

Raninidae infested by parasitic Isopoda (Epicaridea)

Henning Wienberg Rasmussen, deceased, with additional observations by
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Abstract

An unfinished MS by the late H. Wienberg Rasmussen, Copenhagen, regarding observations on bopyriform infestation of fossil decapods, together with a chronological summary of past work by previous authors is reproduced in slightly edited form. Observations subsequent to Wienberg's remarks have been added and a table of known infested species has been included.

Key words: Bopyriform swellings, fossil decapods, discussion, recorded infested species.

Introduction

Henning Wienberg Rasmussen (1920–1980) was an indefatigable writer, who from 1945 until 1979 published numerous papers. Although specializing in echinoderms – particularly crinoids – he unhesitatingly turned his attention to other fields of palaeontology and when SLJ joined the Copenhagen Geological Museum, as personal assistant to Wienberg Rasmussen, Wienberg (as he was affectionately known to friends and colleagues) was already engrossed in describing the vast collection of Upper Cretaceous–Lower Tertiary decapod crustaceans from the Nuussuaq peninsula, West Greenland, that had been collected by the late Professor A. Rosenkrantz, Copenhagen and colleagues during 18 expeditions between 1938–1968. Time absorbing as that Herculean task was, it did not prevent Wienberg from energetically investigating occurrences of bopyriform infestations effecting raninids and mecochirids in the Greenland collection (*q.v.* Collins & Wienberg Rasmussen, 1992); unfortunately, both tasks remained unfinished at the time of death. For comparative purposes and to further his knowledge of Recent forms, Wienberg corresponded with John Markham, a leading authority on the Epicaridea, then at the Bermuda Biological Station, whose reply survives, together with all Wienberg's copious notes in Danish, his hand-written translation into English and typescript, the latter not including his research on the Greenland material which remains handwritten. The wealth of information contained in Markham's letter is a mini-MS in itself, and we include a transcript herein.

In editing the MS we had little to do except bring taxonomic references up to date and correct nuances in punctuation; opinions and observations are strictly Wienberg's. The few comments we have made in text are enclosed in []. Other authors' observations subsequent to Wienberg's remarks, together with those resulting

from our findings, are appended.

At the time of Wienberg's last entry (c. 1980), to his checklist of infested species (not included herein), he had recorded 25 (21 Jurassic, two Cretaceous and two Paleocene) species of crabs with typical bopyriform swellings. However, of these, some have subsequently been transferred to other genera, while others have been relegated to junior synonymy (see Table 2).

Raninidae infested by parasitic Isopoda (Epicaridea)

Among 1,222 specimens of Raninidae from Nuussuaq are 54 with a large swelling of the carapace in the branchial region of either right or left side and one with a swelling in both sides.

From comparison with Recent decapods it is assumed that these swellings are produced by parasitic Isopoda of the suborder Epicaridea, families Bopyridae and Entoniscidae, which live attached in the branchial cavity mainly of Caridea and Anomura, but also in a few Brachyura. They are mainly found in marine Decapoda from littoral to the deep sea (1,570 m), but occur also in decapods from brackish and freshwater, and on land. Most of them live in the branchial cavity of Caridia (*Pandalus*, *Leander*, *Spirontocaris*, *Hippolyte*, *Glyptocrangon*) and in Anomura (Paguroidea, Galatheidae, Porcellanidae, Thalassinoidea), and in a few Brachyura (Xanthidae, Grapsidae, Portunidae, Pinnotheridae). The best studied genera are *Gyge*, *Pseudione* and *Pleurocrypta* (all contained in the Bopyridae) as parasites in *Galathea*, *Munida* and *Upogebia*. Most Epicaridea are restricted to a single, or a few species of decapods as their hosts, but Epicaridea of different species, genus or, even family may occur as a parasite in some species of decapods. A determination of the parasite genus cannot be based on the species of host or on the form of the swelling. Nor is it possible to draw any conclusion on the geological environment

from the presence of the parasite.

The larval parasite generally infests a young decapod and metamorphoses to an adult female, which soon completely fills out the branchial cavity and stays there for the rest of its life, which may be several years. A second intruder metamorphoses to a male [proandrous hermaphrodite] and attaches to the female. The female Bopyridae attaches with head towards the posterior end of its host and ventral side towards the branchiostegite, to which it attaches by its pereopods. The body is ovate, dorsoventrally flattened and asymmetric according to the form of the left or right branchial cavity. Mouth parts are suctorial with piercing mandibles and they are true parasites, living as bloodsuckers. The male is much smaller than the female. The females in Entonischidae are more modified and reduced than in the Bopyridae, and may lose segmentation and appendages, while the male retains isopod features. Although the female grows asymmetrically, the same species of parasite may occur in left or right branchial space, or both.

After moulting, when the carapace is still soft, the carapace bulges in the branchial region to accommodate the parasite, which takes food from its host and harms it to a variable degree in different species, including, in some cases, parasitic castration, but generally, the harm seems small and the host survives to reach normal size for the species.

The number of specimens infested is generally low – about one percent of the population within the area, but locally a higher degree of infestation may occur. Thus, according to Rayner (1935), 3.7–7.4 percent of *Munida gregaria* and *Munida subrugosa* from the Falkland Islands are infested by *Pseudione*, while, according to Tucker (1930), 20–25 percent of *Upogebia littoralis* at Naples are infested by *Gyge*.

The study by Rayner (1935) of *Munida* from the Falkland Islands also shows that out of 5798 specimens of *Munida rugosa*, 395 specimens (6.813 percent) were infested in the right branchial cavity, 20 specimens (0.345 percent) in the left cavity, and 14 specimens (0.241 percent) in both sides. There is no asymmetry in the external form or in function of the two gills of a *Munida* and there seems to be exactly the same probability that a larval isopod should enter the right or left cavity. Also, the asymmetry of the attached female parasite is dependent only on the form of the cavity in which it has become attached. No feature in the morphology or function of the parasite or the host explains why 92 percent of infested specimens have the parasite in the right side only.

Almost the same distribution was found in 3369 specimens of *Munida gregaria*, 114 specimens (3.384 percent) of which being infested in their right side, ten (0.297 percent) specimens in the left side and one specimen (0.003 percent) in both sides. Thus, 91.2 percent was infested in the right branchial cavity.

No reason for the asymmetric distribution of parasites in *Munida* is known. Also, it is unknown whether or not a similar asymmetric distribution is present in other decapods infested by Epicaridea. It is proposed by Houša (1963), that, for some unknown reason in the internal anatomy of the decapods, those infested in their left side

had a greater mortality.

Another unexplained observation is the number of *Munida* with a parasite in both sides. Since this is only seldom found (in fossil decapods) it was assumed by Radwanski (1972) that by some kind of biological regulation, the presence of one epicaridean parasite prevented further infestation by parasites in the branchial cavity of the other side of the host. But actually, if the frequency of parasite infestation was determined by the probability of a larval epicaridean to be washed into the branchial cavity by the stream of water for respiration, as assumed by Houša (1963), we should expect, in the case of *Munida subrugosa* with 6.8 percent infested in the right side, that also 6.8 percent should be infested in the left side (although only 0.345 percent survived). Further, if infestation of one side did not influence one side, the probability of a two-sided infestation would be 6.8 percent \times 0.345 percent = 0.02346 percent, or 1.36 specimens out of 5798 specimens. But actually 14 specimens with a two-sided infestation were found.

So, far from preventing further infestation, it thus seems that the presence of one parasite has weakened the host and reduced its ability to prevent a parasite from attaching also the other branchial cavity. We may assume that the presence of the first parasite harms the host and its vitality so much that it is less capable to clean the gill cavity in case of another parasite arriving. This interpretation may also be supported by the fact that bopyrids and rhizocephalids are found as parasites together in the same host with a frequency much larger than expected from the frequency of these parasites alone in hosts without a second parasite.

In the case of *Munida subrugosa* we may expect that the mortality of specimens infested in both sides is still larger than in specimens infested in left side only (larger than 91 percent) and the number originally infested in both sides may well have been as large, or larger than, the number infested in one of the sides only.

