. Numerous pits on the dorsal surface are scattered among a dense covering of minute granules, running together to produce loops and swirls, particularly round the cardiac region. Minute granules lining the lateral part of the front become more prominent on the orbital margin.

The buccal cavity is quadrate and rimmed laterally; the epistome narrow and triangular.

Male sternites are markedly narrower in relation to carapace width. In the female, the 3rd sternites are divided by a broad cleft, widening posteriorly. Otherwise, general characters of the sternites of both sexes are: triangular 1st and 2nd sternites sharply defined from broad, lozenge-shaped 3rd sternites, separated from the 4th by a deep groove; subquadrangular 4th sternites have an arcuate coxigeal margin terminating in an articular notch, a concave basal margin leads to large rounded-triangular episternites; subtrapezoid sternites 5, and sub-chordate 6th have similar robust episternites.

The male telson extends to about midlength of the 4th sternites; somite 6 is rectangular, short lateral sulci separate otherwise fused 3rd/5th sternites. Triangular telson of female reaches at least to the 3rd/4th sternites; the 6th abdominal somite is rectangular and twice as long as the 3rd/5th somites.

Female chelae robust and slightly heterochelate, the left the larger-carpus subquadrate, subovate in transverse section, lower margin about one third longer than the upper, outer surface smooth. Propodus, a little less than twice the width of carpus, distal height about three fourths the length, reducing proximally, interdigital margin vertical, fingers missing. Carpus of right chela similar to that of left; propodus a little shorter than left, distal height about two thirds the length, the lower margin weakly concave before compressed fixed finger, the lower margin of which is deeply convex for two thirds its length, a large proximal cusp preceeds two smaller ones. Interdigital margin concave. Proximal height of curved dactylus about one fifth the length, corresponding cavities to fixed finger cusps on the occludent margin suggest a distal gape.

? Male right chela has the fixed finger in line with basal margin, half length of propodus, Proximal height about one third that of propodus, occludent margin, sloping directly to tip, has two or three blunt proximal cusps. Dactylus slender, with almost smooth occludent margin producing a gape.

Left cheliped: propodus only a little longer and much the same height as right, fixed finger slightly downcurved with a basal groove; occludent margin with three sharp triangular cusps reducing in size to an upturned tip. Dactylus grooved along upper margin and with contra-corresponding occludent cusps.

Discussion: In having a subcircular outline and transverse depression, *Fredericia* gen. nov. is evidently close to *Palaeograpsus* Bittner, 1875, a genus confirmed in the Goneplacidae by Karasawa and Kato (2001). However, the essential difference of *Fredericia* from *Palaeograpsus* is seen in the fusion of the 3rd/4th male abdominal somites, as well as having a bilobed, weakly sulcate rather than straight front, an incipient lateral spine instead of the two weak spines of *Palaeograpsus* and a weaker, sinuous cervical furrow.

The sternites of *F. barsoei* are remarkably similar to those of *Glyphithyreus bituberculatus* sp. nov., although in *Glyphithyreus* the 3rd sternites of the male as well as the female have a median cleft and there is a longitudinal cleft on the 4th sternites..

Family Panopeidae Ortmann, 1893

Genus *Panopeus sensu lato* H. Milne Edwards, 1834

Type species: *Panopeus herbstii* H. Milne Edwards, 1834 by subsequent designation ICZN Opinion, 1282, 1984.

Range: Lower Eocene - Recent.

***Panopeus bessmanni* sp. nov.**

(Fig. 8; Pl. 7, Figs. 1-3)

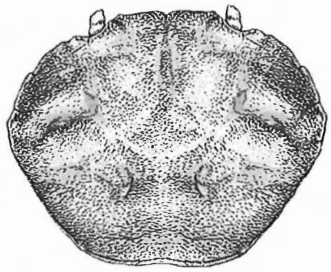


Fig. 8. *Panopeus bessmanni* sp. nov., carapace reconstruction, line drawing.

Diagnosis: Carapace subhexagonal, wider than long, flattened transversely, weakly arched longitudinally; front with weak median notch, two infilled notches in upper orbital margin; ridges well developed on hepatic and epibranchial lobes, weaker on steep-fronted protogastric lobes.

Derivation of name: The species is named for H. C. Bessmann Hansen, collector.

Material: 48 specimens. Holotype. A carapace, MGUH 26805, paratypes, MGUH 26806-26807, GM2003.692-739.

Description: Carapace subhexagonal, broader than long, widest about midlength, quadrilobate in frontal view, the outer pair of lobes lower than inner pair, longitudinally more steeply downturned in front. The orbitofrontal margin occupies about 30 percent of the carapace width, of this the weakly produced front takes up half; it is nearly straight with a weak median sulcus and lined with minute

granules terminating at a notch before thickened upper orbital margins which have a closed fissure in line with the hepatic furrow and (more obvious on internal casts) a shorter one before the external angle. The orbits are circular. The anterolateral margins are broadly curved with thin lateral edges. A weak notch separates insipient 1st and 2nd anterolateral spines; the 3rd spine at the lateral angle is little more than a tubercle and the 4th is sharp and triangular.

The regions are well defined and tumid. From close set gastric pits rather more than half distant from the front, the cervical furrow curves broadly across the base of the mesogastric lobe to the hepatic furrow, turns sharply out and broadens round the hepatic region. Subquadrate, steep-fronted epigastric lobes are well separated from equally steep fronted protogastric lobes. There is an angular ridge on each hepatic lobe. The sharply angled mesogastric lobe has an inconspicuous postero-median groove. A weak groove separates ridged, subovate epibranchial from subpentagonal mesobranchial lobes. The urogastric lobe is depressed and a trilobed cardiac region has three vague nodes in an inverted triangle. Numerous granules on the dorsal surface tend to form rows posteriorly.

