

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*

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Abstract.—The fossil record of the clawed lobster genus, *Homarus*, is appraised. The taxonomic history of *Homarus* and *Hoploparia* is summarized, and a list of species recognized for each is provided. A tabulation of all fossil species of the family Nephropidae permits assessment of nephropid species diversity through time. A new species of *Homarus*, *H. hungaricus*, is recorded from the upper Oligocene (Chattian) Mány Formation at Mány, northern Hungary. The species is known by a single specimen consisting of a partial cephalothorax, a pleon minus telson, and partial chelipeds. *Homarus* is now known by two extant species (*H. americanus* and *H. gammarus*) and six fossil taxa, one of Early Cretaceous (Albian; *H. benedeni*) and five of Cenozoic age (*H. hungaricus* n. sp., *H. klebsi*, *H. lehmanni*, *H. morrissi*, and *H. percyi*). The new fossil *Homarus* differs from modern congeners in aspects of carapace and pleon ornamentation and, especially, cutter claw shape. This is the fourth Oligocene occurrence of a nephropid species; all are *Homarus* and all are from Western Europe. *Homarus* makes its appearance in the fossil record in the Early Cretaceous (Albian) and then is not known again until the Paleogene, despite the fact that nephropid lobsters in general are well known from the Late Cretaceous. Nephropid lobsters are better known from the Cretaceous than from the Cenozoic. Both raw species numbers and numbers corrected (normalized) for epicontinental sea coverage show that shelf-dwelling nephropid lobsters were most diverse during the Late Cretaceous.

Introduction

The clawed lobster family Nephropidae Dana, 1852, consists of 56 Recent and 79 fossil species, arrayed in 19 genera (10 Recent, five fossil, and four both fossil and extant). The Nephropidae has a fossil record extending back to the Lower Cretaceous (Valanginian, ca. 139.8–132.9 Myr).

The clawed lobster genus *Homarus* Weber, 1795 is known by two Recent and six fossil species. In modern oceans, *Homarus* is represented by the American lobster, *H. americanus* Milne Edwards, 1837, and the European lobster, *H. gammarus* (Linnaeus, 1758). These species are morphologically very similar, differing only in the spinosity of the rostrum; *H. americanus* having a spine or two on the underside, and *H. gammarus* lacking these (Beard and McGregor, 2004). The two are capable of artificial breeding (Hauge, 2010). Six fossil species of *Homarus* recognized herein, all European, give the genus a fossil record extending back to the Early Cretaceous (ca. 100 Ma).

To some extent, the extant *Homarus* resembles the extinct *Hoploparia* M'Coy, 1849. Placement of species in these genera has been the subject of much discussion. The separateness of, and differences between, *Homarus* and *Hoploparia* have been long debated and are still not resolved. Many authors have considered

Homarus and *Hoploparia* to be distinct (Mertin, 1941; Glaessner, 1969; Feldmann, 1974; Aguirre-Urreta et al., 1991; Tshudy, 1993; Feldmann and Crame, 1998; Tshudy and Sorhannus, 2003; Ilyin, 2005; Feldmann et al., 2007; De Grave et al., 2009; Schweitzer et al., 2010; Karasawa et al., 2013; and others). Woods (1931), Van Straelen (1936), and Stenzel (1945) viewed the two genera as synonymous. The current view is to separate them. In our opinion, there is not a single character that can be used alone to distinguish the two genera. We use a total evidence approach in drawing generic boundaries—and, even then, with difficulty. Not surprisingly, in cladistic analyses, *Homarus* and *Hoploparia* plot out as sister groups (Tshudy, 1993; Tshudy and Babcock, 1997; Ahyong, 2006; Karasawa et al., 2013).

Hoploparia is most readily distinguished from *Homarus* (Fig. 1) by the ventral extension of the branchiocardiac groove (absent on *Homarus*) and the granulation of the exoskeleton (almost entirely absent on *Homarus*). In addition, the majority of *Hoploparia* display an antennal carina, whether short or long (absent on *Homarus*), as well as postantennal spines (absent on *Homarus*). *Homarus* lacks sculpture and ornamentation on its pleonal terga and pleura (some *Hoploparia* possess these). Claws of *Homarus* are much broader than those of nearly all *Hoploparia* (except for *Hoploparia antarctica* Wilckens, 1907).

There are several species that, although referable to either *Hoploparia* or *Homarus*, more closely resemble the other genus in one or more features. For example, *Homarus klebsi* (Noetling, 1885) and *Homarus morrissi* Quayle, 1987 exhibit a ventral extension of the branchiocardiac groove, as is typical of *Hoploparia*, but are, otherwise, referable to *Homarus*. Conversely, some species referred to *Hoploparia*, such as *H. collignoni* (Van Straelen, 1949), lack the ventral extension of the branchiocardiac groove, but are otherwise characteristically *Hoploparia*. Reference is made to Tshudy (1993) for more examples and discussion.

In the present paper, we appraise the fossil record of *Homarus*. We summarize the taxonomic history of, and confusion between, *Homarus* and *Hoploparia*, provide a redefinition of *Hoploparia*, describe a new fossil species of *Homarus*, list the species recognized for both genera, tabulate all fossil species of the family Nephropidae, and discuss nephropid species diversity through time.

Geological setting

The new species presented herein was collected from the Mány Formation of north-central Hungary. The Mány Formation occurs mostly in the northeastern part of the Transdanubian Mountains. Patchy occurrences are known also from the western and eastern foreland of the Gerecse Mountains and in the Dorog Basin. The thickness of the formation varies between 200 and 600 m. The Mány Formation itself consists of alternating calcareous siltstone, clayey siltstone, cross-bedded sand and sandstone beds, with conglomerate coal stringers and variegated clay intercalations and coal bands (Nagymarosy and Gyalog in Császár, 1997). The formation formed predominantly in the brackish water of a shallow-marine lagoon; however, intercalations with sediments of freshwater origin, as well as those from fully marine settings, are present here.

Deposition of the formation probably started at the end of the ‘Kiscellian’ (Rupelian, early Oligocene) and continued into the ‘Egerian’ (Chattian, late Oligocene) (Gyalog and Budai, 2004). On the basis of the mollusc fauna, the maximum depositional depth of Mány Formation is 20–30 m (Báldi, 1973). According to some researchers (e.g., Sztanó et al., 1998), the Mány Formation should be integrated as a member of the Törökbálint Formation.

Previous occurrences of decapod crustaceans from the Mány Formation include the retroplumid crab *Loerenthopluma lata* Beschin et al., 1996 recovered from borehole Mány-15 (Hyžný and Müller, 2010).

Repositories and institutional abbreviations.—Hungarian Natural History Museum, Budapest (HNHM PAL); Natural History Museum, London (NHMUK).

Systematic paleontology

Order Decapoda Latreille, 1802
 Infraorder Astacidea Latreille, 1802
 Family Nephropidae Dana, 1852

(sensu Tshudy et al., 2009; inclusive of Thaumastocheilidae Bate, 1888)

Genus *Homarus* Weber, 1795

Type species.—*Astacus marinus* Fabricius, 1775, p. 413 (see Holthuis, 1974, for discussion).

Remarks.—The original description (Weber, 1795) of *Homarus* is in Latin. We follow here the emended definition of Holthuis (1974, p. 815–818).

Homarus hungaricus new species Figures 2, 3

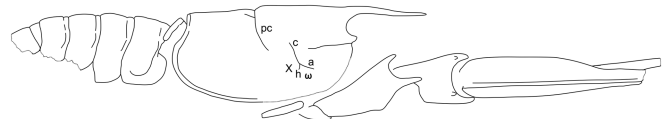


Figure 1. *Homarus benedeni* Pelseener, 1886; line drawing, in right lateral view, showing a morphology similar to that of Recent species of *Homarus* (modified from Pelseener, 1886).

