

***DINOCHELUS STEEPLENSIS*, A NEW SPECIES OF CLAWED LOBSTER (NEPHROPIDAE) FROM THE LONDON CLAY (EOCENE) OF ENGLAND**

Dale Tshudy^{1,*} and Jeff Saward²

¹ Department of Geosciences, Edinboro University of Pennsylvania, Edinboro, PA 16444, USA

² 53 Thundersley Grove, Thundersley, Essex SS7 3EB, UK

ABSTRACT

A new species of clawed lobster, *Dinochelus steeplensis*, is reported from the London Clay (Eocene: Ypresian) of England. This is the first report of *Dinochelus* from the fossil record. The genus was previously known by one recent, deep-water species. Four genera, the fossil *Oncopareia* and extant *Thaumastocheles*, *Thaumastochelopsis* and *Dinochelus*, comprise the thaumastochelid lobsters, a cladistically cohesive group (minus *Dinochelus*) formerly given family-level status as Thaumastochelidae Bate, 1888. These lobsters are united, and readily distinguished from other nephropids, by their short, quadrate, pleonal pleura and by their major claw morphology (a short, bulb-like palm and very long, slender fingers bearing acicular dentition). Also described herein is an occurrence of *Thaumastocheles* sp. from the Miocene of Chile. We now have a monophyletic group of lobsters with a fossil record extending back 90 million years and, with the new fossils reported herein, morphologic end members connected by a range of intermediates. It seems certain that *Oncopareia* is the least derived of the thaumastochelids, and it is reasonable to conclude that *Dinochelus* and *Thaumastocheles* are intermediate between *Oncopareia* and the most derived genus, *Thaumastochelopsis*. The new fossil species, *D. steeplensis*, shows that the carapace and minor claw form of recent thaumastochelids had evolved by the early Eocene (ca. 52-58 mya), and that thaumastochelids were living in outer shelf depths at that time. The new species, being morphologically, stratigraphically, and bathymetrically intermediate between previously known fossil *Oncopareia* and recent *thaumastochelids*, is at least consistent with the previously hypothesized retreat of the thaumastochelids off of the shelf and into deeper waters in the Cenozoic.

KEY WORDS: Decapoda, *Dinochelus*, lobster, London Clay, Nephropidae, *Oncopareia*, *Thaumastocheles*, *Thaumastochelopsis*, Thaumastochelidae

DOI: 10.1163/193724011X615343

INTRODUCTION

In the pioneering publication of Bell (1858), ‘Monograph of the Fossil Malacostracous Crustacea of the London Clay’, the author figured (plate X, no. 9) an unusual specimen of the clawed lobster, *Hoploparia belli* M’Coy, 1849 (= *H. gammaroides* M’Coy, 1849), collected by Dr. Nathaniel Wetherell, probably in the 1840s, from the railway excavations at Chalk Farm, London. Bell labeled this “an abnormal form of the carapace of *H. belli*, or possibly a distinct species”. Bell refrained from describing this single specimen as a new species, with good reason, and went on to remark (pp. 40-41) that it is “...only a mutilated carapace...[and] most probably it is, after all, only an accidentally abnormal condition of *H. belli*”. This specimen, subsequently deposited by Wetherell in the Natural History Museum in London (BM 59132B), is effectively the earliest published reference to the new species described here. More recently, Wetherell’s “mutilated carapace” from Chalk Farm was included as a paratype in the description of *Hoploparia wardi* (Quayle, 1987). This specimen, consisting of an isolated carapace and a few pleonal fragments, might have provided a clue to its true identity had the chelae also been preserved. Renewed interest in collecting the crustacean fossils of the London Clay in the 1970s by members of the

Tertiary Research Group recorded slender claw fragments with distinctive comb-like teeth at Ongar, Essex (Cooper, 1974a). These were tentatively ascribed to the mud shrimp *Ctenocheles* sp. (Cooper, 1974b), but no further effort was made to describe them.

During the mid-1990s, a number of further specimens were collected by the coauthor (JS) and colleagues, especially from Maylandsea and Steeple Bay, Essex. These include well-preserved carapaces and pleons that closely resembled Wetherell’s Chalk Farm specimen (and therefore one of the paratypes of *H. wardi*). However, a few of these specimens also have articulated chelipeds, revealing a distinctive inflated palm on the major claw. Initially considered to be specimens of the previously alluded *Ctenocheles* sp., the lack of a linea thalassinica on the better-preserved carapaces and the distinctive inflated major claws suggested that this species may be more closely allied to the recent clawed lobster genus *Thaumastocheles* Bate, 1888 (Collins and Saward, 2006). Finally, discovery and preparation of more and better specimens from the London Clay of Essex has now provided the answer to this long-running mystery, first raised by Thomas Bell over 150 years ago. The fossil specimens are indeed very similar to the extant clawed

* Corresponding author; e-mail: dtshudy@edinboro.edu

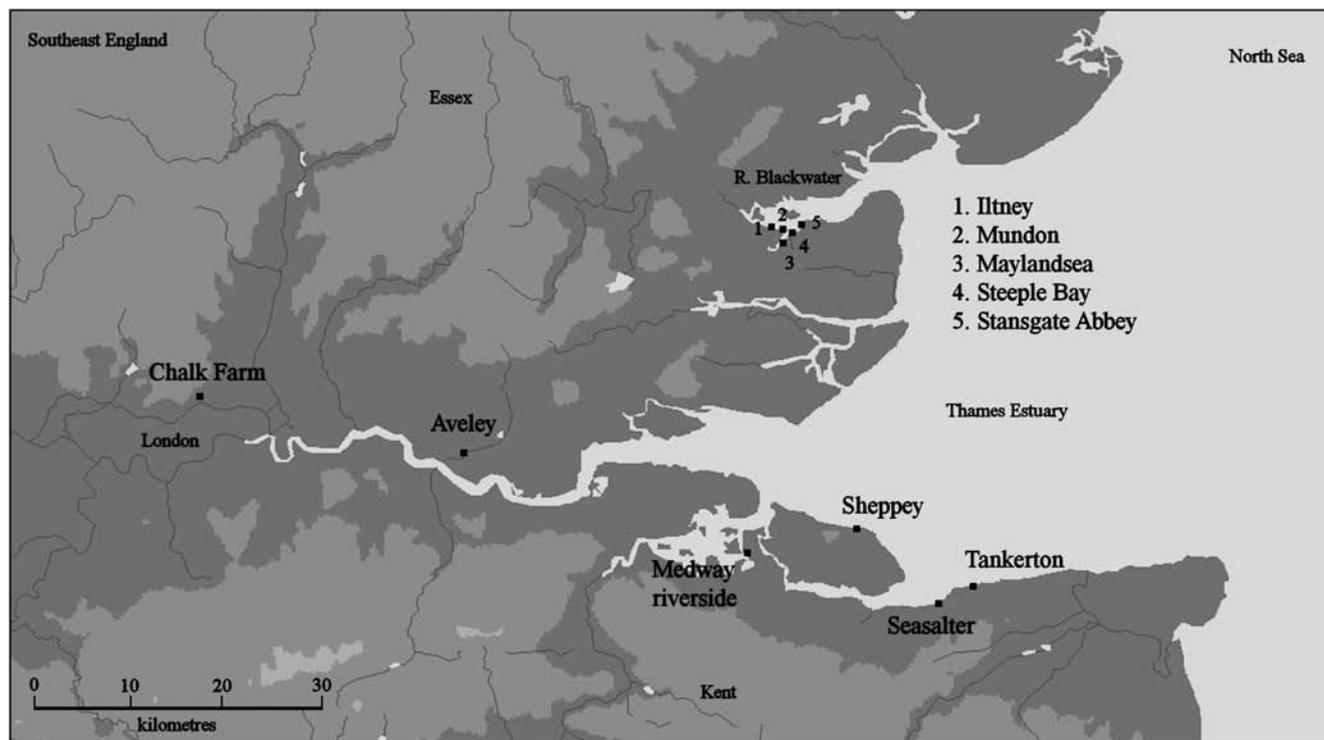


Fig. 1. Map showing collecting localities (numbered or indicated by black squares) in London, Essex and Kent, Southeast England.

lobsters *Thaumastocheles*, *Thaumastochelopsis* Bruce, 1988 and the recently discovered *Dinocheilus* Ah Yong et al., 2010.

Following recent phylogenetic studies (Tsang et al., 2008; Chu et al., 2009; Tshudy et al., 2009), these “thaumastochelid” lobsters are referred to Nephropidae Dana, 1852, the most diverse family of extant marine, clawed lobsters. Thaumastochelid genera were formerly referred to Thaumastochelidae Bate, 1888. The four thaumastochelid genera, *Oncopareia* [4 species: Late Cretaceous (Turonian)-Tertiary (Paleocene)], *Thaumastocheles* (3 extant species), *Thaumastochelopsis* (2 extant species) and *Dinocheilus* (1 recent species, 1 new fossil species reported herein), are closely related [dependably monophyletic in cladistic analyses, e.g., Ah Yong, 2006 (morphological study – minus *Dinocheilus*) and Ah Yong et al., 2010 (molecular study – minus *Oncopareia*], but recent thaumastochelids are nested within Nephropidae in a recent DNA analyses.

Nephropidae has a fossil record extending back to the Early Cretaceous (Valanginian). Twenty nephropid genera (6 extinct, 10 recent only, 4 extant but with fossil record) and 137 species (56 recent, 80 fossil, 1 extant with fossil record) are recognized.

