

## **Taxonomic revision of the extinct clawed lobster genus *Oncopareia* Bosquet, 1854 (Decapoda, Astacidea, Nephropidae)**

**Dale M. Tshudy, Matúš Hyžný, Martina Kočová Veselská, and John W. M. Jagt**

### **ABSTRACT**

*Oncopareia* Bosquet, 1854, is an extinct clawed lobster genus within the clade of thaumastocheliform decapod crustaceans that are characterized by short, quadrate pleura on the pleon and a major claw with a bulbous palm and acicular dentition. In fact, *Oncopareia* is the earliest thaumastocheliform lobster known to date, the oldest example being of Turonian age (~90 Ma). Originally, *Oncopareia* was erected for a single late Maastrichtian species, *O. bredai* Bosquet, 1854, from the southeast Netherlands. The genus has a convoluted taxonomic history that begins with a type species that is an accidental composite of two lobsters that differ at the genus level, the second genus being *Hoploparia* M'Coy, 1849. An analogous situation occurred in *Hoploparia biserialis* Fritsch, in Fritsch and Kafka, 1887, the description of which is partly based on material that is attributable to *Oncopareia*. A number of subsequently erected taxa have been assigned to *Oncopareia*, based solely on isolated cheliped fingers and only later to be recognized as representatives of the ghost shrimp genus *Ctenocheles* Kishinouye, 1926. This was due to convergent evolution of pectinate claws in several distinct decapod lineages. The present contribution summarizes the taxonomic history of *Oncopareia*, redefines the genus and redescribes its type species, and comments on species previously referred to the genus. Herein, in addition to the type species, three distinct *Oncopareia* species are recognized: *Oncopareia esocina* (Fritsch, in Fritsch and Kafka, 1887), *Oncopareia klintebjergensis* Jakobsen and Collins, 1979, and *Oncopareia lunata* (Fritsch, in Fritsch and Kafka, 1887). Other species previously included within *Oncopareia* are either reassigned to other genera or considered of uncertain affinity (incertae sedis).

Dale M. Tshudy. Department of Geosciences, Edinboro University of Pennsylvania, Edinboro, Pennsylvania 16412, USA [dtshudy@edinboro.edu](mailto:dtshudy@edinboro.edu) <https://orcid.org/0000-0001-5382-4378>

Matúš Hyžný. Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, Bratislava, Slovakia. [hyzny.matus@gmail.com](mailto:hyzny.matus@gmail.com) <https://orcid.org/0000-0002-8960-2846>

Tshudy, Dale M., Hyžný, Matúš, Kočová Veselská, Martina, and Jagt, John W.M. 2022. Taxonomic revision of the extinct clawed lobster genus *Oncopareia* Bosquet, 1854 (Decapoda, Astacidea, Nephropidae). *Palaeontologia Electronica*, 25(2):a20. <https://doi.org/10.26879/1190>  
[palaeo-electronica.org/content/2022/3628-lobster-genus-oncopareia](https://palaeo-electronica.org/content/2022/3628-lobster-genus-oncopareia)

Copyright: June 2022 Paleontological Society.

This is an open access article distributed under the terms of Attribution-NonCommercial-ShareAlike 4.0 International (CC BY-NC-SA 4.0), which permits users to copy and redistribute the material in any medium or format, provided it is not used for commercial purposes and the original author and source are credited, with indications if any changes are made.  
[creativecommons.org/licenses/by-nc-sa/4.0/](https://creativecommons.org/licenses/by-nc-sa/4.0/)

Martina Koočová Veselská. Institute of Geology of the Czech Academy of Sciences, v. v. i., Department of Paleobiology and Paleocology, Rozvojová 269, 165 00 Prague 6, Czech Republic and Institute of Geology and Palaeontology, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic. veselskamartina@gmail.com <https://orcid.org/0000-0003-4322-9019>

John W.M. Jagt. Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. john.jagt@maastricht.nl <https://orcid.org/0000-0001-6216-1991>

**Key words:** acicular dentition; convergent evolution; pectinate claws; thaumastocheliform lobsters

Submission: 1 October 2021. Acceptance: 24 May 2022.

## INTRODUCTION

Since Mesozoic times, clawed lobsters have been important components of marine ecosystems (Schweitzer and Feldmann, 2014). They comprise an array of not necessarily related taxa, representatives of which are assigned to a number of distinct families. The most diverse of these is the Nephropidae Dana, 1852, consisting of extinct and extant genera with a stratigraphical range from the Valanginian (Lower Cretaceous) onwards (Tshudy et al., 2018). The taxonomy of fossil nephropid lobsters is convoluted, partly because of usage of rather loosely defined genera such as *Hoploparia* (see Tshudy and Sorhannus, 2003; Tshudy et al., 2018) and *Oncopareia*. Untangling the taxonomy of the latter genus is the major goal of the present contribution.

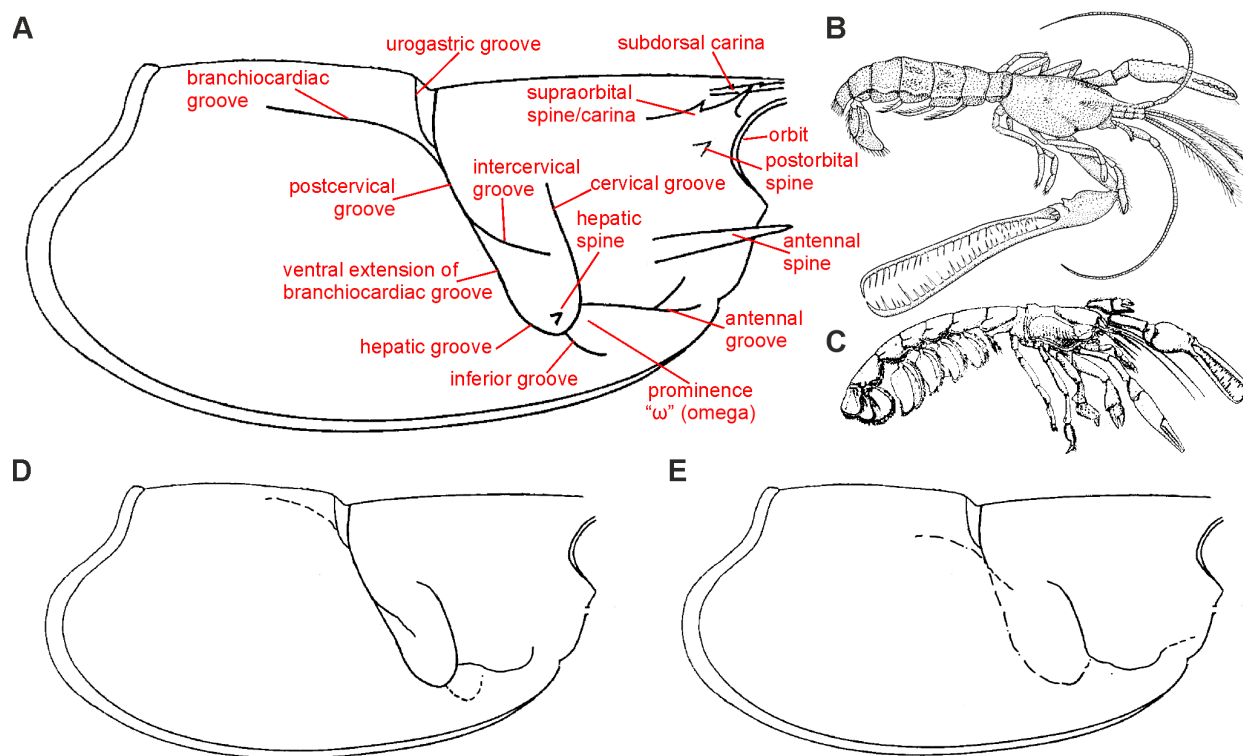
*Oncopareia* was erected for a single late Maastrichtian species, *O. bredai* Bosquet, 1854, from the Kunrade limestone (now Kunrade Formation) in the Kunrade area of southern Limburg, the Netherlands. Unfortunately, the description was based on several specimens belonging to two different lobster taxa, as discussed further below. Since then, a number of extinct lobster taxa have been assigned to *Oncopareia*. The taxonomic history of *Oncopareia bredai* has been discussed on several occasions, although never fully resolved. Feldmann et al. (1990) described four specimens (USNM collections, leg. J.W.M. Jagt) from the Vijlen Member (interval 6; Gulpen Formation; late early Maastrichtian) of the Haccourt-Lixhe area in northeast Belgium and referred them to *O. bredai*. They noted that Bosquet (1854) had not selected a type specimen for his *O. bredai* and advised (Feldmann et al., 1990, p. 29) that a lectotype be designated in a future publication. Tshudy (1993, pp. 275–307), in his unpublished PhD thesis, studied the Bosquet and Ubaghs collections and attempted to untangle the taxonomic confusion surrounding *Oncopareia*. He redefined that genus and its type species, *O. bredai*, and commented on other spe-

cies that were held to be referable to the redefined genus. In discussing convergent evolution in decapod crustacean claws, Tshudy and Sorhannus (2000a, figs. 3–5 = Tshudy, 1993, figs. 38–40) published three plates illustrating *Oncopareia*; some specimens (Tshudy and Sorhannus, 2000a, fig. 5) were later assigned to *Thaumastocheles* Wood-Mason, 1874, by Tshudy and Saward (2012, pp. 10–11). Still, no detailed discussion of the taxonomic history of *Oncopareia* has been published to date, nor has a lectotype been designated in the published literature. Nonetheless, because *Thaumastocheles*-like specimens do exist in the type collection, we herein redefine *O. bredai* on the basis of those specimens.

*Oncopareia*, with its pectinate claws, belongs to thaumastocheliform lobsters (sensu Chang et al., 2017), which are morphologically very similar to each other, and collectively different from other “lobsters” (= morphotype, sensu Schweitzer and Feldmann, 2014). As a group, their record tells an interesting story, of evolution during the Late Cretaceous, of dwelling at shelf depths during that time interval, of a loss of shelf-dwelling habit in the Paleogene (Tshudy and Saward, 2012) and of a reduction or even complete loss of eyes in extant, deep-water representatives (Tshudy and Saward, 2012; Chang et al., 2017). The evolution of this group (as a clade, see Karasawa et al., 2013 and Bracken-Grissom et al., 2014) has recently been assessed by cladistic analysis of morphological, molecular, and combined data (Chang et al., 2017).

Thaumastocheliform lobsters, however, are not the only group of decapod crustaceans possessing pectinate claws (Figure 1). These have been developed independently in several lineages (Tshudy and Sorhannus, 2000a), including polychelid lobsters (Polychelida: Palaeopentachelidae), Astacidea (Erymidae, Nephropidae, Stenochiridae), Axiidea (Ctenochelidae), and Brachyura (Iphiculidae, Leucosiidae), causing diffi-





**FIGURE 1.** Morphology of cephalothorax and a general habitus of studied taxa. A, Cephalothorax of nephropid lobsters with selected morphological characters (modified from Tshudy and Sorhannus, 2003). B, Habitus of thaumastocheliform lobsters, exemplified by *Thaumastocheles zaleucus* (from Calman, 1911). C, Habitus of ctenochelid ghost shrimps, exemplified by *Ctenocheles balssi* (from Kishinouye, 1926). D, Groove pattern of *Oncopareia bredai* Bosquet, 1854 (redrawn from Tshudy and Sorhannus, 2000b, fig. 2.2). E, Groove pattern of *Hoploparia beyrichi* Schlüter, 1862 (redrawn from Tshudy and Sorhannus, 2000b, fig. 2.3).

culties in taxonomic evaluation of fossil occurrences solely based on isolated cheliped elements. In fact, a number of extinct taxa have been assigned to *Oncopareia* based merely on isolated cheliped fingers only to be later recognized as representatives of *Ctenocheles* (Tshudy, 1993). Thus, not only is the generic concept of *Oncopareia* complex, but also the differentiation of *Oncopareia* from other forms can be difficult.

The aims of the present contribution, following up on Tshudy (1993) are threefold: to summarize the taxonomic history of *Oncopareia*, to redefine the genus and redescribe its type species, with designation of a lectotype and, lastly, to present a taxonomic treatment of species previously referred to the genus.

## MATERIAL AND METHODS

The composite nature of the type series of *Oncopareia bredai* was revealed to one of us (DMT) in 1990 when examining specimens contained in the IRScNB collections (Brussels). The

Bosquet Collection was found, after much searching with the late Annie V. Dhondt, and one of the co-authors (JWMJ), in a wooden box under a thick layer of dust in the basement. It seemed possible that the collection had not been examined since it had been transferred to Brussels after Bosquet's death in 1880. Bosquet (1854) discussed specimens contained in three collections, including his own and those of Dr. Van Breda (now in the Department of Palaeontology, The Natural History Museum, London, UK) and the 'Musée Géologique de Harlem' (= Teylers Museum, Haarlem, the Netherlands).

Specimens of *Oncopareia bredai* available for the present study are housed in the IRScNB, MNHN, NHMM, NM, and USNM collections. Approximately 33 specimens are contained in the IRScNB collections; most (25) of these are in the Ubaghs Collection (IG 6521); five in the Bosquet Collection (IG 4285), and three in the Rutot Collection (IG 5425). Bosquet (1854) made frequent reference to specimens in the collections of Dr. Van Breda and of the 'Musée Géologique de Harlem';

we have not re-examined these, if still extant. Other taxa discussed in detail further were studied either firsthand using the type material or via literature surveys (when the material has been lost or was not accessible to us). Details are indicated in the systematic section.

Specimens studied were documented photographically by all co-authors; in some cases, ammonium chloride was used to enhance the contrast prior to photography. Details of geographical and stratigraphical provenance and current repositories are given in respective figure captions.

**Abbreviations.** To denote the repositories of the material illustrated and/or referred to in the text, the following abbreviations are used: ANSP, Academy of Natural Sciences, Philadelphia, USA; IRScNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MGUH, Statens Naturhistorisk Museum (formerly Geological Museum), Copenhagen, Denmark; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NM, National Museum, Prague, Czech Republic; NHMM, Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands; NHMUK, The Natural History Museum, London, UK; TM, Teylers Museum, Haarlem, the Netherlands; USNM, United States National Museum, Washington, DC, USA.

### FOSSIL THAUMASTOCHELES-LIKE LOBSTERS – A HISTORICAL OVERVIEW

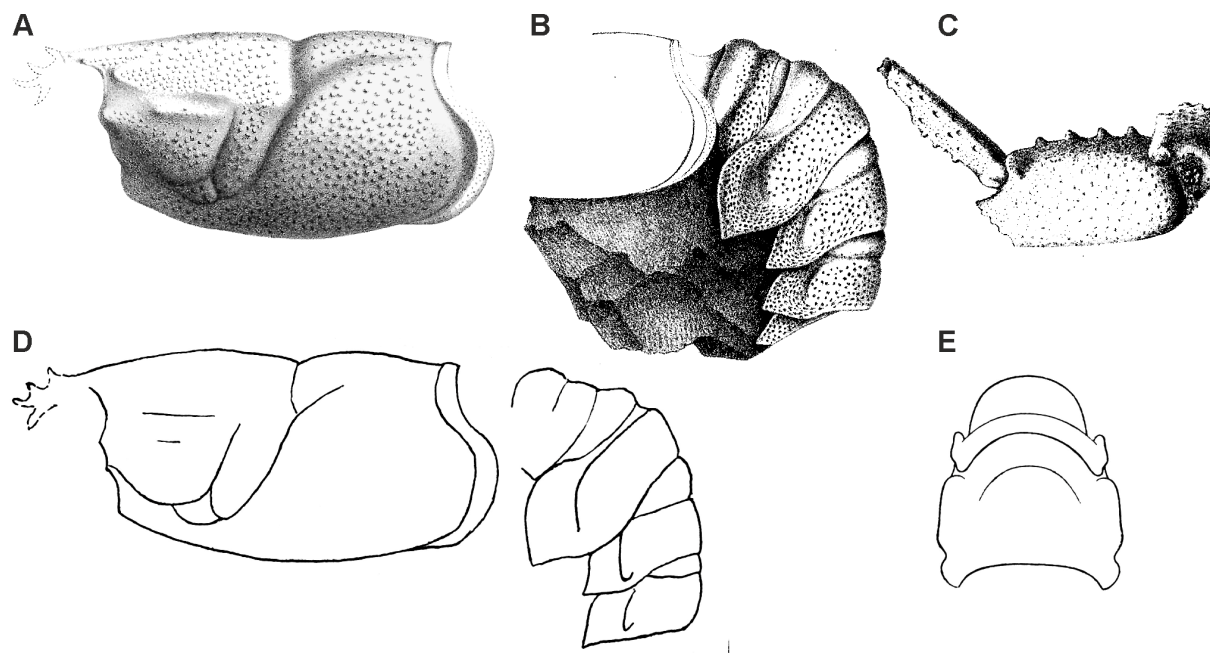
*Oncopareia* was erected for a single late Maastrichtian species, *O. bredai* Bosquet, 1854, from what is now the Kunrade Formation (<https://ncs.naturalsciences.be/cretaceous/kunrade-formation>) in the Kunrade area of southern Limburg, the Netherlands. The taxonomic history of the genus is complex, beginning with a type species that is an accidental composite of two lobsters (Figure 2A–2D) that differ at the genus level: Bosquet (1854) unknowingly established *O. bredai* on the basis of the cephalothorax of one species (Figure 2A) and the pleon (Figure 2B) and claws (Figure 2C) of another. One of the two lobsters comprising the unwitting composite type series of *O. bredai* (sensu Bosquet) is entirely *Hoploparia*-like. The other lobster has a very similar, *Hoploparia*-like cephalothorax but *Thaumastocheles*-like pleon and claws (as discussed further below in the systematic section). These cephalothoraxes belong with the *Thaumastocheles*-like pleons and chelipeds in the Bosquet Collection. Bosquet seems to have attributed the *Thaumastocheles*-like pleon forms to deformation (Bosquet, 1854, footnote on p. 129 [119]). Pelseneer (1886, p. 166), who examined the Bosquet

and Ubaghs collections, was the first to recognize the *Thaumastocheles*-like pleon form as real (i.e., undeformed) and meaningful (he said it was *Thalassina*-like, noting especially the ridge separating the terga and pleura. He illustrated this pleon type in a line drawing (Pelseneer, 1886, fig. 4; Figure 2E here) and referred to it as a new species, *Homarus bosqueti*.

Subsequent to Bosquet's erection of a composite type species, the taxonomic confusion surrounding fossil *Thaumastocheles*-like lobsters became even more serious. Workers in the late 1800s erected new genera at a time when access to information and communication among taxonomists was not what it is today. This led to synonymous genera, even for specimens that were anatomically fairly complete. Other scholars in the late 1800s and early 1900s described isolated chelipeds with bulbous palms and slender fingers armed with acicular denticles; most of these were misidentified at the infraordinal level until recently (Tshudy, 1993).

Schlüter (1862) was the first to describe extinct lobsters with a morphology similar to that of extant *Thaumastocheles* and erected (p. 728) the genus *Nymphaeops*. The type species, *N. coesfeldiensis* (considered herein to be a junior synonym of *O. bredai*; see below), was based on specimens which, although lacking well-preserved claws, were otherwise essentially complete. Schlüter (1862) rightly considered his new species to be distinct from *Hoploparia* mainly because it had a different (i.e., *Thaumastocheles*-like) pleon, with wide, trapezoidal terga and short pleura but also, in his opinion, a different pattern of carapace grooves. In the same paper, he named another new species, *Nymphaeops sendenhorstensis* (considered herein as indeterminate at the generic level), based on a specimen with cephalothorax, partial pleon, and large, isochelous claws.