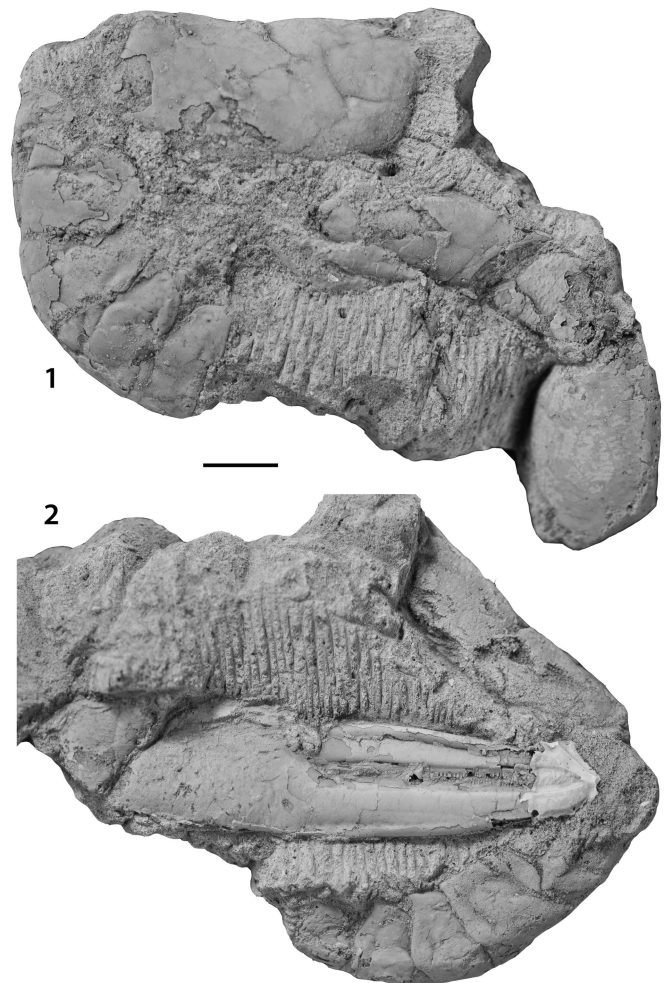


Figure 2. *Homarus hungaricus* n. sp. from the upper Oligocene (Chattian) Törökbálint Formation (HNHM PAL 2015.1): (1) pleon, and lower surface of incomplete, right cheliped; (2) left lateral view of pleon and lower surface of left (cutter) claw. Scale bar equals 10 mm.

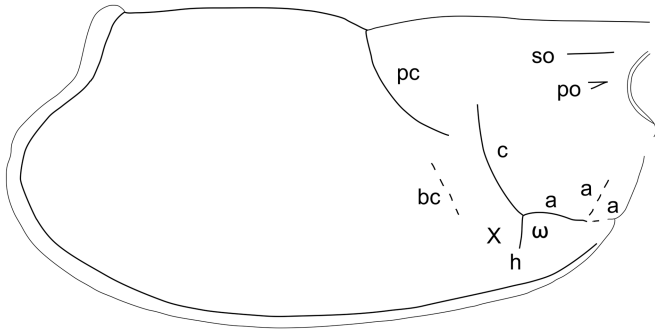


Figure 3. Line drawing (reconstruction) of *Homarus hungaricus* n. sp.; a, antennal groove; bc, branchiocardiac groove; c, cervical groove; h, hepatic groove; pc, postcervical groove; po, postorbital spine; so, supraorbital carina; χ, prominence chi; ω, prominence omega.



Figure 4. Map showing the collecting locality of *Homarus hungaricus* n. sp. near Mány, in the northeast of Fejér County, in the Zsámbék Basin, north-central Hungary.

Holotype.—The holotype and single known specimen of *Homarus hungaricus* n. sp. is from the upper Oligocene (Chattian) Mány Formation at Mány, northern Hungary. It is deposited in the Hungarian Natural History Museum, Budapest as HNHM PAL 2015.1.

Diagnosis.—*Homarus* with narrow chelipeds and postcervical groove extending (as intercervical groove) toward, but not quite reaching, upper part of cervical groove.

Occurrence.—The specimen was recovered from borehole Mány-14 (Má-14), sunk near the village of Mány in north-central Hungary, west of Budapest (Fig. 4), from a depth interval of 401.2–406.7 m. The strata from 170.6–492.3 m belong to the upper Oligocene Mány Formation (Fig. 5).

Description.—Cephalothorax right side mostly preserved. Left side completely absent, beginning at dorsomedian. Cephalothorax posterior margin incomplete. Ventral margin indistinct; cephalothorax ~22 mm in height. While incomplete along margins, overall proportions and proportions of regions (as defined by grooves) are typical of *Homarus-Hoploparia*. Rostrum absent or not exposed.

Postcervical groove extends anteroventrally and concave-forward from (assumedly) dorsomedian (region poorly preserved). Extends anteroventrally (as intercervical groove) toward, but not quite reaching, upper part of cervical groove (Figs. 2, 3).

Region of upper/posterior branchiocardiac groove poorly preserved. Vague ventral extension of branchiocardiac groove extends from lower end of postcervical groove; groove becomes very indistinct along posterior side of subtly inflated prominence χ (terminology of Holthuis, 1974, p. 734; this is the attachment of the adductor testis muscle insertion).

Hepatic groove indistinct as it loops under prominence χ, but better impressed where it separates prominences χ and ω (the mandibular external articulation; see Feldmann and Crame, 1998). Prominence ω triangular, inflated; not underlined by inferior groove. Inferior groove completely absent.

Cervical groove subtly concave forward, angling anteroventrally.

Antennal groove distinct, nearly straight (slightly sinuous) over anterior side of prominence ω. At anteroventral corner of