Oncopareia Bosquet, 1854, sensu Tshudy, 1993 is an extinct, shelf-dwelling lobster known by four named species: type species *Oncopareia bredai* Bosquet, 1854, sensu Tshudy, 1993 (Maastrichtian of Belgium and the Netherlands) (Tshudy and Sorhannus, 2000b); *O. coesfeldiensis* Schlüter, 1862 [“Senonian” (Turonian-Maastrichtian) of Germany]; *O. esocinus* (Fritsch and Kafka, 1887) (upper Turonian of Czech Republic); *O. klintbjergensis* Jakobsen and Collins, 1979 (Paleocene of Denmark). There are also some occurrences referred only to *Oncopareia* sp., including *O.*

sp. (Cretaceous – Upper Senonian of Germany) (Mertin, 1941), and *O.* sp. (Upper Maastrichtian of the Netherlands) (Tshudy, 1993).

Thaumastocheles is a blind, deep dweller with no eye stalks. The type species, *Thaumastocheles zaleucus* Thomson, 1873, is known from the West Indies at 650-1054 m (Holthuis, 1991, p. 25), living in soft mud (ooze). *Thaumastocheles japonicus* Calman, 1913 occurs from Indo-West Pacific from Japan to New Caledonia and Madagascar at 360-1110 m (Chan and de Saint Laurent, 1999, p. 899). *Thaumastocheles dochmiodon* Chan and de Saint Laurent, 1999, can be found from the Indo-West Pacific from Japan to NW Australia at 250-822 m (Chan and de Saint Laurent, 1999, p. 891). A fossil occurrence of *Thaumastocheles* sp., newly reported herein, gives the genus a fossil record as old as Miocene.

Thaumastochelopsis Bruce, 1988, is a blind, deep dweller with very small, moveable eyes with unpigmented corneas (Bruce, 1988). It is known by two recent species, the type species, *T. wardi* Bruce, 1988, from the Coral Sea off NE Australia at 452 m, and *T. brucei* Ah Yong et al., 2007, occurring in the Coral Sea along the Great Barrier Reef at 199-250 m (Ah Yong et al., 2007).

Dinocheilus Ah Yong et al., 2010, is a blind, deep dweller with well developed, moveable eye stalks but unpigmented corneas. Prior to the present study, it was known by a single species, *D. ausubeli*, from the Philippine Sea off of the island of Luzon at a depth of 247-249 m. The new fossil species presented herein reveals that the genus had evolved by the early Eocene (or earlier) and was living in outer shelf depths at that time, unlike its modern thaumastochelid relatives which are dwellers of deeper, continental slope habitats.

SYSTEMATICS

Order Decapoda Latreille, 1802

Infraorder Astacidea Latreille, 1802

Nephropidae Dana, 1852, s. Tshudy et al., 2009 (includes the thaumastocheilids)

Dinochelus Ah Yong, Chan and Bouchet, 2010Type species.—*Dinochelus ausubeli* Ah Yong, Chan and Bouchet, 2010.*Dinochelus steeplensis* n. sp.

Figs. 2, 3

Diagnosis.—*Dinochelus* with pleuron 2 having a straight and sharply defined tergite-pleuron boundary, with pleura 2-5 having a well-developed posteroventrally directed carina, and with pleura 2-3 having symmetrical anterior and posterior margins.

Description.—Cephalic and thoracic regions equally high along dorsomedian (IC 564) (Fig. 2B-C); both regions slightly higher at about midlength (Fig. 2B). Cephalic region rectangular in cross section, being wide and rather flat dorsally (IC 564). Cephalothorax, overall, widest over thoracic region, but, dorsally, widest over cephalic region (IC 564) (Fig. 2E).

Rostrum one half length of cephalic region (IC 563) (Fig. 2A). Rostrum tapers smoothly to distal terminus (IC 563). Dorsal surface transversely rounded over proximal half (IC 564, IC 567, IC 569) but flatter distally (IC 567); with circular or transversely elongate, ovate pits within which are several smaller pits for setal hairs (IC 563). At least one (IC 567) or two (IC 569) lateral spines on each side of rostrum distally. Smooth, shallow median furrow along most [or probably all (uncertain proximally)] of length (IC 567).

Postcervical groove well impressed dorsally and laterally (Fig. 2A-E); crosses the dorsal surface as convex forward arc (IC 564) (Fig. 2E); extends anteroventrally over lateral surface as smooth, slightly concave forward arc to hepatic region (prominence χ of Holthuis, 1974), where it joins hepatic groove. Hepatic groove angles slightly more ventrally than postcervical groove; loops under prominence χ . Cuticle smooth in groove (IC 564). Intercervical groove originates on postcervical groove; extends anteroventrally toward but not reaching cervical groove (IC 564, IC 570). Cervical groove deep, about as sharply and deeply defined as ventral end of postcervical groove; extends dorsally from top of prominence ω (of Holthuis, 1974) to level above antennal spine. Area between cervical and postcervical grooves inflated (IC 564). Inferior groove absent (IC 564). Regions χ and ω inflated (IC 563, IC 564); neither region bears distinct spine (hepatic spine absent), but both have one or more tubercles. Antennal groove well developed (IC 564).

Subdorsal carina absent (IC 564). Supraorbital spine present but no carina behind it (IC 563, IC 564, IC 569). Postorbital spine absent (IC 563, IC 564).

Antennal spine length indeterminate. No distinct antennal carina behind the antennal spine (IC 563, IC 564, IC 571). One specimen (IC 563) (Fig. 2A) with short, indistinct (not sharp) ridge, accentuated by the concavity of carapace surface below it; most specimens show, at most, short, rounded ridge in region. Postantennal region with no trace

of carina (IC 563, IC 564). Cervical spine absent (IC 563, IC 564). Postcervical spine absent (IC 564, IC 571). Gastric tubercle absent (IC 564). Dorsomedian line a smooth band; very thin anteriorly but doubling its width posteriorly (IC 564). Elsewhere, cephalic dorsomedian surface covered with transversely elongate pits over most of surface (IC 564); densely pitted anteriorly; pits form a reticulation around base of rostrum (IC 564). Near postcervical groove, sparse, fine tubercles (IC 564). Cephalic region laterally with scattered tubercles of various sizes (IC 563, IC 564, IC 566, IC 570, IC 571).

Thoracic region flat dorsally; flat region narrower than on cephalic region. Lateral boundary of flattened dorsal region forms corner at which carapace bends ventrally. Dorsomedian ridge present over posterior third of thoracic region (IC 564); terminates just short of posterior margin. Intermediate carina absent (IC 564), although IC 564 shows an inflection in the carapace there. Branchiocardiac groove obvious; extends from postcervical groove to a little more than half way to posterior margin (IC 564). Branchial carina absent (IC 564). Lateral carina absent (IC 564). Inferior carina absent (IC 564). Lateromarginal groove and carina, and posteromarginal groove and carina, well developed, as on other nephropids. Thoracic region rather evenly covered in tubercles. Tubercles somewhat transversely elongate dorsally but round laterally (IC 564). IC 564 also shows some wrinkling/reticulation laterally and, especially, ventrally.

Somite 1 very short; nearly as wide but much shorter than somites 2-6 (Fig. 2B-E). Tergite shortest medially; length (longitudinal dimension) expands laterally (Fig. 2D). Anterior margin (junction with articulating ring) straight; posterior margin a slightly concave-forward arc. Tergite transversely convex. Tergite with transversely elongate pits except on dorsomedian and adjacent to tergite-pleuron boundary, where smooth. A few small granules along anterior margin. An inflated, horizontal terrace on tergite marks the tergite-pleuron boundary; terrace narrows and becomes less inflated posteriorly. Terrace with small tubercles (IC 564).

Pleuron 1 outline triangular; surface highly concave, with a few tubercles anteriorly but smooth posteriorly (Fig. 2B). A very fine raised margin present anteroventrally (IC 564).

Somite 2 tergite subrectangular, wider than long; shortest medially, length expands from median to lateral boundary (Fig. 2D). Anterior and posterior margins slightly concave. Tergite transversely convex, except along lateral margins, where it flattens, forming terrace-like boundary with pleuron. Terrace wider anteriorly than posteriorly, and also slightly inflated anteriorly. Surface variously pitted (more densely so posteriorly) but smooth over an irregular band dorsomedially (and IC 571 has dorsomedian band raised). Dimple-like impression at tergite anterolateral corner; dimple outline and surface irregular. Lateral margin forms sharply defined terrace that overhangs slightly the pleuron below. Just a few pits and tubercles on otherwise smooth surface of lateral terrace (IC 564). IC 565 shows short spines on tergum-pleuron boundary ridge.

Pleuron 2 semicircular-trapezoidal in outline (Fig. 2B). Gently, irregularly convex over interior surface; smooth.