It must now be remembered that in fossil decapods, the presence of an epicaridean parasite is only seen if the decapod survived a moulting by which it obtained a swelling of the carapace. [Thereafter, incidences of moulted carapaces of infested crabs can be expected to be more frequent than infested corpses.]

Fossil decapods with a swollen branchial area of the carapace, probably due to some epicaridean parasite are known from the Jurassic, Cretaceous and Lower Paleocene (Danian). Such swellings were first recorded by McCoy (1854, p. 118) from the Albian raninid *Notopocorystes mantelli* McCoy, 1854 (= *Notopocorystes stokesii* (Mantell, 1844)) and were interpreted by McCoy to be the result of the parasitic isopod *Bopyrus* attached in the branchial chamber.

Quenstedt (1858, p. 779) described a similar swelling in the left gill region of the prosoponid *Prosopon aculeatum* von Meyer from the Upper Jurassic (epsilon) at Oerlingen, Germany. He interpreted the swelling as a deformation.

Von Meyer (1860, p. 220) referred the decapod described by Quenstedt to the galatheid *Gastrosachus wetzleri* von Meyer. He also mentioned (p. 211) that some specimens show a swollen gill

region in either the left or right side due to some disease and that the same might possibly be the case in the incomplete specimen of a *Prosopon acculeatum*.

Bell (1863, pp. 13, 14, pl. 3, fig. 3) figured a *Notopocorystes stokesii* (as *Palaeocorystes stokesi* [sic]) with a large swelling on its left gill region which he described as a specimen infested by a parasite nearly allied to *Bopyrus* found in Recent Palaeomonidae and their allies, but unknown in Brachyura. [At that time raninids were included in the Anomura.]

Gemmellaro (1869, p. 14) described *Prosopon tithonium* from the Upper Jurassic (Tithonian) of Sicily with a swelling in the left branchial area in one of the specimens (pl. 2, fig. 55), but he considered this due to pressure during fossilization.

Blasche (1911, p. 149) was the first to mention a specimen from Stramberg, Czechoslovakia, of a '*Galathea verrucosa* Moericke with a distinct swelling. [Houša (1963) casts doubt on this, adding that no illustration exists.]

Balss (1913, p. 1599) recorded the description of von Meyer (1860) of swellings in the gill region, which he compared with similar swellings in the gill region of Recent Galatheidae illustrated by Milne Edwards & Bouvier (1897). The latter are parasitic isopods of the genera *Gyge* and *Pleurocryptus*. Balss concluded that the swellings in the Jurassic Galatheidae are due to similar parasitic isopods.

Reměš (1921, 1923) described ten specimens from the Upper Jurassic of Stramberg of galatheids (*Galathea*), dynomenids (*Cylothyreus*) and prosopids (*Prosopon*) with swelling in the branchial region, interpreted by him as due to parasitic bopyrids and comparable to such swellings in Recent galatheids (*Galathea squamosa* Leach, 1815 and palaemonids (*Leander squilla* Linné) from the Adriatic Sea.

Van Straelen (1925, p. 50) reviewed some previous records of fossil Brachyura with swollen gill regions similar to swellings caused by parasitic Epicaridea and especially the Bopyridae. He also contributed an infested specimen of *Xantho agassizi* from the Neocomian of Auzerre, Yonne, France [and recorded *Eucorystes carteri* (McCoy, 1854) from the Cambridge Greensand, Upper Albian, of Cambridge]. In 1931 he repeated, in *Fossilium Catalogus*, the species recorded and also corrected *Xantho agassizi* to *Palaeodromites*.

Beurlen (1929, p. 34), described a specimen from the Upper Jurassic (Upper Oxfordian, Corallian) from San Mihiel, Meuse, with both branchial regions swollen due to parasitic bopyrids.

Rathbun (1928, p. 2) showed a specimen of *Notosceles bournei* Rathbun, 1928, from the Lower Paleocene, Midway, Danian of Texas with a swelling on its left side probably due to a parasite. Rathbun (1935, p. 81) figured, and regarded in the same way, a similar swelling in the right side of a specimen of *Raninoides ovalis*, from the Lower Palaeocene, Danian, Sycamore beds of Alabama.

Bachmayer (1948) found pathological swellings of the branchial region in eight specimens of *Galatheites* and one *Pithonoton*

among the numerous decapods collected from Upper Jurassic limestone at Döfles, near Ernstbrunn, Austria. These infestations were interpreted as due to isopods of the family Bopyridae. Among the eight specimens of *Galatheites*, three were infested in the left and five in the right side. In 1955, Bachmayer gave a review of the Isopoda from the Tithonian of Ernstbrunn, Austria, and Stramberg, Czechoslovakia, including abundant new material. He also mentioned (p. 271) Epicaridea, including the family Bopyridae, indicated by swelling in the branchial area of Galatheidae, Prosoponidae and Homolodromidae. Among 3000 crustaceans from the Ernstbrunner limestone, 60 specimens (2 percent) show such swellings; in the Stramberg material they are less common.

Houša (1963, pp. 101–103, pls. 1, 2) gave a very complete and adequate review of previous information. Since Recent species of *Bopyrus* are found only in the cavity of *Leander*, he considered the swelling in fossil decapods [mentioning in particular *Notopocorystes stokesii*] most likely due to some other species of isopod. He also considered an apparent swelling in a specimen of '*Phlyctisoma granulatum*' [= *Palastacus scaber* (Bell, 1863)] figured by Bell (1863, pl. 11, fig. 9) as due to a parasite. In three species of Galatheidae (*Galatheites*, *Mesogalatea*), five specimens were found with a swelling, all of them in the right side. Among the Dromiacea are Prosopidae (*Nodoprosopon*, *Pithonoton*) with eight specimens infested on the left side and twelve on the right side; in the Dynomenidae (*Cylothyreus*, *Cyphonotus*) six specimens are infested in the left side and three in the right side. In the Stramberg material, small or large swellings occur in small as well as in large hosts, indicating that both juvenile and adult decapods may be infested. The difference in size of the swelling may be due to different species of parasites [or according to age and size of host when infested].

Radwanski (1972), in material of more than 500 Prosopidae (*Pithonoton*, *Nodoprosopon*) from the Upper Jurassic (Middle–Upper Oxfordian) of Poland, found seven specimens (less than 1.4 percent) with a swelling of the branchial area, five on the left and two on the right side. He found that infested specimens show normal adult size and concluded that the decapod survived and was not seriously affected by the intruder. For this reason he interpreted the relationship between host and intruder to be commensalism (sharing food) instead of true parasitism. However, parasitism is well documented in Recent Epicaridea, and survival of the host does not exclude parasitism.

From the almost complete absence of fossil specimens infested by isopods on both sides, Radwanski concluded that by some kind of biological regulation, the presence of an isopod in one of the branchial cavities prevented further intrusion or development of isopod larvae also in the other branchial cavity of the specimen. There is, however, no statistical basis for this conclusion. With a frequency of seven specimens infested out of more than 500 Prosoponidae, the probability is less than 0.014 (1.4 percent). If a second infestation was independent of the presence of an isopod on one side, the probability of an infestation in both sides is 0.00098,

or one in 10,204 specimens. The absence of a specimen infested in both sides among 500 specimens studied, is, therefore, without any significance.

Actually, the absence of decapods with both sides infested may be explained by presuming that the parasite is harmful to its host by sucking blood and reducing gill function, and with both sides infested, the host would not survive long enough for the parasite to manifest its presence by a swelling of the carapace after the next ecdysis.

[The following passages remain in English longhand.]

Among 1,295 specimens of raninids [*Lyriedus rosenkrantzi* Collins & Wienberg Rasmussen, 1992 = *Macroacaena rosenkrantzi* (Collins and Wienberg Rasmussen)] from Upper Cretaceous, Maastrichtian concretions in a Lower Paleocene, Danian, conglomerate in Nūsuaq, West Greenland, are 73 specimens (5.64 percent) with a swelling in the branchial region; 32 in the left, 40 in the right side and one in both sides. The difference in frequency of left and right side infestations is rather small and may well be incidental. If infestation on one side is independent of the presence of a parasite on the other side, the probability of the two-sided infestation is $0.0564 \times 0.564 \times 0.5 = 0.16$ percent, or one in 629 specimens – or two in 1.258 – and we find one which has survived long enough to be seen as swelling in the new carapace, but there may have been many that did not survive long enough to be seen in the fossil material.