From the Bosquet Collection, a single claw with a bulbous palm and acicular dentition was referred by Pelseneer (1886, p. 162 [2], fig. 1) to a new genus and species, *Ischnodactylus inaequidens*. Why he described this particular single claw, but failed to mention other claws with acicular denticles, is uncertain. Ironically, the claw he described was one of probably only two specimens at his disposal, which is not an astacidean lobster at all, but an axiidean ghost shrimp referable to the genus *Ctenocheles*. In the same paper, Pelseneer (1886) moved *Hoploparia macrodactyla* Schlüter, in von der Marck and Schlüter, 1868, to *Ischnodactylus*,



**FIGURE 2.** *Oncopareia bredai* (sensu Bosquet, 1854), as a composite species. A, Cephalothorax of *O. bredai* (from Bosquet, 1854, pl. 10, fig. 5). B, Pleon of *Hoploparia beyrichi* Schlüter, 1862 (from Bosquet, 1854, pl. 10, fig. 6). C, Claw of *H. beyrichi* (from Bosquet, 1854, pl. 10, fig. 71b). D, Composite drawing from Mertin (1941, text-fig. 9e). E, Pleonal segments 1 and 2 of *O. bredai* (as *Homarus bosqueti* Pelseneer, 1886; from Pelseneer, 1886, fig. 4).

based on the similarity of its claws to that of the type species.

With two extinct, *Thaumastocheles*-like genera now published (i.e., *Nymphaeops* and *Ischnodactylus*), Fritsch and Kafka (1887) erected the third one, *Stenocheles*, on the basis of three specimens from three different localities. Fritsch and Kafka (1887) described two species, *Stenocheles esocinus* and *S. parvulus*, for this material. Although resembling in many aspects the concept of *Ischnodactylus* published a year before, they made no comparison with it indicating that they were unaware of the latter when they prepared their own manuscript. Later, Hyžný et al. (2014) revised the original material referred to *Stenocheles* by Fritsch and Kafka (1887) and considered all three specimens distinct enough to be attributed to three different species, and erected a new one, *Ctenocheles fritschi* Hyžný, Kočová Veselská, and Dvořák, 2014, to accommodate one of the syntypes of *S. parvulus*. Fritsch and Kafka (1887) did not select a type species for *Stenocheles*; this was done by Glaessner (1969), who designated *Stenocheles esocinus* as such. This species is based on a pleon and associated claw with long, slender fingers and acicular dentition.

Subsequent to Fritsch and Kafka's (1887) work came the discovery of more claws with bul-

bous palms and long, slender fingers and acicular dentition. These claws were referred mostly to *Ischnodactylus* by various authors. Böhm (1891) erected *I. pectiniformis* for a single claw, while Lörenthey and Beurlen (1929) introduced *Hoploparia eocenica* (listed as *I. (?) eocaenicus* by Mertin, 1941) for partly preserved internal molds of cephalothoraxes and separate claws. Rathbun (1935) referred four new species, *I. cookei*, *I. cultellus*, *I. texanus*, and *I. ? dentatus* to this genus; all were based on claw fragments. Finally, Beurlen (1939) assigned claws from the Oligocene of Hungary to *Thaumastocheles*. Most of these chelipeds were misidentified, as will be discussed in detail below.

Mertin (1941, p. 178) expanded the genus *Oncopareia* from one species, i.e., the type, *O. bredai*, to several on the basis of his examination of new, anatomically fairly complete material from the Upper Cretaceous of Braunschweig, northwest Germany. That material revealed the association of fossil remains of *Thaumastocheles*-like claws and pleons for the first time. Much earlier, Pelseneer (1886) had noticed the thaumastocheliform pleons (i.e., with short quadrate pleura) in the Bosquet Collection but he had not recognized the association with any pectinate chelipeds. With that recognition, Mertin (1941) attempted to resolve a

situation wherein extinct *Thaumastocheles*-like lobsters had been described under different names. He synonymized *Stenocheles* Fritsch, in Fritsch and Kafka, 1887, and *Ischnodactylus* Pelseneer, 1886, with *Nymphaeops* Schlüter, 1862, and these, in turn, with *Oncopareia*.

The similarity of a Braunschweig pleon with that of *Stenocheles esocinus* (both of the *Thaumastocheles* type), in addition to some similarities between the *Thaumastocheles*-type claws of the two genera, led Mertin (1941) to relegate *Stenocheles* into the synonymy of *Ischnodactylus*. The similarity of the cephalothorax and pleon of the Braunschweig lobster to that of the type species, *Nymphaeops coesfeldiensis*, led Mertin (1941) to declare *Stenocheles* (= *Ischnodactylus*) a synonym of *Nymphaeops*.

Mertin's (1941) action, however, was too extensive, because not all of the species synonymized possess the *Thaumastocheles*-like pleon and pectinate claw upon which the grouping was based. Far more perplexing, however, is that he synonymized the above forms with *Oncopareia*, a genus which, as described by Bosquet (1854), has neither the *Thaumastocheles*-like pleon, nor claw which unite the three other fossil genera. In fact, the entire anatomy of *Oncopareia* in the original description of Bosquet (1854; but not *Oncopareia* as redefined herein) is highly typical of *Hoploparia*. Mertin's synonymization seems to have been based entirely on the shared possession of a spiny rostrum in his Braunschweig material and in *Oncopareia* (sensu Bosquet, 1854).

Mertin (1941) transferred to *Oncopareia* all three fossil genera, *Nymphaeops*, *Ischnodactylus*, and *Stenocheles*, as well as the fossil species *Hoploparia macrodactylus* and *Enoploclytia paucispina* Schlüter, in von der Marck and Schlüter, 1868. Into the same group, he tentatively moved *Stenocheles parvulus*, *Hoploparia biserialis*, *Homarus muncki* Pelseneer, 1885, and, with some reservation, the extant genus *Thaumastocheles*. He excluded *O. heterodon* Bosquet, 1854, and mentioned that *Nymphaeops belgicus* Forir, 1887, and *Ischnodactylus pectiniformis* were based on material that was insufficient to permit comparison.

Mertin (1941, p. 178) redefined *Oncopareia* to include *Thaumastocheles*-like characteristics; most notably, the pleon and claw with acicular dentition. He did this not because the type species, *O. bredai*, had these features, but because some different, *Thaumastocheles*-like species possessed them, and some of these, in turn, had a spiny rostrum – a generic character for *Oncopareia*

Bosquet, 1854. Thus, on the basis of the shared possession of a spiny rostrum, the *Thaumastocheles*-like extinct species were allied with *O. bredai*, and the latter – being first-named – became the type species. Apparently, Mertin (1941) disregarded the *Hoploparia/Homarus*-like pleon and the absence of *Thaumastocheles*-like claws in Bosquet's original publication. Nonetheless, he did establish *Oncopareia* as an extinct ancestor of *Thaumastocheles* – a concept that gained traction in the literature.

Mertin (1941, p. 180) noted the strong similarity of *Oncopareia* to the extant *Thaumastocheles* (i.e., carapace groove pattern, a very spiny rostrum, a smooth carapace, a lateral ridge on the pleon, pleonal pleura, etc.). He opined (Mertin, 1941, pp. 178, 180) that it was doubtful that the fossil and extant forms could be separated on the genus level.

*Oncopareia* was treated in detail by Tshudy (1993), who examined the type material of *Oncopareia bredai*. Although never published, results of his research found their way into several works dealing with thaumastocheliform lobsters (Tshudy and Sorhannus, 2000a, 2000b; Tshudy and Saward, 2012; Chang et al., 2017). Differences in the cephalothorax groove pattern in *Oncopareia bredai* and *Hoploparia beyrichi* were graphically presented by Tshudy and Sorhannus (2000b, fig. 2) and are redrawn here in Figure 1D–1E. The present contribution, finally, aims to resolve the taxonomic status of *Oncopareia bredai* as the type species of the genus *Oncopareia* and discusses all taxa treated as *Oncopareia* at any time in the light of the present revision.

## SYSTEMATIC PALEONTOLOGY

The systematic section presents all taxa classified as *Oncopareia* at any time. The section starts with species recognized as representatives of *Oncopareia* as revised herein, followed by taxa referable to other genera. All taxa are arranged within the higher-level classification proposed by De Grave et al. (2009); dubious ones are included as well.

DECAPODA Latreille, 1802

ASTACIDEA Latreille, 1802

NEPHROPIDAE Dana, 1852

Genus *Oncopareia* Bosquet, 1854

= *Nymphaeops* Schlüter, 1862 [partim]

= *Ischnodactylus* Pelseneer, 1886 [partim]

= *Stenocheles* Fritsch, 1887 [partim]

**Type species.** *Oncopareia bredai* Bosquet, 1854, by monotypy.

**Diagnosis.** Cephalothorax slightly laterally compressed, with well-developed postcervical, cervical, intercervical, branchiocardiac, and antennal grooves; combined postcervical-branchiocardiac groove parallel with cervical groove; pleon with short, quadrate pleura, and pectinate claw with bulbous palm and acicular dentition.

**Emended description.** Rostrum long, dorso-laterally compressed, spinose. Postcervical groove extending anteroventrally from dorsal midline at about mid-length. Combined branchiocardiac-postcervical groove extending toward hepatic groove, bifurcating at above mid-height on carapace. Anterior extension of postcervical groove extending toward middle of cervical groove. Cervical and postcervical grooves parallel. Ventral extension of branchiocardiac groove extending toward, or to, hepatic groove. Branchiocardiac groove long dorsally; extending from near posterodorsal margin to postcervical groove. Postorbital and supraorbital spine present. Pleonal terga wide, transversely convex; lateral carina at tergum-pleuron boundary. Pleura quadrate, wider than long. Pereiopod 1 chelipeds unequal in size and form. Pectinate claw with short, bulbous palm and very long, slender fingers bearing acicular denticles of varying length. Crusher-type claw robustly constructed.

**Remarks.** *Oncopareia*, as redefined herein, strongly resembles other thaumastocheliform lobsters (nephropids with pectinate claws), such as *Thaumastocheles*, *Thaumastochelopsis* Bruce, 1988 and *Dinocheilus* Ah Yong, Chan and Bouchet, 2010. All of these genera, being representatives of the same clade (Karasawa et al., 2013; Bracken-Grissom et al., 2014), are characterized as having short, quadrate pleura and a major claw with a bulbous palm and acicular dentition. *Oncopareia* differs from these in having: 1) a carapace that is laterally compressed (not dorsoventrally compressed); 2) parallel cervical and postcervical grooves; 3) a major claw palm that is not bilobed; and in lacking: 1) an oblique carina near the posterior corner of the pleura; 2) pleural marginal spines (Tshudy and Saward, 2012, table 1; including additional comparisons). Our present redefinition of *Oncopareia* is based on careful examination of the type material of the type species, i.e., *O. bredai*.

Bosquet's illustrations (1854, pl. 10, figs. 5–8) show the cephalothorax of the lobster (resembling that of both *Hoploparia* and *Thaumastocheles*; his figs. 5, 6<sup>1</sup> and 8; Figure 3A–3C here) and the pleon and claws of another (*Hoploparia*-like; his figs. 6, 7,

7<sup>1</sup>a-b). Bosquet (1854) established *Oncopareia bredai* on the basis of the cephalothorax of one species (which is similar to that of both the extant *Thaumastocheles* and fossil *Hoploparia* [e.g., similar overall shape, groove pattern and spines]) and the pleon and claws of another (*Hoploparia*-like [e.g., a pleon with cordate, pointed pleura; claws of normal nephropid shape]). Bosquet never realized this and failed to recognize the *Thaumastocheles*-like pleons as real (undeformed) and significant.

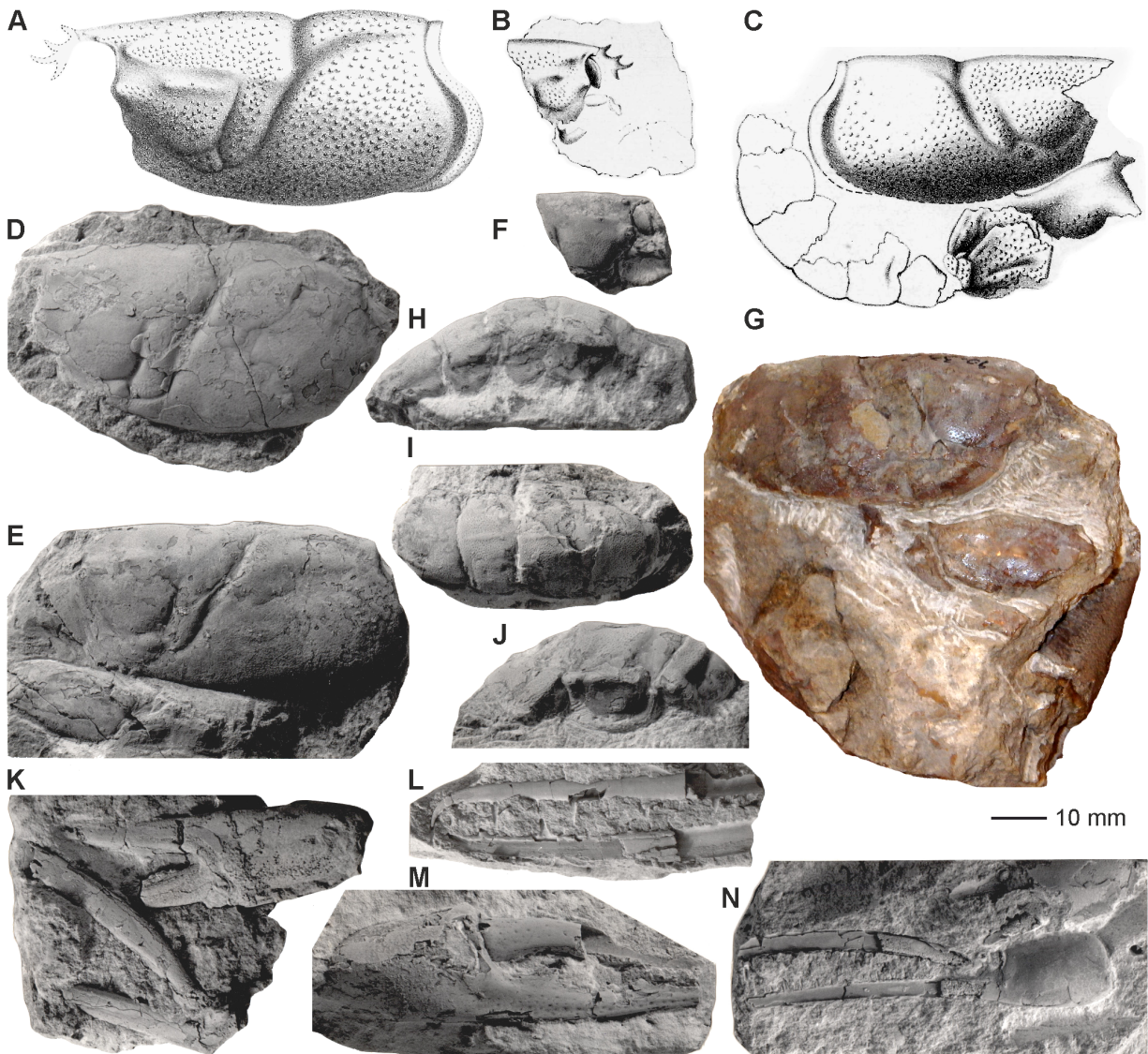
Bosquet (1854, p. 128) referred to his pl. 10, fig. 5 (Figure 3A here) as depicting the most perfect cephalothorax of *Oncopareia* he had examined. The specimen is identified in the plate caption as belonging to his own collection, but it is unknown which specimen of the IRScNB lot this is. However, it does bear a resemblance to IRScNB 90-32c (Ubaghs Collection) (see Tshudy, 1993, fig. 38.1; Tshudy and Sorhannus, 2000a, fig. 3.1; Figure 3D here), although, if it is, it is imperfectly drawn because in this particular specimen the postorbital carina angles upward, instead of downward as illustrated, and the granules in Bosquet's plate 10, figure 5, added by inference from other specimens [as explained in the plate caption] are drawn too coarsely.

The rostrum in Bosquet's plate 10, figure 8 (Figure 3B here), described (footnote on p. 128) as an "impreinte" and added (dashed line) by him to his plate 10, figure 5, might be based on IRScNB 90-15b (Bosquet Collection) (Tshudy and Sorhannus, 2000a, fig. 3.4; Figure 3F here). If so, this "impreinte" is no longer distinct on the actual specimen.

Bosquet's plate 10, figure 6<sup>1</sup> (Figure 3C here, mirrored) depicts a cephalothorax (Van Breda Collection) that is similar to that of plate 10, figure 5, but likewise with unknown repository data. This illustration resembles IRScNB90-17 (Tshudy and Sorhannus, 2000a, fig. 3.5; Figure 3E here) of the Ubaghs Collection.

*Oncopareia* (sensu Bosquet, 1854) included a *Hoploparia*-like (not *Thaumastocheles*-like) pleon, one that Bosquet (1854, p. 128) said bore a close resemblance to that of *Nephrops norvegicus* (Linnaeus, 1758). It seems that Bosquet (1854) did not recognize the *Thaumastocheles*-like pleons as being "real" and informative. It would seem that he attributed the lateral carinae on the pleon to deformation; his footnote on p. 129 says that all of the specimens found are more or less compressed or deformed in the matrix. Specimens IRScNB90-35c (Ubaghs Collection) (Tshudy, 1993, figs. 38.2, 3; Tshudy and Sorhannus, 2000a, figs. 3.2–3.3; Fig-





**FIGURE 3.** *Oncopareia bredai* Bosquet, 1854; upper Maastrichtian (Kunrade Formation) of the Kunrade area, southern Limburg, the Netherlands. A, Cephalothorax in lateral view (from Bosquet, 1854, pl. 10, fig. 5). B, Anterior portion of cephalothorax in lateral view (from Bosquet, 1854, pl. 10, fig. 8). C, Cephalothorax with pleon and tailfan in lateral view (from Bosquet, 1854, pl. 10, fig. 6<sup>1</sup>). D, Cephalothorax in lateral view (IRScNB 90-32c). E, Cephalothorax in lateral view (IRScNB 90-17). F, Anterior portion of cephalothorax in lateral view (IRScNB 90-15b). G, Incomplete individual in lateral view (IRScNB 90-33f, designated lectotype herein). H, I, Pleon in lateral (H) and dorsal (I) views (IRScNB 90-35c). J, Pleonal segments 1–3 in lateral view (IRScNB 90-23b). K, Right (crusher) and left (pectinate) claws of the same individual (IRScNB 90-28). L, Fingers of pectinate claw in lateral view (IRScNB 90-3b). M, Crusher claw in lateral view (IRScNB 90-32a). N, Pectinate claw in lateral view (IRScNB 90-27b). Specimens in D–F and H–N were whitened with ammonium chloride prior to photography.

ure 3H–I here) and IRScNB 90-23b (Ubaghs Collection) (Tshudy, 1993, fig. 38.6; Tshudy and Sorhannus, 2000a, fig. 3.6; Figure 3J here) show the distinctive, *Thaumastocheles*-like terga and short pleura, separated by a prominent ridge.