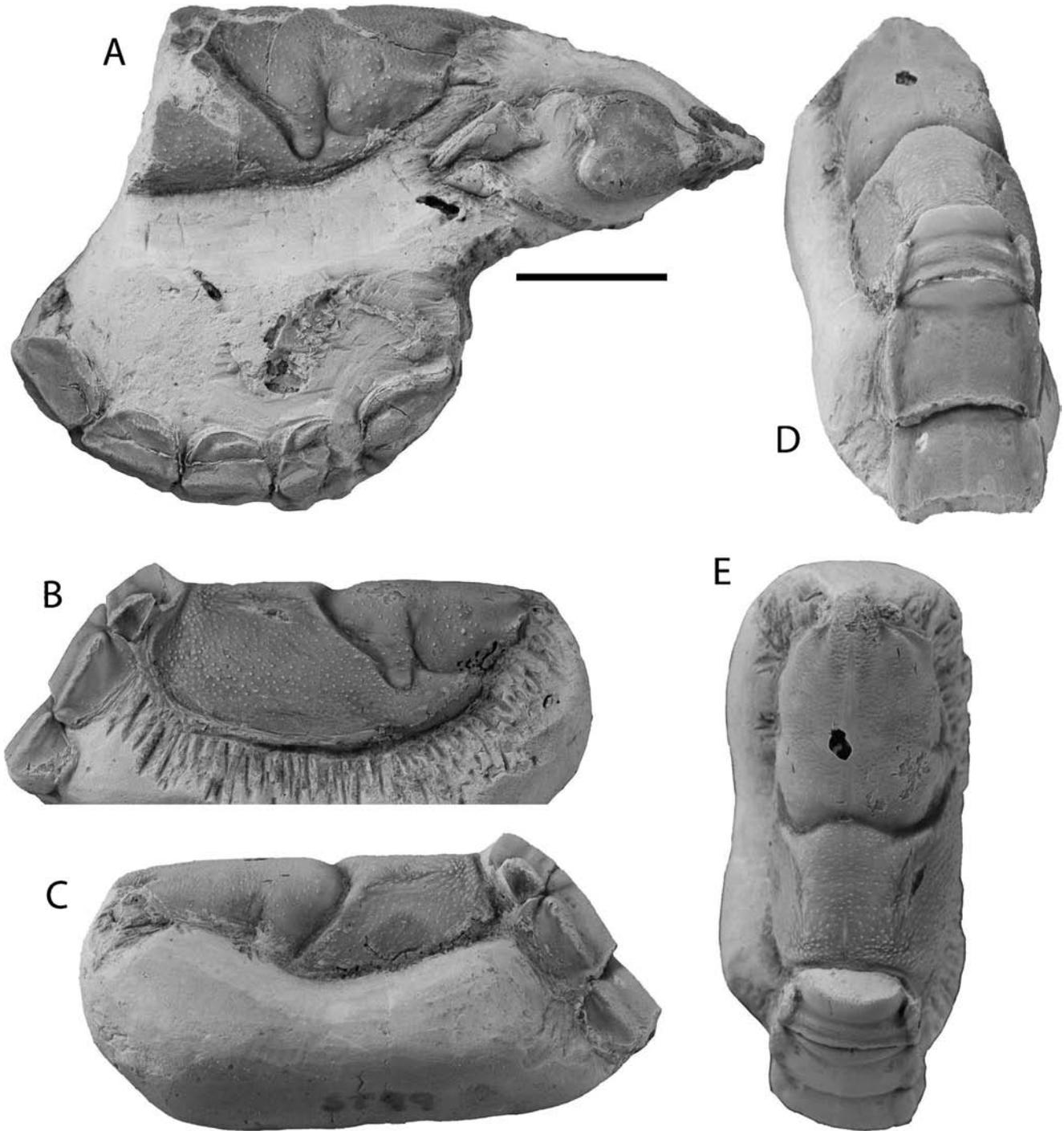


Fig. 2. *Dinochelus steepleensis* n. sp.: A: IC 563, right lateral view of cephalothorax, pleon, and major claw palm; B: IC 564, right lateral view of cephalothorax and pleon segments 1-3; C: IC 564, left lateral view of cephalothorax and pleon segments 1-3; D: IC 564, oblique dorsal view of cephalothorax and dorsal view of pleon segments 1-3; E: IC 564, dorsal view of cephalothorax. Scale bar = 1.0 cm.

Widely, gently inflated along margin; with granules but otherwise smooth (IC 564).

Tergite-pleuron boundary a sharply defined terrace on pleuron 2; transitions from sharp to rounded on 3; rounded on 4-5-6 (IC 563). Pleura 2-5 with posteroventrally-sloping carina just above ventral margin (see IC 563 for pleuron 2) (Fig. 3B). Carina progressively better developed on the more posterior segments; as string of tubercles on subtle ridge on

pleuron 2, but a sharper and progressively higher ridge on 3-5 (IC 563). Pleura 3-5 surfaces concave and mostly smooth (but with some pits dorsally and granules ventrally) between tergite-pleuron boundary and the postero-ventrally directed carina.

Somite 3 tergite rectangular (IC 565) (Fig. 3A). Width (transverse dimension) same as somite 2 (IC 564), but shorter. Anterior margin straight (IC 564, IC 565), posterior

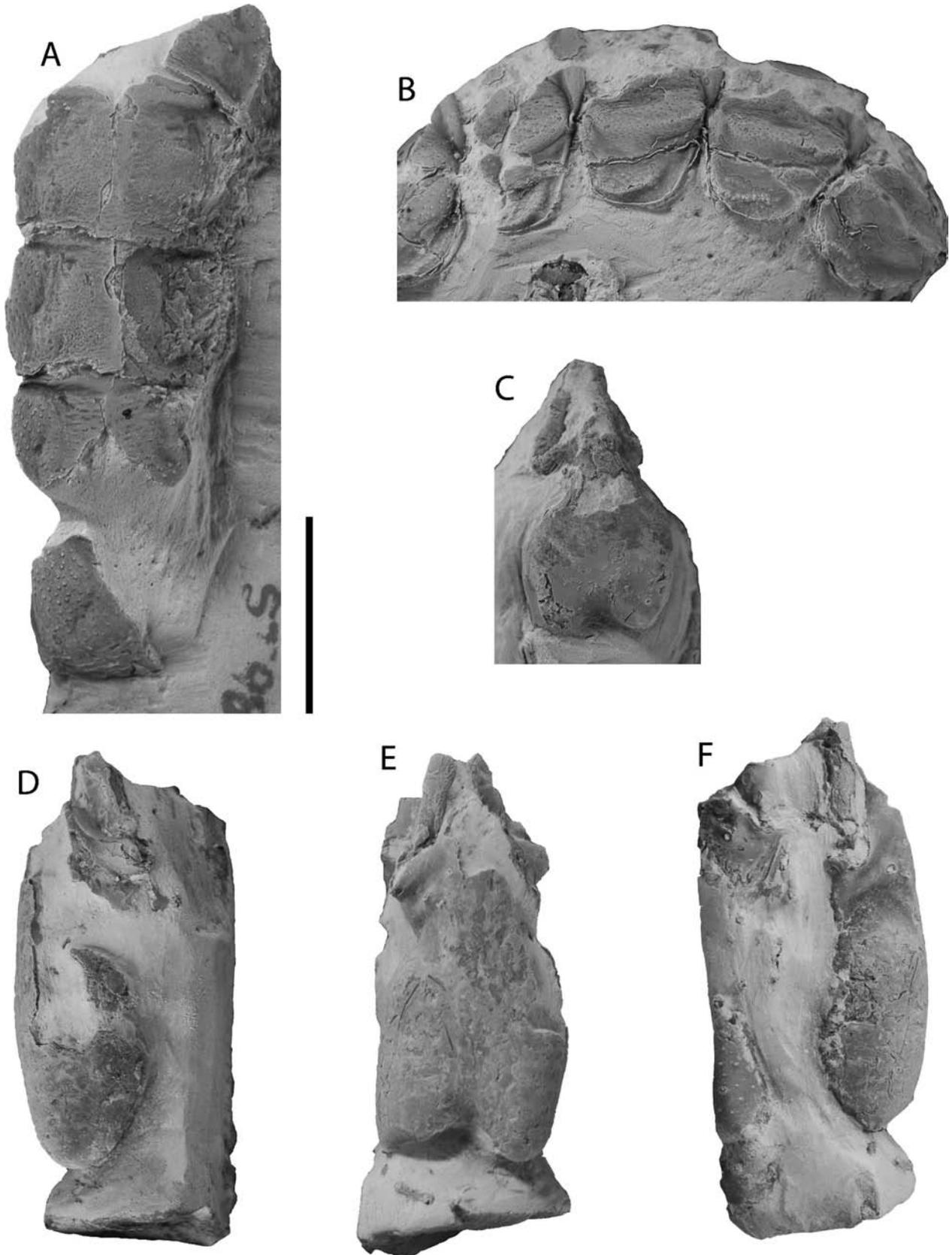


Fig. 3. *Dinochelus steepleensis* n. sp.: A: IC 565, dorsal view of pleon segments 3-6; B: IC 563, right lateral view of pleon segments 2-6; C: IC 564, outer view of major claw palm; D: IC 568, lower view of major claw palm; E: IC 568, outer view of major claw palm; F: IC 568, upper view of major claw palm (right) and minor claw palm (left). Scale bar = 1.0 cm.

margin poorly known. Surface variously and densely pitted but smooth over irregular band (irregular margins) dorsomedially (IC 564, IC 571). Tergite with high (more so on IC 565 and esp. IC 571; less high on IC 564), smooth, dorsomedian ridge; dorsal surface otherwise pitted. Rather flat dorsal region trapezoidal, narrower anteriorly and wider posteriorly (IC 571; less obvious on IC 564, which seems to have tergite 3 with less relief overall). Region falls off rather sharply laterally (IC 565, IC 571; less so on IC 564), making a distinct sunken region bordering the flat region above. Sunken region gives way laterally to slightly inflated and granulated margin which is wider at anterodorsal corner and narrowing posteriorly (IC 564, IC 565, IC 571).

Pleuron 3 trapezoidal (IC 563, IC 564) with very fine raised marginal rim (IC 563); smooth overall, with a few pits near the terrace and a few granules marginally (IC 564), plus carina mentioned above (IC 563).