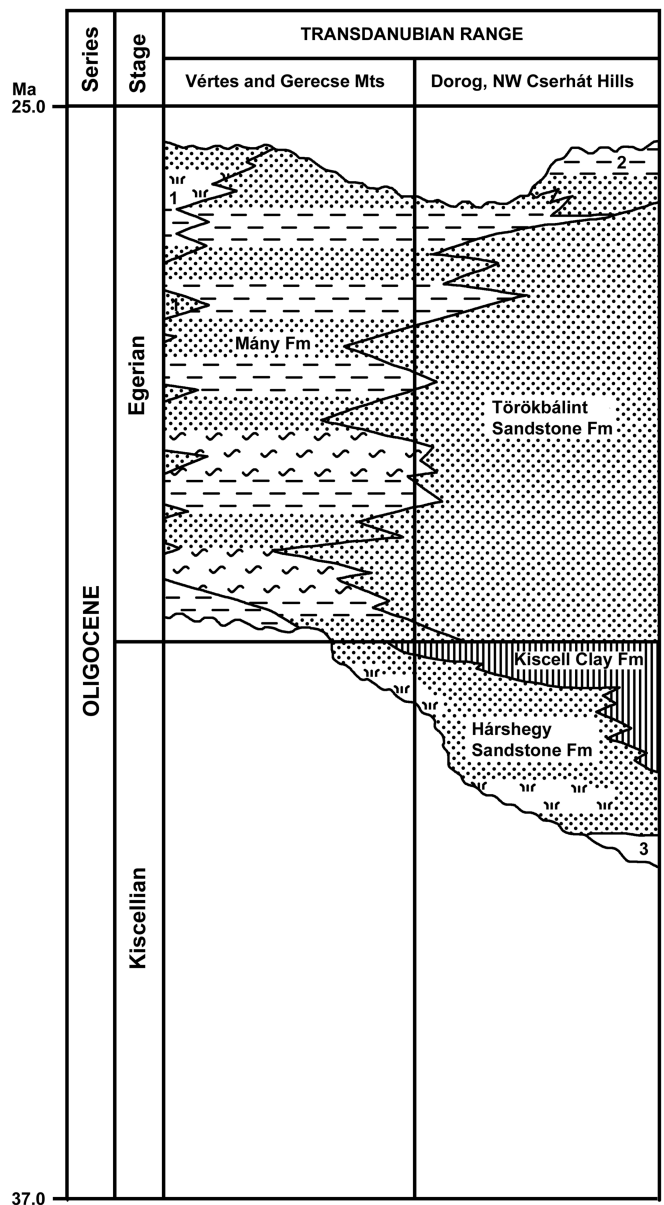


Figure 5. Stratigraphic column (pre-2012; see text) showing the Mány Formation and its lateral equivalent, the Törökbálint Sandstone Formation, as they occur in the Transdanubian Range, Hungary.

prominence ω , antennal groove becomes very faint, bifurcates. Upper branch extends a short distance in direction of base of rostrum. Lower branch extends toward anterior margin, effacing before reaching latter.

Antennal spine not preserved. Antennal and postantennal region smooth, uninflated. Gastro-orbital and buccal grooves absent.

Postantennal spine absent. Hepatic spine absent. Cervical and postcervical spines/spinules absent. Postorbital spine strong at base, angles antero-dorsally. Supraorbital spine region not preserved, but seems to be followed by a nodose, supraorbital carina.

Cuticle of cephalothorax smooth (not granulate), except ventrally, below level of prominence χ , where with low, rounded granules.

Pleon represented by segments one–five (both left and right sides of lobster specimen). All tergites appear to be without sculpture (i.e., lacking grooves, etc.) and with smooth cuticle lacking any surface ornamentation. Tergum-pleuron boundaries unmarked by any ridge, terrace, or other demarcation.

Pleuron one (left side) a parallelogram angling anteroventrally. Pleuron two (left side) subquadrate; anterior margin convex, posterior margin convex at top then concave for remainder. Anteroventral corner rounded; posteroventral corner pointed posteroventrally. Pleura three–five cordate, terminating in sharp, posteroventrally directed point. Pleuron two with broad, submarginal furrow bordering, but well inside, anterior and posterior margins. Pleura three and four with similar furrow bordering upper part of posterior margin. Each pleuron surface broadly, slightly inflated medially and along margin. Pleuron five gently convex overall. Pleura four and five (right side of lobster) with a few low, rounded nodes. Pleura two–five with a large pore near termination. At least the anteroventral margin of pleura three, four, and five with a very fine, rounded, bead for margin; shown best on pleuron five as viewed on right side of lobster, although pleura three, four, and five of left side also show this bead (a similar bead is seen on the anterior, but not posterior, sides of the pleura of *Homarus americanus*). On pleuron five, bead breaks into minute serrations near pleuron termination. Telson not preserved.

Specimen preserved with portions of right (crusher) and left (cutter) claws. Right cheliped rotated inward so that merus, carpus, and propodus lower (ventral) surface and propodus outer margin are exposed. Merus lower surface gently convex overall; cuticle smooth. Merus with strong spine at inner proximal and inner distal corners. Merus outer surface with granules. Carpus lower surface rather flat overall, with strong spine at inner and outer distal corner; cuticle smooth, but with large, transversely elongate pits. Propodus incomplete at approximately mid-length. Manus ovate in cross section. Manus outer margin narrowly squared-off proximally, becoming sharply rounded for most of length. Cuticle of lower surface smooth.

Left (cutter) claw lower surface exposed. Claw elongate, approximately 5x longer than wide (~74 mm long and estimated 15 mm wide). Propodus outer margin sharply rounded. Pollex subovate in crosssection, ~40 mm long, 8.4 mm at widest; thus 0.21x as wide as long. Dactylus ~30 mm long; dactylus subrectangular in cross section. Fingers rather straight, parallel but curving toward each other near terminations. Unsure if

terminations occlude. Cuticle on fingers minutely, densely pitted, especially adjacent to dentition.

Denticles of left cheliped conical, slightly longer than wide, densely arranged, of varying sizes. Smallest ~0.15 mm diameter at base and about twice as long. Larger denticles ~0.3 mm wide at base, ~0.5 mm long. A very few much larger denticles; largest, located proximal of mid-length on pollex, is triangular, ~2 mm wide at base and equally long. Denticles mostly perpendicular to fingers. Largest denticle is distally directed.

Etymology.—The species name derives from the collecting locality in Hungary.

Remarks.—The new species is referred to *Homarus*, but with acknowledgement of similarities to the extinct *Hoploparia*. The new species has: (1) a generally smooth (not granulose) cephalothorax, pleon, and chelipeds; (2) smooth antennal and postantennal regions; (3) only indistinct ventral extension of the branchiocardiac groove; and (4) unsculptured pleonal tergites. Nothing on the cephalothorax or pleon is inconsistent with *Homarus*, but the fossil specimen's cutter claw is elongate and *Hoploparia*-like, thus complicating the generic placement.

Below we compare the late Oligocene (ca. 30 Ma) specimen to all species of *Homarus* known from the Eocene epoch (56.0–33.9 Myr) to the Recent. Given the long history of taxonomic confusion surrounding *Homarus* and *Hoploparia*, we also compare (further below) the new species to all known Eocene–Recent species of *Hoploparia*. No existing species of either genus has a morphology matching that of the new Hungarian fossil.

Comparison to Oligocene (33.9–23.03 Myr) species.—*Homarus klebsi* is known from the lower and upper Oligocene of northern Germany (and, according to specimen labels at the Institut royal des Sciences naturelles de Belgique at Brussels, from the Oligocene ['Tongrien'] of formerly Palmnicken, eastern Prussia [now Kaliningrad, Russian Federation]). *Homarus klebsi* differs from the new species by: (1) its gigantic size, and in having (2) a distinct ventral extension of the branchiocardiac groove and (3) a suprahepatic groove (Noetling, 1885, pl. 7, fig. 1 [same figure in Freess, 1992, pl. 4B]).

Homarus lehmanni Haas, 1889 has been described from the lower Oligocene (Rupelian) of Germany. This species is known only by a fragmentary carpus and fragmentary merus and, therefore, is hardly comparable to the new material. Van Straelen (1936) and Verheyden (2002) considered *H. lehmanni* to be a synonym of *H. percyi* Van Beneden, 1872.

Homarus percyi is known from the lower Oligocene (Rupelian) of northwest Belgium, Germany, and Russia. The claws of *H. percyi* are gigantic, and more robust in proportions than those of the new species; they also have spikes on the propodus upper and lower surface.

Comparison to Eocene (56–33.9 Myr) species.—*Homarus klebsi* (as above). *Homarus morrisoni* Quayle, 1987 from the Eocene of southern England was isolated from *Hoploparia gammaroides* M'Coy, 1849. It differs from the new species in being conspicuously pitted, in having a more granulose prominence ω , a slightly different carapace groove configuration, and a more strongly pitted pleon surface.