Conclusion. From the study of the present collection and a review of previous studies of Recent and fossil decapods with epicaridean parasites, we may conclude that the probability of infestation depends on the ability of the host to prevent a parasite from attaching in the branchial region and is smaller in decapods already weakened by a parasite of the same or another kind. A tendency for parasites to be more common in the right than in the left branchial cavity is found in Recent *Upogebia* and may be indicated in fossil Galatheidae, but is most likely due to increased mortality with a left or two-side parasite. The number of bilaterally infested specimens of *Munida* indicates that many decapods with a parasite in one side have been weakened and infested also in the opposite side, but most of them did not survive. In other groups of decapods there is found no significant difference in frequency of left side or right side parasite.

The size of swellings in [*Macroacaena*] *rosenkrantzi* indicates [Here, Wienberg's Manuscript comes to an end]

[Wienberg also investigated parasitic evidence in *Mecochirus* (= *Mecochirus rostratus* Collins & Wienberg Rasmussen, 1992) from the Maastrichtian of West Greenland. This research remains in longhand, English.]

“Among 2163 specimens of *Mecochirus*, most of them preserved to show only one side, are two specimens (MGUH 28743, GM 1982.276) with a large longitudinal swelling along the upper part of the left branchial region. Both specimens show a normal outline and edge of the carapace, indicating that sediment pressure,

or other kind of postmortem deformation is definitely not the explanation, but most likely a parasite in the branchial cavity. The swellings are less rounded than in other decapods with epicaridean parasites.”

Reply to an enquiry sent by Wienberg to John C. Markham, Bermuda Biological Station, 6th September 1978 :

“Dear Dr. Rasmussen,

Thank you very much for the article by Radwański, which I received about a week ago. Your letter, which just came also contains much information of interest to me.

As Dr. Bromley mentioned, I am deeply involved in the distribution, systematics, and evolution of the Bopyridae. Because those parasites are noncalcified, it is extremely unlikely that any direct fossil remains of them would be found, and so far evidently no such remains have turned up. Thus I must draw inferences from the tenuous fossil evidence provided by the distinctive branchial swelling in their hosts, from the morphology and development of recent parasites and from the known host-selection patterns of living species.

It is of particular interest to find records of parasitism of groups of fossils whose living members completely lack it. I have compiled records of all of the bopyrids on which I have found publications, (so far a total of 500+ species cited in about 1400 papers). From these records I have also derived a file of hosts worldwide, a list which now numbers approximately 600 species of Decapoda. As you commented, there are no recent raniniods known to serve as hosts of bopyrids. It is noteworthy that the whole section Oxystomata is very poorly represented: only two dorippids (*Tymolus japonicus* and a *Tymolus* sp.) and three leucosiids (*Iliacantha subglobosa*, *I. liodactyla* and *Leucosia cranularis*). Another group commonly reported as hosts of bopyrids in the fossil record is the Dromiacea, but only a single recent species, *Hypochooncha* sp., has been recorded as a host of a bopyrid. On the other hand, galatheids are well represented as both fossil and living hosts.

I agree that Radwański's conclusion that the branchial swelling was caused by an animal which was a commensal rather than a parasite seems poorly substantiated. Even among species which have been studied alive the distinction often seems to be a matter of semantics.

You mentioned that you are also studying Cretaceous specimens of *Callianassa*. If you find any with evidence of parasitism, I shall be interested in hearing of it. I don't know whether the issue of the placement of the Thalassinoidea in the Anomura or Palinura has been resolved (Though I would like to have your opinion on the matter). I have become involved in what is essentially a parallel problem of phylogeny. Many recent *Callianassa* spp. and *Upogebia* spp. bear bopyrid parasites which appear to represent genera transitional among those families characteristically found infesting

Macrura, Anomura or Brachyura.

Sincerely yours,

[signed] John C. Markham.”

Also, the numerous callianassid specimens present in the West Greenland collection still await attention.

Wienberg mentioned the larval parasite infesting the decapod, but prior to that, on hatching, the larva undergoes initial development in a copepod host before seeking a decapod as secondary host, in which it waits until the next moulting stage of the host before completing final development which causes the characteristic swelling. Thereafter, the female parasite moults in synchrony with its host (Overstreet, 1983). The male is diminutive and associated with the genital region of the female (Sars, 1899). The earliest known occurrence of a bopyric swelling for brachyurans is from the Oxfordian and for macrurans it is the Toarcian. Although not recognised in the fossil record until the Miocene (Schram, 1979, pp. 240, 242), by inference, and assuming an uninterrupted life-style, it means that copepods must have been coeval with the decapods! Concluding his discussion of infested Jurassic species, Houša (1963) stated that the parasites stopped growth and moulting of their hosts, and that large swellings in adult crabs was the result of late infestation of the crab. However, this opinion is contrary to the presence of obviously infested moults of varying growth-stages which, in multi-evidenced species, equals – or outnumbers – known corpses. It is evident that Wienberg dwelt long upon ratios and probabilities – the value of which is probably best demonstrated in large faunas such as those mentioned by him, namely the Jurassic prosoponids, and Greenland raninids and mecochirids. But a considerable number of species potentially subject to parasitism are known by one or very few specimens, and it would seem logical to expect that as these species become better known, the probability of infested specimens increases. Likewise, the chance occurrence of an infested individual among a mere handful of specimens of a species is no indication of ratio regularity.

Commenting on the value of percentages among fossil forms, Conway Morris (1981), quoting from Bachmayer (1948), Houša (1963), Förster (1969) (chronologically overlooked by Wienberg), and Radwanski (1972), added the important fact that percentages of samples are open to, ‘preferential removal or destruction of distorted carapaces, collector bias etc.’! Conway Morris (1981, p. 495) included the hypothesis that infestation reached a maximum in the Upper Jurassic, “because in the Cretaceous the number of infested species had apparently declined and very few examples are known from the Cainozoic (Rathbun, 1916).” He attributed this as possibly due to the, “evolution of resistant adaptations in many species.”

Nevertheless, while the numerical incidence of individual crabs as well as species of crabs may be greater in the Jurassic, since 1981 considerably more infested species have been made known

from Cretaceous, Tertiary and younger deposits, resulting in a total of 50 known species:

Jurassic 21 (c. 42.2) ; Cretaceous 16 (c. 32.5) ; Palaeocene 3 (c. 6.0) ; Eocene 2 (c. 4.0) ; Miocene 6 (c. 12.0) ; Pleistocene 2 (c. 4.0).

Table 1. Families and the number of infested species therein

Galatheidae	8
Porcellanidae	2
Prosopidae	11
Dynomenidae	4
Homolidae	1
Raninidae	7
Torynomenidae	2
Etyidae	1
Hepatidae	1
Necrocarcinidae	1
Majidae	1
Portunidae	2
Carcineritidae	1
Leucosidae	2
Macrura	6

Houša (1963) pointed out that McCoy (1854) was the first person to note a swelling (which he attributed to *Bopyrus*) on a fossil crab (*Notopocorystes stokesii* (Mantell, 1844); Albian) and briefly surveyed discoveries by other authors. He also discussed asymmetry in the shape and location of swellings, and of the swellings themselves alluding to proof of existence of other species of parasites. Furthermore, he noted slight defects of surface ornament; e.g. he examined a specimen of *Pithonoton marginatum* von Meyer, 1842, which had a large swelling on the right side, the internal cast was covered with small tubercles which were less discernable on the smooth surface of the swelling. Pathogenic deformation of carapaces was also discussed by Förster (1969, p. 51).

