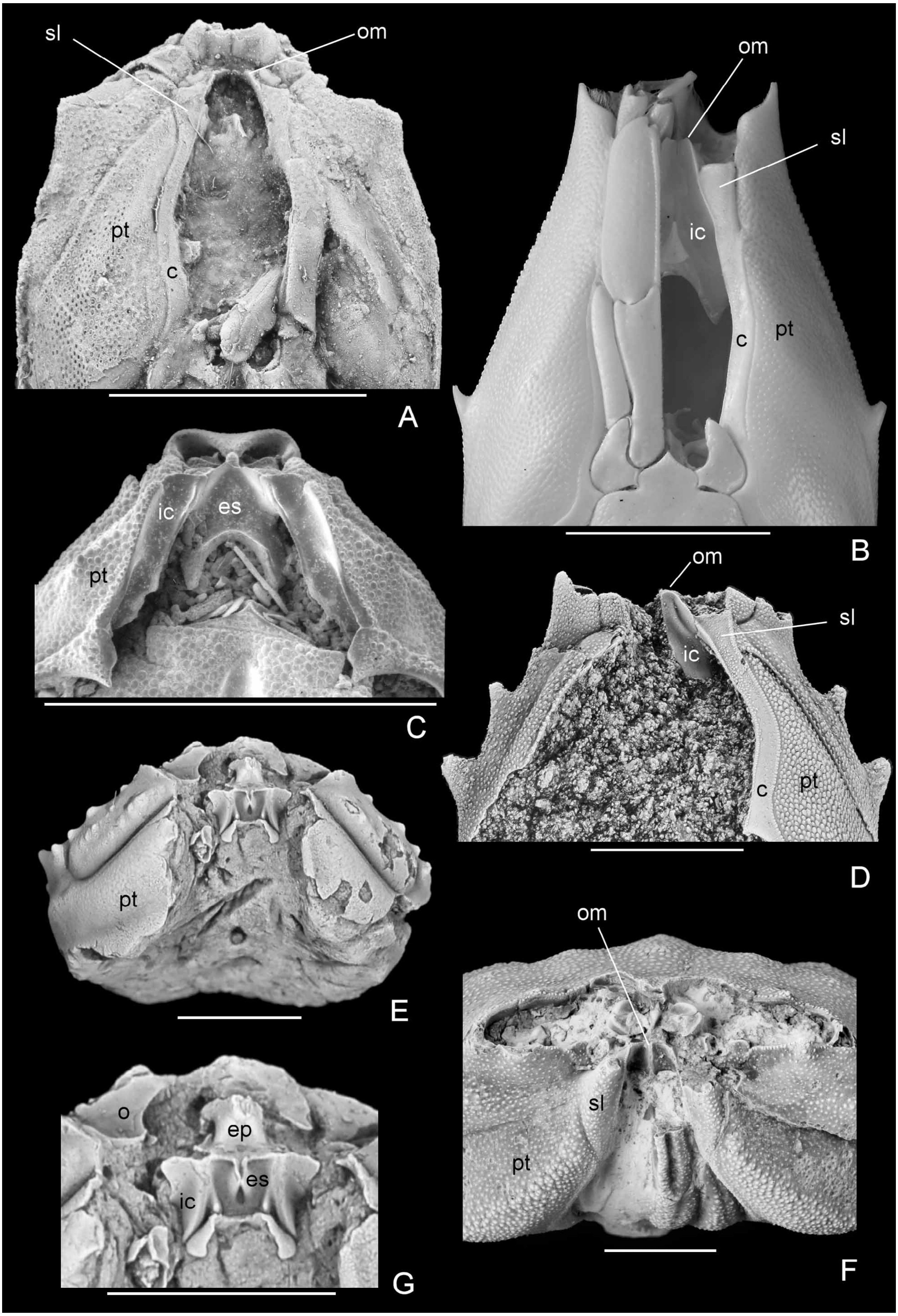
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FIGURE 50. Oxystomian condition in various fossil and extant brachyurans; A, *Marylyreidus punctatus* (Rathbun, 1935b) **n. comb.** (Lyreididae, Marylyreidinae **n. subfam.**), MGSB75297 (*ex* Àlex Ossó-Morales Collection; indeterminate sex); upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County, Texas (U.S.A); ventral view of buccal region; B, *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), MAB k. 2914 (male), Recent, Philippines; ventral view of buccal region; C, *Ebalia cranchii* Leach, 1817 (Leucosioidea, Leucosiidae) (S. Mermuijs Collection, unregistered), Pliocene, Kallo (Antwerpen, northwestern Belgium); ventral view of buccal region; D, *Raninella elongata* A. Milne Edwards, 1862 (Raninidae, Ranininae), MNHN R03934 (**paralectotype**), upper Cenomanian, Le Mans (northwestern France); ventral view of buccal region; E, G, *Necrocarcinus labeschii* (J.-A. [Eudes-]Deslongchamps, 1835) (Necrocarcinidae), MAB k. 2904, Albian, Escalles (Calais, northern France); oblique frontal view showing buccal region and detail of frontal region; F, *Campylostoma matutiforme* Bell, 1858 (Cenomanocarcinidae), NHM In 32654/32655 (indeterminate sex), lower Eocene (Ypresian), Herne Bay (Kent, southern England); detail of frontal view. **c,** buccal collar of pterygostome; **ep,** epistome; **es,** endostome; **ic,** inhalant channel; **o,** orbit; **om,** oxystomian mouth; **pt,** pterygostome; **sl,** subantennary lobe of pterygostome. Scale bars: 5mm.