Comparison to Recent species.—*Homarus americanus* and *H. gammarus*: the fossil specimen is clearly distinct from the American Lobster, *Homarus americanus* (and the extremely similar European lobster, *Homarus gammarus*), differing in aspects of carapace and pleon ornamentation and, especially, cutter claw shape. *Homarus americanus* has no hint of a ventral extension of the branchiocardiac groove. The postorbital spine seems stronger on the fossil specimen than on *H. americanus*. The cephalothorax of *H. americanus* is less granulose below the cervical groove, except for below the antennal groove, where both *H. americanus* and the fossil are granulose. *Homarus americanus* also has, below the prominence χ , a reticulate pattern that is absent on the fossil specimen. *Homarus americanus* lacks a large pore near the termination of pleura two–five (this pore is common on *Hoplopatria* and on some modern nephropid genera, such as *Nephrops*, *Metanephrops* Jenkins, 1972, and *Thymopides*, but, strangely, not *Homarus* [nor on *Nephropsis rosea* Bate, 1888]). On *H. americanus*, on the carpus lower surface, the spine on the inner distal corner is smaller.

The cutter claw of *H. hungaricus* n. sp. is very different from that of *H. americanus* and is, by far, the easiest way to distinguish the two species. The cutter claw pollex on *H. americanus* is, proportionately, twice as wide as that of the fossil. The pollex on *H. americanus* is extremely wide, with a width/length ratio of 0.44 (width = 26.17 mm; length = 59.81 mm) versus 0.21 on the fossil. There are no known fossil species of *Homarus* that have a pollex as wide as that on *H. americanus*. *Homarus morrisoni* (with a broad crusher claw like that on *H. americanus*) has a cutter claw pollex (incomplete; unable to compute a width/length ratio; Quayle, 1987, pl. 64, fig. 7) more closely similar to that of the fossil than to *H. americanus*. The manus is also shaped differently, being proportionately wider on *H. americanus* (e.g., 0.72; width = 34.71 mm; length = 48.07 mm) than the fossil (0.61; width = 15 mm; length = 24.50 mm). The dentition is also very different. The cutter claw of *H. americanus* has small, variably sized denticles that are cylindrical to subconical, and each is concave (crater-like) at its termination (versus the conical, pointed dentition on the fossil).

Genus *Hoplopatria* M'Coy, 1849

Type species.—*Astacus longimanus* Sowerby, 1826, by subsequent designation of Rathbun, 1926.

Remarks.—*Hoplopatria* was erected by M'Coy (1849) as a genus of fossil lobsters that generally resembles *Homarus*, but has a more sculptured (grooved, locally inflated, etc.) and ornamented carapace. In fact, the name *Hoplopatria* (*armagena*) 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 (1849, p. 175–176) distinguished the type species, *Hoplopatria longimana* (Sowerby, 1826), from *Homarus*. Since 1849, the inclusion of more than 50 other fossil species has variously stretched and expanded the definition of *Hoplopatria* to accommodate this or that spine, this or that carina, etc., to the point that *Hoplopatria* is a genus that is difficult to characterize (Tshudy and Sorhannus, 2003).

Redefinition by Tshudy (1993).—Tshudy (1993, p. 71–72) redefined *Hoplopatria* as follows: "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 (see Tshudy, 1993, p. 463–464; Tshudy and Babcock, 1997, p. 257, for a discussion of the homologies of the branchiocardiac and postcervical grooves). The groove patterns on Triassic and Jurassic Erymidae Van Straelen, 1925 and the Jurassic chilenophoberids (now *Stenochiridae* Beurlen, 1928; see Karasawa et al., 2013), *Chilenophoberus* Chong and Förster, 1976, *Palaeophoberus* Glaessner, 1932, and *Pseudastacus* Oppel, 1861, show convincingly that the more ventrally directed branch of the postcervical groove (sensu Holthuis, 1974) is actually part of the branchiocardiac 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.

Hoplopatria: a wastebasket genus?—Tshudy and Sorhannus (2003) proposed that *Hoplopatria* is a "wastebasket" genus, one with a broad range of variation and, in cladistic analyses, containing non-*Hoplopatria*. They presented the following points:

1. *Hoplopatria* has been expanded in a de facto fashion to an extent that, today, there is so much variation among lobster species referred to *Hoplopatria* that the genus is difficult to characterize and to code for cladistic analysis without using many polymorphic character states. Tshudy (1993) encountered this while attempting to write an emended diagnosis of the genus. His diagnosis (1993, p. 71–72; see above), by necessity, was rife with descriptions of how character states "typically" occur. Moreover, some of his other statements, such as "thoracic region lacks carinae," are invalidated by one or a few species (e.g., presence of thoracic carinae on *Hoplopatria antarctica* Wilckens, 1907, and *Hoplopatria bearpawensis* Feldmann in Feldmann, Bishop, and Kammer, 1977).

2. *Hoplopatria* has been expanded in a de facto fashion to an extent that, "the morphologies of some Recent genera (e.g., *Eunephrops* Smith, 1885 and *Nephropides* Manning, 1969) seem easily accommodated within the fossil genus *Hoplopatria*" (Tshudy and Sorhannus, 2003, p. 700), and that, "if found in fossil form," ... "*Nephropides* and *Eunephrops* would very likely

be referred to *Hoploparia*” (Tshudy and Sorhannus, 2003, p. 701; supporting details in their paper).

3. *Hoploparia* is paraphyletic. Cladistic results showed other nephropid genera scattered throughout the *Hoploparia* results.

To these points, we here add:

4. The range of variation in *Hoploparia* is inconsistent with that in Recent genera (i.e., species of *Hoploparia* are morphologically more different from each other than are some other nephropid genera). For example, the modern *Thymopides* Burukovsky and Averin, 1977, and *Thymops* Holthuis, 1974 are, in external morphology, more closely similar to each other (seen best in a quick, comparative glance at each, but for details, see Tshudy, 1993) than many species of *Hoploparia* are to each other. The same is true for *Homarus* and *Homarinus* Kornfield, Williams, and Steneck, 1995 (likewise, and details in Tshudy, 1993), and especially *Thaumastocheles* Wood-Mason, 1874 and *Thaumastochelopsis* Bruce, 1988.

Tshudy and Sorhannus (2003) did not propose a solution to the problem (i.e., they did not present a revision of *Hoploparia* in that particular paper, but hoped to stimulate discussion and new characters and cladograms that would lead to a consensus and, subsequently, revision). Feldmann et al. (2007, p. 702–703) rebuffed the idea that *Hoploparia* was a wastebasket genus, noting that they were “struck by how similar the species currently referred to *Hoploparia* are to one another.” But they did not comment directly on the points (above) made by Tshudy and Sorhannus (2003). Thus, in our opinion, the definition and species composition of *Hoploparia* remain problematic.

It would seem that a consensus from species-level cladistic analyses would be a reasonable way of dividing the current contents of *Hoploparia* into smaller groups. We do not believe that a single published cladistic analysis or cluster analysis is a firm enough basis for disrupting the taxonomic stability of fossil lobsters. We cite, as an example of the apparent fallibility of computer analyses, a recently published (Schweitzer and Feldmann, 2014) cluster analysis of extant lobster genera. Among the curious results is that *Thaumastocheles* and *Thaumastochelopsis* are well separated, and each is paired with a lobster that looks much less like it than does its former family-mate (former family Thaumastochelidae). Indeed, Ah Yong et al. (2007, p. 206–207) opined that the “differences between *Thaumastocheles* and *Thaumastochelopsis* are minor, and whether or not both genera should be recognized requires further study.” With results this strange, it seems unreasonable to make sweeping, formal changes to taxonomy on the basis of a single, computerized analysis.