A massive right-side swelling on a young male *Hoplitocarcinus atlanticus* (Roberts, 1962) (Pl. 3, Fig. 1) from the Upper Cretaceous of the Northern Atlantic Coast of the USA, almost entirely obliterates surface nodes peculiar to that species. Contrastingly, the corpse of a young *Hepatus lineatinus* Collins & Todd (*in* Todd & Collins, 2005) (BMNH PI IC440) from the Middle Miocene of Panama has a large swelling on the left side which merely disturbs the dorsal surface ornament (Pl. 3, Fig. 2).

With but two exceptions, rare carapaces of *Protomunida munidoides* (Segerberg, 1900), from the Paleocene Middle Danian of Fakse, Denmark (Pl. 3, Fig. 3) and *Galathea weinfurteri* Bachmayer, 1950, from the Miocene Badenian of Rákos, Hungary (Müller, 1982, pl. 22, fig. 5), all known fossil galatheids are from Jurassic deposits and are well documented by earlier authors.

Of two known species of *Palaeodromites* with bopyriform swellings, infestation in the earlier, *Palaeodromites oxythyriiformis* (Gemmellaro, 1870), from the Tithonian of Czechoslovakia, is known to occur in both left and right sides and, while the carapace

of *Palaeodromites octodentatus* (Milne Edwards, 1865), from the Hauterivian of Yonne, France, is much abraded, has remnants of a swelling on the right side (Pl. 5).

Carter (1898, p. 28) when referring to specimens of *Necrocarcinus labeschei* (Deslongchamps, 1835), was non-committal when he remarked, "Specimens having the branchial region rendered tumid by some Bopyriform parasites are of frequent occurrence." A tablet in the Sedgwick Museum, Cambridge, from the Carter Collection (Pl. 4), has four of these 'mentioned' specimens from the Upper Albian Cambridge Greensand; all have swellings on the right side and, as far as can be ascertained, all are moults. The first carapace has an extraordinarily large swelling which caused a 'ridge' curving from near the anterior metabranchial tubercle to the margin, whilst on carapace No. B 23185 only the 'flangelike' rim of the swelling remains.

As indicated by moulted carapaces (Museum de Harvre) and G. Breton Collection, from the raulinatus Zone, Lower Albian, Pays de Bray, France, the essentially Albian species *Notopocorystes stokesii* (Mantell, 1844) became prone to infestation early in its phylogenetic development and its role as host continued to the final stages in *N. s. serotinus* Wright & Collins, 1972. The three, much the same sized carapaces figured (Pl. 1, Figs. 1–3), from the raulinatus Zone, of Bully, le Havre, are rather more than half grown and presumably moults; two have a robust ovate swelling on the right side and one, a similar swelling on the left side.

A well preserved corpse of *N. s. stokesii*, from the Gault (Albian) of Folkestone, (Pl. 1, Figs. 5a–c), in the Natural History Museum, London, (BMNH In 31278) has two quite dissimilar swellings; that on the right is typically sub-spherical and overlapping the margin, whereas that on the left, occupying about the same area, is shallower, rather diffuse, and leaving the posterolateral margin visible from above. Moreover, the dorsal granular ornament is sharp and well-defined, in contrast to the sparsely granulated, almost glossy surface on the right side.

A second tablet from the Carter Collection (Pl. 2), in the Sedgwick Museum, has eleven infested carapaces of *N. s. serotinus* from the Cambridge Greensand. The nodular state of preservation renders some doubt on whether the carapaces are of corpses or moults, but with two indeterminate exceptions (situated 4, 8 on tablet), four (2, 3, 6, 10) are possibly corpses, the others being possible moults. Two have bilateral swellings, six have swellings on the left side and three on the right. All swellings except that of the third are reasonably well advanced; on that carapace a small swelling occupies the extreme anterior 'corner' of the branchial region, indicative of possible infestation of the crab at a later stage of life.

Carter's specimens from the Cambridge Greensand are augmented by ten carapaces in the Natural History Museum, London. Of these, two have a left swelling and both are considered to be moults (Pl. 1, Figs. 13, 17). Among those with right swellings, a corpse (I 3695; Pl. 1, Fig. 12), has the largest swelling among the specimens seen, but unfortunately, pre-fossil fractures on the left

side impair contrast of the sides. Carapace In 29883 is of a corpse, whereas carapace 39369, more or less equal in size, is a moult (Pl. 1, Figs. 13, 15). The swellings in all but one carapace are typically sub-spherical; that of 29797 (Pl. 1, Fig. 16), however, has a ridge parallel to the branchiocardiac furrow similar to the one seen on the carapace of *Necrocarcinus labeschei* mentioned above.

From evidence accrued it is apparent that the majority of fatalities among *N. stokesii* s.l. occurred among individuals that were less than half-grown.

Also among the raninids, a carapace of a *Cretacorantina testacea* (Rathbun, 1926), from the Coon Creek member, Ripley Formation of Union County, Mississippi, has a typical swelling on the left side (pers. comm., G. A. Bishop).

Infested carapaces of *Macroacaena rosenkrantzi* (Collins & Rasmussen, 1992) from the Maastrichtian of West Greenland, (Pl. 13, Figs. 5–7) that promoted Wienberg's study of parasitism in crabs range in size from 18 mm–36 mm in length (from posterior margin to base of rostrum). Strangely, the contemporary *Macroacaena succedania* (Collins & Rasmussen, 1992), was, apparently, not affected.

A large right-hand swelling on *Torynomma australis* Feldmann *et al.*, 1993, (BMNH BAS In.2422) (Pl. 3, Fig. 4) (Campanian of Antarctica) was considered by those authors probably to have been caused by a bopyrid. Later in 1993, Feldmann attributed a proportionately large swelling in the right-hand branchial chamber of *Torynomma flemmingi* Glaessner, 1980 (Upper Cretaceous, New Zealand) to bopyric infestation. Feldmann (2003) gave a brief survey of parasitism in crabs (*sensu lato*) and noted (p. 114) that "all fossil occurrences of bopyrids are in galatheids, porcellanids, or in the so-called primitive crabs".

An extremely tumid swelling occupying the entire right branchial region of a *Withersella crepitans* Wright & Collins, 1972, was figured by Wright (1997, fig. 1) from the Aptian, Crackers Beds, Isle of Wight.

The only known infested oxyrhynch, *Mithacia libiniodes* Bell, 1858 (Rayner *et al.* in prep) from the London Clay (Ypresian) of Tankerton, Kent, has a large, regular swelling in the left branchial region.

When discussing Recent *Philyra*, Stebbing (1893, p. 128), noted that, "*Philyra pisum* de Haan, is said to be infested by a *Bopyrus*", concluding that, "the parasite referred to would no doubt stand under some other generic name". Two known fossil infestations of leucosiids are, *Philyra granulosa* Morris & Collins, 1991 (BMNH In.6106) (Pl. 3, Fig. 9), from the Miocene, Miri Formation, of Brunei, which has a massive left-side swelling, while that in *Philyra syndactyla* Ortmann, 1892, from the Middle Pleistocene Atsumi Group, Aichi Prefecture, Japan (Kobayashi *et al.*, 2008, in this volume), is on the right (Pl. 3, Fig. 10). In both instances the swelling occupies the entire branchial cavity.

In contrast to normally circular swellings, a *Gastrosacus wetzleri* von Meyer, 1851 (Pl. 3, Fig. 11), from the Tithonian of Moravia (BMNH In. 38256) has an irregular, reniform swelling occupying

the right side. Further examples of irregular swellings are provided by a large, but shallow swelling on the left side of a *Petrolithses magnus* Müller, 1984 (pl. 23, fig. 4), that slightly expands that side and noticeably emphasises the course of branchiocardiac furrow. A male corpse of *Portunus woodwardi* Morris & Collins, 1991 (Pl. 3, Fig. 13) from the Upper Miocene of Brunei, is unusual in that the massive swelling on the left side, “so strongly affected the natural development of the branchiostegal areas, as well as the dorsal region that all the anterolateral spines [on the left side] became completely atrophied and the lateral angle rounded” (*op cit* p. 8). This distortion contrasts sharply with the ‘normal’ swelling on the right side of *Charybdis* sp. (Karasawa and Nobuhara, 2008, in this volume) from the early Pliocene, Gusakube Formation, Okinawa Prefecture of Japan (Pl. 3, Fig. 18).