Upper margin of the epistome is ridged and minutely beaded, there is a thin median notch in the basal margin for the head of the endostome. Subovate antennular fossae are twice the length of the circular orbits; the subrectangular basal antennular segment is ridged along the upper margin and finely granulated in the upper lateral angle. The basal antennal segment is subquadrate and the orbital peduncle is medially constricted.

Third maxilliped endopodites are one third longer than broad with convex opposing margins, a concave lateral margin is finely beaded; a deep groove at inner third extends almost the entire length and a weaker groove borders the lateral margin. Poorly preserved exopodites are about the same width of the inner portion of the endopodites.

Sternites of both sexes more or less similar: a convexi-concave groove separates weakly tumid, triangular 1st/2nd sternites from wide, subtriangular 3rd sternites; 4th sternites, deeply separated from the 3rd, subquadrate with sinuous anterior margin. 5th, and slightly larger 6th elements chordate, both appearing subquadrate when covered by the abdomen; 5th and 6th elements are overlapped by narrow, triangular episternites from preceding elements. The entire surface is densely granulated.

Male abdominal trough extends two thirds into 4th sternal elements, sides of abdomen almost straight, diverging weakly from the midline: telson semiovate, about twice length of rectangular 6th somite, 5th and 4th somites are a little shorter.

Female abdominal trough extends to anterior margin of the 4th sternites; the abdomen is wider and the sides are only a little more divergent than those of the male. The telson is relatively longer, about twice length of rectangular 6th somite, 5th and 4th somites a little shorter than the 6th.

Abdomina of both sexes are smooth, in contrast to the minutely granulated sternites.

Male chelae marginally heterochelate: right merus length almost equals height, a shallow groove bounds the carpal margin, upper margin thin, minutely beaded, surface minutely granulated. Carpus rounded triangular, about one fifth as long as propodus, nearly as long as high, propodal margin bounded by ridge. Propodus, distal height about four fifths length, upper and lower margins weakly convex, upper edge flattened between finely beaded ridges, lower edge rounded, carpal margin oblique, interdigital margin slightly concave, vertical. Fixed finger in line with basal margin, half length of propodus, proximal height one third of propodal height; occludent margin sloping directly to tip, has two or three blunt cusps proximally. Dactylus very slender, occludent margin smooth, producing a gape.

Left cheliped: propodus only a little longer and much the same height as right, fixed finger slightly downcurved with basal groove; occludent margin with three sharp, triangular cusps reducing in size to upturned tip. Dactylus grooved along upper margin and with contra-corresponding occludent cusps.

Discussion: The ridges and lobation of *Panopeus bessmanni* sp. nov. fall within the considerable degree of variation of the anatomical characters among the eleven fossil species (including the fossil occurrence of the Recent *Panopeus herbstii*) recognised by Schweitzer (2000). Although the lobation of *P. bessmanni* is rather more pronounced than generally seen on European species, it approaches that of *Panopeus olearis* (Rathbun, 1926), Oligocene, Alaska, which immediately differs in having a rounded, less angulate cardiac region, *Lophopanopeus bellus* (Stimpson, 1860) referred to by Rathbun (1926) has essentially similar lobation to that of *P. bessmanni*, but has more quadrate epigastric lobes and lacks ridges.

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Plate 1

Fig. 1. *Pagurus langei* sp. nov. Holotype, MGUH 26771, plaster cast of outer surface of right cheliped and domicile gastropod, *Volutocorbis* sp., a, carpus; b, propodus and part of dactylus; c, merus.

Fig. 2. *Ctenocheles anderseni* sp. nov. Holotype, MGUH 26772, inner surface of right chela, together with paratype, MGUH 26773, an external mould of a left chela; 2 a, silicone rubber cast of left chela, MGUH 26773.

Fig. 3. *Ctenocheles anderseni* sp. nov. Paratype, MGUH 26774, two left propodi in the same nodule; 3a, enlargement of tip of fixed finger; 3b, opposite side of the same nodule showing dactylus.

Fig. 4. *Ctenocheles anderseni* sp. nov. Paratype, MGUH 26775, outer surface of right dactylus.