Tshudy (1993) noted that, despite the range of variation among species of *Hoploparia*, there were no obvious correlations between character states that would make subdividing the genus easy. In other words, he did not (and we do not) see certain spines associated with certain thoracic carinae, etc. Instead, each species of *Hoploparia* seems like a random sample from a grab bag of character states. Feldmann et al. (2007, p. 703) independently found the same.

Comparison of the new species to Miocene (23.03–5.33 Myr) *Hoploparia* species.—*Hoploparia gazdzicki* Feldmann

and Crame, 1998, from the lower Miocene of Antarctica, is a good *Hoploparia* that differs from the new species in having a granulose cephalothorax, a much more distinct ventral extension of the branchiocardiac groove, and a pleon with the tergum-pleuron surface separated by a distinct ridge.

Comparison of the new species to Eocene (56–33.9 Myr) *Hoploparia* species.—*Hoploparia alpinus* (Van Straelen, 1936) from the lower Upper Eocene (‘Auversien’) of Switzerland is fairly complete and well preserved, and “clearly a *Hoploparia*” (Tshudy, 1993, p. 73), but we cannot verify species identification without having seen the actual specimen or at least a whitened photograph. Tshudy (1993) was unable to locate the holotype and sole specimen known. Van Straelen (1936) cited ‘Le Musée d’Histoire naturelle de la Ville de Neuchâtel’ as the repository. From the description and photocopied photographs in Van Straelen (1936, figs. 1, 2), *Hoploparia alpinus* has pleonal pleura 3–5 narrower near the terminations than those of the new species. *Hoploparia alpinus* also appears to have relatively smaller chelipeds than those on the new species. Chelipeds on the new species are approximately 1.5x longer, or more, than the cephalothorax.

Hoploparia corneti Van Straelen, 1921, from the lower Eocene (Ypresian) of Belgium, is assigned to *Hoploparia*, based on granulation of the skeleton and the ventral extension of the branchiocardiac groove (Tshudy, 1993, p. 109). Van Straelen (1921, p. 138) wrote that *H. corneti* most closely resembles *H. gammaroides*. Tshudy (1993) was unable to locate material during his dissertation work; *H. corneti* differs from the new species in having granulation and a distinct branchiocardiac groove.

Hoploparia gammaroides M’Coy, 1849, from the lower Eocene of England and Belgium, is a good *Hoploparia* that differs from the new species in having a granulose cephalothorax and pleonal pleura that are more sickle-shaped/hook-like (see especially pleuron 3 [e.g., NHMUK 59127 and 59118] and with posterior margins more indented).

Hoploparia groenlandica Ravn, 1903 has been recorded from the lower Eocene of Greenland. We have examined a latex cast; cephalothorax, pleon, and claws all support identification as *Hoploparia*. It differs from the new species in having a distinct ventral extension of the branchiocardiac groove, a carapace surface covered by slightly squamiform granulations, and perhaps a more distinct sculpture (grooves) on the pleon.

Hoploparia johnsoni Rathbun, 1935, from the Middle Eocene of Alabama, U.S.A., is a good *Hoploparia* with a granular cephalothorax. It differs from the new species in having a granular cephalothorax, a better-defined ventral extension of the branchiocardiac groove, a hepatic spine, some spines on the postantennal region, and a better-defined sculpture (grooves) of the pleon.

Hoploparia wardi Quayle, 1987, from the lower Eocene of southern England, also is a good *Hoploparia* with a granular cephalothorax; Quayle removed it from *H. gammaroides*. It can be differentiated from the new species in having a granular cephalothorax, a hepatic spine, spines on the antennal region, and a more distinct ventral extension of the branchiocardiac groove.

Fossil record of *Homarus* and *Hoploparia*

The fossil record of *Homarus* is equivocal, depending on which species are referred to the genus. Six fossil species recognized herein, all European, give the genus a fossil record extending back to the Early Cretaceous (ca. 100 Ma). These are: *Homarus benedeni* Pelseneer, 1886 (Albian of France; Fig. 1), *H. morrisi* (Eocene of southern England), *H. klebsi* (late Eocene–late Oligocene of western Europe), *H. percyi* Van Beneden, 1872 (Oligocene of Europe), *H. lehmanni* Haas, 1889 (early Oligocene of Germany), and *H. hungaricus* n. sp. (late Oligocene of Hungary). Schweitzer et al. (2010) listed eight species of *Homarus*, but their list contains several differences from ours (Appendix 1).

Its oldest, and sole Cretaceous, occurrence (*H. benedeni*, of Albian age) is based on material that we have not been able to examine first hand. Line drawings in Pelseneer (1886, p. 49–50) show that *H. benedeni* is very *Homarus*-like and not at all suggestive of *Hoploparia*. Based on these line drawings, we are confident that *Homarus* is known from the Albian (ca. 100 Ma).

Some of the Paleogene occurrences exhibit a combination of *Homarus*- and *Hoploparia*-like morphological features (Appendix 1) (e.g., a ventral extension of the branchiocardiac groove [*H. klebsi*, *H. morrisi*] or a long subdorsal carina [*H. klebsi*]).

Table 1 presents the stratigraphic distribution of species of *Homarus*. *Homarus* first appears in the fossil record in the Early Cretaceous (Albian) and then is not known from the Late Cretaceous, despite the fact that nephropid lobsters in general are well known from that time interval. This stratigraphic distribution makes one wonder if we are looking at one lineage, or if the Paleogene species are convergent with the Albian form.

Hoploparia is the best known fossil genus of clawed lobster, with a record extending from the Lower Cretaceous (Valanginian) to the Neogene (Miocene). Fifty-eight species are known: 18 from the Lower Cretaceous, 33 from the Upper Cretaceous (31, plus one carryover from the Lower Cretaceous and one extending into the Paleogene), and nine Paleogene and Neogene (eight, plus one carryover from the Upper Cretaceous) (Table 2). *Hoploparia* was cosmopolitan in geographic range, extending from Canada (i.e., the Late Cretaceous *H. bennetti* Woodward, 1900 from Vancouver, and *H. albertanensis* Tshudy et al., 2005 from Alberta) and Greenland (i.e., the early Eocene *H. groenlandica* Ravn, 1903) to the Antarctic Peninsula (i.e., the Campanian–Maastrichtian *H. antarctica*, the

Campanian–Paleocene *H. stokesi* (Weller, 1903), and the early Miocene *H. gazdzicki* Feldmann and Crame, 1998).

Nephropid lobster diversity through time

Moving beyond alpha taxonomy and phylogenetic studies, some recent papers have examined lobster diversity through time (Tshudy, 2003 for the family Nephropidae; Schweitzer and Feldmann, 2014, 2015 for all lobsters). We revisit that herein for the family Nephropidae. A tally of fossil nephropid species per geological age is presented in Appendix 2, and diversity through time is graphed in Figure 6 (data and calculations in Appendix 3).

The known diversity of fossil nephropids really only equates to known shelf-depth diversity (i.e., marginal shelf and epicontinental sea diversity) (Tshudy, 2003). Lobsters that lived on the continental slope and at greater depths are never collected as fossils.

High sea levels, and therefore epicontinental seas, increase known fossil lobster diversity in two ways: (1) they increase lobster habitat, and (2) they fossilize lobsters where they can be collected today (those fossilized below modern sea level are not collected). Effect #1 produces a real increase in diversity (i.e., a real signal) and so, of course, should not be corrected for. Effect #2 biases the record in favor of time intervals (geological ages here) of high sea levels and, thus, we should at least attempt to correct for it.