Bosquet made no mention of the single *Thaumastocheles*-like claw pair in his collection (IRScNB 90-36a), likely because very little of the

distinctive major claw is exposed. There may be others in the Bosquet Collection that we have not seen. The Ubaghs Collection contains several *Thaumastocheles*-like claws, some in obviously heterochelous pairs. Specimen IRScNB 90-28 (Tshudy, 1993, fig. 39.1; Tshudy and Sorhannus, 2000a, figs. 4.5–4.8; Figure 3K here) constitutes a heterochelous claw pair, including a *Thaumasto-*

*cheles*-like pectinate claw (fingers only). Specimen IRScNB 90-27b (Tshudy, 1993, fig. 39.3; Tshudy and Sorhannus, 2000a, fig. 3.3; Figure 3N here) is a complete, *Thaumastocheles*-like pectinate claw, with bulbous palm and delicate fingers bearing acicular dentition. Specimen IRScNB 90-19f (Tshudy, 1993, fig. 39.5–8) is another bulbous, *Thaumastocheles*-like palm, while specimen IRScNB 90-3b (Tshudy, 1993, fig. 39.2; Tshudy and Sorhannus, 2000a, fig. 3.2; Figure 3L here) shows acicular dentition. Finally, specimen IRScNB 90-32a (Tshudy, 1993, fig. 39.4; Tshudy and Sorhannus, 2000a, fig. 3.4; Figure 3M here) is a nearly complete crusher claw. The crusher claw in Bosquet's plate 10, figure 7 (Bosquet Collection) and the claw in plate 10, figure 7<sup>1</sup>a, b (Van Breda Collection) are referred herein to *Hoploparia beyrichi* (see below).

The other species of *Oncopareia* recognized herein are confidently referred to the genus. Published illustrations reveal nothing to distinguish *O. coesfeldiensis* from *O. bredai*, leading us to synonymize both taxa. The holotype of *O. esocina* suggests that its pleonal pleura are bordered by a marginal carina, narrower than that on *O. bredai*, while *O. lunata* has a slightly different groove pattern. *Oncopareia klintebjergensis* differs from *O. bredai* in several aspects, including the longer, shallower orbits, the more ventral position of prominence “ω” (omega) on the carapace, and in the claw denticles which are directed more sharply distally.

*Oncopareia bredai* Bosquet, 1854

- Figures 1D, 2A, 3A–N, 4A–E, 5A–L, 6A–C, 7A–K partim 1854 *Oncopareia bredai* Bosquet, p. 128, pl. 10, figs. 5, 6<sup>1</sup> and 8 [non pl. 10, figs. 6, 7 and 7<sup>1</sup>a, b = *Hoploparia beyrichi*].
- 1862 *Nymphaeops coesfeldiensis* Schlüter, p. 728, pl. 13, figs. 3, 6.
- 1868 *Nymphaeops coesfeldiensis* Schlüter; Schlüter in von der Marck and Schlüter, p. 295.
- 1868 *Enoploclytia paucispina* Schlüter in von der Marck and Schlüter, p. 303, pl. 44, fig. 6.
- 1879 *Nymphaeops coesfeldiensis* Schlüt.; Schlüter, p. 597, pl. 15, fig. 1, 2.
- 1886 *Homarus bosqueti* Pelseneer, p. 166 [6], fig. 4.
- partim 1887 *Hoploparia biserialis* Fritsch in Fritsch and Kafka, p. 35, pl. 5, fig. 2

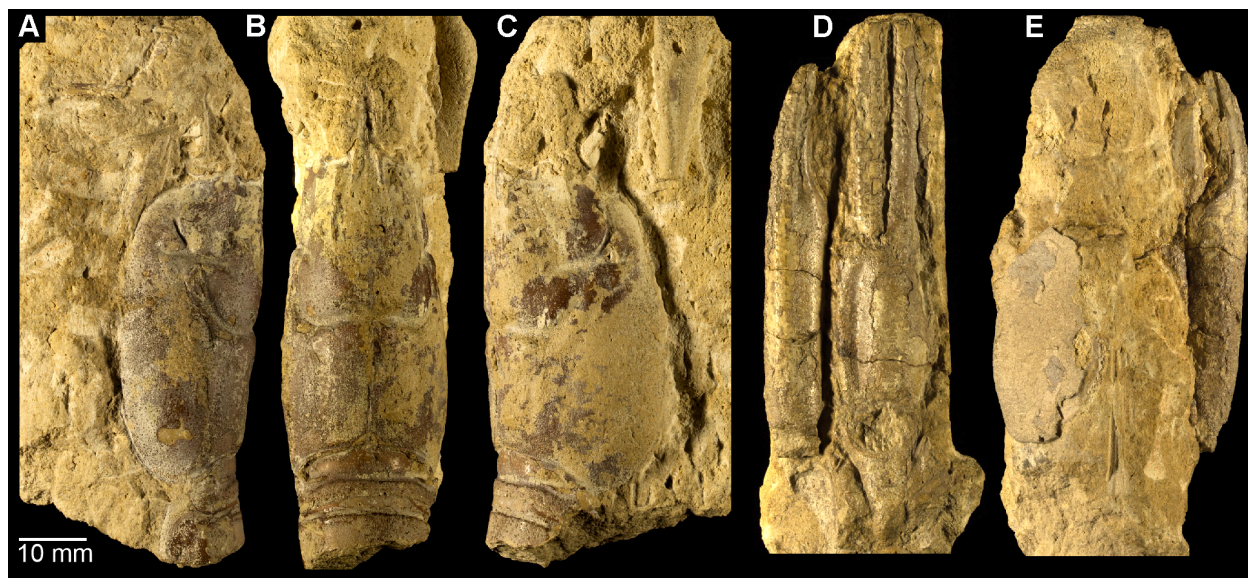
[non text-fig. 56; pl. 3, fig. 5, pl. 5, fig. 1 = *Hoploparia biserialis*].

- 1929 *Nymphaeops coesfeldiensis* Schlüter; Glaessner, p. 279.
- 1941 *Oncopareia bredai* Bosquet; Martin, p. 183, fig. 9 [cephalothorax, but not pleon, and necessarily rostrum]
- ?1941 *Oncopareia coesfeldensis* [sic] (Schlüter); Martin, p. 182, text-figs. 9a, ?9b, 10b–d, k–m; pl. 3, figs. 2–7.
- ?1941 *Oncopareia cf. coesfeldensis* [sic] (Schlüter); Martin, p. 187, pl. 3, fig. 9.
- 1964 *Ctenocheles coesfeldiensis* (Schlüter); Secretan, p. 152.
- 1990 *Oncopareia bredai* Bosquet; Feldmann et al., p. 26, text-fig. 4; pl. 1, figs. 4–6.
- 2000a *Oncopareia bredai* Bosquet; Tshudy and Sorhannus, p. 484, figs. 3, 4.
- 2000b *Oncopareia bredai* Bosquet; Tshudy and Sorhannus, fig. 2.2.
- 2010 *Oncopareia bredai* Bosquet; Schweitzer et al., p. 31.
- 2010 *Oncopareia coesfeldiensis* (Schlüter); Schweitzer et al., p. 31.
- 2016 *Oncopareia bredai* Bosquet; Feldmann et al., p. 23.
- 2016 *Oncopareia coesfeldiensis* (Schlüter); Feldmann et al., p. 23, fig. 20.3b.

**Type material.** IRScNB 90-33f (lectotype; specimen consisting of cephalothorax, partial pleon, left [crusher] palm, and basis through merus of right claw), IRScNB 90-3b (Tshudy, 1993, fig. 39.2; incomplete cheliped); IRScNB 90-15a, b (Tshudy, 1993, fig. 38.4; cephalothorax fragment), IRScNB 90-17 (Tshudy, 1993, fig. 38.5; cephalothorax), IRScNB 90-18, 90-19b, c, g, i, k, q (Tshudy, 1993, fig. 39.5–8; incomplete cheliped), IRScNB 90-22a, c, 90-23b (Tshudy, 1993, fig. 38.6; partial pleon), IRScNB 90-26a, 90-27a, b (Tshudy, 1993, fig. 39.3; b: complete cheliped), IRScNB 90-28a, b (Tshudy, 1993, fig. 39.1; incomplete pair of chelipeds), IRScNB 90-32a, c, e (a: cheliped; c: cephalothorax [Tshudy, 1993, fig. 38.1]), IRScNB 90-34, 90-35a, c (Tshudy, 1993, fig. 38.2–3; pleon) and IRScNB 90-36a, 90-37 and 90-40.

Bosquet (1854, pl. 10, figs. 5–8) did not explicitly select a type when erecting *Oncopareia bredai*, but did illustrate five specimens, all unregistered. However, he did cite collections by name. As





**FIGURE 4.** *Oncopareia bredai* Bosquet, 1854; cephalothorax with associated pleonal segments 1 and 2 and both claws (MNHN R03408) from the upper Maastrichtian (Kunrade Formation) at Kunrade, the Netherlands. A, Cephalothorax in left lateral view. B, Cephalothorax in dorsal view. C, Cephalothorax in right lateral view. D, Both claws. E, Crusher claw in lateral view.

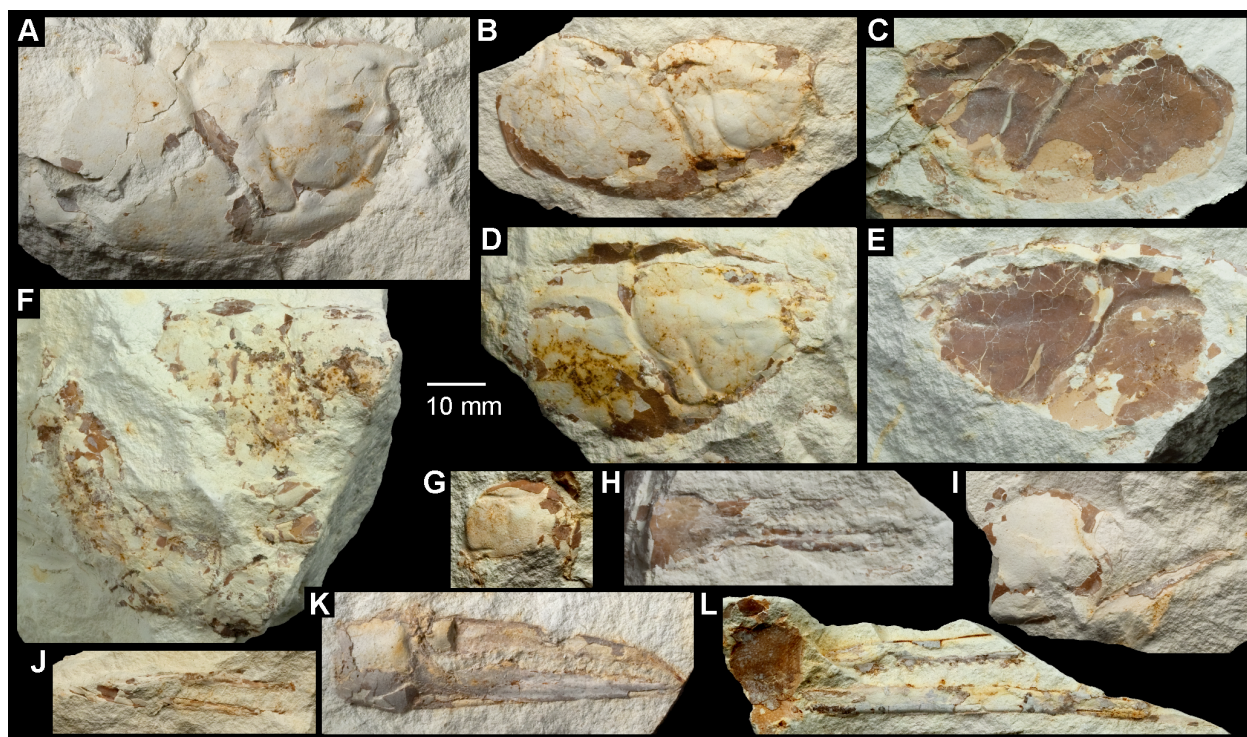
Bosquet did not designate type specimens, his illustrated specimens were not identified by museum/specimen numbers and none of the specimens that we have examined could be confidently matched up with his illustrations, it seems best to designate a lectotype for *Oncopareia bredai*. Specimen IRScNB 90-33f (Figure 3G here), from the “type series” of *O. bredai* (sensu Bosquet, 1854), according to the label accompanying the specimen, is designated lectotype here. The specimen consists of a cephalothorax, partial pleon, left (crusher) palm, and basis through merus of the right claw. This specimen serves well as the lectotype because it includes a cephalothorax and its associated, distinctive, *Thaumastocheles*-like pleon.

**Additional material.** Four specimens from the upper lower Maastrichtian (Gulpen Formation, Vijlen Member, interval 6) of Haccourt, north-east Belgium, originally described by Feldmann et al. (1990), i.e., a near-complete cephalothorax and pleon with fragments of appendages (USNM 444296), an incomplete pleon with tailfan (USNM 444297), an incomplete cephalothorax with fragments of pleon and appendages (USNM 444298), as well as a fragmentary cephalothorax and chelipeds (USNM 444299). From the same locality and stratigraphical level come seven additional specimens (Figure 5), preserving partial cephalothoraxes, pleons, claws, and partial tailfans (NHMM JJ 6741, JJ 6764, JJ 6839, JJ 7194, JJ 14618, JJ

15534, and JJ 15836). One claw (NHMM JJ 5932) is from the Zeven Wegen Member (Gulpen Formation, late Campanian) at the CBR-Lixhe quarry (Lixhe, north-east Belgium). One specimen, a cephalothorax with associated pleonal segments 1 and 2 and both claws (MNHN R03408; Figure 4) is from the upper Maastrichtian (Kunrade Formation) at Kunrade, the Netherlands. Two syntypes of *Hoploparia biserialis* Fritsch, in Fritsch and Kafka, 1887 (NM O3470 and NM O6861) originated from the Turonian of Vináry, Czech Republic, and representing isolated cephalothoraxes (Figure 6); NM O3470 was figured by Fritsch and Kafka (1887, pl. 5, fig. 2). These two specimens are removed from the type series of *H. biserialis* herein (see below for further details).

The only material referred to *Nymphaeops coesfeldensis* (Figure 7) that we have studied in person includes a few fragmentary specimens of pectinate and crusher claw (NHMM HB 393 and HB 756; Figure 7J–K) from the Vaals Formation (lower Campanian) of Haccourt, north-east Belgium, recorded by Jagt and Bongaerts (1986). In addition, there is a single, near-complete cephalothorax, with associated appendages (NHMM JJ 9974), from the same locality and stratigraphical level (Figure 7I). In this respect, it is of note that Bosquet (1860, 1868) listed, but did not illustrate, *O. bredai*, from the so-called ‘Hervien’ in the Liège-Limburg Basin. This corresponds nowadays with the Vaals Formation of early Campanian age. We

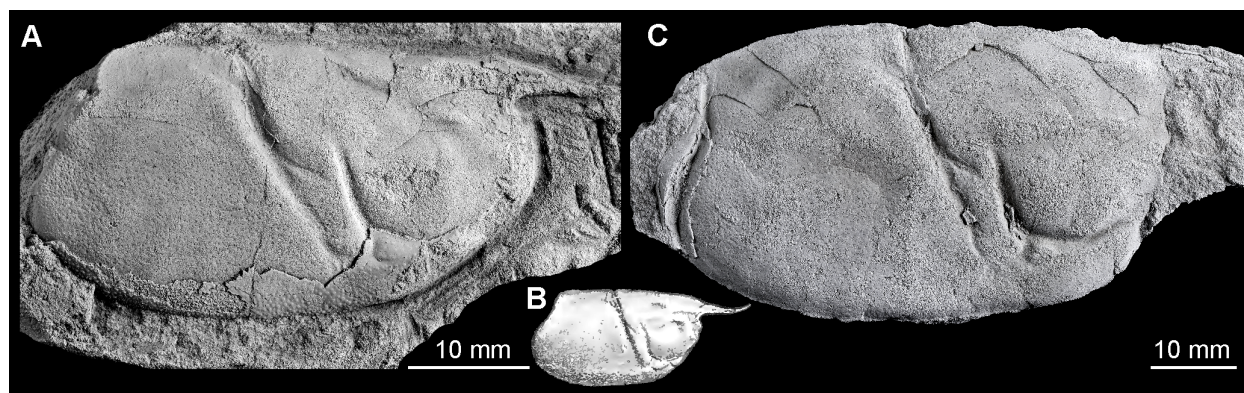




**FIGURE 5.** *Oncopareia bredai* Bosquet, 1854, cephalothoraxes, partial pleons and isolated claws; with exception of H (which is from the upper Campanian Zeven Wegen Member), all are from the Vijlen Member, interval 6 (upper lower Maastrichtian) at the CPL/CBR quarry complex near Haccourt and Lixhe, north-east Belgium. A, Cephalothorax in right lateral view (NHMM JJ 15836). B, C, Cephalothorax in right lateral view, and counterpart (NHMM JJ 6741). D, E, Cephalothorax in right lateral view, and counterpart (NHMM JJ 14618). F, Fragmentary cephalothorax and pleon in right lateral view (NHMM JJ 6764). G, Isolated pleura (NHMM JJ 6741). I, Fragment of cephalothorax and pectinate claw (NHMM JJ 14618). J, pectinate claw in lateral view (NHMM JJ 15534). K, crusher claw in lateral view (NHMM JJ 7194). L, fragmentary pectinate claw in lateral view (NHMM JJ 6839).