Scale bars: 10 mm

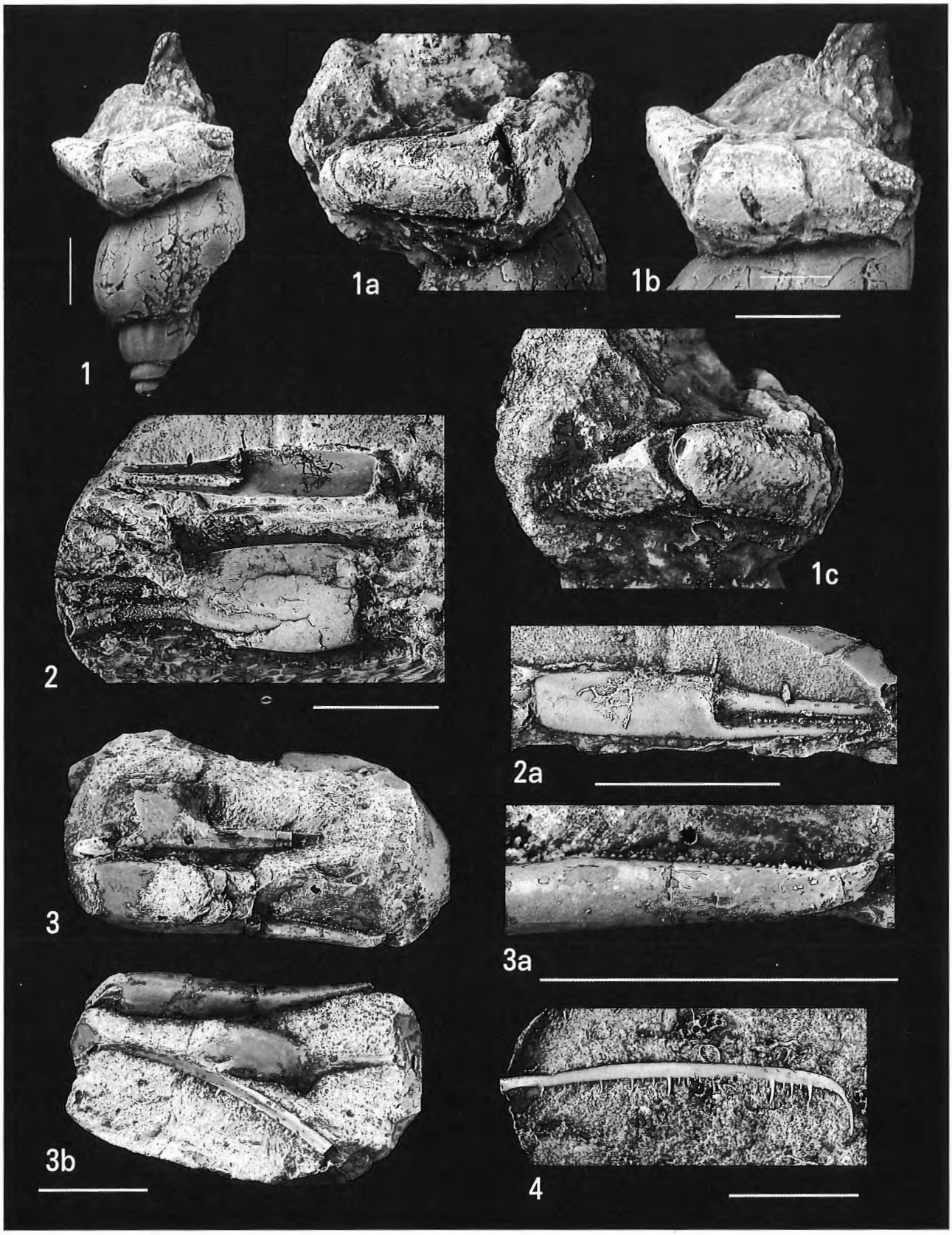

1
1a
1b
1c
2
2a
3
3a
3b
4

Plate 2

Figs. 1-7. *Basinotopus tricornis* sp. nov.

Fig. 1. Paratype, MGUH 26776, dorsal view of a female, 1b, enlargement of sternites.

Fig. 2. Paratype, MGUH 26777, dorsal view of carapace.

Fig. 3. Silicon rubber cast of external mould of holotype, MGUH 26778, showing well preserved frontal region.

Fig. 4. Paratype, MGUH 26779, outer surface of right cheliped and meri of 1st and 2nd pereiopods.

Fig. 5. A silicone rubber cast of external mould of Paratype, MGUH 26780, 5a, right lateral and 5b, frontal view.

Fig. 6. Paratype, MGUH 26781, outer surface of left chela.

Fig. 7. Paratype, MGUH 26782, ventral view showing buccal and pterygostomian regions.

Fig. 8. *Basinotopus lamarckii* (Desmarest). MGUH 26783, London Clay, Isle of Sheppey, 8a, poorly preserved carapace, 8b, enlargement of rostrum, 8c, outer surface of left chela.