In Raninoidea (with the exception of Notopodinae, see below) the basal articles of the antennules and antennae are expanded and form the floor of the orbital cavities. The shape of the antennae and antennules matches and coincides with each other; their inner (medial) surfaces are excavated and together they form a passage for the exhalant waterflow. As such they form an extension of the oxystomian mouth (see below), bridging the distance between the tip of the oxystomian mouth and the sediment surface when buried. The tip of the mxp3 may just overlap the antennae to close the circuit. In addition to acting together as a funnel, the antennae may be separated from the antennules and admedial waterways between the antennules and antennae are created. Action of the mxp2 scaphognathite creates an inhalant current through this artificial passage. Such a mechanism is seen in Lyreididae, where both exhalant and inhalant currents are regulated frontally. Lyreidids lack Milne-Edwards openings as well as posterior inhalant openings; they have no modifications to form an exostegal channel between the pterygostome and chelipeds. The Notopodinae is another group that lacks inhalant openings at the base of the chelipeds or below the posterior carapace margin. Here the articles of the flagellae of the antennae are cylindrical with many interlocking setae at the medial surfaces, together forming a straw (see Bourne 1922b: pl. 7, fig. 56). The precise performance of this modification for the inhalant current needs to be studied in more detail. The basal elements of the antennae are preserved in well-preserved specimens of *Notopus mulleri* from the Maastrichtian type area (Late Cretaceous; southeastern Netherlands, northeastern Belgium), their geometry being homologous to their extant congeners.

All raninoids show the oxystomian condition. The endostome is elongated, overlapping the epistome and proepistome, and forms the 'oxystomian mouth' under the front. Here, the exhalant channel is formed thanks to expansion and modification of both the exopodite and endopodite of the mxp1; the long exopodite, devoid of flagellum, is the most effective agent in forming the operculiform floor of the anterior part of the deeply excavated sides of the endostome. Laterally, the deeply excavated channels are fused to the pterygostome. The oxystomian condition has so far not been assessed in any detail in the fossil record, being often not exposed as a result of insufficient preparation. One specimen of *Raninella elongata*, from the upper Cenomanian of Le Mans (northern France) clearly shows the forwardly elongated endostome, expanded in deep exhalant channels. In another lyreidid, *Macroacaena johnsoni*, the exhalant channels are obvious in one of the paratypes (Waugh *et al*. 2009: fig. 11.1, right (ventral) view).