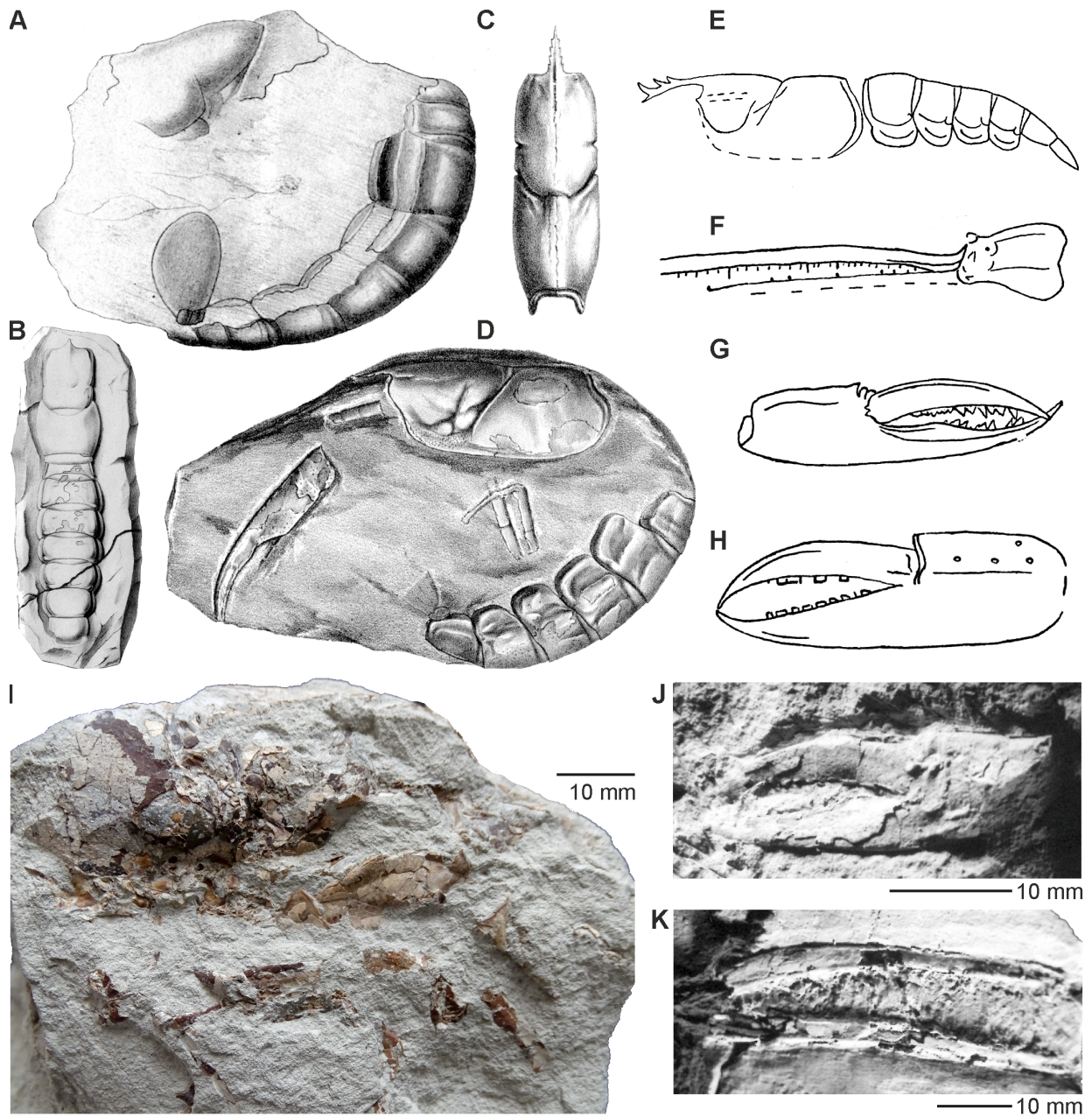
have attempted to borrow Schlüter's 1862 type specimen and other individuals from the 'Akademie zu Münster', but these may have fallen victim to air raids during World War II. We are aware of larger suites of specimens of nephropid lobsters con-

tained in the Karl-Heinz Hilpert Collection at the Ruhrmuseum (Essen, Germany; see Jagt et al., 2004; Van Bakel et al., 2005) that may include topotypical material of *Nymphaeops coesfeldien-*



**FIGURE 6.** *Oncopareia bredai* Bosquet, 1854; isolated cephalothoraxes from the upper Turonian (uppermost part of the Jizera Formation) at Vinary near Vysoké Mýto, Czech Republic. A, Isolated cephalothorax in lateral view (NM O3470). B, Digital copy of Fritsch and Kafka (1887, pl. 5, fig. 2). C, Isolated cephalothorax in lateral view (NM O6861). Both specimens were whitened with ammonium chloride prior to photography.





**FIGURE 7.** *Nymphaeops coesfeldiensis* Schlüter, 1862 (= *Oncopareia bredai* Bosquet, 1854, as here understood). A, Incomplete cephalothorax with associated pleon in lateral view (from Schlüter, 1862, pl. 13, fig. 3). B, Cephalothorax and pleon in dorsal view (from Schlüter, 1862, pl. 13, fig. 6). C, Reconstruction of cephalothorax in dorsal view (from Schlüter, 1879, pl. 15, fig. 2). D, Near-complete individual in lateral view (from Schlüter, 1879, pl. 15, fig. 1). E, Cephalothorax and pleon in lateral view (from Mertin, 1941, text-fig. 9a). F, Pectinate claw (from Mertin, 1941, text-fig. 10k). G, Crusher claw (from Mertin, 1941, text-fig. 10b). H, Crusher claw (from Mertin, 1941, text-fig. 10d). *Nymphaeops coesfeldiensis* Schlüter, 1862 (= *Oncopareia bredai* Bosquet, 1854, as here understood) from the Vaals Formation (lower Campanian) at the former CPL SA quarry, Haccourt, north-east Belgium (I–K). I, Near-complete cephalothorax with associated appendages in lateral view (NHMM JJ 9974). J, Crusher claw (NHMM HB 393). K, Fingers of pectinate claw (NHMM HB 756). Figure parts A–H not to scale.

sis. A detailed assessment of this material is deferred to another occasion.

**Diagnosis.** *Oncopareia* with pleura having prominent, rounded, marginal carina; intercervical groove extending toward below upper end of cervical groove; pectinate claw denticles perpendicular to longitudinal axis of fingers.

**Emended description.** Carapace laterally compressed, twice as long as high. Postcervical groove intersecting dorsal median line slightly posteriorly to mid-length on carapace. Postcervical groove long, well incised dorsally and laterally; extending ventrally over dorsal surface, then, as combined branchiocardiac-postcervical groove, angling anteroventrally to hepatic groove. Hepatic groove deeply incised, joining cervical and antennal grooves in semicircular loop. Cervical groove originating at level of base of orbit, paralleling postcervical groove except at upper end of cervical groove, which is deflected anteroventrally. Prominence “ω” distinct. Intercervical groove narrow, extending anteroventrally from postcervical groove, at level just above cervical groove origin, toward, but not reaching, lower portion of cervical groove; intercervical groove terminating at level of mid-height on cervical groove. Cervical groove and antennal groove together forming a smooth, semicircular arc. Antennal groove vague anterior to prominence “ω”; curving toward antennal spine, effacing well before reaching spine. Branchiocardiac carina broad, subtle; extending from near posterior margin to postcervical groove, curving downward near groove. Antennal region flat, featureless. Very shallow branchiocardiac groove present; most evident near postcervical groove. Posteromarginal carina wide, smooth, with a few pits. Cephalic region granulose, with a row of setal pits extending from top of cervical groove to near antennal spine. Antennal spine strong; supraorbital and postorbital spines slightly smaller. Thoracic region pitted dorsally, with granules generally sparse laterally but dense ventrally.

Pleonal terga wide, convex. Each segment with lateral carina at tergum-pleuron boundary. Pleura short; at least pleura 2 and 3 with blunt ventral margin.

Tergum 2 rectangular. Anterior margin straight, posterior margin subtly convex backward, lateral margins subtly convex, locally indented near posterior margin. Anterior margin depressed laterally; depressed area progressively widening toward pleuron. Tergum coarsely and densely pitted. Lateral carina prominent, rounded, widest anteriorly.

Pleuron trapezoidal, convex axially; upper surface coarsely pitted, lower surface smooth.

Terga 3–6 of similar width. Tergum 3 rectangular. Anterior margin slightly concave forward, lateral margins slightly convex, widest at mid-length, subtly indented locally near posterior margin. Anterior margin depressed laterally. Tergum coarsely, densely pitted except on smooth dorsomedian keel, depression along anterior margin, and in subtle furrow adjacent to upper limit of lateral carina. Summit of lateral carina well defined, extending obliquely ventrally posteriorly. Pleuron trapezoidal; ventral and posterior margins shorter than dorsal and anterior margins. Pleuron concave overall; margins convex. Surface mostly smooth, granulose ventrally. Surface locally swollen at anteroventral corner, maybe with spine.

Tergum 4 trapezoidal, wider anteriorly than posteriorly. Lateral margins convex along most of length; straight for a short distance posteriorly. Tergum coarsely and densely pitted except on smooth dorsomedian keel. Lateral carina extending from near anterior margin to posterior margin, curving posteroventrally over anterior half and extending on level over posterior half. Upper surface of carina very broad, inflated. Carina summit rounded, distinct. Pleuron margins convex, with sharply rounded, posteroventrally directed termination. Upper surface almost smooth, lower surface granulose. Small, dome-like swelling anteroventrally.

Tergum 5 rectangular. Lateral margins convex. Tergum smooth on dorsomedian keel, otherwise coarsely and densely pitted. Lateral carina as on segment 4. Pleuron round. Small, dome-like swelling anteroventrally. Pleuron upper surface granulose, lower surface densely granulose. Pleural margins 4–5 with very narrow, rounded, raised margin.

Sixth tergum trapezoidal, much wider anteriorly. Lateral margins slightly convex. Tergum subtly convex, densely and coarsely pitted, sparsely so dorsoventrally. Tergum dropping off sharply laterally. Posteriorly, tergum concave laterally between subtly convex dorsum and drop off. Pleuron triangular, very short, highest near anteroventral corner. Small, dome-like swelling anteroventrally. Pleuron granulose. Telson with round granules.

Claws strongly dissimilar in form; relative size of left and right claw varying. Crusher claw very *Hoploparia*-like; delicate pectinate claw with bulbous palm, long fingers and acicular dentition much like that of extant *Thaumastocheles*.

Pectinate claw with bulbous palm approximately twice longer than thick. Large process on at least

one side of palm receiving spine at base of dactylus. Palm surface with minute granules. On at least one surface of palm, spine distally near base of fixed finger. Fingers long, slender, with acicular denticles of varying length, of formula ADCDBD-CDA ("A" being largest), in one plane. Fixed finger nearly straight, widest at base; width tapering very gradually distally. Dactylus slightly curved; widest over proximal portion near mid-length. Fingers proximally triangular in cross section; otherwise compressed. Tips of fingers not occludent; one slightly shorter than other. Most denticles straight, angling slightly distally. Some larger denticles slightly curving, angling distally at base, proximally at end. Surface of both fingers pitted.

Crusher palm shape varying between specimens. On most, left palm nearly twice as long as wide. Palm widening distally over proximal half; margins parallel over distal half. Palm compressed, slightly thicker proximally; upper and lower surfaces gently convex. Palm surface variously granulose, pitted. Upper and lower palm surfaces very subtly concave at base of fixed finger. Both surfaces with spine submedially, near base of fixed finger. Sub-medial process on upper and lower distal margin articulating with spines on dactylus base. Inner margin somewhat flattened, with a few alternating spines on upper and lower edges. Outer margin rounded; axis with band of setal pits; upper surface of outer margin with irregular row of spines directed slightly distally. Fingers moderately strong, ovate in cross section. Fixed finger occlusal surface with multi-cusped platform proximally; otherwise with blunt, conical denticles. Dactylus with upward and distally-directed spine proximally on corner of upper/non-occluding surfaces. Dactylus dentition conical; pattern varying between specimens. Merus (IRScNB 90-17 and 90-33f) large, strongly compressed laterally, widening distally; upper proximal corner terminating in long point. Upper palm surface variously pitted, granulose.

On two specimens (IRScNB 90-33f and 90-32a; latter with small, *Thaumastocheles*-like claw), crusher claw palm proportionately shorter than on other specimens, and widening distally over entire length, giving subtriangular outline; upper and lower surfaces more convex than on other specimens; palm thickens distally.

**Remarks.** Pelseneer (1886) was the first to note the *Thaumastocheles*-like morphology in Bosquet's type series. He examined both the Bosquet and Ubaghs collections but did not recognize Bosquet's combining of the two lobster species. He did, however, realize the uniqueness of one of the *Thau-*

*mastocheles*-like pleons and referred to this as a new species, *Homarus bosqueti*. Pelseneer (1886) correctly described the terga as being less convex than those of *O. bredai*, but his figures 3 and 4 show the opposite. *Homarus bosqueti* is considered herein to be a junior objective synonym of *Oncopareia bredai*.

A re-examination of the syntype series of *Hoploparia biserialis* has revealed that two isolated cephalothoraxes assigned to this species by Fritsch himself (one of them being figured in Fritsch and Kafka, 1887, pl. 5, fig. 2), belonged to a different genus. Indeed, there is an imminent difference in the groove pattern between the two cephalothoraxes assigned to *H. biserialis* shown in Fritsch and Kafka (1887, pl. 5, figs. 1 and 2), one of them belonging to *H. biserialis* and another being reassigned to *O. bredai* herein. We were not able to identify any morphological differences between the type material of *O. bredai* and the Czech material here attributed to that species.

The type specimen of *Nymphaeops coesfeldiensis* has not been located; it is here considered lost. Our examination of the original figures (Schlüter, 1862, pl. 13, figs. 3, 6; Schlüter, 1879, pl. 15, figs. 1, 2, refigured herein in Figure 7) has not revealed any difference from the material of *O. bredai* leading us to recognize *N. coesfeldiensis* as a junior subjective synonym of *O. bredai*. In this respect, it is important to note that Mertin (1941) lumped material from several 'Senonian' localities into one species, i.e., *O. coesfeldiensis*. Whether or not all of the specimens Mertin (1941) assigned to *O. coesfeldiensis* are correctly referred to one species is uncertain. His unwhitened photographs are difficult to interpret and his line drawings do not seem to be consistent with the photographs. For example, he did not connect the branchiocardiac and cervical grooves ventrally (as hepatic groove) in his figure 9a. Cephalothoraxes and pleons in his plates strongly resemble those of *O. bredai* as revised herein. Mertin (1941, p. 187, pl. 3, fig. 9) also listed *Oncopareia* cf. *coesfeldiensis* from the lower 'Senonian' of north-central Germany and *Oncopareia* sp. (Mertin, 1941, p. 187, text-fig. 10e, f and n) from the upper 'Senonian' of the same area. The latter shows heterochelous claws, the pectinate claw having acicular dentition.

*Oncopareia bredai* differs from its congeners by the intercervical groove extending toward below the top of the cervical groove. In *O. bredai*, the marginal carina on pleonal pleura is wider than that on *O. esocina*. The pectinate claw of *O. bredai* possesses denticles which are perpendicular to the

longitudinal axis of the fingers, unlike those in *O. klintebjergensis* which are angled distally.

**Range and occurrence.** *Oncopareia bredai* was first described from what is now the Kunrade Formation, a lateral equivalent of part of the Maastricht Formation, of late Maastrichtian age, and exposed in the eastern part of southern Limburg, the Netherlands. Subsequent records are from the Vijlen Member, interval 6 (Gulpen Formation), of late early Maastrichtian age, as exposed at the former SA Ciments Portland Liegeois (CPL) quarry near Haccourt and the adjacent Ciments Belge Réunion (CBR) quarry, province of Liège, north-east Belgium. Czech occurrences, referred to *Hoploparia biserialis* by Fritsch, in Fritsch and Kafka (1887) originate from the uppermost part of the Jizera Formation (upper Turonian) at Vinary near Vysoké Mýto in the Bohemian Cretaceous Basin, Czech Republic. The stratigraphical level of *N. coesfeldi* was indicated as 'Senonian', both lower and upper, of north-central and northwest Germany by Mertin (1941); in current terminology, this would correspond to the lower and upper Campanian.

*Oncopareia esocina* (Fritsch in Fritsch and Kafka, 1887)

Figure 8A–E

- |       |  |
|-------|--|
| 1887  | <i>Stenocheles esocinus</i> Fritsch in Fritsch and Kafka, p. 40, text-fig. 59; pl. 4, fig. 7.                      |
| 1887  | <i>Ischnodactylus esocinus</i> (Fritsch in Fritsch and Kafka); Forir, p. 189.                                      |
| 1893  | <i>Stenocheles esocinus</i> Fritsch in Fritsch and Kafka; Frič, p. 106, text-fig. 137.                             |
| 1894  | <i>Stenocheles esocinus</i> Fritsch in Fritsch and Kafka; Frič, p. 102, text-fig. 137.                             |
| 1929  | <i>Ischnodactylus esocinus</i> (Fritsch in Fritsch and Kafka); Glaessner, p. 226.                                  |
| 1941  | <i>Oncopareia esocinus</i> (Fritsch in Fritsch and Kafka); Mertin, p. 181, text-fig. 8b.                           |
| ?1941 | <i>Oncopareia</i> cf. <i>esocinus</i> (Fritsch in Fritsch and Kafka); Mertin, p. 181, text-fig. 8c; pl. 3, fig. 1. |
| 2010  | <i>Oncopareia esocinus</i> (Fritsch in Fritsch and Kafka); Schweitzer et al., p. 31.                               |
| 2016  | <i>Oncopareia esocinus</i> (Fritsch in Fritsch and Kafka); Feldmann et al., p. 23, fig. 20.3a.                     |

**Material examined.** Part and counterpart of the holotype, NM O3467 and NM O3468 (respectively) in the palaeontological collections of the National Museum in Prague.

**Diagnosis.** *Oncopareia* with second pleonal somite tergite-pleuron boundary marked by arcuate, concave-upward, ridge. Second pleuron quadrate.

**Remarks.** This species is known from a single specimen representing a pleon and associated major claw, both of which are characteristic of *Oncopareia*. Pleonal terga are wide and convex with lateral carina at tergum-pleuron boundary on each segment. The pectinate claw with bulbous palm possesses long, slender fingers with acicular dentition. The material is flattened in fine-grained siliceous to calcareous claystones. The second pleonal somite on *O. bredai* differs from that of *O. esocina* in being shorter and less quadrate, and in having the tergite-pleuron boundary ridge straighter. Also, pleura bordered by marginal carina are narrower on *O. esocina* than those on *O. bredai*.

**Range and occurrence.** This species is known from the lower Coniacian (*Cremnoceramus crassus* inoceramid Zone) of the Teplice Formation (Rohatce Member) at Oškobrh near Poděbrady in the Czech Republic (Fritsch and Kafka, 1887). The material reported by Mertin (1941, p. 181) from the lower 'Senonian' (i.e., Coniacian-lower Campanian) of Salzberg near Quedlinburg, northern Germany, is certainly referable to *Oncopareia*, although based solely on Mertin's photographs of an unwhitened specimen, we cannot judge whether this belongs to *O. esocina*, or not.