Scale bars: 10 mm, except fig. 8b: 5 mm

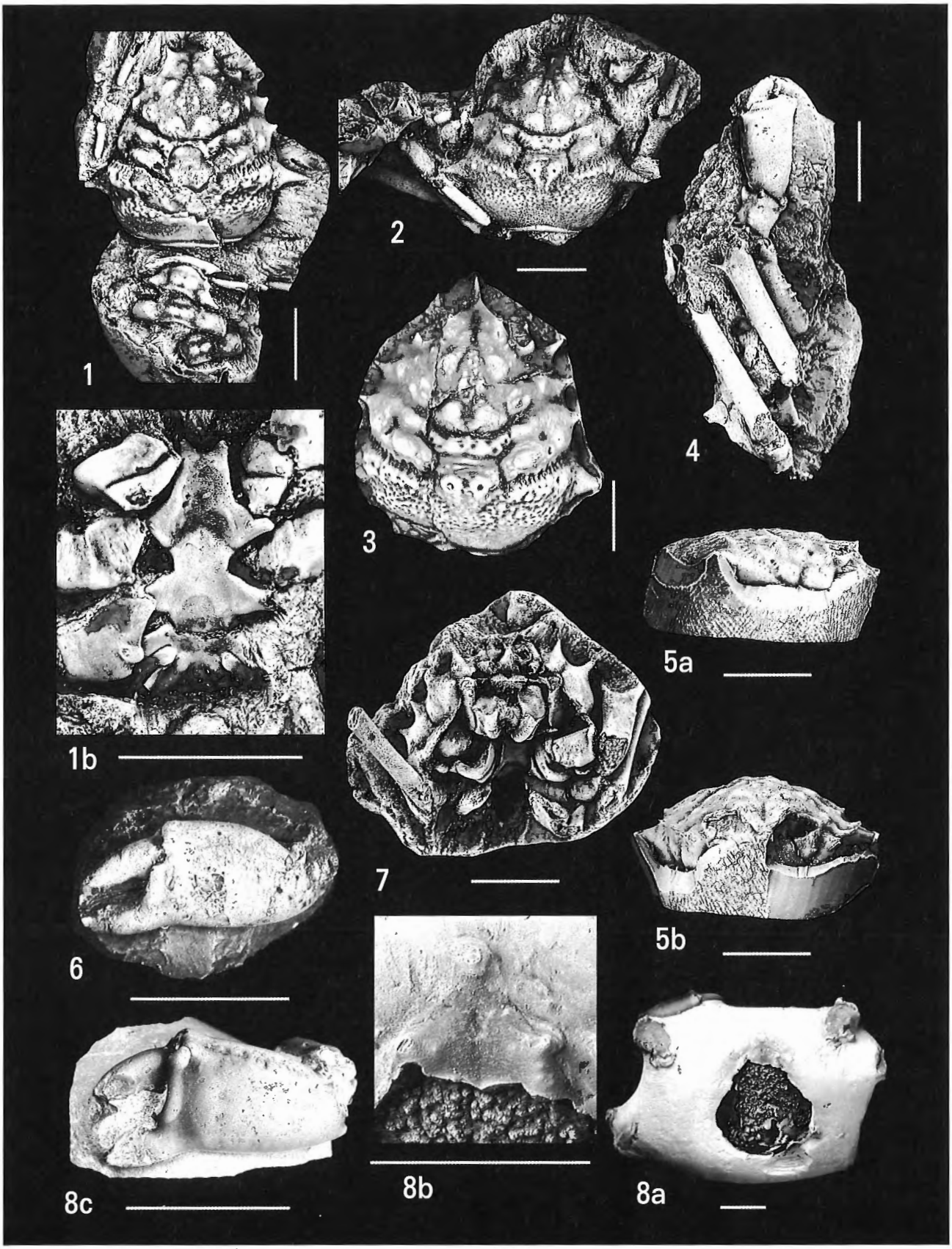

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3
4
5a
1b
7
5b
6
8c
8b
8a

Plate 3

Figs. 1-3. *Goniochele madseni* sp. nov.

Fig. 1. Holotype, MGUH 26784, 1a, dorsal view, 1b, frontal view.

Fig. 2. Paratype, MGUH 26785, 2a, ventral surface of a female; 2b, enlargement of 3rd maxillipedes; 2c, silicone rubber cast of inner surface of right chela.

Fig. 3. Reconstruction of dorsal surface.

Fig. 4. *Goniochele angulata* Bell (Natural History Museum London, IC 48212) from London Clay, Isle of Sheppey, Kent, a, b. ventral and dorsal views of a female.

Fig. 5. *Laeviranina treldenaesensis* sp. nov. Holotype, MGUH 26786, 5a, dorsal; 5b, ventral; 5c, frontal; 5d, right lateral view; 5e, enlargement of sternite. Note damaged dorsal area attributed to gastric corruption.

Scale bars: 10 mm, except fig. 2c: 5 mm

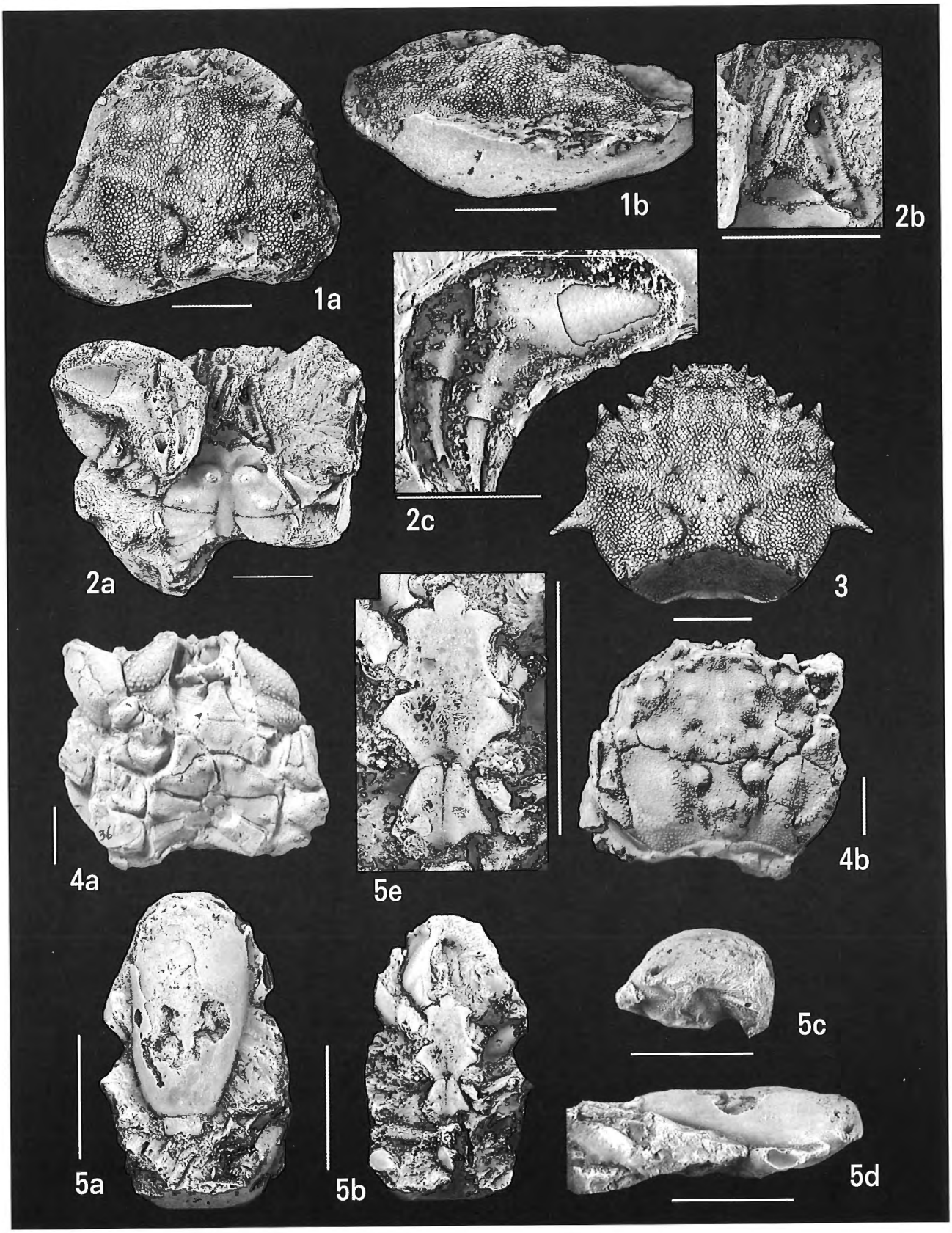

1a
1b
2a
2b
2c
3
4a
4b
5a
5b
5c
5d
5e

Plate 4

Figs. 1-6. *Falsiportunites longispinosus* gen. et sp. nov.