Somite 4 (IC 563, IC 565, IC 571) tergite similar to tergite 3 (Fig. 3A). Tergite rectangular (IC 565). Width and length same as somite 3 (IC 565); sculpture also similar. Surface variously and densely pitted but smooth over a raised dorsomedian band which is irregular in width (IC 571). Rather flat dorsal region trapezoidal, narrower anteriorly and wider posteriorly (IC 565). Trapezoid is bordered by a broad oblique furrow which gives way to an inflated lateral termination of tergite; lateral part is broader and higher anteriorly and narrower, lower posteriorly (IC 565, IC 571). Tergite-pleuron boundary is a rounded ridge, its apex concave up as viewed laterally.

Pleuron 4 smaller than 3 but similar in outline (albeit just a bit more angular, and proportionately longer and narrower), topography, and ornamentation; although oblique carina better developed on 4 than 3 (IC 564). Pleuron 4 with a few marginal spines posteriorly.

Somite 5 (IC 565, IC 564, IC 569, IC 571) shorter, narrower than preceding (Fig. 3A). Tergite divided into dorsal portion and lateral portion by hemispherical furrow arcing from the tergite lateral margin (IC 565); anterior end reaches lateral margin but posterior end does not (IC 565). Dorsal part with transversely elongate pits, except over the mostly smooth dorsomedian line, which has a few smaller round pits (IC 565). Lateral portions inflated over a semicircular region extending dorsomedially from tergite-pleuron boundary; this region has low, posteriorly directed, tubercles (IC 565). Short but deep, kidney-shaped dimple marks the posterior portion of the semicircular raised area (IC 565). Tergite-pleuron boundary similar to preceding, although ridge fades to obscurity on posterior part (IC 569); rounded ridge lacks any ornamentation (IC 569, IC 571, IC 564).

Pleuron 5 smaller than preceding, trapezoidal (IC 564) to subtriangular (IC 569, IC 571); ornamentation as on previous pleura (IC 564, IC 571), with a few marginal spines posteriorly.

Somite 6 (IC 563, 563, 570, IC 569, IC 571) of a very different shape, being longer and proportionately longer than 2-5 (IC 563, IC 569), but nowhere well preserved (Fig. 3A). Flat dorsally, broadly inflated laterally (IC 569). Rather flat dorsal region smooth, with some pits (IC 564). Inflated lateral part with short, low, posteriorly directed spinules (IC

563, IC 571). Tergite-pleuron boundary rounded (especially anteriorly) and indistinct (IC 563).

Pleuron 6 a long (longitudinally) but narrow (transversely) crescent ($\sim 2.8\times$ longer than high; IC 563) with very fine raised marginal carina (IC 563). Long, central, longitudinal concavity across pleuron curves posterodorsally, interrupting tergite-pleuron boundary a short distance from posterior margin (IC 563). Central, sharply concave part of pleuron smooth, without granules. Tuberculate submarginal carina as in 3-5, though not quite as high.

Telson (IC 569, IC 570) shows inflated antero-medial portion from which two raised, diverging rays extend. Uropod (IC 569) protopod bilobed; both lobes with spines and spinules on margin. Exopod of uropod with distal margin (proximal to diarsis) denticulate (IC 563). One specimen (IC 563) shows, albeit in fragmentary condition on both left and right sides, distal article slightly broader than one half the exopod width.

First pereopods strongly asymmetrical. Major claw with bulb-like palm (Fig. 3C-F) and slender, elongate fingers. Minor claw smaller, with cylindrical palm. Unknown whether or not pereopods 2-5 are chelate. Merus of major claw (IC 564) terminates with distal, lower corner a knob-like projection extending anteroventrally. Merus outer edge ridge-like; termination inflated along margin; bears at least one tubercle or spine (IC 564). Major claw palm bulblike, bilobed (IC 563, IC 568). Upper bulb articulates with carpus; lower bulb hangs free (Fig. 2A). Fingers open in horizontal plane, i.e., inward and outward; dactylus on inside. In outer view, palm thickest over bulblike, proximal portion (IC 563) but flares abruptly and greatly to articulate with the dactylus (Fig. 3C, E). Outer surface over bulb portion broadly rounded and smooth except for scattered granules (IC 563, IC 566, IC 568). Upper surface with few spines of various size distally, near dactylus (IC 563, IC 566; IC 568, IC 571 might be spinier than others). Largest spine on upper surface near articulation with dactylus (IC 563, IC 566, IC 568). Lower surface ornamentation similar, and, as on upper, spine near articulation with dactylus (IC 566, IC 563). Dactylus a flattened equilateral triangle at articulation with palm. Margins of triangular dactylus base rounded (IC 563, IC 568). Interior of triangle sunken within rounded margins (IC 568). Each side (lateral margin) of triangle has one spine near articulation (IC 563, IC 568). Dentition of major claw unknown.

Minor claw is left claw on all specimens (IC 563, IC 565, IC 566, IC 567, IC 569, IC 571), as appears to always be in thaumastochelids. Palm of minor claw not bulbous but cylindrical and thinner than on major claw (IC 563, IC 568, IC 569, IC 571) (Fig. 3F), ca. 16.9 mm long, ca. 4 mm diameter; $4.2\times$ longer than thick (IC 568). Upper surface of palm with spines; lower surface smooth (IC 569, IC 571). Carpus distal end concave; receives convex proximal end of palm.

Remarks.—A few specimens [IC 563, IC 569, and a non-type specimen from Stansgate Abbey (in Div. B2)] preserve what appear to be eyestalks. The question of whether these were functional or vestigial remains.

Antennules/antennae are poorly known. Peduncle segments are imperfectly preserved on a few specimens (IC 563, IC 566, IC 570). IC 563 (left side) shows a spine on

Table 1. Diagnostic characters of thaumastochelid genera. The first five characters distinguish *Oncopareia* from extant thaumastochelid genera. Unique states in bold.

Character	<i>Oncopareia</i>	n. sp.	<i>Dinochelus</i>	<i>Thaumastocheles</i>	<i>Thaumastochelopsis</i>
Carapace shape	lat-comp	dv-comp	dv-comp	dv-comp	dv-comp
Cervical and post-cervical grooves	parallel	divergent	divergent	divergent	divergent
Pleura oblique carina near post corner	absent	present	present	present	present
Major claw palm bilobed	no	yes	yes	yes	yes
Minor claw palm strongly or delicately constructed	strong	delicate	delicate	delicate	delicate
Eyestalks	present	present	present	absent	present
Moveable eyes	present	?	present	absent	present
Basal antennal segments	?	?	large	small	short
Exopod maxilliped 2	?	?	well developed	well developed	rudimentary
Exopod maxilliped 3	?	?	well developed	well developed	rudimentary
Maxilliped 3 arthrobranch	?	?	2	2	1
Maxilliped 3 podobranch	?	?	well developed	well developed	rudimentary
Epistome medially narrow or wide	?	?	narrow	wide	wide
Exopod distal article narrow or wide	?	wide	wide	wide	narrow
Cephalic region wider anterior or posterior to cervical groove	?	posterior	posterior	anterior	?
Pleura marginal spines	absent	few	few	present	present

the distal, inner edge of one elongate segment, probably the antennal scale. IC 568 and IC 563 shows segments of the antennule or antennal flagella.

The new fossil species resembles four nephropid genera, the “thaumastochelids”, which include the fossil *Oncopareia* and the recent *Thaumastocheles*, *Thaumastochelopsis*, and *Dinochelus*. The new fossil species more resembles extant genera than it does the fossil *Oncopareia*. Differences between the four genera are summarized in Table 1.

The extant genera *Thaumastocheles*, *Thaumastochelopsis*, and *Dinochelus* are morphologically very similar. In fact, Ah Yong et al. (2007, pp. 206-207) expressed the opinion that the “differences between *Thaumastocheles* and *Thaumastochelopsis* are minor, and whether or not both genera should be recognized requires further study”. For example, Ah Yong et al. noted that the dentition of the major claw of *Thaumastocheles dochmiodon* and *Thaumastochelopsis brucei* is very similar, as is the dentition of the major claw of *Thaumastochelopsis wardi* and *Thaumastocheles japonicus*. We add here, it could be argued that *Dinochelus* and *Thaumastocheles* are (morphologically) even more similar than are *Thaumastocheles* and *Thaumastochelopsis*.

In the current study, we compared the new fossil material directly with specimens of *Thaumastocheles zaleucus*, *T. japonicus*, and *T. dochmiodon*, and with *Oncopareia*, *Thaumastochelopsis*, and *Dinochelus* via the literature and, for *Oncopareia*, unpublished photos from previous studies.

The new fossil species cannot be referred to the fossil genus, *Oncopareia*. Differences between the new fossil species and *Oncopareia bredai* sensu Tshudy, 1993 are as follows. 1) *Oncopareia bredai* has a laterally-compressed, *Hoploparia*-like cephalothorax. That of the new fossil species is flatter dorsally, as on recent thaumastochelids. 2) On *O. bredai*, the cervical and postcervical grooves are parallel, whereas on the new species (IC 564, IC 563) these grooves diverge dorsally. 3) *Oncopareia bredai* pleura lack the oblique (angling posteroventrally) sloping carina on/near the posteroventral corner. This carina is well developed on pleura 2-6 on the new fossil form. 4) *Oncopareia bredai* has a major claw palm lacking the bilobed form seen on the new fossil and the recent thaumastochelids. 5) *Oncopareia bredai* has a minor claw that is strong and *Hoploparia*-like. The new fossil has a minor claw more like that of recent thaumastochelids.

Eleven criteria (listed below, and Table 1), used in combination, distinguish the extant thaumastochelid genera. However, only four of these eleven features are preserved on the fossil specimens and therefore helpful in placing the new fossil material in one or the other genus. Based on these four features (#1, 9, 10, 11 below), the new fossil material is most similar to *Dinochelus*.