The contribution of the chelipeds in burying is very limited (Faulkes 2006: 147), their role in forming a respiratory channel being a reason. Bourne (1922b: 58, 59) suggested that the spines on the lower cheliped margin of *Ranina* had a raking function. In addition, it may also be possible that these spines functioned as surface extension of the exostegal channel. Notopodines notably have chelae atypical of the Raninoidea, with tall palm, smooth lower margin, and a diminutive fixed finger. This group likely buries into a different substrate, and their respiratory system is different: they do not depend on an exostegal channel. Symethines have claws that are atypical of Raninoidea, the palm being bulbous, with long, slender fingers having teeth only on prehensile margins, the complete structure resembling a pectinate claw. Such a claw is most probably modified for feeding, not for a respiratory function.

A 'hairy patch' can be found on the pterygostome, under the merus of the cheliped of most raninoids, extending posteriorly on the branchiostegite. The upper and lower margins of the cheliped merus may also have a line of dense setae. The exostegal waterway is laterally closed when the cheliped is pressed against the body, from the anterolateral margin up to the base of the cheliped. The inner surface of the merus is smooth and matches the opposing pterygostome, thus the cheliped may be moved while the exostegal waterway remains intact. The exostegal channel is also medially limited in *Ranina ranina*. The inner margin of the cheliped dactylus is lined with dense setae, which limits the exostegal waterway medially. This feature is found to have distinct variation within the species, and more study is called for to determine their precise function.