*Oncopareia klintebjergensis* Jakobsen and Collins, 1979

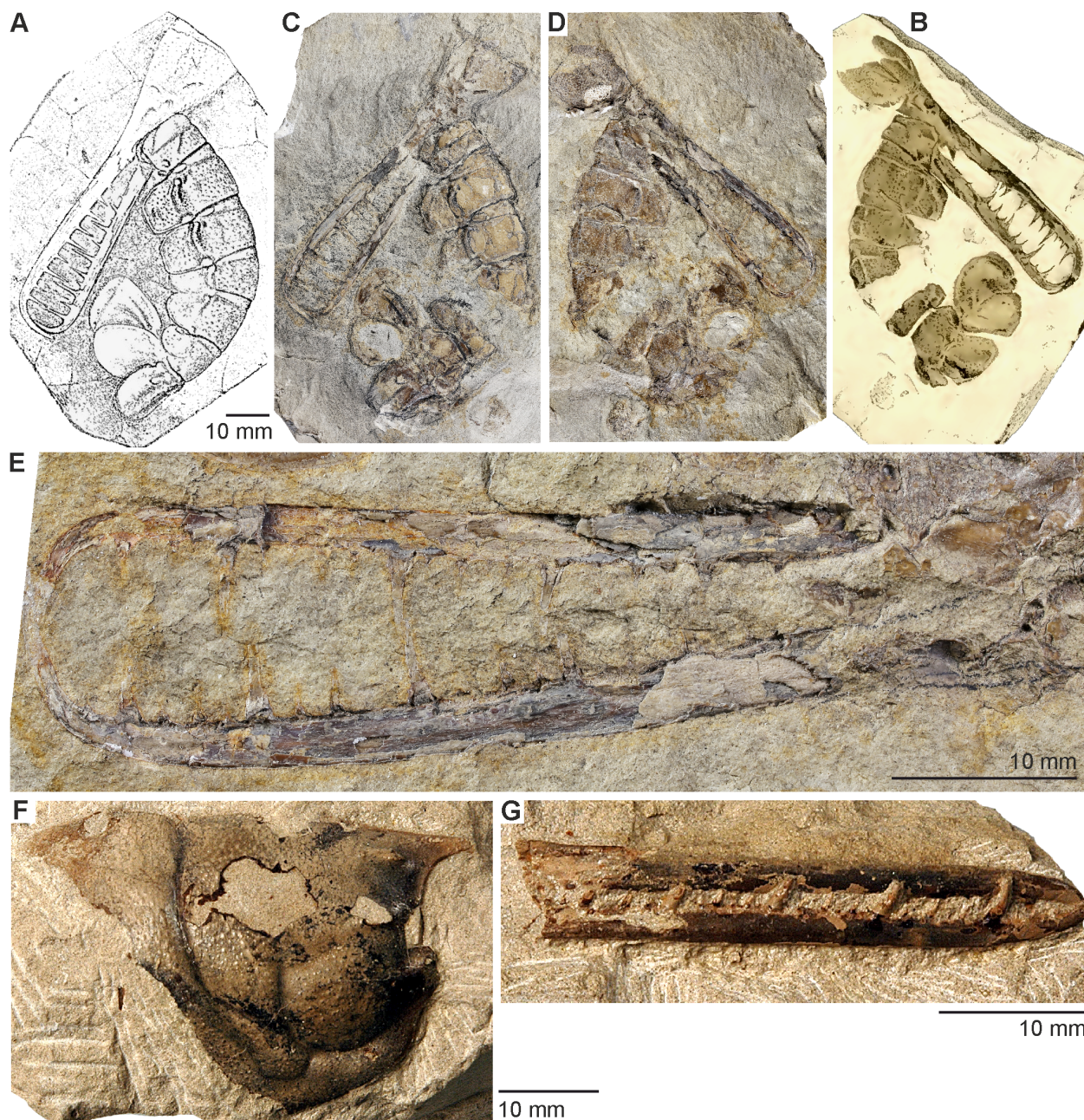
Figure 8F–G

- |      |   |
|------|---|
| 1979 | <i>Oncopareia klintebjergensis</i> Jakobsen and Collins, p. 61, pl. 1, figs. 1, 2.            |
| 2010 | <i>Oncopareia klintebjergensis</i> Jakobsen and Collins; Schweitzer et al., p. 32.            |
| 2016 | <i>Oncopareia klintebjergensis</i> Jakobsen and Collins; Feldmann et al., p. 23, fig. 20.3c–d |

**Material examined.** Holotype MGUH 14437 (incomplete cephalothorax), paratype MGUH 14438 (right cheliped fingers).

**Diagnosis.** *Oncopareia* with long, almost straight orbital margin; cervical and combined branchial-





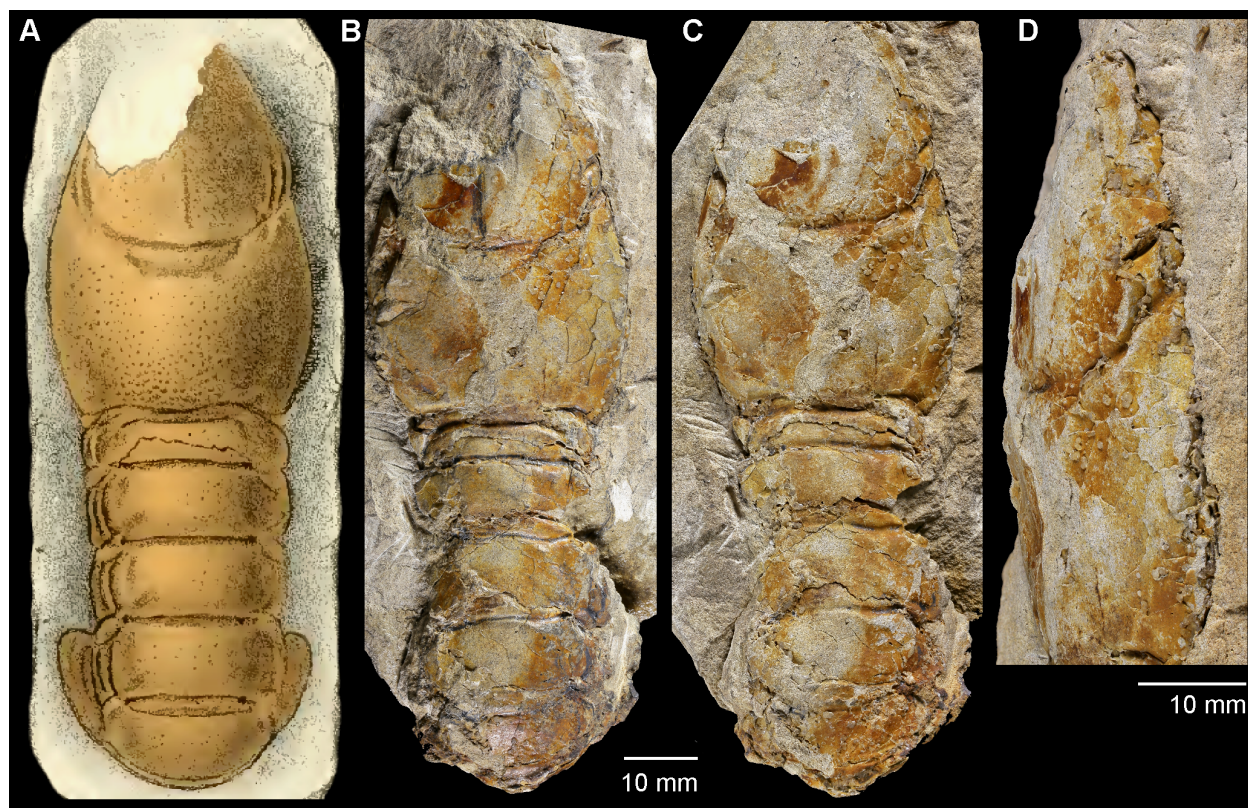
**FIGURE 8.** Species of *Oncopareia* based on fragmentary specimens. A–E. *Oncopareia esocina* (Fritsch, in Fritsch and Kafka, 1887); pectinate claw with associated pleon and tailfan from the lower Coniacian (Teplice Formation) at Oškobrh near Poděbrady, Czech Republic. A, Digital copy of figure from Fritsch and Kafka (1887, text-fig. 59). B, Digital copy of figure from Fritsch and Kafka (1887, pl. 4, fig. 7). C, Part of the holotype (NM O3467). D, Counterpart of the holotype (NM O3468). E, Detailed view of pectinate claw. F, G, *Oncopareia klintebjergensis* Jakobsen and Collins, 1979; Paleocene (Lellinge Greensand Limestone) of Klintebjerg, Denmark. F, Incomplete cephalothorax in lateral view (holotype). G, Fingers of pectinate claw (paratype).

postcervical grooves concave-forward and with two spines behind orbit.

**Remarks.** *Oncopareia klintebjergensis* is based on the anterior portion of a single cephalothorax and part of its associated right cheliped (Jakobsen and

Collins, 1979). The species differs from *O. bredai* in several aspects, including the longer, shallower orbits, the more ventral position of prominence “ $\omega$ ” on the carapace, and in the claw denticles which are angled distally.





**FIGURE 9.** *Oncopareia lunata* (Fritsch, in Fritsch and Kafka, 1887); incomplete cephalothorax with pleon from the lower-middle Turonian (Bílá Hora Formation) in Prague, Czech Republic (NM O3473). A, Digital copy of the figure from Fritsch and Kafka (1887, pl. 5, fig. 6). B, Holotype in dorsal view with morphological features highlighted by pencil (presumably by Fritsch himself). C, Holotype in dorsal view with pencil marks removed. D, Holotype in lateral view.

**Range and occurrence.** Paleocene Lellinge Greensand Limestone of Klintebjerg, eastern Sjælland, Denmark.

*Oncopareia lunata* (Fritsch in Fritsch and Kafka, 1887)

Figure 9A–D

- |       |   |
|-------|---|
| 1887  | <i>Nymphaeops? lunatus</i> Fritsch in Fritsch and Kafka, p. 35, pl. 5, fig. 6.                            |
| 1929  | <i>Nymphaeops? lunatus</i> ; Glaessner, p. 279.   |
| 1941  | <i>Oncopareia lunatus</i> (Fritsch in Fritsch and Kafka); Mertin, p. 180.                                 |
| 2000a | <i>Oncopareia ?lunatus</i> (Fritsch in Fritsch and Kafka); Tshudy and Sorhannus, pp. 481, 484-appendix 1. |
| 2010  | <i>Oncopareia lunatus</i> (Fritsch in Fritsch and Kafka); Schweitzer et al., p. 32.                       |

**Material examined.** Holotype, NM O3473, in the palaeontological collections of the National Museum in Prague.

**Diagnosis.** *Oncopareia* with arcuate (concave-up) intercervical groove extending toward upper part of cervical groove.

**Description.** This species is known by a single specimen preserving part of a dorsoventrally flattened cephalothorax (without rostrum and anterior region) and the pleon in dorsal aspect. The pleon itself is connected to the cephalothorax. Long post-cervical groove intersects dorsal median line slightly posteriorly to mid-length on carapace; as combined branchiocardiac-postcervical groove, extending anteroventrally to hepatic groove; then, bifurcating at third-height of carapace and as arcuate intercervical groove curving toward, but not reaching, the level of top of cervical groove. Branchiocardiac groove absent posteriorly and beginning as branchiocardiac-postcervical groove; after bifurcating extending ventrally to join semicircular hepatic groove. Cervical groove well incised, short. Anteroventral part of cephalothorax, in region of antennal and inferior grooves, not preserved. Pleura short; pleonal terga wide, convex with a lateral carina at tergum-pleuron boundary.

**Remarks.** Mertin (1941) referred this species to *Oncopareia* based on the short pleura; he did not comment on the cephalothorax grooves. Tshudy (1993, pp. 300–301), based on the published illustration, assigned the single specimen with *Oncopareia*-like pleon to “*Oncopareia?*”; the uncertainty was based on the urogastric groove on the cephalothorax, which is unknown in *Oncopareia*. Personal re-examination of the type material by one of us (MKV) confirmed the attribution of the species to *Oncopareia*. In this respect, it should be stressed that the original restoration of this form (Fritsch and Kafka, 1887, pl. 5, fig. 6) does not fully correspond with the original specimen. Fritsch pencil marked the specimen to highlight morphological features, and, as a result, two distinct transverse grooves crossing the dorsal midline of the cephalothorax appeared in his drawing. These grooves look to be the urogastric and postcervical grooves, the former being known in several nephropid genera, but not in *Oncopareia*. However, after washing the specimen, it turned out that Fritsch marked an extra line (i.e., a potential urogastric groove) on this particular specimen. In actual fact, there is only one transverse groove crossing the dorsal midline, the postcervical groove. Thus, caution must be exercised when dealing with Fritsch’s taxa on the basis of published drawings only.

*Oncopareia lunata* differs from *O. bredai* in having a considerably shorter cervical groove, a more arcuate intercervical groove oriented toward the level of the top of the cervical groove. In addition, it lacks a posteriorly defined branchiocardiac groove. In view of the fact that *O. lunata* is incompletely known (i.e., lacking the anterior region of the cephalothorax and chelipeds), further comparison with *O. bredai* is not possible.

**Range and occurrence.** The occurrence of *O. lunata* is so far limited to shallow-marine marlstones of the Bílá Hora Formation (lower–middle Turonian) in the Prague area, Czech Republic.

*Oncopareia* sp. 1

- 1993            *Oncopareia* sp. Tshudy, p. 303.  
2000a        *Oncopareia bredai* Bosquet; Tshudy  
                 and Sorhannus, figs. 4.5–4.8.

**Material examined.** Three specimens, IRScNB 90-19f, 90-19h and 90-19m (one complete and two incomplete palms).

**Description.** Palm bulbous, about 1.7x longer than wide; widest and thickest near distal end. Upper and lower surfaces convex. Outer margin rounded; inner margin with very prominent, broad, flat-topped keel. Keel higher, narrower, proximally;

lower, broader distally. Palm upper surface with very fine (IRScNB 90-19f) or fine (IRScNB 90-19m) granules, with spine near outer-proximal corner. Lower surface and outer margin smooth. Inner marginal keel bearing a few stout, alternating spines on keel edges; otherwise with minute, densely distributed granules.

**Remarks.** These specimens are distinguished from *O. bredai* on the basis of the prominent keel on the inner margin of the claw.

**Range and occurrence.** Upper Maastrichtian (Kunrade Formation) of Kunrade, southern Limburg, the Netherlands.

*Oncopareia* sp. 2

- 1941            *Oncopareia* sp. Mertin, p. 187, text-  
                 fig. 10e, f, n.

**Material examined.** None.

**Remarks.** Known only by an incomplete major and minor claw. Solely on the basis of Mertin’s (1941) photographs of unwhitened specimens, we cannot judge whether this material belongs to *O. esocina*, or not. However, it certainly is referable to *Oncopareia*.

**Range and occurrence.** Upper ‘Senonian’ of Königslutter, east of Braunschweig, north-central Germany (Mertin, 1941); in current terminology this would correspond to the upper lower Campanian.

Genus *Hoploparia* M’Coy, 1849

**Type species.** *Astacus longimanus* Sowerby, 1826, by the subsequent designation of Rathbun (1926).

**Diagnosis (after M’Coy, 1849, pp. 175–176).** Carapace minutely granulose, oblong, tumid, slightly compressed, a little deeper than wide, ending in front in a strong sharp rostrum, the sides of which are strongly carinate and smooth, or with few very minute teeth; beneath the orbits the cheeks are prolonged forwards about half the length of the rostrum.

**Diagnosis (after Feldmann et al., 2016, p. 16).** Subcylindrical carapace smooth; rostrum long, with suprarostal spines; supraorbital spine present; scaphocerite present; subdorsal carina present; cervical groove and postcervical groove well-developed, postcervical groove extending from midline to about midheight of carapace where it joins hepatic groove to encircle adductor testis muscle attachment; branchiocardiac groove weak; strong heterochely of pereopod 1; major chelipeds with fingers with strong, domal denticles on occlusal surfaces; minor chelipeds with finer, spinose denticles on occlusal surfaces; pereopods 2 and 3 chelate; terga smooth or weakly ornamented;



subrectangular telson; exopodite of uropods with diaeresis.

**Diagnosis (after Tshudy et al., 2018, p. 174).**

Rostrum long, spinose. Postcervical groove well impressed over most of length; becomes subtler as it extends anteriorly toward cervical groove. Branchiocardiac groove (dorsally) usually present. Ventral extension of branchiocardiac groove typically extends to hepatic groove. Urogastric groove typically absent. Cervical groove well impressed; extends from level of orbit to junction of hepatic and antennal grooves. Median carina typically absent. Submedian carina present on a few species. Subdorsal carina present. Supraorbital spine present, typically followed by supraorbital carina. Postorbital spine typically present; gastrolateral and hepatic spine typically absent. Antennal carina absent, short, or extending to near cervical groove. Thoracic region lacks carinae. Pleonal terga unornamented, mostly unsculptured; typically with a narrow transverse furrow along posterior margin. Pleura elongate, typically cordate, ending in a point. Telson surface with a pair of submedian ridges converging posteriorly. Telson without lateral spines but with posterolateral spines. Scaphocerite present. Claws typically unequal; upper and lower surfaces lacking carinae. Exoskeleton generally granulated.

**Remarks.** *Hoploparia* was erected by M'Coy (1849) for fossils that generally resembled *Homarus* but had a more sculptured (grooved, locally inflated, etc.) and ornamented carapace. In fact, the name *Hoploparia* refers to the lobster's "spiny cheeks", the locally inflated and ornamented regions on the anteroventral sides of the cephalothorax. *Homarus* lacks these locally inflated "cheeks" and is less spiny. M'Coy's diagnosis, reprinted here, distinguished the type species, *Hoploparia longimana*, from *Homarus*.

*Hoploparia* is readily distinguished from *Oncopareia* in the nature of the chelipeds and pleon. Claws are never pectinate in *Hoploparia* and pleura 3-5 in *Oncopareia* are characteristically quadrate, not cordate and pointed as in *Hoploparia*.

*Hoploparia beyrichi* Schlüter, 1862

Figure 1E, 2B–C, 10A–M

Partim 1854 *Oncopareia bredai* Bosquet, p. 127, pl. 10, figs. 6, 7, 7<sup>1</sup> [not pl. 10, figs. 5, 6<sup>1</sup>]

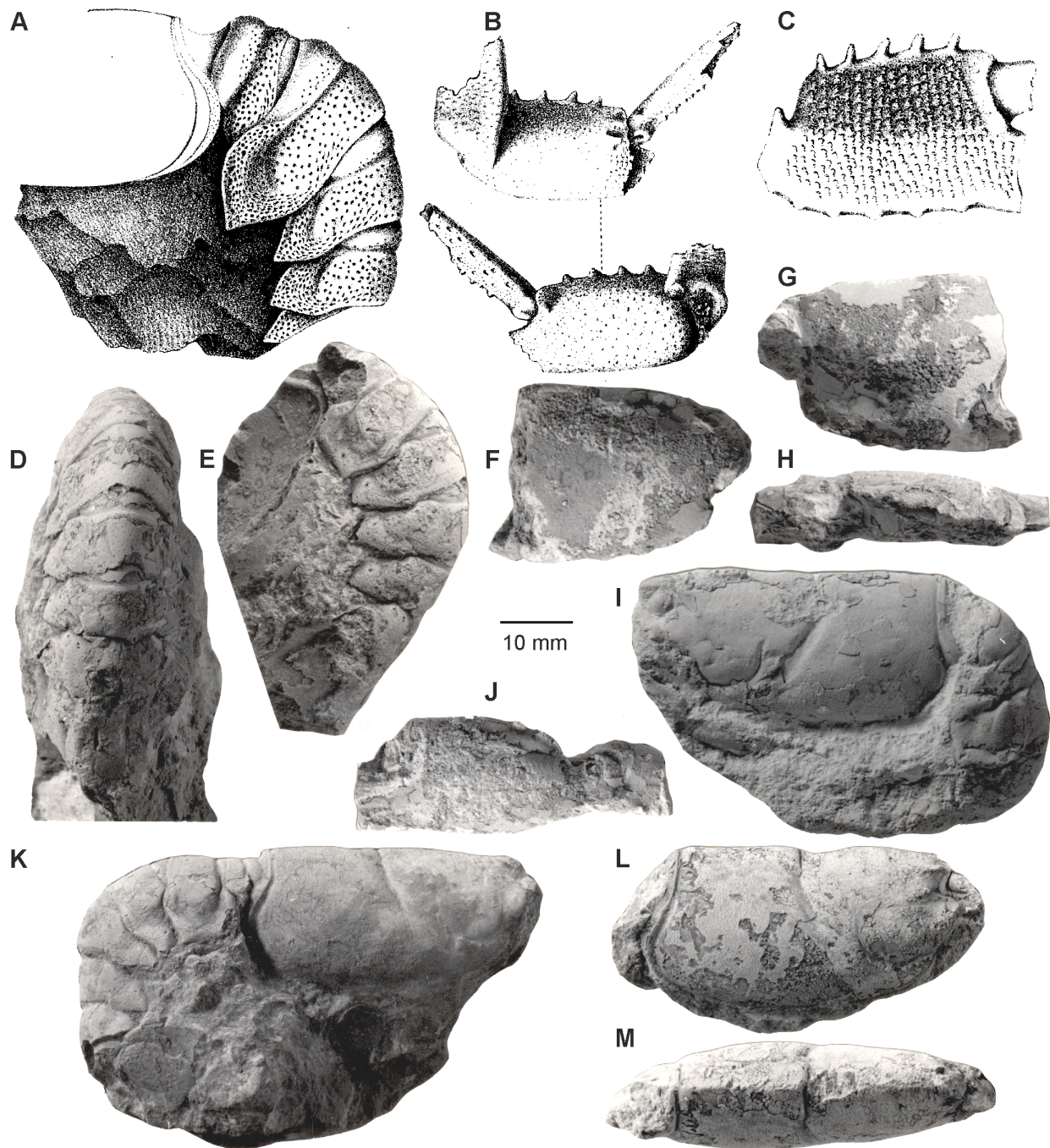
1862 *Hoploparia beyrichi* Schlüter, p. 721, pl. 13, fig. 4.