Schweitzer *et al.* (1999, fig. 3.6), drew attention to a carapace of *Xanthosia wintoni* Rathbun, 1935, from the upper Albian/Cenomanian of Texas, with an inflated area on the right side which was considered to be a bopyric infestation; this swelling caused considerable distortion to the lateral margin.

As well as occurrences in *Mecochirus rostratus* (Pl. 3, Fig. 18), noted above, a bopyriform swelling has been recorded in only five other macruran species. Hitherto, the earliest undisputed occurrence of decapod infestation was from the Oxfordian. However, the range is considerably extended to the Toarcian by a carapace of *Eryma* sp. Soergel in Böhm, 1913 (p. 622, pl. 24, fig. 9) (Pl. 3, Fig. 14), which was overlooked by Glaessner (1929), from the Toarcian of Jefbel Island, Indonesia. This carapace has a distinct reniform swelling (reminiscent of that seen in *Gastrosacus wetzleri*) on the right side characteristically close to, and parallel to the branchiocardiac furrow coincident with similar swellings in later forms and contrary to the normal development of the branchial region in other erymids.

The recording of a ‘distinct swelling’ on the right side of *Phlyctisoma granulum* Bell, 1863 (pl. 11, fig. 9) (= *Palastacus scaber* (Bell, 1863)), from the Upper Albian of England, was dispelled by Förster (1969) and rightly considered by Wienberg (on his list of infested species) as a concretion. In Woods (1930, pl. 23, figs. 9a, b), the ‘swelling’ has been erased. On the other hand, if Houša had erred in respect of figure numbers and intended to refer to Bell’s pl. 11, fig. 10, this specimen presents a very different aspect – one much more attributable to parasitic infestation. As figured, on the left side a ‘ridge’ bounds the anterior margin of the branchiocardiac furrow (which is wider than the right side); behind the furrow are three swellings increasing in size posteriorly in three distinct stages, apparently coincident with the 2nd–4th pleurobranch areas. We enter it as a provisional recording.

Woods (1929, p. 89), on drawing attention to a swelling on the carapace of a specimen (BM In 28219, Pl. 3, Fig. 15), of *Hoploparia dentata* (Rømer, 1841), from the Speeton Clay (Hauterivian), of Speeton, Yorkshire, remarked that, “the branchial region on the right side is much swollen as if infested with *Bopyrus* ...” as, indeed it is; the ‘regular’-shaped swelling occupies

practically the whole branchial region on that side.

A young *Hoploparia gammaroides* (McCoy, 1849) (Rayner Coll.) from the London Clay of Tankerton, Kent, has a massive, regular swelling on the right side causing that side of the carapace to inflate by about one third of its radius. Although split along the dorsal midline, there is little or no disturbance in the juxtaposition of the sides, as generally observed among moults, and the split may be attributed to pre-fossil compression-fracturing of a corpse (Pl. 3, Fig. 16).

In contrast, a moult of a juvenile *Hoploparia trigeri* (Van Straelen, 1936) (Pl. 3, Fig. 17) from the Cenomanian of Le Mans, France, in the Natural History Museum, Le Mans (Regt. No. N2003-01-3785), has a low, noticeably irregular swelling in the left branchial region, commencing with a rounded ‘ridge’ parallel to the branchiocardiac furrow. Whether or not the infested side influenced the lobster to lay on the right side to moult is open to conjecture.

Nowadays, it appears to be the trend to refer to all branchial swellings in fossil crabs to bopyrid origin. However, Houša (1963), and Wienberg (above) discussed a number of other epicaridean genera infesting recent decapods, and mentioned carapaces with other deformities. Being soft bodied, no skeletal evidence of various potential parasitic genera can be determined. It would seem, therefore, that a broader outlook leading to adoption of ‘bopyriform swellings’ should prevail.

With the upsurge of the description of new species and the growing awareness of pathological conditions among fossil decapods leading to re-examination of ‘old collections’, together with occurrences arising from subsequently collected material and newly described species, many other instances of bopyriform infestation have come to notice, and substantially increased the taxonomic diversity among species. It is inevitable that with subsequent revision of individual species, or familial groups (*e.g.*, Wehner, 1988) a number of synonymies among considered-established species has introduced unfamiliar taxa. See Table 2.

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Table 2. Fossil decapods with bopyriform swellings. The first author indicates the earliest known recognition of infestation, subsequent recordings follow; synonyms and/or misnomers, preceded by authors, are enclosed in { }.

			left	Sides right	both
<i>Gastrosacus latirostris</i> Beurlen, 1929	Oxfordian,	France	x	x	x
Beurlen, 1929; Houša; 1963, Förster, 1969;	Rasmussen MS				
<i>Gastrosacus wetzleri</i> von Meyer, 1851	Portlandian,	Germany	x	x	
	Kimmeridgian,	France			
	Tithonian,	Czechoslovakia			
Quenstedt, 1858; Houša, 1963; Förster, 1969; Rasmussen MS					
<i>Gastrosacus meyeri</i> (Moericke, 1889)	Tithonian,	Austria	x	x	
{Bachmeyer, 1948 <i>Galatheites meyeri</i> }	Rasmussen MS				
<i>Galathea weinfurteri</i> Bachmeyer, 1950	Miocene,	Hungary	x		
Müller, 1984					
<i>Galatheites zitteli</i> (Moericke, 1889)	Tithonian,	Czechoslovakia, Austria	x	x	
{Remeš, 1921, 1923, <i>Galathea antiqua</i> ; Houša, 1963, <i>Galathietes antiquus</i> ;					
Rasmussen MS <i>Gastrosachus zitteli</i> and <i>Gastrosacus antiquus</i> }					
Houša, 1963, Förster, 1969					
<i>Mesogalathea striata</i> (Remeš, 1895)	Tithonian,	Czechoslovakia, Austria	x	x	
{Remeš, 1921, 1923, <i>Galathea striata</i> }	Houša, 1963, Förster, 1969, Glaessner, 1969,				
Rasmussen MS					
<i>Paragalathea verrucosa</i> (Moericke, 1889)	Tithonian,	Czechoslovakia	x	x	
{Blaschke, 1911, ' <i>Galathea</i> ' <i>verrucosa</i> ; Förster, 1969, <i>Galatheites verrucosus</i> }					
<i>Protomunida munidoides</i> (Segeberg, 1900)	Danian,	Denmark		x	
{Rasmussen MS <i>Munida</i> }					
<i>Petrolisthes magnus</i> Müller, 1984	Miocene,	Hungary	x		
Müller, 1984					
<i>Pisidia</i> cf. <i>kokai</i> (Müller, 1984)	Miocene,	Hungary	x		
Müller, 1984					
<i>Cyclothyreus latus</i> Moericke, 1889	Tithonian,	Czechoslovakia	no data recorded		
{Förster, 1969 <i>Prosopon latum</i> }					
<i>Cyclothyreus reussi</i> (Gemmellaro, 1869)	Tithonian,	Czechoslovakia, Austria, Sicily	x	x	
{Remeš, 1921, 1923; Houša, 1963; Rasmussen MS <i>Cyclothyreus strambergensis</i> ;					
Bachmeyer, 1948, <i>Cycloprosopon reussi</i> ; Förster, 1969, <i>Prosopon tithonotum</i>					
Gemmellaro) Förster, 1969					
<i>Longodromites excisus</i> (von Meyer, 1857)	Tithonian,	Czechoslovakia	x		
{Houša, 1963, Förster, 1969; Rasmussen MS, <i>Nodoprosopon ovale</i> (Moericke,					
1889)} Wehner, 1988	Oxfordian,	Germany		x	
<i>Nodoprosopon heydeni</i> von Meyer, 1860	Oxfordian,	Poland	x		
Radwanski, 1972, Rasmussen MS					
<i>Nodoprosopon mirum</i> (Morricke, 1889)	Tithonian,	Germany	x		
Wehner, 1988					
<i>Nodoprosopon ornatum</i> (von Meyer, 1860)	Tithonian,	Germany		x	
Wehner, 1988					
<i>Nodoprosopon spinosum</i> (von Meyer, 1842)	Tithonian,	Germany	x		
Förster, 1969	Oxfordian,	France			
<i>Pithonoton bidentatum</i> (Reuss, 1858)	Tithonian,	Czechoslovakia	x	x	
{Reuss, 1858; Remeš, 1921, 1923; Houša, 1963; Förster, 1969, <i>Goniodromites</i>					
<i>bidentatum</i> ; Rasmussen MS <i>P. (G.) bidentatum</i> ; <i>P. (G.) polyodon</i> Reuss, 1859;					
Förster, 1969; Rasmussen MS; Remeš, 1921, <i>Prosopon complanatum</i>					
von Meyer, 1860, <i>P. complanatifforme</i> ; Moericke, 1889, <i>P. polyodon</i> ;					
Rasmussen MS <i>Pithonoton complanatifforme</i> }					
<i>Pithonoton globosum</i> (Remeš, 1895)	Tithonian,	Czechoslovakia	x	x	
{Remeš, 1921, 1923; Houša, 1963 <i>Goniodromites globosum</i> }	Rasmussen MS				
<i>Pithonoton katholickyi</i> (Remeš, 1895)	Tithonian,	Czechoslovakia		x	
{Remeš, 1921, 1923 <i>Prosopon katholickyi</i> ; Houša 1963, Förster, 1969, Rasmussen MS					
<i>Nodoprosopon katholickyi</i> }					
<i>Pithonoton marginatum</i> von Meyer, 1842	Tithonian,	Czechoslovakia		x	
Houša, 1963; Förster, 1969, Glaessner, 1969, Rasmussen MS;					
Radwanski, 1972	Oxfordian	Poland			
<i>Pithonoton rostratum</i> (von Meyer, 1840)	Oxfordian,	Poland	x		
Radwanski, 1972					