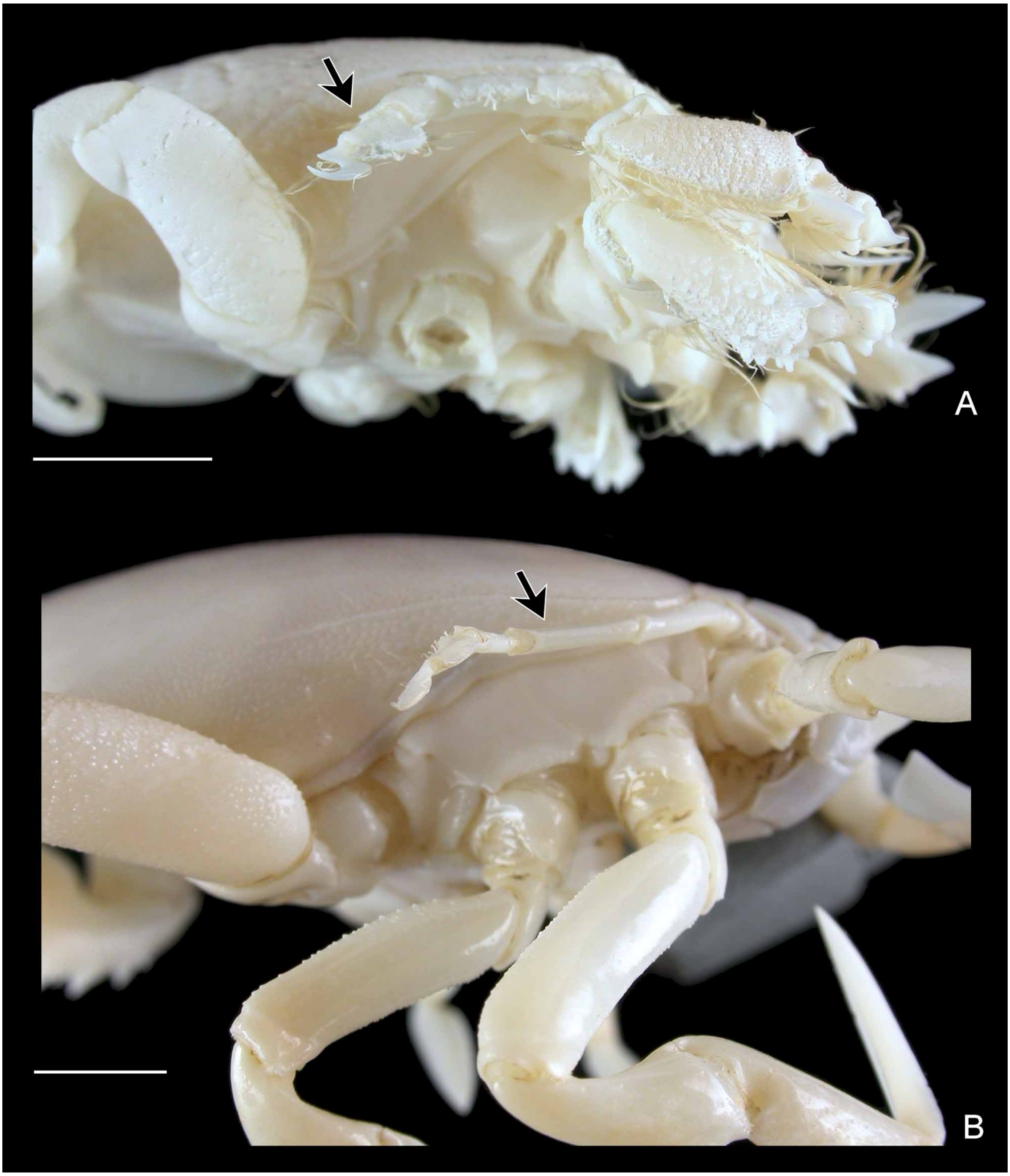

FIGURE 51. Orientation of P5 in Raninoidea; A, *Symethis corallica* Davie, 1989 (Raninidae, Symethinae), MNHN-B20795 (**holotype**, female), Coral Sea, Chesterfield Islands; B, *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), MNHN-B13364 (male). Arrows indicate filiform P5. (photographs by J.-F. Dejouannet) scale bars: 5mm.

In Lyreididae and Notopodinae, groups in which posterior respiratory openings are absent, the exposed pleurites 5–7 form a rather flat plate, not distinctly overhung by the branchiostegite. The low branchiostegite is in prolongation of the exposed pleurites. The exposed pleurites are excavated and concave in other Raninoidea. This region appears as a smooth, polished surface in all cases. The exposed pleurites are flat in Symethinae, but the low branchiostegite is not in prolongation, but rather overhangs the region. This excavated, lateral area acts together with the modified P5.

The P5 is reduced in most raninoids. Such a reduction is weak in Ranininae and Notopodinae (virtually absent in *Ranina*), the leg nearly reaching the size of other pereiopods. The P5 is rather long and strongly setose in all raninoids. The shape of the P5 articles is such that, when placed alongside the carapace, the P5 closely matches the posterolateral margin of the carapace, any gap closed by fringes of setae. The P5 thus forms the roof of the water-chamber enclosed between the preceding pereopods and the thoracic flanks formed by the excavated surface of the branchiostegite and exposed pleurites. Whereas the P2–P4 are the prime movers of sand, the P5 contributes little when burying (Faulkes 2006: 147). Their main function is apparently creating a lateral path for water to flow to the posterior respiratory openings. Implementation of this lateral water conduit is ‘by no means primitive but a definite specialisation’ (Bourne 1922b: 53).

Raninoids (except Lyreididae and Notopodinae) have acquired a new, posterior entrance to the branchial chamber in the form of inhalant openings situated between the tergite of the abdominal somite 1 and the P5 coxa. Števčić (2005: 26) used this feature to characterise Raninoidea: ‘supplementary paired inhalant opening between coxae of last pair of legs and terga of first abdominal segment’. Lyreidids and notopodines, however, do not possess such an opening, which may be replaced or completed by arrangements in the frontal region. Henri Milne Edwards (1837: 192, 193; atlas, pl. 21, fig. 2) was the first to observe this unique mechanism, which Bourne (1922b: 57) discussed at length stating:

> ‘*In the Raninidae, however, the arrangements differ from those usually observed in crabs. There is, in most of them, a pair of posterior respiratory orifices situated between the tergum of the first abdominal somite and the coxa of the last pair of pereiopods. When the abdomen is extended or only slightly flexed, water can pass freely into or out of these orifices, but they are pretty effectively closed when the abdomen is closely flexed under the thorax*’.