- 1886 *Homarus bredai* (Bosquet); Pelse-neer, p. 164, figs. 2, 3.  
 1929 *Hoploparia bredai* (Bosquet); Glaes-sner, p. 216.  
 1941 *Oncopareia bredai* Bosquet; Martin, fig. 9<sup>e</sup> [pleon only].  
 1993 *Hoploparia beyrichi* Schlüter; Tshudy, figs. 17.1–17.14.  
 2000b *Hoploparia beyrichi* Schlüter; Tshudy and Sorhannus, fig. 2.3.  
 2010 *Hoploparia beyrichi* Schlüter; Schweitzer et al., p. 28.  
 2018 *Hoploparia beyrichi* Schlüter; Tshudy et al., p. 182.

**Material examined.** Holotype, Museum für Naturkunde Berlin, MB. A. 209; also several specimens deposited in the IRScNB collections, including those in the Bosquet (IG 4285; IRScNB 90-33a, c, g, i), De Jaer (IG 8261; IRScNB 90-24a, b) and Ubaghs (IG 6521; IRScNB 90-19j, n, 90-20, 90-22b, 90-32b, d, f and 90-39c) collections.

**Diagnosis.** Cephalothorax with little relief; antennal carina absent. Postorbital and supraorbital spine prominent; supraorbital followed by short carina. Pleonal terga and pleura with little relief; surfaces pitted. Claws slightly unequal in form and size.

**Description.** Carapace laterally compressed, twice as long as high. Postcervical groove intersecting dorsal midline at just posterior to mid-length on carapace. Postcervical groove extending transversely across dorsal surface; combined branchiocardiac and postcervical groove extending anteroventrally to level of antennal groove in slightly concave-forward arc; well impressed dorsally, becoming progressively fainter ventrally. Anterior extension of postcervical groove extending toward, but not reaching, middle of cervical groove. Hepatic groove very subtle or absent. Cervical groove subparallel to, and more vertical than, postcervical groove; originating at level of base of orbit. Cervical and antennal grooves together forming a semicircular arc. Antennal groove anteriorly curving upward, reaching carapace margin well below antennal spine. Branchiocardiac groove very short on most specimens, long on the single large specimen. Supraorbital spine followed by short carina. Postorbital spine round. Wide, flat, postero-marginal carina with elongate pits dorsally, smooth or pitted laterally. Surface of thoracic region with transversely elongate pits dorsally and laterally, granules ventrally.



**FIGURE 10.** *Hoploparia beyrichi* Schlüter, 1862; upper Maastrichtian (Kunrade Formation), Kunrade area, southern Limburg, the Netherlands. A, Pleon in lateral view (from Bosquet, 1854, pl. 10, fig. 6). B, Right claw in inner and outer lateral views (from Bosquet, 1854, pl. 10, fig. 7<sup>1</sup>). C, Incomplete right claw (from Bosquet, 1854, pl. 10, fig. 7). D, E, Pleon in dorsal (D) and lateral (E) views (IRScNB 90-32f). F–H, Fragmentary claw (right propodus) in inner lateral (F), outer lateral (G) and dorsal (H) views (IRScNB 90-19j). I, Cephalothorax with associated incomplete pleon in lateral view (IRScNB 90-32d). J, Right claw (propodus and carpus) in inner lateral view (IRScNB 90-24b). K, Cephalothorax with associated pleon (holotype, MB. A. 209). L–M, Cephalothorax in lateral (L) and dorsal (M) views (IRScNB 90-33g). Specimens were whitened with ammonium chloride prior to photography.

Pleon laterally compressed. Terga rectangular, strongly convex, sparsely pitted. Pleura long, more densely pitted than terga. Pleuron 2 quadrate; anterior margin rounded, anteroventral corner rounded, ventral margin straight, posterior margin recurved, posteroventral corner terminating in posteriorly directed point. Pleura 3–5 cordate, terminating in point; pleuron 6 triangular. Pleura gently inflated axially, traversed by very broad, subtle, oblique ridge extending posteroventrally from anterodorsal corner of pleuron; carina most pronounced on second pleuron and becoming progressively less obvious on posterior segments. Pleura directed posteriorly relative to terga. A single, large pit present posteroventrally on pleuron 2, anteroventrally on pleura 3–5.

Claws slightly unequal in form and size. Right palm larger than left; right palm slightly longer than wide; left palm slightly more elongate. Palms widening distally; rapidly so near proximal articulation. Right palm upper surface gently convex; pitted proximally, but most of surface with flat, scale-like granules of varying size; pits along distal edges of most scales. Lower surface slightly more convex than upper surface, mostly pitted. Inner margin angular, slightly upturned, with at least four large, conical, slightly upturned spines; all but most proximal spine directed slightly distally; space between spines increasing distally. Outer margin angular, pitted.

Left palm upper surface gently convex, pitted. Lower surface convex, with very fine, very low, transversely elongate granules. Inner margin angular, with at least four large, conical, slightly upturned spines; all but most proximal spine directed distally. Outer margin broadly rounded proximally, becoming progressively narrower distally; sharply rounded at base of fixed finger.

**Remarks.** The holotype from the upper Maastrichtian (Kunrade Formation) of Kunrade, southern Limburg, the Netherlands, consists of an imperfectly preserved cephalothorax lacking the rostrum and a slightly better-preserved pleon lacking the telson. Schlüter (1862, p. 722) considered the specimen distinct from *O. bredai*, mainly on the basis of its carapace grooves and ornamentation and named it *Hoploparia beyrichi*. The pleons and claws that Bosquet (1854) described, illustrated and referred to *Oncopareia bredai* also belong to *H. beyrichi*; thus, some specimens from the syntype collection of *O. bredai* actually belong to *H. beyrichi*. Bosquet's figure 6 depicts the pleon of IRScNB 90-33a, and figure 7 the major claw, IRScNB 90-33c. Figure 7<sup>1</sup>a–b may correspond to

IRScNB 90-24b; if not, the palms are very similar. Cephalothoraxes IRScNB 90-24a and 90-33g are referred to *H. beyrichi* as well.

The cephalothoraxes of *H. beyrichi* and *O. bredai* are strikingly similar considering the fundamental differences between the pleons and claws of the two species. There are, however, consistent differences between them. First, the hepatic groove is deeper in *O. bredai* than in *H. beyrichi*. Schlüter (1862, p. 722) described, in different terms, that the hepatic groove circumscribed the protuberance “χ” on *O. bredai* but not on his new species, *H. beyrichi*. Secondly, the cervical groove on *O. bredai* more nearly parallels the ventral portion of the branchiocardiac groove than on *H. beyrichi*. Finally, *O. bredai* is ornamented with granules, whereas *H. beyrichi* is covered dorsally and laterally with pits. Schlüter (1862, p. 722) noted that *H. beyrichi* lacked granules but was ornamented with an extremely fine sculpture.

**Range and occurrence.** Upper Maastrichtian of Belgium and the Netherlands.

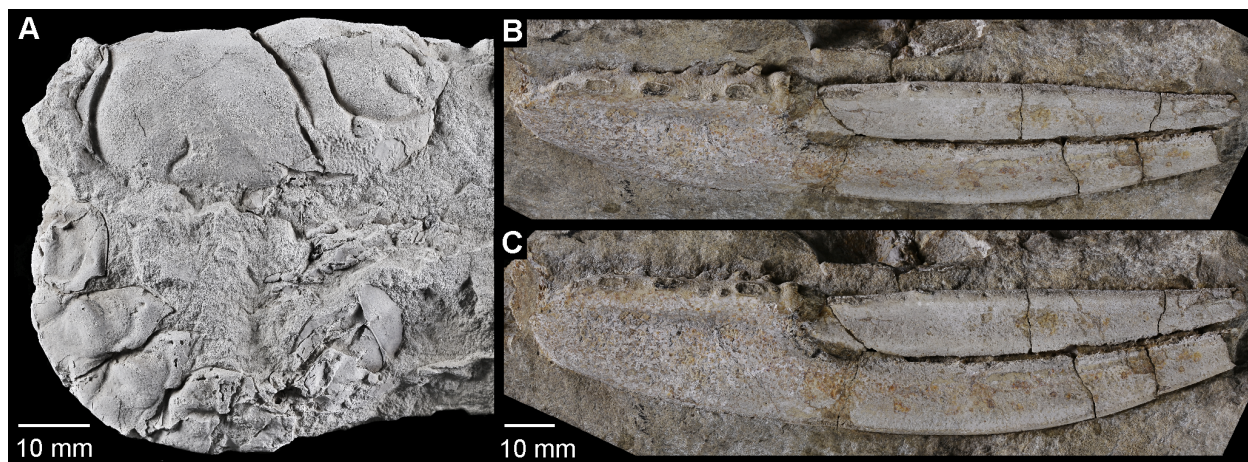
*Hoploparia biserialis* Fritsch in Fritsch and Kafka, 1887

Figure 11A–C

- Partim 1887 *Hoploparia biserialis* Fritsch in Fritsch and Kafka, p. 35, text-fig. 56, pl. 3, fig. 5; pl. 5, fig. 1 [non pl. 5, fig. 2 = *Oncopareia bredai* Bosquet, 1854]
- 1929 *Hoploparia biserialis* Fritsch in Fritsch and Kafka; Glaessner, p. 216.
- 1941 *Hoploparia “biserialis”* Fritsch in Fritsch and Kafka; Mertin, p. 176, text-fig. 7h.
- 1941 ?*Oncopareia biserialis* (Fritsch in Fritsch and Kafka); Mertin, text-fig. 8a.
- 2010 *Hoploparia biserialis* Fritsch in Fritsch and Kafka; Schweitzer et al., p. 28.
- 2010 *Oncopareia biserialis* [sic] Fritsch in Fritsch and Kafka; Schweitzer et al., p. 31.
- 2018 *Hoploparia biserialis* Fritsch in Fritsch and Kafka; Tshudy et al., p. 182.

**Material examined.** Four specimens in the original Fritsch Collection from the National Museum in Prague, labelled as *Hoploparia biserialis*, including NM O4044 (Orig. #91; cephalothorax and pleon), NM O3470 (Orig. #86; cephalothorax), NM O3457





**FIGURE 11.** *Hoploparia biserialis* Fritsch, in Fritsch and Kafka, 1887; lower–middle Turonian (Bílá Hora Formation) in Prague, Czech Republic. A, Cephalothorax with pleon and tailfan in lateral view (lectotype, NM O4044). B–C, Isolated right cutter claw in dorsal (B) and lateral (C) views (NM O3457). Specimen in A was whitened with ammonium chloride prior to photography.

(Orig. #87; isolated cutter claw) and NM 06861 (cephalothorax). NM O4044 (Figure 11A) is herein designated lectotype of the species.

**Diagnosis.** *Hoploparia* with combined postcervical and branchiocardiac grooves extending to hepatic groove. Antennal carina missing. Cutter claw elongate, with fingers longer than palm.

**Remarks.** Two specimens, NM O3470 and NM O6861, representing isolated cephalothoraxes of *O. bredai* were removed from the type collection of *H. biserialis* (see above). The remaining specimens, NM O4044 and NM O3457, confidently confirm placement in the genus *Hoploparia*. The long, pointed pleura of *H. biserialis* NM O4044 (see Fritsch and Kafka, 1887, text-fig. 56; Figure 11A here) are clearly *Hoploparia*- or *Homarus*-like and very unlike those of *Oncopareia*. No claw pairs are known from this specimen. The isolated cutter claw NM O3457 (e.g., Fritsch and Kafka, 1887, pl. 3, fig. 5; Figure 11B–C here) is *Hoploparia*-like; with a subtriangular palm, the inner margin of which has numerous large, anteriorly directed spines in two rows; fingers are long and robust, lack dentition on occlusal margins and become narrower distally.

It is important to note, that Martin (1941) considered these two specimens of *H. biserialis* (sensu Fritsch and Kafka, 1887), NM O3457 and NM O4044, to belong to different taxa. The isolated cutter claw NM O3457 (Martin, 1941, text-fig. 7h), in Martin's (1941) view closely resembling that of *H. longimana*, was referred to as *Hoploparia* “*biserialis*”, whereas the carapace with pleon NM O4044 (Martin, 1941, text-fig. 8a) was treated as ?*Oncopareia biserialis*. This pleon with cordate, pointed

pleura, and cephalothorax with smooth rostrum did not deter Martin (1941, p. 181) from placing the species in *Oncopareia*, which, by his definition, possesses a “stark bedornten” (strongly spiny) rostrum. Although the material comes neither from the same locality nor the same lithostratigraphic unit, we here refer both these specimens to *Hoploparia biserialis*, following Fritsch and Kafka (1887).

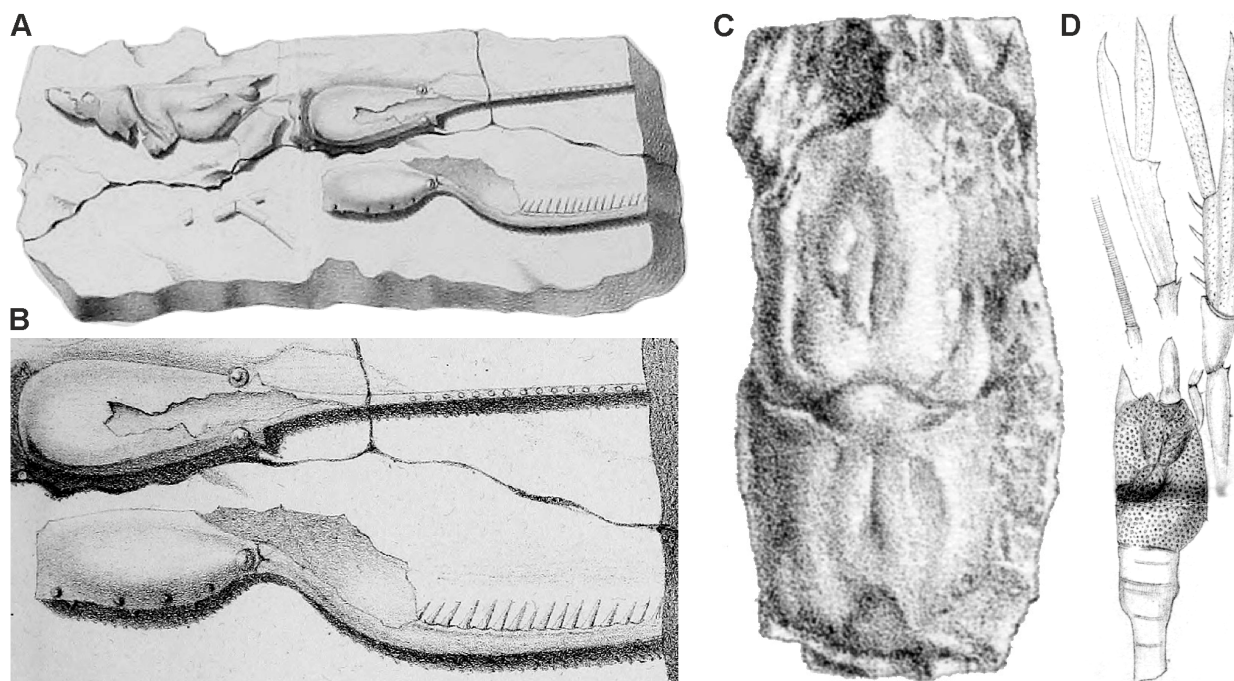
**Range and occurrence.** Upper Cretaceous, lower–middle Turonian of the Czech Republic; NM O3457 comes from the middle Turonian (lower part of the Jizera Formation) at Bechlín near Roudnice nad Labem and NM O4044 is from the lower–middle Turonian (Bílá Hora Formation) of Bílá Hora (‘Weissenberg’) in Prague.

#### *Hoploparia muncki* Pelseneer, 1885

- |      |   |
|------|---|
| 1885 | <i>Hoploparia muncki</i> Pelseneer, p. 44 [8], fig. 1.              |
| 1929 | <i>Hoploparia muncki</i> Pelseneer; Glaessner, p. 221.              |
| 1941 | <i>Oncopareia muncki</i> (Pelseneer); Martin, p. 188, text-fig. 8d. |
| 2010 | <i>Hoploparia muncki</i> Pelseneer; Schweitzer et al., p. 30.       |
| 2010 | <i>Oncopareia muncki</i> (Pelseneer); Schweitzer et al., p. 32.     |
| 2018 | <i>Hoploparia muncki</i> Pelseneer; Tshudy et al., p. 183.          |

**Material examined.** None.

**Remarks.** Tshudy (1993, pp. 147–148) and Tshudy et al. (2018) maintained Pelseneer's (1885) referral to *Hoploparia*, based on its antennal carina (albeit short), the diverging submedian carinae of the tel-



**FIGURE 12.** Astacidean lobsters with uncertain affinities. A-B, "*Hoploparia*" *macroductyla* Schlüter, in von der Marck and Schlüter, 1868; fragmentary cephalothorax with associated claws (from Schlüter, 1862, pl. 11, fig. 5). C, "*Nymphaeops*" *belgicus* Forir, 1887; cephalothorax in dorsal view (from Forir, 1887, pl. 7, fig. 1). D, "*Nymphaeops*" *sendenhorstensis* Schlüter, 1862; cephalothorax with pleon and chelipeds (from Schlüter, 1862, pl. 14, fig. 5).

son, and the granulation of the cephalothorax, pleon and telson. Its pleonal pleura are more like those of *Homarus* than those of *Hoploparia*.

**Range and occurrence.** Upper Cretaceous, lower Maastrichtian (Ciply-Malogne Phosphatic Chalk Formation; see Robaszynski et al. (2002) of the Mons Basin, southern Belgium).

#### ASTACIDEA INCERTAE SEDIS

"*Hoploparia*" *macroductyla* Schlüter in von der Marck and Schlüter, 1868  
Figure 12A–B

- 1862 *Hoploparia longimana* (Sowerby); Schlüter, p. 723, pl. 11, fig. 5.
- 1868 *Hoploparia macroductyla* Schlüter in von der Marck and Schlüter, p. 295.
- 1886 *Ischnodactylus macroductyla* (Schlüter); Pelseneer, p. 163.
- 1929 *Ischnodactylus macroductylus* (Schlüter); Glaessner, p. 226.
- 1941 *Oncopareia macroductylus* (Schlüter); Mertin, p. 179.
- 1993 *Oncopareia? macroductyla* (Schlüter); Tshudy, p. 301.
- 2010 *Oncopareia macroductylus* (Schlüter); Schweitzer et al., p. 32.