<i>Prosopon aculeatum</i> von Meyer, 1860 {Quenstedt, 1858, <i>Gastrosacus wetzleri</i> Glaessner, 1969}	Tithonian,	Germany	no data recorded		
<i>Palaeodromites octodentatus</i> (Milne Edwards, 1865) { <i>Xantho aggazzi</i> Van Straelen, 1928; Förster, 1969, <i>Cyphonotus octodentatus</i> Rasmussen MS}	Hauterivian,	France		x	
<i>Palaeodromilites oxythyriiformis</i> (Gemmellaro, 1870) {Remeš, 1921, 1923, <i>Prosopon oxythyriiforme</i> ; Houša, 1963, <i>Cyphonotus oxythyriiformis</i> } Förster, 1969	Tithonian,	Czechoslovakia	x		x
<i>Hoplitocarcinus atlanticus</i> (Roberts, 1962) {Bishop, 1986, <i>Homolopsis atlantica</i> }	Camapnian,	USA			x
<i>Withersella crepitans</i> Wright & Collins, 1972 Wright, 1997	Aptian,	Isle of Wight			x
<i>Torynomma flemmingi</i> Glaessner, 1980 Feldmann, 1993	Cretaceous,	New Zealand			x
<i>Torynomma australis</i> Feldmann <i>et al.</i> , 1993 Feldmann <i>et al.</i> , 1993	Cretaceous,	Antarctica			x
<i>Cretacorantina testacea</i> (Rathbun) G. A. Bishop, pers. comm.	Cretaceous,	USA.	x		
<i>Notopocorystes s. stokesii</i> (Mantell, 1844) {McCoy, 1854, ' <i>Notopocorystes mantelli</i> '; Bell, 1863, <i>Palaeocorystes stokesi</i> } Förster, 1969	Albian,	England	x	x	x
<i>Notopocorystes s. serotinus</i> Wright & Collins, 1972 Herein	Albian,	England	x	x	x
<i>Eucorystes carteri</i> (McCoy, 1854) Van Straelen, 1925	Albian,	England	no data recorded		
<i>Macroacaena rosenkrantzi</i> (Collins & Rasmussen, 1992) {Rasmussen MS <i>Acantharanina</i> sp.; Collins & Rasmussen, 1991, <i>Lyreidus rosenkrantzi</i> }	Maastrichtian,	W. Greenland	x		x
<i>Notosceles bournei</i> Rathbun, 1928 Rathbun, 1928; Rasmussen MS	Lower Palaeocene,	Texas			x
<i>Raninoides ovalis</i> Rathbun, 1935 Rathbun, 1935; Rasmussen MS	Lower Palaeocene,	Alabama			x
<i>Xanthosia wintoni</i> Rathbun, 1935 Schweitzer Hopkins <i>et al.</i> , 1999	Albian/Cenomanian,	Texas			x
<i>Hepatus lineatinus</i> Collins & Todd, 2005 Collins & Todd <i>in</i> Todd & Collins, 2005	Miocene	Panama	x		
<i>Necrocarcinus labeschii</i> (Deslongchamps, 1835) Carter, 1898	Upper Albian,	England		x	x
<i>Charybdis</i> sp. Karasawa & Nobuhara, 2008	Pliocene,	Japan			x
<i>Portunus woodwardi</i> Morris & Collins, 1991 Morris & Collins, 1991	Miocene,	Brunei	x		
<i>Philyra granulosa</i> Morris & Collins, 1991 Morris & Collins, 1991	Miocene,	Brunei	x		
<i>Philyra syndactyla</i> Ortmann, 1892 Kobayashi <i>et al.</i> , 2008	Pleistocene,	Japan			x
<i>Mecochirus rostratus</i> Collins & Rasmussen, 1992 Collins & Rasmussen, 1992	Maastrichtian,	W. Greenland	x		
<i>Eryma</i> sp. Soergel <i>in</i> Böhm, 1913 Herein	Toarcian,	Jefbie Island			x
<i>Hoploparia dentata</i> (Rœmer, 1841) Woods, 1929	Hauterivian,	England			x
<i>Hoploparia gammaroides</i> Bell, 1858 Herein	Eocene,	England			x
<i>Hoploparia trigeri</i> (Van Straelen, 1936) Breton & Collins, 2007	Cenomanian,	France	x		
? <i>Palastacus scaber</i> (Bell, 1863) Herein	Albian,	England			x
<i>non Phlyctisoma granulatum</i> Bell, 1863 {Houša, 1963; Förster 1969 <i>Palastacus scaber</i> (Bell, 1803); Bell, 1863, Rasmussen MS, <i>Phlyctisoma granulatum</i> ; Glaessner, 1969, <i>Phlyctisoma</i> }	Albian,	England	x		

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Plate 1

Figs. 1–8. *Notopocorystes stokesii* (Mantell). **1–3**, Plaster casts of infested carapaces from the Lower Albian raulinianus Zone, Bully, le Havre, France (Le Havre Museum, 7832, 7692, 7686): **4**, BMNH I 364, ? Moults, Gault (Middle Albian) ?subzone, Folkestone, Kent: **5a–c**. Bilateral swellings on a male corpse (BMNH 31278) Gault ?Diploceras cristatum Subzone, Folkstone, Kent: **6**, BMNH I 3072, ?Moults, Gault (Middle Albian) ?subzone, Folkestone, Kent: **7 & 8**, Moults with bilateral swellings (BMNH 604494, In 30047) Gault, ? Subzone, Folkestone, Kent.

Figs. 9–18. *Notopocorystes stokesii serotinus* Wright & Collins. Cambridge Greensand (any one of numerous small, short-lived exposures dug for phosphate) Cambridgeshire, in the Department of Palaeontology, Natural History Museum, London. **9**, In 29795, corpse: **10**, In 29798, moult: **11**, In 29800, ?corpse, a small, ovate swelling: **12**, I 3695, corpse-largest swelling seen, the carapace has prefossil fractures, distorting left side, so true proportions of swelling are impaired: **13**, 39369, moult: **14**, In 29796, moult retaining elements of female abdomen. **15**, In 29883, corpse: **16**, In 29797, moult - ridge developed similar to that seen on *Necrocarinus labeschi*: **17** 29801, moult: **17**, 29799, ?corpse: **18**, 44312, moult.