1, 2) *Thaumastocheles* has no eyes. *Thaumastochelopsis* has small pigmentless eyes that are slightly moveable. *Dinochelus* has well-developed pigmentless eyes that are elongate and moveable. The eyestalk on the new fossil form

is preserved on a few specimens but the question of whether these were functional or vestigial remains. The orbit on the new fossil is subtle. Orbits, unfortunately, are unreliable in predicting eye size. In fact, the observed relationship is opposite the expected. That is, *Thaumastocheles zaleucus* has vestigial orbits but no eyes. Conversely, orbits are absent on *Thaumastochelopsis* and *Dinochelus* which have at least small eyes.

3) Basal antennal segments are proportionately larger in *Dinochelus* than *Thaumastocheles* and *Thaumastochelopsis* (Ahyong et al., 2010, p. 529). Condition is unknown in the new fossil form.

4, 5) *Thaumastocheles* (Holthuis, 1974, p. 728) and *Dinochelus* (Ahyong et al., 2010, p. 528) have a maxilliped 2 and 3 with a well developed exopod. *Thaumastochelopsis* has a maxilliped 2 and 3 with only an exopod "reduced to small, scale-like rudiments" (Bruce, 1988, p. 908). Condition is unknown in the new fossil form.

6) *Thaumastocheles* (Holthuis, 1974, p. 728) and *Dinochelus* (Ahyong et al., 2010, p. 528) have a maxilliped 3 with two arthrobranches. *Thaumastochelopsis* has a single, small arthrobranch here (Bruce, 1988, p. 909). Condition is unknown in the new fossil form.

7) On *Thaumastocheles* (Holthuis, 1974, p. 728) and *Dinochelus* (Ahyong et al., 2010, p. 528), maxilliped 3 epipod has a well developed podobranch. *Thaumastochelopsis* lacks a functional podobranch here (Bruce, 1988, p. 908). Condition is unknown in the new fossil form.

8) Epistome medially is narrower on *Dinochelus* than on *Thaumastocheles* and *Thaumastochelopsis*. Condition is unknown in the new fossil form.

9) On *Thaumastocheles* and *Dinochelus*, the exopod of the uropod has an article beyond the diarsis that is wider than it is on *Thaumastochelopsis*. On *Dinochelus* and *Thaumastocheles* (*T. zaleucus*), this article is about one half (*Dinochelus*) or a little greater than one half (*Thaumastocheles*) the exopod width. On *Thaumastochelopsis*, this article is narrower, being "reduced to a small, mobile, oval lobe" (Bruce, 1988, p. 908), much less than one half [ca. 14% the exopod width, measured from Bruce's (1988) figure 3H] the exopod width. On the new fossil form, one specimen (IC 563) shows, albeit in fragmentary condition on both the left and right sides, an article comparable in width to that of *Thaumastocheles* and *Dinochelus*.

10) In *Thaumastocheles*, as viewed dorsally, the cephalic region is wider anterior to the cervical groove than it is posterior to the cervical groove. On *Dinochelus* and the new fossil species, the cephalic region is wider posterior to the cephalic groove.

11) Pleural marginal spines are numerous on *Thaumastocheles* and *Thaumastochelopsis* but few on recent *Dinochelus*.

Thus, while we emphasize the morphologic similarity of the extant thaumastochelid genera to each other, and of the new fossil species to all of these, we declare the new fossil species most similar to *Dinocheles* based on criteria #1, 9, 10, 11.

What is preserved on the new species *D. steeplensis* is very similar to the type species *D. ausubeli*, but the two

Table 2. Presence (1 or 2) or absence (0) of certain carapace spines and carinae on fossil and recent thaumastochelids, as well as two mainstream nephropids. Thaumastochelids: "TZ" = *Thaumastocheles zaleucus*, "TJ" = *Thaumastocheles japonicus*, "TD" = *Thaumastocheles dochmiodon*, "TW" = *Thaumastochelopsis wardi*, "TB" = *Thaumastochelopsis brucei*, "DA" = *Dinochelus ausubeli*, "DS" = *Dinochelus steeplensis* n. sp. Other nephropids: "HA" = *Homarus americanus*, "NN" = *Nephrops norvegicus*.

	TZ	TJ	TD	TW	TB	DA	DS	HA	NN
Subdorsal carina	0	0	0	0	0	0	0	0	1
Supraorbital spine	1	0	0	1	1	1	1	1	1
Supraorbital carina	0	0	0	0	0	0	0	1	1
Postorbital spine	0	0	0	1	1	0	0	1	1
Metorbital spines	0	1	2	2	1	0	0	0	0

can be distinguished at the species level by the following criteria.

1) On pleura 2-5, the posteroventrally directed carina is better developed on *D. steeplensis*.

2) On pleura 2-5, the tergite-pleuron boundary is more sharply defined, and straighter, on *D. steeplensis*.

3) On pleura 2 and 3, the anterior and posterior margins are more symmetrical on *D. steeplensis*. On *D. ausubeli*, the posteroventral margin is more sharply convex.

In terms of carapace ornamentation, the new fossil species is very similar to *Dinocheles ausubeli* [and also *Thaumastocheles zaleucus* (Table 2)], but subtle differences include: 4) on the gastric region of the cephalothorax, spines/spinules are more anteriorly directed on *D. ausubeli*; 5) the thoracic region is more spiny/spinulose on *D. steeplensis*; 6) *D. steeplensis* has a few more spines near the base of the rostrum.

Given the similarity of the *Dinochelus* and *Thaumastocheles*, it seems prudent to further compare the new fossil to species of *Thaumastocheles*. The new species *D. steeplensis* is distinguished from *T. zaleucus* in having: 1) a less reticulated lateral-ventral carapace surface (more reticulated on *T. zaleucus*); 2) a much narrower smooth region of the cephalic dorsomedian [wider, triangular on *T. zaleucus* (On *T. zaleucus*, the smooth area is, at its widest, approximately 1/3 the width of the flattened dorsal surface. On the fossil, the smooth area is, at most, 1/13 width.); 3) pleuron 2 with an oblique, posteroventrally-oriented carina on the posteroventral part (very subtle-absent on *T. zaleucus*); 4) pleuron 3 trapezoidal (missing anterior leg on *T. zaleucus*); 5) a pleonal segment 4 tergite-pleuron boundary lacking a short, spinulose carina anteriorly which is present on *T. zaleucus*; 6) pleuron 4 lacking an extension of the posteroventral corner (extended on *T. zaleucus*); 7) a major claw palm inner (upper inner) surface spinier than on that of *T. zaleucus*.

Dinochelus steeplensis is distinguished from *T. japonicus* in having: 1) a less reticulated lateral-ventral carapace surface (more reticulated on *T. japonicus*); 2) pleonal tergite 4 barely inflated laterally (somewhat inflated on *T. japonicus*); 3) on pleura 2 and 3, an oblique, posteroventrally-oriented carina on the posteroventral part (absent on *T. japonicus*); 4) pleuron 4 lacking an extension of the posteroventral corner (extended on *T. japonicus*); 5) a major claw palm upper surface with few or no spines (*T. japonicus* has several spines).

Table 3. Measurements and calculated ratios for carapace shape on the new fossil species, *Dinochelus steeplensis* n. sp., Recent species of *Thaumastocheles*: *T. zaleucus* (USNM 170685; 1 female, 1 unknown); *T. japonicus* (USNM 107527; 1 female), *Thaumastocheles dochmiodon* (USNM 288422; 3 males), and *Thaumastochelopsis* and *Dinochelus* species measured from published photographs.

	L _c	L _a	L _p	L _a /L _p	H _c	H _c /L _c
<i>T. zaleucus</i> 1	42.9	26.0	16.9	1.54	26.1	0.61
<i>T. zaleucus</i> 2	54.6	34.1	20.5	1.66	32.1	0.59
<i>T. japonicus</i>	25.0	14.5	10.5	1.38	12.5	0.50
<i>T. dochmiodon</i> 3	32.5	18.2	14.3	1.27	16.0	0.49
<i>T. wardi</i>	17.7	11.0	6.7	1.64	9.5	0.54
<i>T. brucei</i>	14.8	8.7	6.9	1.26	9.3	0.63
<i>D. ausubeli</i>	26.1	15.3	10.8	1.42	11.6	0.44
<i>D. steeplensis</i>	22.1	12.4	9.5	1.30	12.0	0.54

Dinochelus steeplensis is distinguished from *T. dochmiodon* in having: 1) pleonal segment 2 with tergum-pleuron boundary sharp (rounded on *T. dochmiodon*); 2) on pleura 2 and 3, an oblique, posteroventrally-oriented carina on the posteroventral part (absent on *T. dochmiodon*); 3) tergite 4 barely inflated laterally (inflated on *T. dochmiodon*); 4) a tergite 5 with kidney-shaped dimple on the posterolateral part (absent on *T. dochmiodon*); 5) claw palm upper surface with few or no spines (*T. dochmiodon* has several spines).

In overall carapace proportions, the new fossil is similar to extant thaumastochelids. H_c/L_c for *D. steeplensis* = 0.54; extant species = 0.44-0.63 (Table 3, column 6). L_a/L_p for *D. steeplensis* = 1.30; extant species = 1.26-1.66 (Table 3, column 4).

The new fossil species has a rostrum intermediate in length for extant thaumastochelids, which show appreciable variation in this regard. L_{rostrum}/L_a for *D. steeplensis* = 0.52 as compared to extant species showing a range of 0.38-0.79 (Table 4).