**Material examined.** None.

**Remarks.** Mertin (1941, p. 186) examined Schlüter's illustrated specimen and noted that: 1) the specimen's claws were not as well preserved as the illustration indicated; 2) the cephalothorax and shape of the claw palms were indistinguishable from those of *Oncopareia coesfeldiensis*; and that 3) the claw denticles were not of uniform length, as erroneously depicted in Schlüter, but of different lengths, as in *O. coesfeldiensis*. According to Mertin (1941), the only difference between Schlüter's specimen and *O. coesfeldiensis* was that the palm of the former had two rows of large spines on the upper edge; these spines being absent in *O. coesfeldiensis*. Mertin (1941) declared the specimen referable to *O. coesfeldiensis* but did not discuss the specimen's presumably equal claws, the latter indicated by Schlüter's illustration and in Pelseneer's remarks (1886, p. 163). Unfortunately, without the re-examination of the original material (which has not been traced) it is difficult to state whether the morphology of both claws as depicted is genuine. Based on the apparent lack of important characters and poor preservation of the original material we consider "*Hoploparia*" *macroductyla* an astacidean lobster with unknown affini-

ties (*Astacidea incertae sedis*), at least for the time being.

**Range and occurrence.** Upper lower ‘Senonian’ of Dülmen, northwest Germany (Mertin, 1941, p. 179); in current terminology this would mean the Dülmener Schichten of early Campanian age.

*“Nymphaeops” belgicus* Forir, 1887

Figure 12C

- 1887 *Nymphaeops belgicus* Forir, p. 157, pl. 7, fig. 1.  
 1929 *Nymphaeops belgicus* Forir; Glaessner, p. 279.  
 2010 *Oncopareia belgicus* (Forir); Schweitzer et al., p. 31.

**Material studied.** None.

**Remarks.** Tshudy (1993, pp. 369–370) concluded that the cephalothorax illustrated in dorsal view in Forir’s (1887) plate was probably not a nephropid. Mertin (1941, p. 188) wrote that the specimen was too poorly preserved to permit any comparison to *Oncopareia*.

**Range and occurrence.** Upper Cretaceous, ‘middle Senonian’, probably lower Maastrichtian, of the Liège-Limburg Basin, northwest Belgium and the southeast Netherlands (Forir, 1887, p. 160).

*“Nymphaeops” sendenhorstensis* Schlüter, 1862

Figure 12D

- 1862 *Nymphaeops sendenhorstensis* Schlüter, pp. 732–734, pl. 14, fig. 5.  
 1886 *Nymphaeops sendenhorstensis* Schlüter; Pelseneer, p. 173.  
 1929 *Nymphaeops sendenhorstensis* Schlüter; Glaessner, p. 279.  
 1941 *Nymphaeops sendenhorstensis* Schlüter; Mertin, p. 180.  
 1993 *“Nymphaeops” sendenhorstensis* Schlüter; Tshudy, pp. 28, 370–371.  
 2010 *Oncopareia sendenhorstensis* (Schlüter); Schweitzer et al., p. 32.

**Material studied.** None.

**Remarks.** The generic identity of *N. sendenhorstensis* is uncertain. Tshudy (1993, pp. 285, 370–371) concluded that the cephalothorax, pleon (with broken pleura) and heavy, isochelous claws were unlike those of *Oncopareia*, and treated the specimen as *“Nymphaeops” sendenhorstensis*.

**Range and occurrence.** Upper Cretaceous, upper ‘Senonian’ (probably late Campanian) of Sendenhorst, near Münster, western Germany (Mertin, 1941, p. 180) and lower Maastrichtian of the Liège-Limburg Basin, northeast Belgium and the southeast Netherlands (Pelseneer, 1886, p. 173).

*“Stenocheles” parvulus* Fritsch in Fritsch and Kafka, 1887

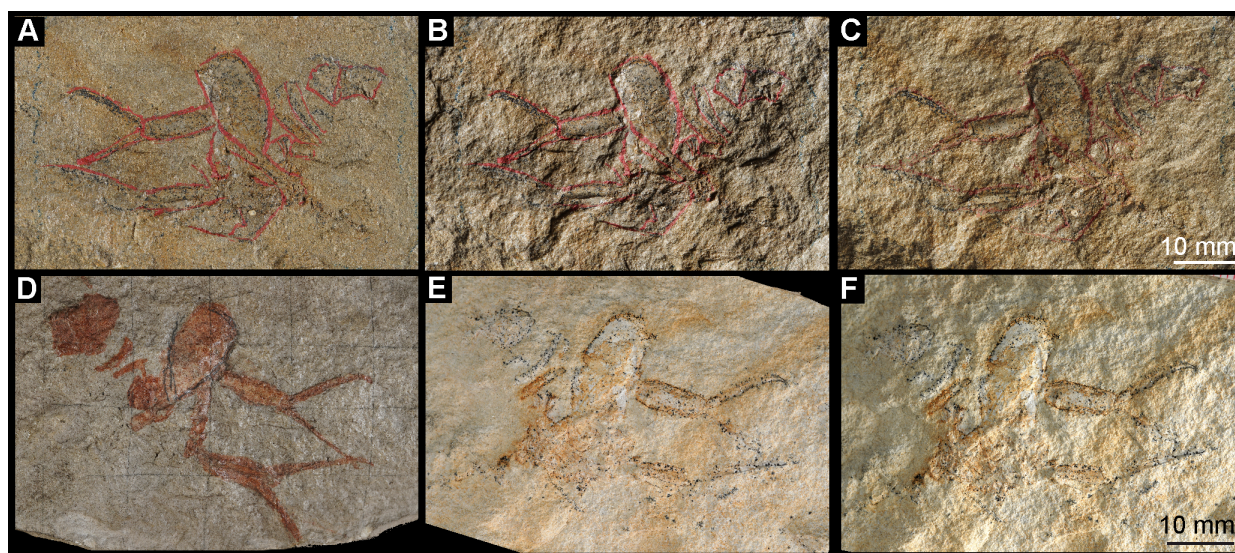
Figure 13A–F

- partim 1887 *Stenocheles parvulus* Fritsch in Fritsch and Kafka; p. 40, pl. 3, fig. 3 [non fig. 4 = *Ctenocheles fritschi* Hyžný, Kočová Veselská and Dvořák, 2014]  
 partim 1929 *Ischnodactylus parvulus* (Fritsch in Fritsch and Kafka); Glaessner, p. 226.  
 1941 ?*Oncopareia parvulus* (Fritsch in Fritsch and Kafka); Mertin, p. 185, text-fig. 10g.  
 1969 ?*Oncopareia parvulus* (Fritsch in Fritsch and Kafka); Glaessner, p. R459.  
 2010 *Oncopareia parvulus* (Fritsch in Fritsch and Kafka); Schweitzer et al., p. 32.  
 2014 ?*Oncopareia parvulus* (Fritsch in Fritsch and Kafka), Hyžný et al., p. 246, figs. 1B, 1C, 2B.

**Material studied.** Lectotype (designated by Hyžný et al., 2014), NM O3455 (part), and NM O9092 (counterpart).

**Remarks.** Mertin (1941, p. 198) expressed uncertainty regarding the generic placement of this species, but (p. 179) referred it to “?*Oncopareia*”. Tshudy (1993) concluded that the two specimens upon which *S. parvulus* was based (see Fritsch and Kafka, 1887, pl. 3, figs. 3, and 4) represented two different taxa but was unable to refer either specimen to a known genus and assigned both to “*Stenocheles*”. Hyžný et al. (2014) restudied these two specimens and recognized them as belonging to separate taxa, representing two entirely different infraorders. The heterochelous specimen NM O3456 (Fritsch and Kafka, 1887, pl. 3, fig. 4) became the holotype of *Ctenocheles fritschi* and the isochelous specimen NM O3455 (part) and NM O9092 (counterpart) (Fritsch and Kafka, 1887, pl. 3, fig. 3) was designated lectotype of *S. parvulus* (= ?*Oncopareia parvulus* sensu Hyžný et al., 2014). A new re-examination of the material by one of us (MKV) shows a very poorly preserved specimen with some portions being drawn onto the fossil (Figure 13A). The specimen not only does not correspond to details presented in the illustration provided by Fritsch and Kafka (1887, pl. 3, fig. 3), but also does not preserve sufficient taxonomically important characters to define the species. Moreover, its assignment to *Oncopareia* or *Ctenocheles*





**FIGURE 13.** “*Stenocheles*” *parvulus* Fritsch, in Fritsch and Kafka, 1887; lectotype from the lower–middle Turonian (Bílá Hora Formation) in Prague, Czech Republic. A–C, Part of the specimen (NM O3455) under various light conditions. D–F, Counterpart of the same (NM O9092), including the historical cast (D).

is highly dubious. The palms of *S. parvulus* are more elongate than is characteristic of either *Ctenocheles* or *Oncopareia*. The finger/palm length ratios on both specimens are smaller than on *Ctenocheles*, and much smaller than on *Oncopareia*. Importantly, the genus *Stenocheles* cannot be used for *S. parvulus*, because the type species of *Stenocheles* is *Stenocheles esocinus* (as designated by Glaessner, 1969), which is here reassigned to *Oncopareia*, thereby making *Stenocheles* a junior subjective synonym of *Oncopareia* (see above). Therefore, we refer *S. parvulus* to “*Stenocheles*” and consider “*Stenocheles*” *parvulus* a taxon of unknown affinities (*incertae sedis*). The classification of this dubious taxon at the infraordinal level is here considered only a matter of convenience rather than an assignment based on important characters.

**Range and occurrence.** Upper Cretaceous, lower–middle Turonian (Bílá Hora Formation) of Bílá Hora (‘Weissenberge’) in Prague, Czech Republic (Fritsch and Kafka 1887, p. 40).

AXIIDEA de Saint Laurent, 1979

CTENOCHELIDAE Manning and Felder, 1991

Genus *Ctenocheles* Kishinouye, 1926

**Type species.** *Ctenocheles balssi* Kishinouye, 1926, by monotypy.

*Ctenocheles cookei* (Rathbun, 1935)

Figure 14A–B

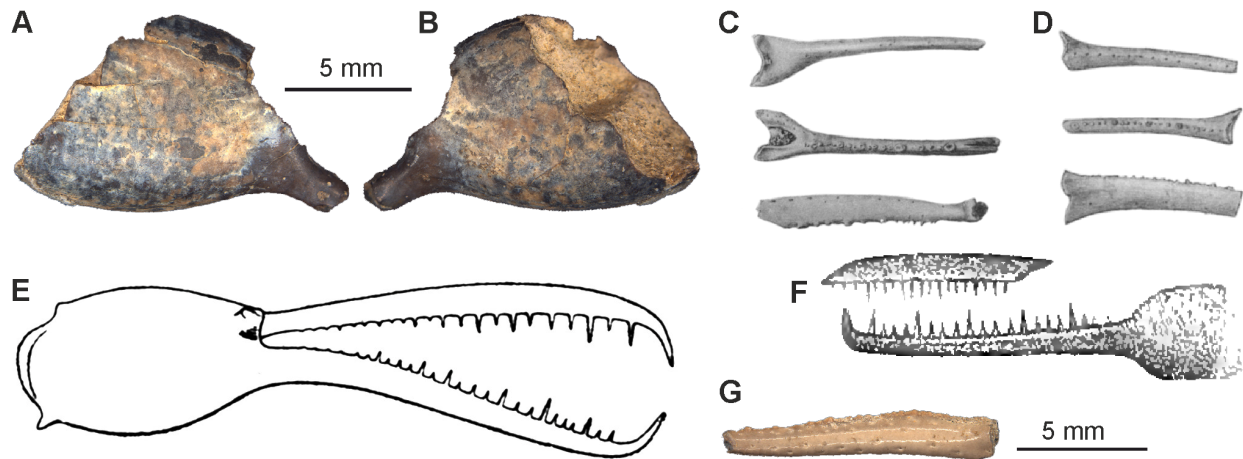
1935 *Ischnodactylus cookei* Rathbun, pp. 63–64, pl. 14, figs. 1–6.

1935 *Ischnodactylus cookei lowei* Rathbun, p. 64.  
 1941 *Oncopareia cookei* (Rathbun); Martin, p. 179.  
 2010 *Oncopareia cookei* (Rathbun); Schweitzer et al., p. 31.  
 2010 *Ctenocheles cookei* (Rathbun); Schweitzer et al., p. 40.  
 2014 *Ctenocheles cookei* (Rathbun); Hyžný and Dulai, table 2.  
 2015 *Ctenocheles cookei* (Rathbun); Hyžný and Klompmaker, supplement 1.

**Material examined.** Tshudy (1993, p. 361) examined the holotype (USNM 371511) and identified the two incomplete palms of isolated claws as *Ctenocheles cookei lowei*.

**Remarks.** Martin (1941) synonymized *Ischnodactylus* with *Oncopareia* and considered *I. cookei* to be a species of *Oncopareia*. On the basis of palm shape and the downflexed fixed finger, Tshudy (1993, pp. 360–361) classified the isolated claw material of *Ischnodactylus cookei* as belonging to the axiidean ghost shrimp genus *Ctenocheles*. Hyžný and Dulai (2014) and Hyžný and Klompmaker (2015) also recognized this form as a representative of *Ctenocheles*.

**Range and occurrence.** Lower Eocene (Succanoochee beds of the Midway Formation) of Wilcox County, Alabama; and upper Eocene (Jackson



**FIGURE 14.** Non-astacidean decapod species with pectinate claws. A–B, *Ctenocheles cookei* (Rathbun, 1935), left propodus in inner (A) and outer (B) lateral views (holotype, USNM 371511). C–D, *Ctenocheles cultellus* (Rathbun, 1935), incomplete dactylus (A) and fixed finger (B) in upper, lower and lateral views (from Rathbun, 1935, pl. 14, figs. 7–12). E, *Ctenocheles inaequidens* (Pelseneer, 1886), right major claw (holotype, from Pelseneer, 1886, text-fig. 1). F, ?*Ctenocheles pectiniformis* (Böhm, 1891), isolated claw (from Böhm, 1891, pl. 1, fig. 2, 2a). G, ?*Ischnodactylus dentatus* Rathbun, 1935, isolated finger (USNM MO 495109).

Formation) of Yazoo City, Mississippi, USA (Rathbun, 1935).

*Ctenocheles cultellus* (Rathbun, 1935)  
Figure 14C–D

- |      |   |
|------|---|
| 1935 | <i>Ischnodactylus cultellus</i> Rathbun, p. 64, pl. 14, figs. 7–12.         |
| 1941 | <i>Oncopareia cultellus</i> (Rathbun); Mertin, p. 179.                      |
| 1956 | <i>Ischnodactylus cultellus</i> Rathbun; Roberts, p. 6, text-fig. 1.        |
| 2010 | <i>Oncopareia cultellus</i> (Rathbun); Schweitzer et al., p. 31.            |
| 2010 | <i>Ctenocheles cultellus</i> (Rathbun); Schweitzer et al., p. 40.           |
| 2014 | <i>Ctenocheles cultellus</i> (Rathbun); Hyžný and Dulai, table 2.           |
| 2015 | <i>Ctenocheles cultellus</i> (Rathbun); Hyžný and Klompmaker, supplement 1. |

**Material examined.** The holotype, ANSP 30429.

**Remarks.** Tshudy (1993) referred the type material of the species to *Ctenocheles*, an assignment corroborated by Hyžný and Dulai (2014) and Hyžný and Klompmaker (2015).

**Range and occurrence.** Eocene: several occurrences in Alabama, Mississippi and New Jersey, USA (Rathbun, 1935).

*Ctenocheles inaequidens* (Pelseneer, 1886)  
Figure 14E

1886

*Ischnodactylus inaequidens* Pelseneer, p. 162 [2], text-fig. 1.

1929

*Ischnodactylus inaequidens* Pelseneer; Glaessner, p. 226.

1941

*Oncopareia inaequidens* (Pelseneer); Mertin, p. 179, text-fig. 10o.

1993

*Ctenocheles inaequidens* (Pelseneer); Tshudy, pp. 361–362.

2010

*Oncopareia inaequidens* (Pelseneer); Schweitzer et al., p. 32.

2010

*Ctenocheles inaequidens* (Pelseneer); Schweitzer et al., p. 40.

2014

*Ctenocheles inaequidens* (Pelseneer); Hyžný and Dulai, table 2.

2015

*Ctenocheles inaequidens* (Pelseneer); Hyžný and Klompmaker, supplement 1.

**Material examined.** Tshudy (1993) examined the holotype (IG 4285, IRScNB 90-36b), a single claw.

**Remarks.** Tshudy (1993) confidently referred this species to *Ctenocheles*; this placement has subsequently been corroborated by Hyžný and Dulai (2014) and Hyžný and Klompmaker (2015).

**Range and occurrence.** Upper Maastrichtian, Kunrade Formation of the Kunrade area, southern Limburg, the Netherlands (Pelseneer, 1886, p. 164).

?*Ctenocheles pectiniformis* (Böhm, 1891)  
Figure 14F



- 1891 *Ischnodactylus pectiniformis* Böhm, p. 42, pl. 1, fig. 2, 2a.  
 1929 *Ischnodactylus pectiniformis* (Böhm); Glaessner, p. 226.  
 1941 *Oncopareia pectiniforme* [sic] (Böhm); Mertin, p. 179, text-fig. 10p.  
 2010 *Oncopareia pectiniformis* (Böhm); Schweitzer et al., p. 32.

**Material studied.** None.

**Remarks.** Although Tshudy (1993, p. 365) concluded that the generic identity of the specimen, known only by a single claw, was uncertain, the downflexed fixed finger as depicted by Böhm (1891, pl. 1, fig. 2) is very much like those in *Ctenocheles*. In view of the fact that this species was studied by us only through published figures, we are reluctant to assign *I. pectiniformis* without any reservations. Nevertheless, assignment to *Oncopareia* seems to be excluded.

**Range and occurrence.** Upper Cretaceous, 'Senonian' of Bayern, southern Germany.

CTENOCHELIDAE INCERTAE SEDIS  
*"Ischnodactylus" texanus* Rathbun, 1935

- 1935 *Ischnodactylus texanus* Rathbun, p. 27, pl. 3, figs. 4–6.  
 1941 *Oncopareia texanus* (Rathbun); Mertin, p. 179.  
 2010 *Oncopareia texanus* (Rathbun); Schweitzer et al., p. 32.

**Material studied.** Tshudy (1993, p. 365) examined several non-type specimens, all claw fragments, contained in collections of the Texas Memorial Museum.

**Remarks.** Tshudy (1993, p. 365) concluded that the studied material very likely did not belong to a nephropid, and that the palm was too rectangular to fit into *Ctenocheles*. The material as figured by Rathbun (1935) exhibits a morphology that is typical of the minor chelae of *Ctenocheles* (for details see Hyžný and Dulai, 2014) and major chelae of *Gourretia* and *Dawsonius*. Confident generic assignment is pending discovery of better material.

**Range and occurrence.** Lower Cretaceous (Albian) at several localities in the Duck Creek Limestone, Denton Clay and Paw Paw Clay of northeast Texas (Rathbun, 1935, pp. 27–28).