In the absence of published information on rock exposure area per geological age, Tshudy (2003) normalized known species diversity for area of epicontinental sea coverage by using the sea level curve by Vail et al. (1978). Figure 6 herein updates the results of Tshudy (2003) in the light of species-level taxonomic additions and changes (since 2003)—the Oligocene species count has increased from two to four, and the Turonian–Coniacian–Santonian count from 15 to 22. Figure 6 shows known species diversity (white bars) for clawed lobsters of the family Nephropidae and normalized diversity for epicontinental sea coverage (black bars).

As in the 2003 study, both known species diversity (i.e., raw numbers) and normalized numbers indicate that the diversity of shelf-dwelling nephropids was highest during the Late Cretaceous; higher than in the Early Cretaceous and the post-Cretaceous. Tshudy (2003) interpreted the reduction in the Paleogene and Neogene as resulting not from the end-Cretaceous extinction, but largely from the nephropid general abandonment of shelf depths in the Paleogene.

Schweitzer and Feldmann (2014) compiled and interpreted (all) lobster diversity through time at the levels of infraorder, superfamily, family, and genus. Among the potential biases that they recognized was rock volume (first discussed by Raup, 1976a, b; later by Signor, 1985; and discussed in the context of nephropid lobsters by Tshudy, 2003, p. 179). Tshudy (2003) considered rock volume as less important than rock exposure area in biasing the lobster record through time, in that only exposed rocks yield lobster fossils (with very few exceptions, e.g. the new species described here, lobsters are unrecognizable in drill cuttings). Schweitzer and Feldmann (2015, p. 635) again noted the importance of the “uneven rock record” in interpreting diversity through time, this time acknowledging

Table 1. Stratigraphic distribution of species of *Homarus*.

Recent
<i>H. americanus</i> Milne Edwards, 1837
<i>H. gammarus</i> (Linnaeus, 1758)
Paleogene: Oligocene (33.9–23.03 Myr)
<i>H. hungaricus</i> n. sp.
<i>H. klebsi</i> (Noetling, 1885) (Eocene–Oligocene)
<i>H. lehmanni</i> Haas, 1889
<i>H. percyi</i> Van Beneden, 1872
Paleogene: Eocene (56.0–33.9 Myr)
<i>H. klebsi</i> (Noetling, 1885) (Eocene–Oligocene)
<i>H. morrisi</i> Quayle, 1987
Cretaceous: Albian (113–100.5 Myr)
<i>H. benedeni</i> Pelseneer, 1886

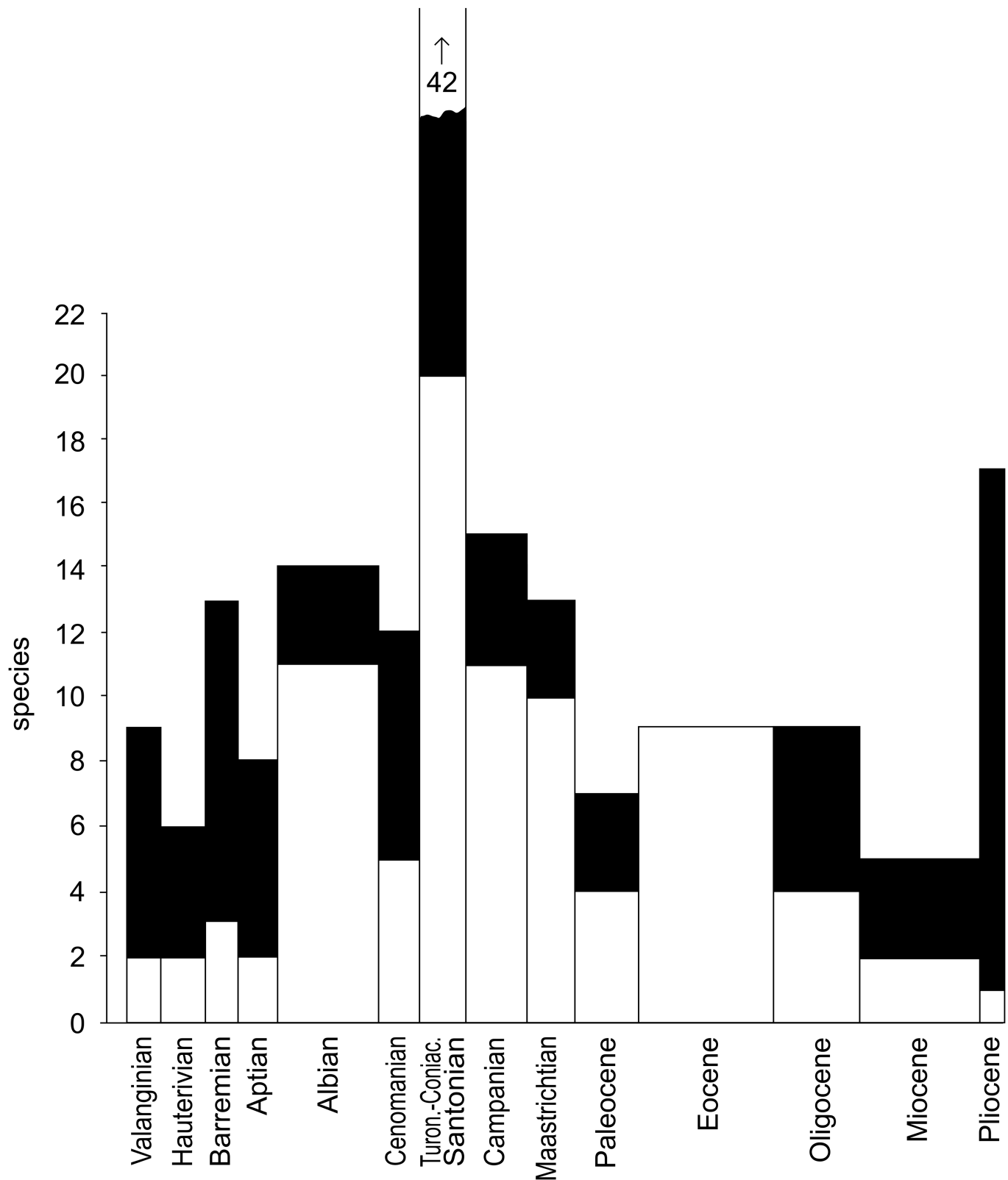


Figure 6. Known species diversity (white bars) for clawed lobsters of the family Nephropidae and diversity normalized for epicontinental sea coverage (black bars) using the sea-level curve of Vail et al. (1978) for geological ages (Valanginian–Pliocene) as per Tshudy (2003). This figure updates that of Tshudy (2003).

exposure area, albeit interchangeably with rock volume. In neither paper did they acknowledge the attempt by Tshudy (2003; “Vail Curve method”) at normalizing/correcting for

exposure area. Also, Schweitzer and Feldmann (2014, p. 823, fig. 1A) used “number of maps with outcrops of a given age” as a proxy for rock volume; neither is necessarily correlated with

Table 2. Stratigraphic distribution of species of the Nephropidae, compiled for three time intervals: Early Cretaceous, Late Cretaceous, and Paleogene and Neogene (data from Appendix 2).