Fig. 1. Holotype, MGUH 26787, latex cast of a female, 1a, dorsal view, 1b, ventral view, 1c, enlargement of abdomen.

Fig. 2. Paratype, MGUH 26788, acid prepared silicone rubber cast of a male, 2a, dorsal view, 2b, ventral view.

Fig. 3. Paratype, MGUH 26789, enlargement of a male abdomen.

Fig. 4. Paratype, MGUH 26790, outer surface of chelae.

Fig. 5. Paratype, MGUH 26791, silicone rubber cast of a carapace.

Fig. 6. Paratype, MGUH 26792, 6a, silicone rubber cast of female abdomen, 6b, enlargement of 3rd maxillipedes.

Scale bars: 10 mm

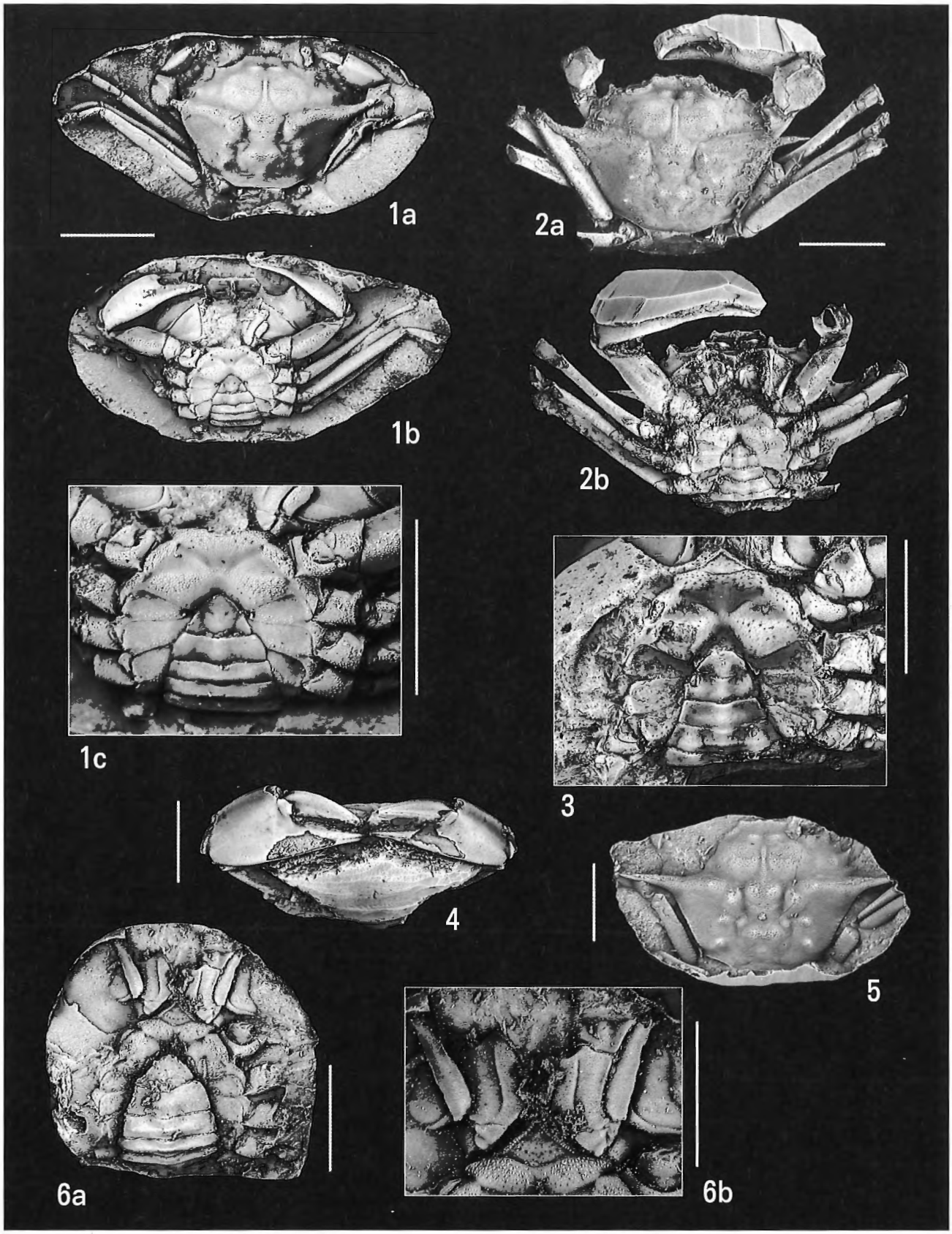

1a
2a
1b
2b
1c
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6a
6b

Plate 5

Figs. 1-5. *Glyphithyreus bituberculatus* sp. nov.

Fig. 1. Paratype, MGUH 26793, acid prepared cast of dorsal surface of a female carapace.

Fig. 2. Holotype, MGUH 26794, 2a, silicone rubber cast of dorsal view, 2b, left lateral view, 2c, frontal view of male carapace.

Fig. 3. Paratype, MGUH 26795, outer surface of a right cheliped.

Fig. 4. Paratype, MGUH 26796, 4a, latex cast of external mould of ventral surface of a female; 4b, enlargements of abdomen, 4c, enlargement of 3rd maxillipedes.

Fig. 5. Paratype, MGUH 26797, 5a, acid prepared silicone rubber cast of ventral surface of a male, 5b, enlargement of abdomen.