Bar scale equals 10 mm

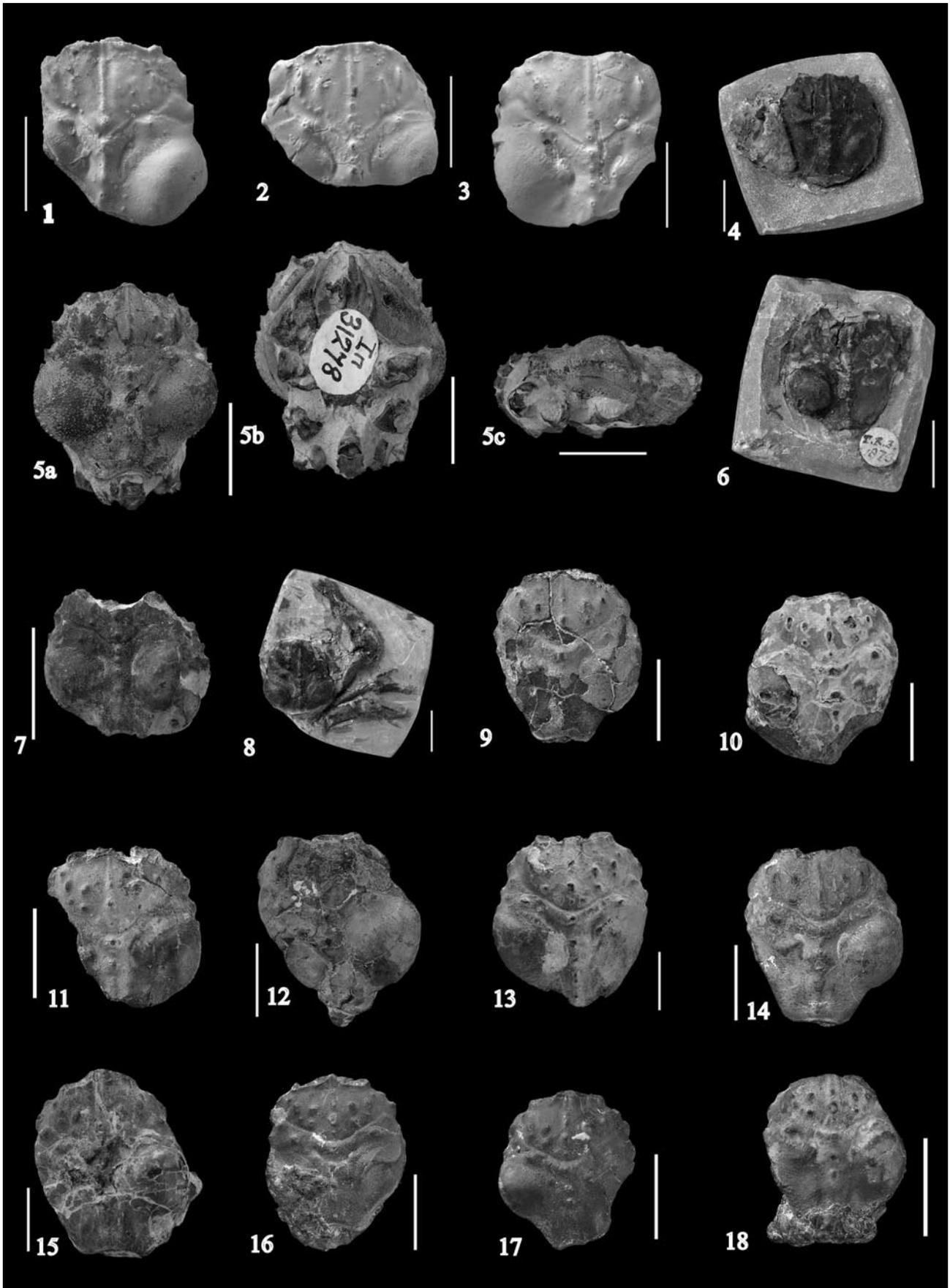


Plate 2

Notopocorystes stokesii serotinus Wright & Collins. Cambridge Greensand (any one of numerous small, short-lived exposures dug, for phosphate) Cambridgeshire. A historic Tablet of specimens in J. Carter's Collection, Sedgwick Museum, Cambridge. B22952–22962 – from left to right: **1**, ? moult: **2**, ? corpse: **3**, ?corpse, a small swelling occupying extreme upper 'corner' of left branchial region: **4**, status indeterminable: **6**, ?corpse: **7**, ?moult: **8**, status indeterminable: **9**, ? moult: **10**, ?corpse: **11**, ?moult.

Bar scale equals 20 mm.

Carter Collection.



With branchial parasite

Genus Palaeocorystes
 Species Stokesii. (Mantell)
 Locality Cambridge. B22952-62
 Rock Cambridge Greensand.

—————
 20 mm

Plate 3

- Fig. 1. *Hoplitocarcinus atlanticus* (Roberts) , Late Cretaceous, Merchantville Formation, Delaware, USA, (G.A. Bishop Coll.) , with a right-side swelling.
- Fig. 2. *Hepatus lineatinus* Collins & Todd, (BMNH PI IC440), Middle Miocene, Panama, with a left-side swelling.
- Fig. 3. *Protomunida munidoides* (Segeberg), MGUH 24358, Paleocene Middle Danian, Fakse, Denmark, with a left-side swelling.
- Fig. 4. *Torynomma australis* Feldmann *et al.*, (BMNH BAS In.2422), Campanian, Antarctica, with a right-side swelling.
- Figs. 5–7. *Macroacaena rosenkrantzi* (Collins & Rasmussen), Maastrichtian, Nuussuaq, W. Greenland, (MGUH 28740–28741–28742) with swellings on left, right and both sides.
- Fig. 8. *Withersella crepitans* (Wright & Collins), Cretaceous, Lower Greensand, Isle of Wight, England, (BMNH IC 5), with extraordinarily tumid swelling on right side.
- Fig. 9. *Philyra granulosa* Morris & Collins, (BMNH In.6106), Miocene, Miri Formation of Brunei, with a left-side swelling.
- Fig. 10. *Philyra syndactyla* Ortmann, Pleistocene, Atsumi Group, Aichi Prefecture, Japan, (Kobayashi Coll.), with a right-hand swelling.
- Fig. 11. *Gastrosacus wetzleri* von Meyer, (BMNH In 38256), Tithonian, Moravia, with an irregular, reniform swelling occupying the right side.
- Fig. 12. *Charybdis* sp., (MFM Coll.), early Pliocene, Okinawa Prefecture, Japan, with a right-hand swelling.
- Figs. 13a, b. *Portunus woodwardi* Morris & Collins, (BMNH In 61924), Miocene, Miri Formation of Brunei, with massive distortion of left side, dorsal and left lateral views.
- Fig. 14. *Eryma* sp. from the Toarcian of Jefbel Island, Indonesia, with a swelling on the right side, from the original illustration in Soergel, *in* Böhm, 1913, depositry unknown).
- Fig. 15. *Hoploparia dentata* Roemer, (BMNH 28219), Hauterivian, Speeton Clay, Speeton, Yorkshire, with a right-side swelling.
- Fig. 16. Plaster cast of *Hoploparia gammaroides* (McCoy), Lower Eocene London Clay (Ypresian), Tankerton, Kent, (D. Rayner, Kent, Coll). Dorsal view of a corpse of a young individual with a massive regular swelling distorting carapace to about one third of its radius.
- Fig. 17. Plaster cast of *Hoploparia trigeri* (Van Straelen), Cenomanian Couche a Crustacés, Natural History Museum, Le Mans, 2003-01-3785, with a moderate swelling commencing with a rounded ridge parallel with the branchiocardiac furrow.
- Fig. 18. *Mecochirus rostratus* Collins & Rasmussen, (MGUH 28743), Maastrichtian, Nuussuaq, W. Greenland, left lateral view of a swelling below the branchiocardiac furrow.