Paleogene Period and Neogene Period (66–2.6 Myr)	
<i>Homarus</i>	= 5
<i>Hoploparia</i>	= 9 (8 + <i>H. stokesi</i> extending up from Late Cretaceous)
<i>Metanephrops</i>	= 2 (1 + <i>M. jenkinsi</i> extending up from Late Cretaceous)
<i>Nephrops</i>	= 1
<i>Oncopareia</i>	= 1
<i>Dinochelus</i>	= 1
Total	= 19
Late Cretaceous Epoch (Cenomanian Age [100 Ma]–end of Maastrichtian Age [66 Ma])	
<i>Hoploparia</i>	= 33 (31 + 2 [<i>H. tshudyi</i> extending up from Early Cretaceous, and <i>H. stokesi</i> extending into Paleogene])
<i>Jagtia</i>	= 1
<i>Metanephrops</i>	= 2 (1 + <i>M. jenkinsi</i> extending into Paleogene)
<i>Oncopareia</i>	= 3
<i>Palaeonephrops</i>	= 1
<i>Paraclytia</i>	= 4
Total	= 44
Early Cretaceous Epoch (Valangian Age [ca. 139 Ma]–end of Albian Age [100 Ma])	
<i>Homarus</i>	= 1
<i>Hoploparia</i>	= 18
Total	= 19

rock exposure area. Nonetheless, the work of Schweitzer and Feldmann (2015), and now ours, corroborates the long-held hypothesis that, whatever the cause, clawed lobsters largely abandoned shallow-water environments over geological time.

Conclusion

Homarus is known by two Recent and six fossil species. The fossil species are all European, and give the genus a record extending back to the Early Cretaceous. *Homarus* makes its appearance in the fossil record in the Early Cretaceous (Albian) and then is not known again until the Paleogene, despite the fact that nephropid lobsters in general are well known from the Late Cretaceous.

The separateness of, and differences between, *Homarus* and the extinct *Hoploparia* have long been debated. In our opinion, *Hoploparia* is most readily distinguished from *Homarus* by the ventral extension of the branchiocardiac groove (absent on *Homarus*) and the granulation of the exoskeleton (almost entirely absent on *Homarus*). In addition, the majority of *Hoploparia* display an antennal carina (absent on *Homarus*), as well as postantennal spines (absent on *Homarus*). *Homarus* lacks sculpture and ornamentation on its pleonal terga and pleura (some *Hoploparia* possess these). Claws of *Homarus* are much broader than those of nearly all *Hoploparia*. *Hoploparia*, the best-known fossil genus of clawed lobster, is known by 58 species.

Diversity of shelf-dwelling nephropid lobsters was highest during the Late Cretaceous. Raw tallies of species diversity numbers, as well as numbers corrected (normalized) for epicontinental sea coverage, indicate that clawed lobsters largely abandoned shallow-water environments over geological time.

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Accessibility of supplemental data

Data (appendices 2 and 3) available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.qr818>

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APPENDIX 1

Alphabetical list of species of *Homarus* and *Hoploparia*.

Homarus – two Recent (R) and six fossil (F) species

1R. *Homarus americanus* H. Milne Edwards, 1837.

2R. *H. gammarus* (Linnaeus, 1758). Schweitzer et al. (2010) listed this species as *H. vulgaris* H. Milne Edwards, 1837; this is a junior synonym of *H. gammarus*.

1F. *H. benedeni* Pelseneer, 1886 (Albian, France). Schweitzer et al. (2010) listed this as *Hoploparia benedeni*. Tshudy (1993, p. 65) maintained Pelseneer's (1886) assignment to *Homarus* as based on very *Homarus*-like line drawings in the latter paper.

2F. *H. hungaricus* n. sp. (Oligocene, Hungary).

3F. *H. klebsi* (Noetling, 1885) (Eocene-Oligocene, northwest Europe). Schweitzer et al. (2010) listed this as *Hoploparia klebsi*, but Tshudy (1993, p. 68-69) assigned it to *Homarus*, albeit with reservation. *Homarus klebsi* is known from beautifully preserved and illustrated specimens (drawings in Noetling, 1885). Generic placement is a tough call; claws are like those of Recent *Homarus*, but cephalothorax and pleon have aspects fitting either *Homarus* or *Hoploparia* (Tshudy, 1993, p. 68). Like *Homarus*: (1) absence of antennal carina; (2) absence of postantennal spines; (3) lack of sculpture on pleonal terga and pleura; (4) general lack of granulation on exoskeleton. Like *Hoploparia*: (1) distinct ventral extension of branchiocardiac groove; (2) long, subdorsal carina.

Most workers have retained the species in *Hoploparia* (Glaessner, 1929; Bachmayer and Mundlos, 1968; Eichbaum, 1971; Förster and Mundlos, 1982; Freess, 1992; Verheyden, 2002; Polkowsky, 2014). Van Straelen (1936) transferred it to *Homarus* (as did one of us, DT), but he believed there was no difference between *Homarus* and *Hoploparia*. Moths and Braasch (2005) referred the species to *Homarus*, noting the long-standing confusion of the genera but not explaining their generic assignment.

Homarus klebsi is a gigantic lobster, possibly synonymous with *Homarus percyi*. Reference is made to Moths and Braasch (2005) for a list of synonyms. At least, the coincidence of great size (very unusual among fossil nephropids), claw morphology, and stratigraphic and geographic occurrence indicate that *Homarus klebsi* and *H. percyi* are very closely related. Verheyden (2002, p. 181-182) found no differences between the claws of the two species.

4F. *H. lehmanni* (Oligocene, Germany). This species is known by a fragmentary carpus and fragmentary merus (Haas, 1889). Van Straelen (1936) and Verheyden (2002) considered *H. lehmanni* to be a synonym of *H. percyi*. Tshudy (1993, p. 69) maintained Haas' identification but did not examine the original material. Schweitzer et al. (2010) erroneously had the species double listed, under *Homarus* and *Hoploparia*.

5F. *H. morrisi* (Eocene, southern England). In 1990, one of us, DT, examined type and non-type specimens and supported Quayle's removal of several specimens from *Hoploparia*

gammaroides from the London Clay of southeast England, based on the general absence of granulation of the exoskeleton, absence of a supraorbital carina, antennal carina, and post-antennal spines, the lack of sculpture on the pleonal terga and pleura, and the very robust morphology of the claws (Tshudy, 1993, p. 70). The species does, however, resemble *Hoploparia* in having a ventral extension of the branchiocardiac groove.

6F. *Homarus percyi* (Oligocene, Europe). Schweitzer et al. (2010) listed this as *Hoploparia*, but Tshudy (1993, p. 71) maintained Van Beneden's (1872) original placement in *Homarus*, as did other workers (Delheid, 1895; Van Straelen, 1920, 1936; Geys and Marquet, 1983; Verheyden, 2002); none to our knowledge has moved species *percyi* to *Hoploparia*. Reference is made to Verheyden (2002, p. 179) for list of synonyms and possible synonyms. The species is known mostly by its chelipeds, which, being very robust, are better referred to *Homarus* than *Hoploparia*. This species is very similar to *H. klebsi*; the two are unique among all nephropids for their gigantic size and their claw morphology. One *Homarus percyi* claw is 0.4 meters in length (Van Beneden, 1872).

Hoploparia – 58 fossil species

Eocene (n = 6), Oligocene (n = 0), and Miocene (n = 1) occurrences are indicated because they are most relevant for morphological comparisons to Oligocene *Homarus hungaricus* n. sp.