We are unsure of any taxonomic differences in major claw palm shape, owing to small sample size and the possibility of ontogenetic variation among our small sample. Elongation varies ontogenetically. Simple inspection of the data (Table 5) indicates that larger individuals of *D. steeplensis* have more elongate palms. Relative length of the major palm and carapace (column 8), likewise, appears

Table 4. Measurements and calculated ratios for rostrum length for the new fossil species, *Dinochelus steeplensis*, Recent species of *Thaumastocheles*: *T. zaleucus* (USNM 170685; 1 female, 1 unknown), *T. japonicus* (USNM 107527; 1 female), *T. dochmiodon* (USNM 288422; 3 males), and *Thaumastochelopsis* and *Dinochelus* species measured from published photographs.

	L _{rostrum}	L _a	L _{rostrum} /L _a
<i>T. zaleucus</i> 1	11.6	26.0	0.45
<i>T. zaleucus</i> 2	14.3	34.1	0.42
<i>T. japonicus</i>	5.2	14.5	0.36
<i>T. dochmiodon</i> 1	8.0	19.6	0.41
<i>T. dochmiodon</i> 2	7.8	20.6	0.38
<i>T. dochmiodon</i> 3	7.9	18.2	0.43
<i>T. wardi</i>	6.8	10.4	0.67
<i>T. brucei</i>	6.9	8.7	0.79
<i>D. ausubeli</i>	5.8	15.3	0.38
<i>D. steeplensis</i> n. sp.	ca. 8.0	ca. 15.5	0.52

to be vary ontogenetically more than taxonomically. The large specimen of *T. zaleucus* has a palm proportionately longer (Table 5; columns 5, 6) than that of *T. dochmiodon*, *T. japonicus* and the *D. steeplensis*. On *T. zaleucus*, major claw palm is thickest at articulation with dactylus. Palm on *D. steeplensis*, *T. dochmiodon*, and *T. japonicus* is wider over the proximal, bulb-like portion than at the dactylus articulation (Table 5; compare columns 3, 4).

Etymology.—The species name refers to Steeple Bay on the River Blackwater, Essex, United Kingdom, where the first diagnostic specimens (type series and others) were collected and recognized by the current co-author (JS) and Mr. R. J. Williams in 1996 and 1997.

Types.—The holotype, IC 563, and eight paratypes (listed below), all collected by Saward, are in the collection of the Natural History Museum. IC 563: cephalothorax, pleura, major claw palm, minor claw palm. IC 564: cephalothorax, pleonal somites 1-3. IC 565: pleonal tergites. IC 566: cephalothorax, major claw palm. IC 567: cephalothorax. IC 568: major claw palm. IC 569: cephalothorax, somites 2-6, both claws proximally. IC 570: cephalothorax. IC 571: cephalothorax, somites 2-6, both claws proximally. Additional material: BM 59132B (figured by Bell, 1858, plate X, no. 9), London Clay, probably Division B, Chalk Farm, London; also in the Natural History Museum, London.

Occurrence.—London Clay (Eocene: Ypresian) of the counties of Essex and Kent, in southeast England, in what is commonly referred to as the London Basin. Localities include: Chalk Farm, London; Aveley, Maylandsea (IC 568, IC 569, IC 570), Steeple Bay (IC 563, IC 564, IC 565, IC 566), Stansgate Abbey Farm (IC 567), Mundon Stone Point, and Iltnay, Essex; Tankerton (IC 571), Medway riverside, Seasalter and the Isle of Sheppey, Kent (Fig. 1).

Dating from ca. 54-51 Ma (King, 1981), the London Clay is an extensive deposit of marine sediments consisting mainly of silty clays, and clayey and sandy silts, has a maximum thickness of over 150 m and underlies much of the county of Essex, parts of adjacent Suffolk and North Kent and also extends beneath London to Hampshire and the Isle of Wight in southern England.

In total, around 70 specimens have been collected by the coauthor (JS) at sites in Essex (by far the majority from Steeple Bay) and Kent over the last 20 years. These, and a further 20 or so specimens found by other collectors (predominantly in Kent), and the single historic example housed in the Natural History Museum in London, have been inspected in the course of writing this paper. The vast majority are little more than fragments, typically crushed carapaces and pleonal sections; fewer than ten specimens have articulated chelae, and then only the inflated palm is commonly preserved in any detail. This typically poor preservation of what was clearly a thin-shelled crustacean with weakly calcified carapace and pleon, and the superficial resemblance to distorted specimens of *H. gammaroides*, would suggest that more specimens may exist in collections from the above locations (and maybe from elsewhere where London Clay is exposed in southern and eastern England), either overlooked, misidentified as *Hoploparia*, or consigned to the scrap bin as little more than worthless fragments.

Table 5. Measurements and calculated ratios for major claw palm shape on the new fossil species and recent *Thaumastocheles* and species of *Dinocheilus*: *T. zaleucus* (USNM 170685; 1 female, 1 unknown), *T. japonicus* (USNM 107527; 1 female), *T. dochmiodon* (USNM 288422; 3 males). L_{palm} = palm length; T_{palm} = maximum thickness of proximal, bulb-like portion of palm (i.e. not at articulation with dactylus) as held in view of (bilobed) outer surface; $W_{\text{palm-p}}$ = width of proximal, bulb-like portion of palm as held in view of upper surface; $W_{\text{palm-d}}$ = width of palm at articulation with dactylus; L_a = length of cephalic region of cephalothorax.

	L_{palm}	T_{palm}	$W_{\text{palm-p}}$	$W_{\text{palm-d}}$	$L/W_{\text{palm-p}}$	L/T	L_a	L_{palm}/L_a
<i>T. zaleucus</i> 2	30.4	16.5	17.8	18.7	1.71	1.84	34.1	0.89
<i>T. zaleucus</i> 3	25.2	13.5	14.7	14.9	1.71	1.86	NA	NA
<i>T. japonicus</i>	9.2	6.1	7.3	6.1	1.26	1.51	14.5	0.63
<i>T. dochmiodon</i> 1	11.7	7.3	9.0	6.2	1.30	1.60	19.6	0.60
<i>T. dochmiodon</i> 2	11.8	7.8	9.2	7.0	1.28	1.51	20.6	0.57
<i>T. dochmiodon</i> 3	10.7	6.9	7.7	5.7	1.39	1.55	18.2	0.59
<i>D. ausubeli</i>	10.3	7.3	NA	NA	NA	1.41	15.3	0.67
<i>D. steeplensis</i> IC 563	8.7	7.5	7.4	5.9	1.18	1.16	ca. 15.5	0.56
<i>D. steeplensis</i> IC 566	8.4	NA	ca. 7.8	6.0	1.08	NA	NA	NA
<i>D. steeplensis</i> IC 568	14.7	NA	9.6	ca. 9.0	1.53	NA	NA	NA

Five divisions of the London Clay are recognized (King, 1981), A through E, each representing a transgressive-regressive sedimentary cycle. *Dinocheilus steeplensis* is known almost exclusively from Division B. Division B represents the maximum marine transgression, with deep water (estimated by King to be at least 200 meters deep) covering southeast England.

Associated crustacean fauna at the majority of Division B localities includes the clawed lobster *Hoploparia gammaroides* M'Coy, 1849 (the most common crustacean in the London Clay), occasional specimens of the non-clawed/spiny lobster *Linuparus scyllariformis* Bell, 1858, the very rare *Glyphea scabra* Bell, 1858 and fragments of an undescribed *Callianassa* species. Crabs are uncommon (less than 5% of specimens found), but at least 13 species in 12 genera have been reported.

Thaumastocheles Bate, 1888

Type species.—*Astacus zaleucus* Thomson, 1873.

Thaumastocheles sp.

Oncopareia sp. Tshudy, 1993, pp. 303-307, fig. 40.

Oncopareia sp. Tshudy and Sorhannus, 2000b, p. 481, figs. 5, 7.

Material.—One specimen (4280) borrowed from Museo Nacional de Historia Natural. Anterior portion of sternum and attached chelipeds exposed. Left and right chelipeds with partial or complete basis, ischium, merus, carpus, propodus and dactylus.

Occurrence.—Miocene age (ca. 24-5 mya) gray siltstone of Fiordo San Pablo, Tres Montes, southern Chile. Specimen label includes: Fiordo San Pablo, immediately west of Fiordo Newman, interior of Golfo Tres Montes; coordinates approximately 46°39.09 latitude, 75°09.80 longitude. The only stratigraphic information given is "levels of concretions with abundant siltstone 'hedgehog plates' (placas de erizo en limolitas), with whale bones".

Description.—Claws very unequal in size and form; right claw larger. On major claw, palm crushed, approximately 14 mm long. Fingers approximately 3× as long as palm.

Fingers approximately 45 mm long, slender, of similar thickness, subrectangular in cross section. Dactylus approximately 2 mm wide at midlength, propodus slightly less wide. Distal ends of claws strongly incurved, non-occluding; dactylus longer. Dactylus with sharp, slender, upright denticles of two general sizes. Longest denticle 3 mm long, just under 0.5 mm wide at base. Large denticles approximately 4 mm apart. Small denticles less than half as long and wide as large denticles.