Bar scale equals : 10 mm except for fig. 3: 5 mm

Specimens prefixed by BMNH are in the Natural History Museum London; MGUH are in the Geological Museum, Copenhagen; MFM is in the Mizunami Fossil Museum.

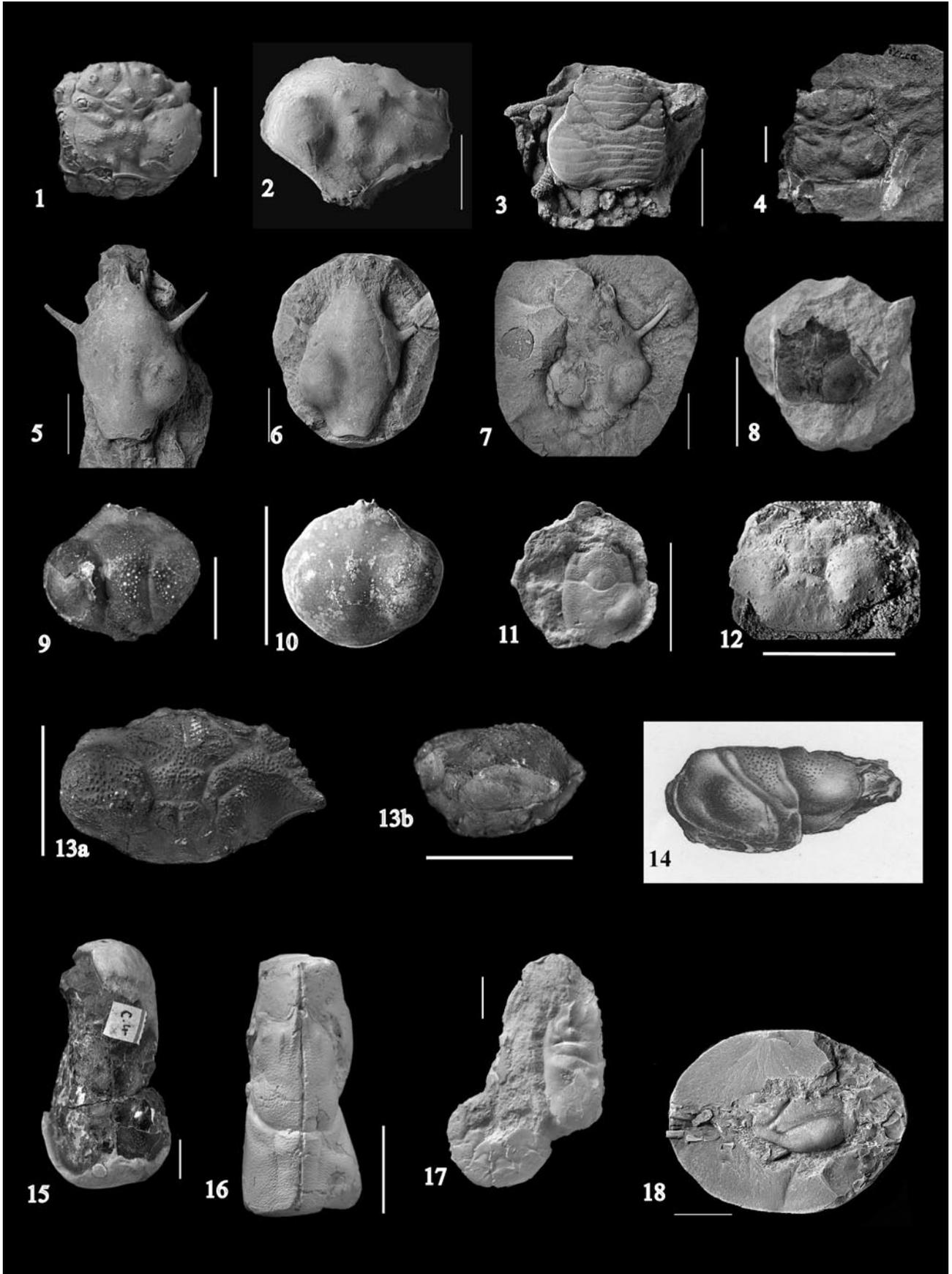


Plate 4

Necrocarinus labescheii (Deslongchamps). Cretaceous Uppermost Albian, Cambridge Greensand (any one of numerous small, short-lived exposures dug for phosphate) Cambridgeshire, England. A historic Tablet of specimens in J. Carter's Collection, Sedgwick Museum, Cambridge. **B23184–B23187** – all moults. Left to right, **B23184**, a large swelling commencing with a rounded ridge more or less parallel with the branchiocardiac furrow: **B23185**, swelling represented by little more than peripheral rim: **B23186** & **B23187** with moderate to large regular swellings.

Bar scale equals 20 mm

Plate 5

A historic Tablet of Van Straelen's record of *Palaeodromites octodentatus* (Milne Edwards), Cretaceous Hauterivian of Yonne, France. No. 3651, Muséum d'Auxerre, France.

Bar scale equals 10 mm

HPlate 4

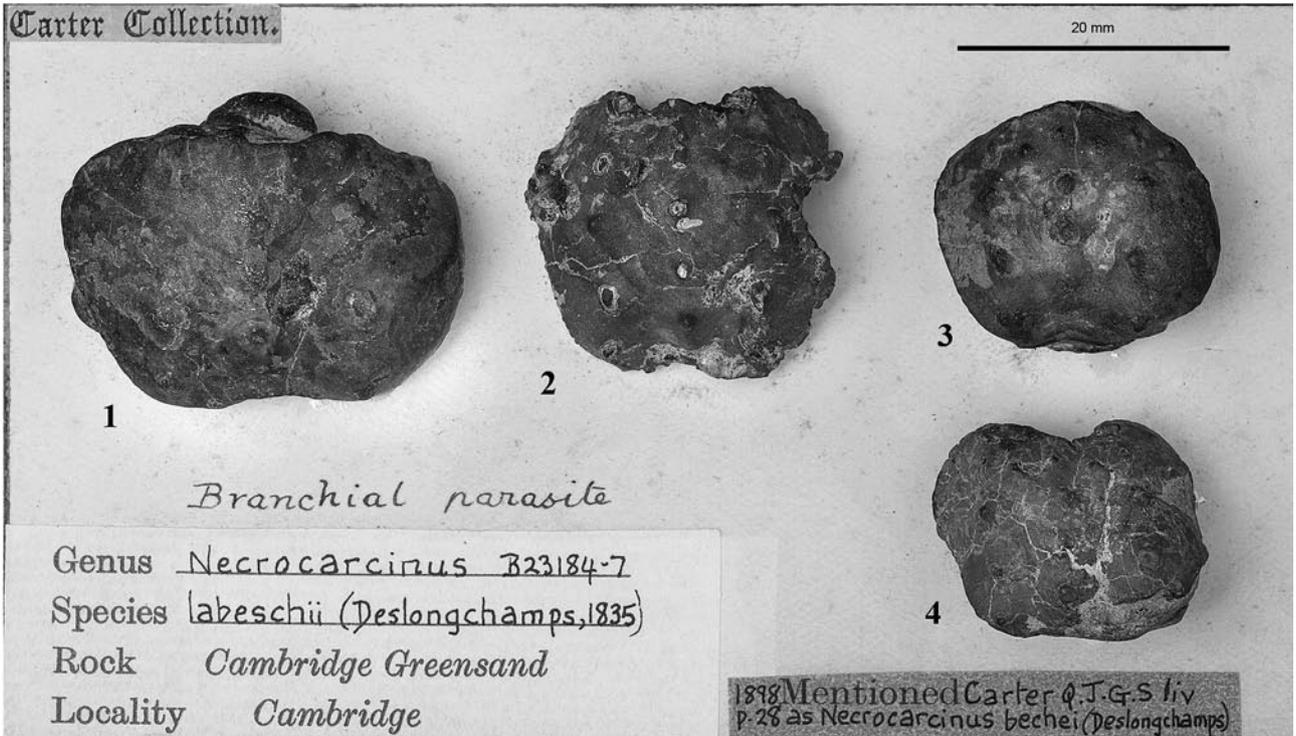


Plate 5