BRACHYURA Latreille, 1802  
 PODOTREMATA INCERTAE SEDIS  
*"Oncopareia" heterodon* Bosquet, 1854

- 1854 *Oncopareia? heterodon* Bosquet, p. 131, pl. 10, fig. 9a, b.

- 1886 *Oncopareia heterodon* Bosquet; Pelseneer, p. 173.  
 1929 *Hoploparia? heterodon* (Bosquet); Glaessner, p. 219.  
 2010 *Hoploparia heterodon* (Bosquet); Schweitzer et al., p. 30.  
 2014 *Oncopareia heterodon* Bosquet; Jagt et al., p. 100, pl. 5, figs. 1, 2.

**Material studied.** One of us (JWMJ) has recognized several isolated fingers in the Bosquet Collection (IRScNB), embedded in matrix, which might be Bosquet's originals (see Jagt et al., 2014, pl. 5, figs. 1, 2). There is a lot of additional material, from various levels within the upper Gulpen (Lanaye Member) and lower/middle Maastricht Formation (Valkenburg to Emael members) in the Liège-Limburg Basin (Belgium, the Netherlands). The best-preserved specimen to date is the one illustrated by Jagt et al. (2014, pl. 5, figs. 3, 4).

**Remarks.** Bosquet (1854) referred this form "avec doute" to *Oncopareia*. Known mostly by claw fingers, with only a single partial cheliped known to date; these probably belong to a brachyuran, a podotreme crab of uncertain affinities, as indicated by Jagt et al. (2014). We follow their opinion here.

**Range and occurrence.** Upper Gulpen (Lanaye Member) and lower/middle Maastricht Formation (Valkenburg to Emael members), all upper Maastrichtian, of southern Limburg (the Netherlands) and adjacent Belgian provinces of Liège and Limburg.

DECAPODA INCERTAE SEDIS  
*"Ischnodactylus" dentatus* Rathbun, 1935  
 Figure 14G

- 1935 *Ischnodactylus (?) dentatus* Rathbun, p. 65, pl. 14, figs. 19–22.  
 1941 *Oncopareia dentatus* (Rathbun); Mertin, p. 179.  
 2010 *Oncopareia dentatus* (Rathbun); Schweitzer et al., p. 31.  
 2010 *Ctenocheles dentatus* (Rathbun); Schweitzer et al., p. 40.  
 2014 *Ctenocheles dentatus* (Rathbun); Hyžný and Dulai, table 2.  
 2015 *Ctenocheles dentatus* (Rathbun); Hyžný and Klompmaker, supplement 1.

**Material examined.** A single isolated finger, USNM MO495109 (holotype).

**Remarks.** According to Rathbun (1935, p. 65), each of the fingers studied by her was equipped with "low, triangular, thick" (i.e., not acicular) denti-

tion, unlike that of *Oncopareia* or *Ctenocheles*. Although Hyžný and Dulai (2014) and Hyžný and Klompmaker (2015) treated *Ischnodactylus dentatus* as a representative of *Ctenocheles*, they did not discuss the species in detail. In the present taxonomic re-evaluation, we propose to remove this taxon from *Ctenocheles*, based on the lack of acicular dentition, typical of the genus. Unfortunately, the isolated fingers are difficult to assign to any particular group of decapod crustacean. Similar fingers can be present equally in some brachyuran crabs or axiidean ghost shrimp.

**Range and occurrence.** Middle Eocene of Mississippi, USA (Rathbun, 1935).

### CONCLUSIONS

*Oncopareia* is an extinct clawed lobster genus within the clade of thaumastocheliform nephropid lobsters, characterized by short, quadrate pleura on the pleon and a major claw with a bulbous palm and acicular dentition. *Oncopareia* is the earliest *Thaumastocheles*-like lobster with the oldest example being of early to middle Turonian age. Originally, *Oncopareia* was erected for a single late Maastrichtian species, *O. bredai*, from the Netherlands. The genus has a convoluted taxonomic history that begins with a type species that is an accidental composite of two lobsters that differ at the generic level. Subsequent to Bosquet's (1854) erection of a composite type species, the taxonomic confusion surrounding *Thaumastocheles*-like fossils became even more serious. Workers in the late 1800s erected new genera at a time when access to information and communication among taxonomists were not what they are today. This led to synonymous genera, even for specimens that were anatomically fairly complete. Other scholars in the late 1800s and early 1900s described isolated chelipeds with bulbous palms and slender fingers armed with acicular denticles; most of these were misidentified at the infraordinal level until

recently. Mertin (1941) tried to rectify all of this by bringing all fossil lobsters with pectinate claws into one genus; a reasonable approach, but he went one step too far in synonymizing *Thaumastocheles*-like lobsters with *Oncopareia*. In fact, most of Mertin's (1941) synonyms are not thaumastochelids at all, but instead refer to claws of other decapod crustaceans showing convergence, whereas still others are of uncertain affinity. Nonetheless, it became entrenched in the literature that *Oncopareia* was closely related to *Thaumastocheles*. Based on the redescription of the type species, *Oncopareia bredai*, presented herein, we have been able to revise all taxa previously attributed to the respective genus. Besides the type species, three other *Oncopareia* species are recognized herein. Other taxa, once attributed to *Oncopareia*, are reassigned to other astacidean or axiidean genera. Taxa based on poorly preserved material are considered of uncertain affinity (*incertae sedis*).

### ACKNOWLEDGMENTS

S. Charbonnier (Muséum National d'histoire Naturelle, Paris) and J. Sklenář (National Museum, Prague) provided access to the material contained at the respective institutions. S.L. Jakobsen (Geomuseum Faxe, Denmark) is acknowledged for taking a new set of photographs of the type material of *Oncopareia klintebjergensis*. J.W. Stroucken (Natuurhistorisch Museum Maastricht) is thanked for taking photographs of some of the material deposited in NHMM. Constructive criticism of C.E. Schweitzer (Kent State University, Ohio) and an anonymous reviewer greatly improved the original manuscript. The research of MH was supported by Slovak Research and Development Agency (APVV 17-0555). The research of MKV was supported by the Centre for Geosphere Dynamics (UNCE/SCI/006) and by RVO 67985831 of the Institute of Geology of the Czech Academy of Sciences, v. v. i.

### REFERENCES

- Ahyong, S.T., Chan, T.Y., and Bouchet, P. 2010. Mighty claws: a new genus and species of lobster from the Philippine deep sea (Crustacea, Decapoda, Nephropidae). *Zoosystema*, 32:525-535. <https://doi.org/10.5252/z2010n3a11>
- Beurlen, K. 1939. Neue Decapoden-Krebse aus dem ungarischen Tertiär. *Paläontologische Zeitschrift*, 21:135-160. <https://doi.org/10.1007/BF03043252>
- Böhm, J. 1891. Die Kreidebildung des Fürbergs und Sulzbergs bei Siegsdorf in Oberbayern. *Palaeontographica*, 38:1-106.

- Bosquet, J. 1854. Les crustacés fossiles du Terrain Crétacé du Limbourg. Verhandeligen uitgegeven door de Commissie belast met het Vervaardigen eener geologische Beschrijving en Kaart van Nederland, 2:1-127 [10-137]. A.C. Kruseman, Haarlem.
- Bosquet, J. 1860. Versteeningen uit het Limburgsche krijt [sic]. In Staring, W.C.H. De bodem van Nederland. De zamenstelling en het ontstaan der gronden in Nederland ten behoeve van het algemeen beschreven: 362-418. A.C. Kruseman, Haarlem.
- Bosquet, J. 1868. Liste des fossiles du massif crétacé du Limbourg. In Dewalque, G. : Prodrome d'une description géologique de la Belgique: 355-387. J.-G. Carmanne, Liège.
- Bracken-Grissom, H.D., Ah Yong, S.T., Wilkinson, R.D., Feldmann, R.M., Schweitzer, C.E., Breinholt, J.W., Bendall, M., Palero, F., Chan, T.-Y., Felder, D.L., Robles, R., Chu, K.-H., Tsang, L.-M., Kim, D., Martin, J.W., and Crandall, K.A. 2014. The emergence of lobsters: phylogenetic relationships, morphological evolution and divergence time comparisons of an ancient group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Systematic Biology*, 63:457-479. <https://doi.org/10.1093/sysbio/syu008>
- Bruce, A.J. 1988. *Thaumastochelopsis wardi*, gen. et sp. nov., a new blind deep-sea lobster from the Coral Sea (Crustacea: Decapoda: Nephropidea). *Invertebrate Taxonomy*, 2:903-914. <https://doi.org/10.1071/IT9880903>
- Calman, W.T. 1911. The life of Crustacea. Methuen & Co., London.
- Chang, S.-C., Tshudy, D., Sorhannus, U., Ah Yong, S.T., and Chan, T.-Y. 2017. Evolution of the thaumastocheliform lobsters (Crustacea, Decapoda, Nephropidae). *Zoologica Scripta*, 46:372-387. <https://doi.org/10.1111/zsc.12205>
- Dana, J.D. 1852. Macrura. *Conspectus crustaceorum & conspectus of the Crustacea of the Exploring Expedition under Captain C. Wilkes, U.S.N. Proceedings of the Academy of Natural Sciences of Philadelphia*, 6:10-28.
- De Grave, S., Pentcheff, N.D., Ah Yong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaître, R., Low, M.E.Y., Martin, J.W., Ng, P.K. L., Schweitzer, C.E., Tan, S.H., Tshudy, D., and Wetzer, R. 2009. A classification of living and fossil genera of decapod crustaceans: The Raffles Bulletin of Zoology, Suppl. 21:1-109.
- de Saint Laurent, M. 1979. Vers une nouvelle classification des Crustacés Décapodes Reptantia. *Bulletin de l'Office Nationale de Pêche de Tunisie*, 3:15-31.
- Feldmann, R.M., Jagt, J.W.M., and Tshudy, D.M. 1990. Late Maastrichtian isopod and decapod Crustacea from Haccourt (Liège), northeastern Belgium. *Mededelingen Rijks Geologische Dienst*, 44:23-35.
- Feldmann, R.M., Schweitzer, C.E., and Karasawa, H. 2016. Part R, revised, Volume 1, Chapter 8J : Systematic descriptions: infraorder Astacidea. *Treatise Online*, 74:1-28.
- Forir, H. 1887. Contributions à l'étude du système crétacé de la Belgique. II. Études complémentaires sur les crustacés: *Annales de la Société géologique de Belgique*, 14:155-175.
- Frič, A. 1893. Studien im Gebiete der Böhmischen Kreideformation. Paläontologische Untersuchung der einzelnen Schichten. V. Priesener Schichten. *Archiv der Naturwissenschaftlichen Landesdurchforschung von Böhmen*, 9:1-134.
- Frič, A. 1894. Studie v oboru křídového útvaru v Čechách. V. Březenské vrstvy. *Archiv pro přírodovědné prozkoumání Čech 9. V kommissi knihkupectví Fr. Řivnáče, Prague*.
- Fritsch, A. and Kafka, J. 1887. Die Crustaceen der böhmischen Kreideformation. Selbstverlag in Commission von F. Rivnáč, Prague.
- Glaessner, M.F. 1929. Crustacea Decapoda, Pars 41. In J.F. Pompeckj (ed.), *Fossilium Catalogus*, 1. Animalia. Junk, Berlin.
- Glaessner, M.F. 1969. Decapoda. In Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology*, Part R, Arthropoda 4(2):R399-R651. Geological Society of America, Boulder, and The University of Kansas Press, Lawrence.
- Hyžný, M. and Dulai, A. 2014. Deep-water fossorial shrimps from the Oligocene Kiscell Clay of Hungary: taxonomy and palaeoecology. *Acta Palaeontologica Polonica*, 59:947-965. <https://doi.org/10.4202/app.2012.0078>
- Hyžný, M. and Klompmaker, A.A. 2015. Systematics, phylogeny, and taphonomy of ghost shrimps (Decapoda): a perspective from the fossil record. *Arthropod Systematics & Phylogeny*, 73:401-437.

- Hyžný, M., Kočová Veselská, M., and Dvořák, P. 2014. On the occurrence of *Ctenocheles* (Decapoda, Axiidea, Callianassidae) in the Bohemian Cretaceous Basin. *Bulletin of Geosciences*, 89:245-256. <https://doi.org/10.3140/bull.geosci.1421>
- Jagt, J.W.M. and Bongaerts, H.L. 1986. Kreeftresten uit de Formatie van Vaals (Onder-Campanien, Boven-Krijt) in de groeve Ciments Portland Liégeois, Haccourt, Liège (B.). *Natuurhistorisch Maandblad*, 75:76-80.
- Jagt, J.W.M., Fraaije, R.H.B., and Van Bakel, B.W.M. 2014. Decapod crustacean 'odds and ends' from the Maastrichtian type area (southeast Netherlands, northeast Belgium). In Fraaije, R.H.B., Hyžný, M., Jagt, J.W.M., Krobicki, M., and Van Bakel, B.W.M. (eds.), *Proceedings of the 5<sup>th</sup> Symposium on Mesozoic and Cenozoic decapod crustaceans*, Krakow [sic], Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geologica*, 147:95-115.
- Jagt, J.W.M., Fraaije, R.H.B., Van Bakel, B.W.M., and Coole, Y. 2004. New data on the raninid crab *Cretacorantina schloenbachi* (Schlüter, 1879) (Late Cretaceous, NW Germany). *Bulletin of the Mizunami Fossil Museum*, 30(for 2003):51-55.
- Jakobsen, S.L. and Collins, J.S.H. 1979. Decapod Crustacea from the Paleocene of Zealand, Denmark. *Proceedings of the Geologists' Association*, 90:61-64. [https://doi.org/10.1016/S0016-7878\(79\)80033-4](https://doi.org/10.1016/S0016-7878(79)80033-4)
- Karasawa, H., Schweitzer, C.E., and Feldmann, R.M. 2013. Phylogeny and systematics of extant and extinct lobsters. *Journal of Crustacean Biology*, 33:78-123. <https://doi.org/10.1163/1937240X-00002111>
- Kishinouye, K. 1926. Two rare and remarkable forms of macrurous Crustacea from Japan. *Annotationes Zoologicae Japonenses*, 11:63-70.
- Latreille, P.A. 1802. Histoire naturelle, générale et particulière, des Crustacés et des Insectes. Ouvrage faisant suite aux oeuvres de Leclerc de Buffon, et partie du Cours complet d'Histoire naturelle rédigé par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres, Volume 3. F. DuFart, Paris.
- Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Editio decima) 1. Laurentius Salvius, Holmiae.
- Lőrenthey, E. and Beurlen, K. 1929. Die fossilen Dekapoden der Länder der Ungarischen Krone. *Geologica Hungarica, Series Palaeontologica*, 3:1-421.
- Manning, R.B. and Felder, D.L. 1991. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea). *Proceedings of the Biological Society of Washington*, 104:764-792.
- M'Coy, F. 1849. On the classification of some British fossil Crustacea with notices of new forms in the university collection at Cambridge. *The Annals and Magazine of Natural History*, 4:161-179, 330-335.
- 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.
- Pelseneer, P. 1885. Notice sur un Crustacé de la Craie Brune des environs de Mons. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 4(2):37-46 [1-10].
- Pelseneer, P. 1886. Notice sur les Crustacés décapodes du Maestrichtien du Limbourg. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 4(2):161-175 [1-15].
- Rathbun, M.J. 1926. Phylum Arthropoda, p. 184-191, pls. 63-68. In Wade, B. (ed.), *Fauna of the Ripley Formation on Coon Creek, Tennessee*. United States Geological Survey Professional Paper, 137.
- Rathbun, M.J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America, Special Papers*, 2:1-160.
- Robaszynski, F., Dhondt, A.V., and Jagt, J.W.M. 2002. Cretaceous lithostratigraphic units (Belgium). In Bultynck, P. and Dejonghe, L. (eds.), *Guide to a revised lithostratigraphic scale of Belgium*. *Geologica Belgica*, 4(1-2) (for 2001):121-134.
- Roberts, H.B. 1956. Early Tertiary decapod crustaceans from the Vincentown Formation in New Jersey. *Bulletin of the Wagner Free Institute of Science*, 31:5-12.
- Schlüter, C. 1862. Die macruren Decapoden der Senon- und Cenoman-Bildungen Westphalens. *Zeitschrift der deutschen geologischen Gesellschaft*, 14:702-749.
- Schlüter, C. 1879. Neue und weniger gekannte Kreide- und Tertiärkrebse des nördlichen Deutschlands. *Zeitschrift der deutschen geologischen Gesellschaft*, 31:586-615.

- Schweitzer, C.E. and Feldmann, R.M. 2014. Lobster (Decapoda) diversity and evolutionary patterns through time. *Journal of Crustacean Biology*, 34:820-847.  
<https://doi.org/10.1163/1937240X-00002288>
- Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H., and Schweigert, G. 2010. Systematic list of fossil decapod crustacean species. *Crustaceana Monographs*, 10:1-222.
- Secretan, S. 1964. Les crustacés décapodes du Jurassique supérieur et du Crétacé de Madagascar. *Mémoires du Muséum national d'Histoire naturelle Paris*, C14:1-226.
- Sowerby, G.B. 1826. Description of a new species of *Astacus*, found in a fossil state at Lyme Regis. *Zoological Journal*, 2:493-494.
- Tshudy, D. 1993. Taxonomy and evolution of the clawed lobster families Chilenophoberidae and Nephropidae. Unpublished PhD dissertation, Kent State University, Kent, Ohio.
- Tshudy, D. and Saward, J. 2012. *Dinochelus steeplensis*, a new species of clawed lobster (Nephropidae) from the London Clay (Eocene) of England. *Journal of Crustacean Biology*, 32:67-79. <https://doi.org/10.1163/193724011X615343>
- Tshudy, D. and Sorhannus, U. 2000a. Pectinate claws in decapod crustaceans: convergence in four lineages. *Journal of Paleontology*, 74:474-486.  
<https://doi.org/10.1017/S0022336000031735>
- Tshudy, D. and Sorhannus, U. 2000b. *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.  
<https://doi.org/10.1017/S0022336000031449>
- Tshudy, D. and Sorhannus, U. 2003. *Hoploparia*, the best-known fossil clawed lobster (Family Nephropidae), is a "wastebasket" genus. *Journal of Crustacean Biology*, 23:700-711.  
<https://doi.org/10.1651/C-2353>
- Tshudy, D., Hyžný, M., Dulai, A., and Jagt, J.W.M. 2018. Appraisal of the fossil record of *Homarus* (nephropid lobster), with description of a new species from the upper Oligocene of Hungary and remarks on the status of *Hoploparia*. *Journal of Paleontology*, 92:170-182.  
<https://doi.org/10.1017/jpa.2017.65>
- Van Bakel, B.W.M., Fraaije, R.H.B., and Jagt, J.W.M. 2005. A new Early Campanian species of *Xanthosia* (Decapoda, Brachyura) from northwestern Germany. *Crustaceana*, 78:285-295.  
<https://doi.org/10.1163/1568540054286547>
- von der Marck, W. and Schlüter, C. 1868. Neue Fische und Krebse aus der Kreide von Westphalen. *Palaeontographica*, 15:269-305.
- Wood-Mason, J. 1874. Blind Crustacea. *Proceedings of the Asiatic Society of Bengal*, 1874:180-181.