Scale bars: 10 mm

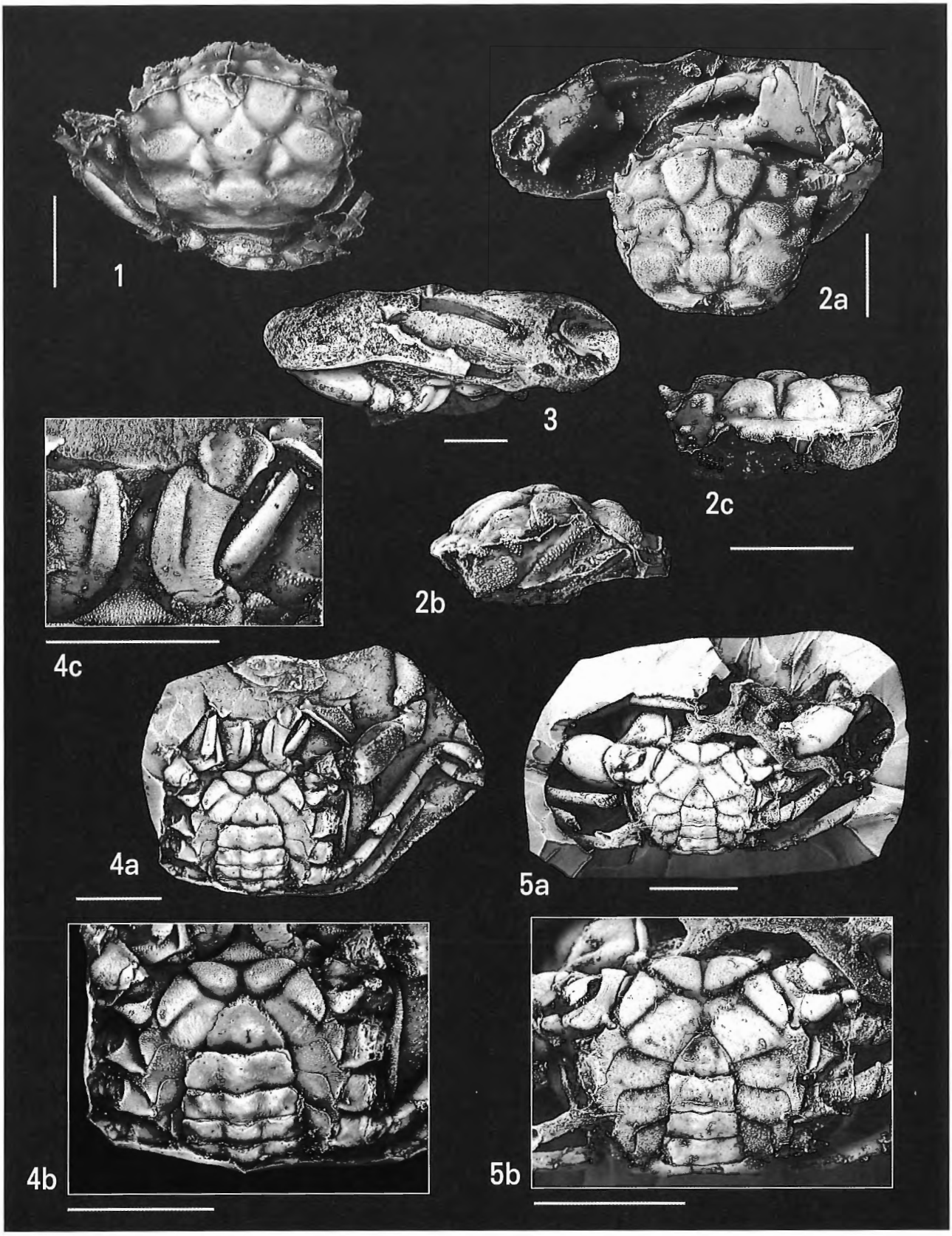

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2a
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2c
2b
4c
4a
5a
4b
5b

Plate 6

Figs. 1-7. *Fredericia barsoei* gen. et sp. nov.

Fig. 1. Holotype, MGUH 26798 of a male, 1a, dorsal view, 1b, ventral view, 1c, inclined frontal view, 1d, frontal view.

Fig. 2. Paratype, MGUH 26799 of a male, 2a, exposing both chelipeds, 2b, enlargement of outer surface of right chela.

Fig. 3. Paratype, MGUH 26800, a carapace, 3a, frontal view, 3b, left lateral view.

Fig. 4. Paratype, MGUH 26801, outer surface of left chela.

Fig. 5. Paratype, MGUH 26802, acid prepared silicone rubber cast of ventral surface of a male.

Fig. 6. Paratype, MGUH 26803, silicone rubber cast of male sternites and abdomen.

Fig. 7. Paratype, MGUH 26804, female sternites and abdomen.