On minor claw, palm subrectangular, 8.6 mm long, 6.2 mm wide, not inflated. Cuticle smooth. Fingers rather strongly curving outward, and in parallel. Dactylus approximately 3 mm wide at articulation with propodus. Fixed finger slightly narrower than dactylus; nearly 2 mm wide at midpoint along length. Fingers taper smoothly distally. Dactylus with sharp, densely-spaced teeth of two general sizes; all directed slightly distally. Largest denticle located near midpoint along length; 1.3 mm wide, 3.5 mm high. Large denticles approximately 2 mm apart, usually with two or three small denticles between. Small denticles approximately one half size of large denticles. Clusters of setal pits faintly preserved in two alternating rows on dactylus, also distributed over propodus. On both chelipeds, ischium and merus strong. Merus approximately 14 mm long, with spines along lower margin.

Remarks.—The Miocene fossil specimen is referred herein to *Thaumastocheles*, with acknowledgement to its similarity also to *Thaumastochelopsis wardi*. Its major claw (what is preserved) is indistinguishable from that of *Thaumastocheles japonicus*, and its minor claw is very similar as well.

The major claw has a finger:palm length ratio (3.2:1) within the range of recent thaumastochelids (2.6:1-4.1:1) and unlike that of fossil *Oncopareia* (2.0:1-2.3:1). The major claw fingers and upright dentition of the Miocene fossil specimen most resemble those of *Thaumastocheles japonicus* and *Thaumastochelopsis wardi*. The finger:palm length ratio of measured *T. japonicus* specimens (USNM 106926, 107527) is 3.5:1. The fingers of *Thaumastochelopsis wardi* are somewhat incomplete and, so, a ratio cannot be accurately determined (but is >3.0:1). For preservational reasons, there is no discernable denticle formula on the Miocene specimen that could be compared to the recent

species. In summary, what is known of the major claw of the fossil specimen is indistinguishable from that of *Thaumastocheles japonicus* and *Thaumastochelopsis wardi*.

The minor claw palm is more blocky than tubular, having a length:width ratio (1.7:1) more like that of *Oncopareia* (1.3:1-1.9:1) and recent *Dinochelus* (1.5:1) than that of most recent thaumastochelids (2.2:1-3.7:1). However, dentition on the Miocene fossil is acicular, like that of recent thaumastochelids and unlike that of fossil *Oncopareia*. Its finger:palm length ratio (1.5:1) is intermediate between that of *Thaumastocheles japonicus* (1.8-2.0:1) and *Thaumastochelopsis wardi* (1.2-1.3:1). Its fingers both curve outward, as they do on *T. japonicus*, but not on *T. wardi*. In summary, the minor claw of the Miocene specimen is most similar to that of *T. japonicus*.

EVOLUTION AND BATHYMETRIC DISTRIBUTION OF THAUMASTOCHELIDS

The geologically oldest known thaumastochelid genus, *Oncopareia*, is morphologically intermediate between the fossil *Hoploparia*, which has a “mainstream” or “stem nephropid” morphology, and the distinctive, recent thaumastochelids. *Oncopareia* has a *Hoploparia*-like carapace and minor claw, but a pleon and major claw like those of recent thaumastochelids. Therefore, *Oncopareia* is interpreted intuitively as an evolutionary intermediate between *Hoploparia* and recent thaumastochelids (Mertin, 1941; Tshudy and Babcock, 1997; Tshudy and Sorhannus, 2000b). Cladistic analyses support the close relationship of *Oncopareia* and recent thaumastochelids. They show *Oncopareia* as either unresolved from the recent thaumastochelids (Tshudy and Babcock, 1997; Tshudy and Sorhannus, 2000a) or as a sister taxon to the recent thaumastochelids which, together, form a sister group to other, “mainstream” nephropids (Tshudy and Sorhannus, 2000b; Ah Yong, 2006). Prior to this paper,

all fossil thaumastochelids had been referred to *Oncopareia*. The fossils newly presented herein are more reasonably referred to their extant thaumastochelid genera. As revised, the geologically oldest and youngest occurrences of *Oncopareia* are Late Cretaceous (Turonian age, ca. 90 mya) and Paleocene (ca. 58-66 mya).

Now at hand is a group of lobsters, known to be monophyletic, with a fossil record extending back 90 million years, with morphologic end members connected by a range of intermediate morphologies. Future morphological cladistic analysis of all thaumastochelid species will more thoroughly evaluate the derivedness and relationships of each. For now, it seems certain that *Oncopareia* is the least derived of the thaumastochelids, and straightforward and safe enough to conclude and that *Dinochelus* and *Thaumastocheles* are intermediate between *Oncopareia* and the most derived genus, *Thaumastochelopsis* (Table 1).

The new fossil species, *D. steeplensis*, gives *Dinochelus* a fossil record, and shows that the carapace form and minor claw form of recent thaumastochelids had evolved by the early Eocene (ca. 52-58 mya). The interpretation that *Thaumastochelopsis* is most derived morphologically is indicated mostly by its reduced branchial formula, but also by the reduction of the exopod distal article (Ahyong et al., 2010; Table 1). Additionally, *Dinochelus* generally lacks marginal spines on the pleura; these spines are present (presumably a derived feature) on *Thaumastocheles* and *Thaumastochelopsis*.

The new fossil species, *Dinochelus steeplensis*, shows that thaumastochelids were living in outer shelf depths at that time. The new species, being morphologically, stratigraphically, and bathymetrically intermediate between previously known fossil *Oncopareia* and recent *thaumastochelids*, is at least consistent with the previously hypothesized (Tshudy and Sorhannus, 2000b) retreat of the thaumastochelids off of

Table 6. Bathymetric distribution of fossil and recent thaumastochelids. * *Oncopareia coesfeldiensis* is known from the Senonian (Turonian – Maastrichtian) European Epoch from 89.3 ± 1 to 65.5 ± 0.3 Ma.

Epoch	Inner shelf	Outer shelf	Slope and deeper
Recent			<i>Thaumastocheles</i> <i>T. dochmiodon</i> (250-822 m) <i>T. japonicus</i> (360-1110 m) <i>T. zaleucus</i> (650-1054 m) <i>Thaumastochelopsis</i> <i>T. brucei</i> (199-250 m) <i>T. wardi</i> (452 m) <i>Dinochelus</i> <i>D. ausubeli</i> (247-249 m)
Pliocene			
Miocene	<i>Thaumastocheles</i> sp.		
Oligocene			
Eocene		<i>Dinochelus steeplensis</i> n. sp.	
Paleocene	<i>Oncopareia klintebjergensis</i>		
Maastrichtian	<i>O. bredai</i>		
Campanian	<i>O. coesfeldiensis</i> *		
Santonian			
Coniacian			
Turonian	<i>O. esocinus</i>		
Cenomanian			

the shelf and into deeper waters. *Oncopareia* is known from sediments deposited in shallow, shelf depths (Table 6). For preservational (more accurately, sampling) reasons (deepwater sediments/rocks are almost never exposed in outcrops), we will likely never know about any ancient deepwater (continental slope and deeper) thaumastochelids. So, we don't know how long the thaumastochelids have inhabited deep water. What seems clear, though, is that the thaumastochelids abandoned shelf depths in the Tertiary. All six modern thaumastochelid species are deepwater dwellers (Table 6) and have either reduced (*Dinochelus*) or greatly reduced (*Thaumastochelopsis*), blind eyes or no eyes at all (*Thaumastochelids*). The Miocene occurrence of *Thaumastochelids* sp. from southern Chile, is the last known occurrence of *Thaumastochelids* on the continental shelf.

The abandonment of shelf depths is apparent in some other clawed lobster lineages (*Metanephrops*; Feldmann and Tshudy, 1989; Tshudy et al., 2007), and clawed lobsters in general (Tshudy, 2003). Fossil species diversity counts (both raw and normalized data) indicate that nephropids largely abandoned the continental shelf in the Cenozoic (ca. late Eocene-early Oligocene) (Tshudy, 2003). Today, of the 57 recent species of nephropid lobster, 4 inhabit the shelf (<200 m), 7 inhabit the shelf and deeper habitats (< and >200 m), and 46 are known from continental slope and deeper habitats (>200 m).

ACKNOWLEDGEMENTS

The authors would especially like to thank M. Rayner, D. Rayner, D. Savage, R. J. Williams and C. Millbank, all tireless field-workers of the London Clay, for access to their collections and loans and donations of specimens used for comparative purposes and description in this paper, and also to the staff of the Sedgwick and Natural History Museums in England, past and present, who have tolerated our rummaging through their cabinets in search of further specimens. Additional thanks go to the various members of the Tertiary Research Group, the Essex Rock and Mineral Society and the Medway Fossil and Mineral Society, whose willingness to share their knowledge and finds have revolutionized our understanding of the London Clay crustacean fauna of Southeast England. We thank I. Henriquez, Museo Nacional de Historia Natural, Chile, and E. Pérez, Servicio Nacional de Geología y Minería, Chile, for their help with locality information for the Miocene specimen of *Thaumastochelids* sp. Finally, we thank R. Feldmann for whitening and photographing the fossil specimens, D. Mitchell for Photoshop help in preparing the plates, and R. Feldmann and one anonymous reviewer for their helpful criticisms.