Implementation of the posterior respiratory opening is poorly understood in raninoids. Except for its function in the respiratory system, we may suspect that it is used as a temporary event during back-burrowing and, together with a reversed respiratory current, to spout water out of the posterior orifices to aid in ‘liquifying’ the substratum. Such hypothesis must be tested with live animals. Water reaches the posterior orifices through the lateral water-conduit, formed by the: 1) excavated exposed pleurites, 2) filiform P5 as the roof, and 3) remaining pereiopods and their setation as the outer barrier. The formation of this lateral water-conduit is ‘by no means primitive but a definite specialisation, and I have attributed it to the burrowing habits of the family’ (Bourne 1922b: 53). Water can flow posteriorly over the P5 coxa and enters underneath the first abdominal somite into this posterior branchial entrance (Figs. 52B; 53A–C). This entrance is created by outgrowths of pleurite 7 (laterally) and sternite 8 (medially), which leave a narrow opening close to the carapace, and so a new channel to the branchial chamber (Fig. 52A). This feature was studied in a single fossil specimen of *Raninoides glabra* (Woodward, 1871) (Raninoidinae). In this unusually preserved specimen, the carapace was eroded away, thus exposing the pleurites and sternites in dorsal view.

Little is known about the function of the spines on the frontal margin of raninoids. Members of Ranininae and Notopodinae may have distinct spines along a wide orbitofrontal margin, which is densely setose. When these spines break the surface of the sediment, water may be filtered through the setae, and drawn through the wide, deep orbital cavities towards the oxystomian mouth. The notopodine *Lianira* Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991, represented by three species in the Eocene of northern Italy, is characterised by distinctly projected, wide, spiniform orbital margins (Beschin *et al*. 1991: figs. 4, 5; pls. 1–4; Beschin *et al*. 2007: fig. 3, pl. 1, figs. 1–4; De Angeli & Beschin 2007: figs. 2.1–2.3), which may serve for such a function. The function of the orbitofrontal margin in respiration must be tested with live animals.

Sternite 4 is connected to the pterygostome in all raninoids; the Milne-Edwards openings are absent. The only exception is Marylyreidinae **n. subfam.** (Lyreididae), in which the mxp3 coxae are intercalated between the thoracic sternum and pterygostome (Fig. 25D, E), a primitive condition. The mxp3 coxa is flabelliform, and the Milne-Edwards openings were possibly present. *Marylyreidus* **n. gen.** shows an intermediate condition of the respiratory system, resembling the disposition seen in the Palaeocorystoidea.

Respiration in the Palaeocorystoidea. All Palaeocorystoidea show a large, flabelliform mxp3 coxa, which is intercalated between the thoracic sternum and pterygostome, and inserted anterior to the P1. A Milne-Edwards opening is present, contrary to the raninoid condition where this pre-cheliped inhalant opening is absent. It may thus be concluded that the respiratory mechanism must have functioned differently.

Several modifications to the respiratory system are discernible in the Palaeocorystoidea: modification of the carapace and chelipeds, pterygostome and branchiostegite; setation on antero-ventral regions; oxystomian condition of endostome and mxp3; modification of the antennae; and flabelliform mxp3 coxae.

The anterolateral margin of palaeocorystoids typically bears multiple, mostly spiniform teeth. The Cenomanocarcinidae and Necrocarcinidae, two groups considered basal within Palaeocorystoidea, have convex anterolateral margins with spiniform teeth and a narrow, clearly upraised orbitofrontal margin. The anterolateral teeth adjacent to the orbits are pointed almost anteriorly. In contrast to Necrocarcininae, Paranecrocarcininae have granular anterolateral margins without teeth or spines.