1. *Hoploparia albertaensis* Tshudy, Donaldson, Collom, Feldmann and Schweitzer, 2005
2. *H. alpinus* (Van Straelen, 1936) – Eocene
3. *H. antarctica* Wilckens, 1907
4. *H. arbei* Aguirre-Urreta, 1989
5. *H. aspera* Harbort, 1905
6. *H. bearpawensis* Feldmann, in Feldmann, Bishop and Kammer, 1977
7. *H. bennetti* Woodward, 1900
8. *H. beyrichi* (Schlüter, 1862)
9. *H. biserialis* Fritsch, 1887
10. *H. blossomana* Rathbun, 1935
11. *H. brittonestrus* (Stenzel, 1945). Feldmann et al. (2007) and Schweitzer et al. (2010) listed this as *Homarus*, but one of us (DT) had referred it to *Hoploparia* (Tshudy, 1993, p. 103) as based on ornamentation of the cephalothorax and the shape and ornamentation of the claws. We (this paper) agree with Feldmann et al. (2007, p. 702-703) that the species is *Homarus*-like in lacking a ventral extension of the branchiocardiac groove.
12. *H. buntingi* (Feldmann and Holland Jr, 1971)
13. *H. catalunica* Garassino, Artal and Pasini, 2009
14. *H. collignoni* (Van Straelen, 1949)
15. *H. columbiana* Beurlen, 1938
16. *H. corneti* Van Straelen, 1921 – Eocene
17. *H. davisii* (Stenzel, 1945). Feldmann et al. (2007) and Schweitzer et al. (2010) listed this as *Homarus*, but one of us (DT) had referred it to *Hoploparia* as based on ornamentation of the cephalothorax (Tshudy, 1993, p. 109). We agree with Feldmann et al. (2007, p. 702-703), who said that

- species was *Homarus*-like in lacking a ventral extension of branchiocardiac groove.
18. *H. dentata* (Roemer, 1841)
 19. *H. dentonensis* Rathbun, 1935
 20. *H. edwardsi* (Robineau-Desvoidy, 1849)
 21. *H. fraasi* (Böhm, 1891)
 22. *H. gabbi* Pilsbry, 1901
 23. *H. gazdzicki* Feldmann and Crame, 1998 – Miocene
 24. *H. gammaroides* McCoy, 1849 – Eocene
 25. *H. georgeana* Rathbun, 1935
 26. *H. gladiator* Pilsbry, 1901
 27. *H. groenlandica* Ravn, 1903 – Eocene
 28. *H. hakelensis* (Fraas, 1878). Schweitzer et al. (2010) listed this as *Homarus* but one of us (DT) had supported Chong and Forster's (1976) reference to *Hoploparia*; they noted its strong antennal ridge and unequal claws (Tshudy, 1993, p. 127).
 29. *H. hemprichi* (Mertin, 1941)
 30. *H. horrida* Schweitzer and Feldmann, in Schweitzer et al. (2003)
 31. *H. intermedia* Secrétan, 1964 (According to Charbonnier et al., 2012, a junior synonym of *H. collignoni*. Tshudy, 1993, p. 130, tentatively regarded the species as separate from *H. collignoni*).
 32. *H. johnsoni* Rathbun, 1935 – Eocene
 33. *H. kamimurai* Kato and Karasawa, 2006
 34. *H. kamuy* Karasawa and Hayakawa, 2000
 35. *H. longimana* (Sowerby, 1826)
 36. *H. mcnairyensis* Rathbun, 1929
 37. *H. mesembria* Etheridge, Jr., 1917
 38. *H. mickelsoni* Bishop, 1985. Schweitzer et al. (2010) listed this as *Homarus*, but one of us (DT) had referred it to *Hoploparia* (Tshudy, 1993, p. 146) as based on cephalothorax ornamentation, including long subdorsal and supraorbital carinae. It does, however, lack a ventral extension of the branchiocardiac groove (as emphasized by Feldmann et al., 2007) and does possess a urogastric groove; both *Homarus*-like features.
 39. *H. minima* de Tribolet, 1876
 40. *H. miyamotoi* Karasawa, 1998
 41. *H. muncki* Pelseneer, 1886
 42. *H. natsumiae* Karasawa, Ohara and Kato, 2008
 43. *H. pelseneeri* (Van Straelen, 1936)
 44. *H. pusilla* Secrétan, 1964
 45. *H. riddlensis* Feldmann, 1974
 46. *H. schlueteri* Tribolet, 1874
 47. *H. sculpta* Secrétan, 1964 (According to Charbonnier et al., 2012, a junior synonym of *H. collignoni*. Tshudy, 1993, p. 150 regarded the species as distinguishable from *H. collignoni* based on its “distinctly different” abdomen.)
 48. *H. senonensis* Forir, 1887
 49. *H. shastensis* (Rathbun, 1929)
 50. *H. stokesi* (Weller, 1903)
 51. *H. tennesseensis* Rathbun, in Wade, 1926
 52. *H. travisensis* (Stenzel, 1945). Schweitzer et al. (2010) listed this as *Homarus*, but one of us (DT) had referred the species, known only by an incomplete palm, to *Hoploparia* (Tshudy, 1993, p. 183).
 53. *H. triboleti* Borissjak, 1904
 54. *H. trigeri* Van Straelen, 1936
 55. *H. tshudyi* Schweitzer and Feldmann, 2001
 56. *H. uzbekensis* Feldmann et al., 2007
 57. *H. wardi* Quayle, 1987 – Eocene
- Removed, as synonyms, from the list of Schweitzer et al. (2010)
1. *H. belli* M'Coy, 1849 (syn. *H. gammaroides*) (see Tshudy, 1993, p. 122)
 2. *H. saxbyi* M'Coy, 1854 (syn. *H. longimana*) (see Tshudy, 1993, p. 131)
 3. *H. victoriae* Quayle, 1987 (syn. *H. gammaroides*) (see Tshudy, 1993, p. 122)
- Referred to *Hoploparia* by Schweitzer et al. (2010), but here transferred to a genus other than *Hoploparia* or *Homarus*
1. *Hoploparia nephropiformis* Schlüter, 1874 to *Paraclytia* Fritsch, 1887 (see Tshudy, 1993, p. 314).
 2. *Hoploparia scabra* Bell, 1863 to *Palaeastacus* Bell, 1850 (see Tshudy, 1993, p. 371).
- Genus uncertain
1. *Homarus neptunianus* Polkowsky, 2005 – known only by a single fixed finger (pollex), which could even belong to a crab claw (see also Polkowsky, 2014).
 2. *Hoploparia calcarifera* Schlüter, 1879 – holotype, and sole specimen known, is lost; identification at generic and specific levels is uncertain without examination of the original material (Tshudy, 1993, p. 106).
 3. *Hoploparia eocaenica* Lörenthey, in Lörenthey and Beurlen, 1929 – identity of the three specimens is unknown, but none is suggestive of *Hoploparia* (Tshudy, 1993, p. 363). Referred to *Hoploparia* by Schweitzer et al. (2010).
 4. *Hoploparia falcifer* Fritsch, in Fritsch and Kafka, 1887 – known only by claws; generic identity unknown (Tshudy, 1993, p. 115). Referred to *Hoploparia* by Schweitzer et al. (2010).
 5. *Hoploparia heterodon* – as used in Schweitzer et al. (2010). *Oncopareia? heterodon* Bosquet, 1854 is known only by claw fingers which are now assumed to have belonged to a crab (Tshudy, 1993, p. 371; Jagt et al., 2014).
 6. *Hoploparia? suecica* Schlüter, 1874 – we have been unable to locate the repository; an identification is impossible on the basis of the illustration in Schlüter (1874) alone (Tshudy, 1993, p. 180). Referred to *Hoploparia* by Schweitzer et al. (2010).
 7. *Hoploparia? sulcicauda* Schlüter, 1874 – material is lost; the generic identity remains unknown (Tshudy, 1993, p. 181). Referred to *Hoploparia* by Schweitzer et al. (2010).
 8. *Hoploparia tarrantensis* Rathbun, 1935 – we have examined the holotype; it probably is not a nephropid (Tshudy, 1993, p. 364).

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