Scale bars: 10 mm

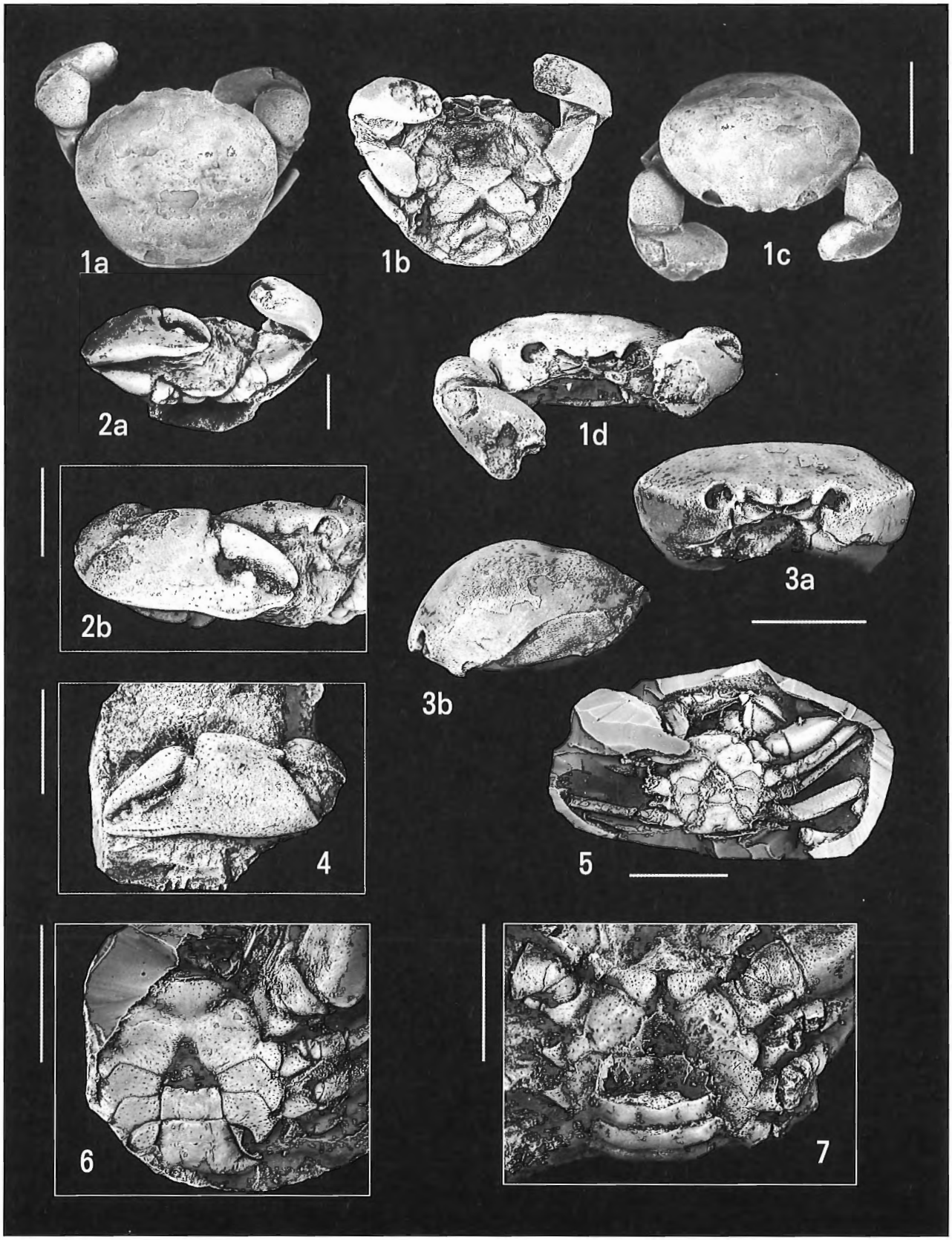

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1d
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3a
3b
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Plate 7

Figs. 1-3. *Panopeus bessmanni* sp. n ov.

Fig. 1. Holotype, MGUH 26805 of a carapace, 1a, dorsal view, 1b, frontal view.

Fig. 2. Acid prepared silicone rubber cast of paratype, MGUH 26806 of a female, 2a, dorsal view, 2b, frontal view, 2c, ventral view, 2d, enlargement of left chela, 2e, enlargement of sternites and abdomen, 2f, right anterolateral margin.

Fig. 3. Acid prepared silicone rubber cast of paratype, MGUH 26807 of a male, 3a, dorsal, 3b, ventral view, 3c, enlargement of included gastropod, *Limacina* sp., 3d, left-hand 3rd maxillipede, 3e, enlargement of female sternites and abdomen.