REFERENCES

- Ahyong, S. T. 2006. Phylogeny of the clawed lobsters (Crustacea: Decapoda: Homarida). *Zootaxa* 1109: 1-14.
- , T.-Y. Chan, and P. Bouchet. 2010. Mighty claws: a new genus and species of lobster from the Philippine deep sea (Crustacea, Decapoda, Nephropidae). *Zoosystema* 32: 525-535.
- , K.-H. Chu, and T.-Y. Chan. 2007. Description of a new species of *Thaumastochelopsis* from the Coral Sea (Crustacea: Decapoda: Nephropoidea). *Bulletin of Marine Science* 80: 201-208.
- Bate, C. S. 1888. Report on the Crustacea Macrura collected by H. M. S. "Challenger" during the years 1873-1876. Reports on the Scientific Results of the Voyage of H. M. S. Challenger, (Zoology) 24: 1-942. (Published by Order of Her Majesty, London.)
- Bell, T. 1858-63. A Monograph of the Fossil Malacostracous Crustacea of Great Britain. Part I. Crustacea of the London Clay: 1-44. Palaeontographical Society [Monograph], viii + 40 pp.
- Bosquet, J. 1854. Monographie des crustacés fossils du terrain Crétacé du Duché de Limbourg. Verhandelingen uitgegeven door de commissie belast met het vervaardigen eener geologische beschrijving en kaart van Nederland 2: 1-137, Plates 1-10, 1 table.
- Bruce, A. J. 1988. *Thaumastochelopsis wardi*, gen. et sp. nov., a new blind deep-sea lobster from the Coral Sea (Crustacea: Decapoda: Nephropoidea). *Invertebrate Taxonomy* 2: 903-914.
- Calman, W. T. 1913. A new species of the crustacean genus *Thaumastochelids*. *Annales and Magazine of Natural History* 8: 229-233.
- Chan, T.-Y., and M. de Saint Laurent. 1999. The rare lobster genus *Thaumastochelids* (Decapoda: Thaumastochelidae) from the Indo-Pacific, with description of a new species. *Journal of Crustacean Biology* 19: 891-901.
- Chu, K. H., L. M. Tsang, K. H. Ma, T.-Y. Chan, and P. K. L. Ng. 2009. Decapod phylogeny: what can protein-coding genes tell us? pp. 89-99. In, J. W. Martin, K. A. Crandall, and D. L. Felder (eds.), *Decapod Crustacean Phylogenetics*. CRC Press, Boca Raton.
- Clouter, F., T. Mitchell, D. Rayner, and M. Rayner. 2000. London Clay Fossils of the Isle of Sheppey. Medway Lapidary and Mineral Society, Gillingham, England.
- Collins, J. S. H., and J. Saward. 2006. Three new genera and species of crabs from the Lower Eocene London Clay of Essex, England. *Bulletin of the Mizunami Fossil Museum* 33: 67-76.
- Cooper, J. 1974a. Report of field meeting to High Ongar, Essex. *Tertiary Times* 2: 18-22. Reprinted *Tertiary Research* 22: 97-101 (2004).
- . 1974b. The stratigraphic distribution of the English palaeogene decapod Crustacea. *Tertiary Times* 2: 83-85. Reprinted *Tertiary Research* 22: 142-143 (2004).
- Dana, J. D. 1852. Crustacea. Part I. United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N. Vol. 13. C. Sherman, Philadelphia.
- Feldmann, R. M. 1993. Additions to the fossil decapod crustacean fauna of New Zealand. *New Zealand Journal of Geology and Geophysics* 36: 201-211.
- , and A. Gaździcki. 1997. A new species of *Glyphea* (Decapoda: Palinura) from the La Meseta Formation (Eocene) of Seymour Island, Antarctica. *Acta Palaeontologica Polonica* 42: 437-445.
- , and P. A. Maxwell. 1999. A new species of glypheid lobster, *Glyphea christeyi* (Decapoda: Palinura), from the Eocene (Bortonian) Waihao Greensand, South Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics* 42: 75-78.
- , and D. M. Tshudy. 1989. Evolutionary patterns in macrurous decapod crustaceans from Cretaceous to early Cenozoic rocks of the James Ross Island region, Antarctica, pp. 183-195. In, J. A. Crame (ed.), *Origins and Evolution of the Antarctic Biota*. Geological Society Special Publication 47.
- Fritsch, A., and J. Kafka. 1887. Die Crustaceen der böhmischen Kreideformation. Prague, Selbstverlag in commission von F. Rívnác, 53 pp., plates 1-10.
- George W., and S. Vincent. 1977. A foreshore exposure of London Clay at Steeple, Essex. *Tertiary Research* 1: 105-108.
- , and ———. 1982. An exposure of London Clay at Maylandsea (Lawling Creek), Essex. *Tertiary Research* 4: 39-43.
- Glaessner, M. F. 1969. Decapoda, pp. R400-R533, R626-R628. In, R. C. Moore (ed.), *Treatise on Invertebrate Paleontology*, R 4(2). Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.
- Hewitt, R. 1988. Outline of research on the ecology and evolution of the Eocene nautilid cephalopods from the London Clay, England. *Tertiary Research* 10: 65-81.
- Holthuis, L. B. 1974. Biological results of the University of Miami deep-sea expeditions. 106. The lobsters of the superfamily Nephropoidea of the Atlantic Ocean (Crustacea: Decapoda). *Bulletin Marine Science* 24: 723-884.
- . 1991. FAO Species Catalogue. Vol. 13. Marine Lobsters of the World. An Annotated and Illustrated Catalogue of Species of Interest to Fisheries Known to Date. FAO Fisheries Synopsis. Vol. 125. Food and Agriculture Organization of the United Nations, Rome.
- Jakobsen, S. L., and J. S. H. Collins. 1979. New middle Danian species of anomurans and brachyuran crabs from Fakse, Denmark. *Bulletin of the Geological Society of Denmark* 44: 89-100.
- King, C. 1981. The stratigraphy of the London Clay and associated deposits. *Tertiary Research Special Paper*, No. 6.
- . 1984. The stratigraphy of the London Clay formation and Virginia Water formation in the coastal sections of the Isle of Sheppey (Kent, England). *Tertiary Research* 5: 121-158.
- Latreille, P. A. 1802. Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite à l'histoire naturelle

- générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Vol. 3. F. DuFart, Paris.
- M'Coy, F. 1849. On the classification of some British fossil Crustacea, with notices on the new forms in the University Collection at Cambridge. The Annals and Magazine of Natural History, series 2 4: 161-179, 330-335, 392-414.
- Mertin, H. 1941. Decapode Krebse aus dem Subhercynen und Braunschweiger Emscher und Untersenon sowie Bemerkungen über einige verwandte Formen in der Oberkreide. Nova Acta Leopoldina 10: 1-264.
- Miller, J. S. 1821. A Natural History of the Crinoidea or Lily-Shaped Animals, with Observations on the Genera Asteria, Euryale, Comatula, and Marsupites. Bryan and Co., Bristol.
- Milne Edwards, H. 1837. Histoire Naturelle des Crustacés; comprenant l'anatomie, la physiologie et al classification de ces animaux, 2. Paris.
- Quayle, W. J. 1987. English Eocene Crustacea (Lobsters and Stomatopod). Palaeontology 30: 581-612.
- , and J. S. H. Collins. 1981. New Eocene crabs from the Hampshire Basin. Palaeontology 24: 733-758.
- Rayner, D., T. Mitchell, M. Rayner, and F. Clouter. 2009. London Clay Fossils of Kent and Essex. Medway Fossil and Mineral Society, Rochester, England.
- Richer de Forges, B. 2006. Découverte en mer du Corail d'une deuxième espèce de glyphéide (Crustacea, Decapoda, Glypheoidea). Zoosystema 28: 17-29.
- Schlüter, C. 1862. Die Macruren decapoden der Senon- und Cenomanbildung Westphalens. Zeitschrift der deutschen Geologischen Gesellschaft 14: 702-749.
- Sumbler, M. G. 1996. British Regional Geology: London and the Thames Valley. 4th Edition. HMSO for the British Geological Survey, London.
- Thomson, C. W. 1873. Notes from the "Challenger" IV. Nature 8: 246-249.
- Tsang, L. M., K. Y. Ma, S. T. Ah Yong, T.-Y. Chan, and K. H. Chu. 2008. Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. Molecular Phylogenetics and Evolution 48: 359-368.
- Tshudy, D. 1993. Taxonomy and evolution of the clawed lobster families Chilenophoberidae and Nephropidae. Unpublished PhD Dissertation, Kent State University.
- . 2003. Clawed lobster (Nephropidae) diversity through time. Journal of Crustacean Biology 23: 178-186.
- , and L. E. Babcock. 1997. Morphology-based phylogenetic analysis of the clawed lobsters (family Nephropidae and the new family Chilenophoberidae). Journal of Crustacean Biology 17: 253-263.
- , and U. Sorhannus. 2000a. *Jagtia kunradensis*, a new genus and species of clawed lobster (Decapoda: Nephropidae) from the upper Cretaceous (upper Maastrichtian) Maastricht formation, The Netherlands. Journal of Paleontology 74: 224-229.
- , and ———. 2000b. Pectinate claws in decapod crustaceans: convergence in four lineages. Journal of Paleontology 74: 474-486.
- , T.-Y. Chan, and U. Sorhannus. 2007. Morphology based cladistic analysis of *Metanephrops*: the most diverse extant genus of clawed lobster (Nephropidae). Journal of Crustacean Biology 27: 463-476.
- , D. R. Robles, T.-Y. Chan, K. C. Ho, K. H. Chu, S. T. Ah Yong, and D. Felder. 2009. Phylogeny of marine clawed lobster families Nephropidae Dana 1852 and Thaumastochelidae Bate 1888 based on mitochondrial genes, pp. 357-368. In, J. W. Martin, K. A. Crandall, and D. L. Felder (eds.), Decapod Crustacean Phylogenetics. CRC Press, Boca Raton.
- Williams, R. J. 2002. Observations on the London Clay excavation at Aveley, Essex. Tertiary Research 21: 95-111.
- Woods, H. 1925-1931. A Monograph of Fossil Macrurous Crustacea of England. Paleontographical Society, London.

RECEIVED: 8 May 2010.

ACCEPTED: 21 June 2011.