Scale bars: 10 mm, except figs. 3c and 3d: 5 mm

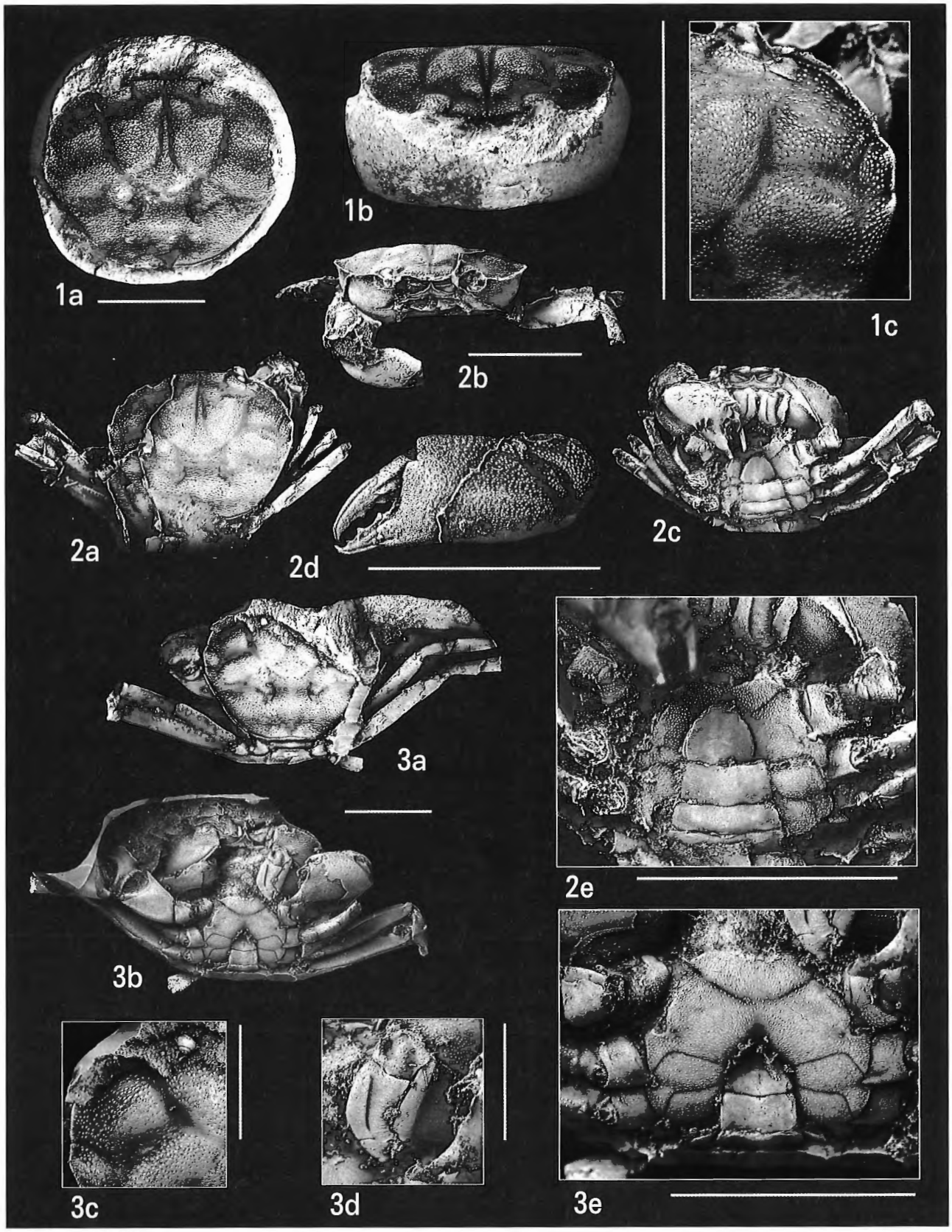

1a
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2a
2b
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2e
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3c
3d
3e

Plate 8

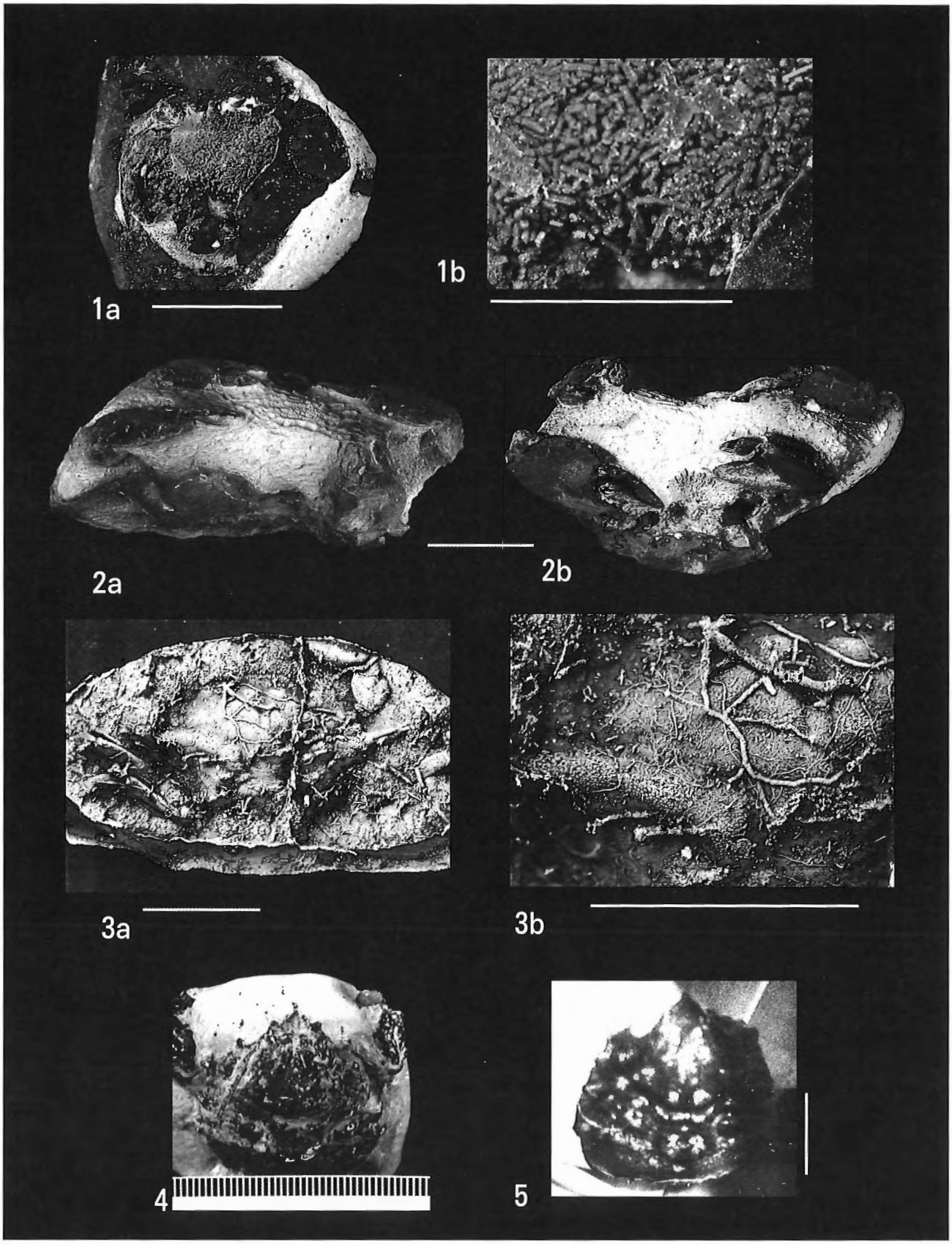
Fig. 1. *Panopeus bessmanni* sp. nov. MGUH 26808, 1a, pellet filled internal cavity of carapace, 1b, enlargement of right median area.

Fig. 2. *Falsiportunites longispinosus* sp. nov. MGUH 26809, 2a, frontodorsal view of one carapace preserved over another, interpreted as a possible postmoult/death occurrence, 2b, frontoventral view showing juxtaposition of chelipeds.

Fig. 3. *Falsiportunites longispinosus* sp. nov. MGUH 26810, acid prepared silicone rubber cast of carapace and accompanying presumed infilled worm burrows.

Figs. 4, 5. *Basinotopus lamarckii* (Desmarest) Fig. 5, a carapace (In 48212), Natural History Museum, London) with a well preserved front, yet lacking the detail preserved on, Fig. 6, a carapace (C19324) in the Sedgwick Museum, Cambridge, U. K.

scale bars: 10 mm


1a
1b
2a
2b
3a
3b
4
5