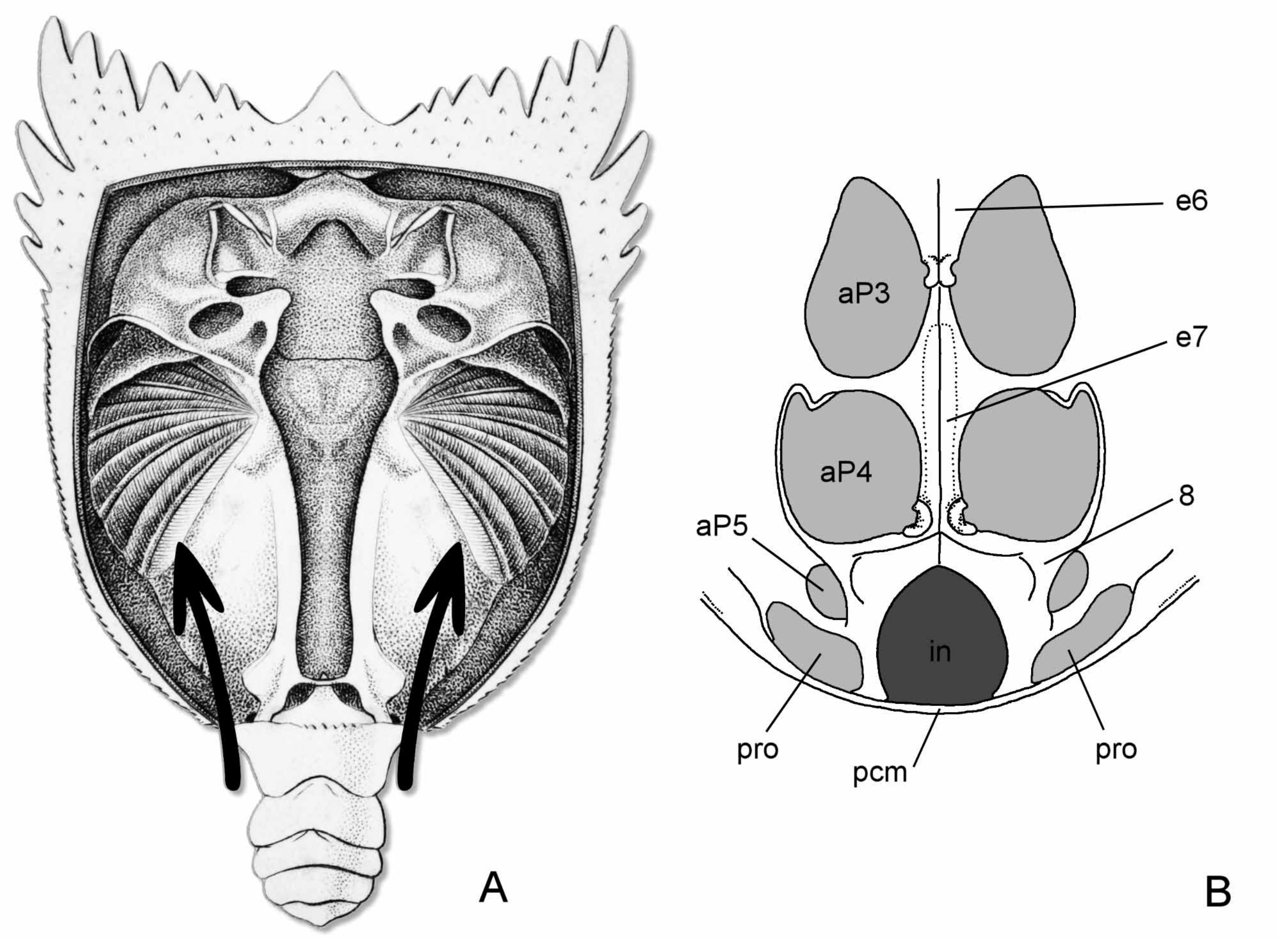

FIGURE 52. Posterior respiratory openings in selected raninids; A, *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), dorsal view, carapace partially removed to reveal branchial chambers (modified after H. Milne Edwards 1839: pl. 4, fig. 4); B, *Notopoides latus* Henderson, 1888 (Raninidae, Raninoidinae) (male), posterior thoracic sternites showing posterior respiratory opening (modified after Gordon 1966: fig. 2a). **8,** thoracic sternite 8; **aP3, aP4, aP5,** arthrodial cavities of P3, P4, P5; **e6, e7,** episternites 6, 7; **in,** intestinal canal; **pcm,** posterior carapace margin; **pro,** posterior respiratory opening.

Palaeocorystids have wide orbits, occupying the anterior margin of the carapace. The anterolateral margins are rather straight, with long, spiniform teeth. *Notopocorystes* has a slightly narrower orbitofrontal margin, here considered to be a basal character within Palaeocorystidae.

Orithopsids have a distinctly wide, straight, orbitofrontal margin, with long, flattened orbital spines, separated by deep, open notches. The lateral carapace margins are straight, the anterolateral margin being armed with long spines (see also Marangon & De Angeli 1997: fig. 2.1; Schweitzer *et al.* 2003a: figs. 14.1–14.3; Guinot *et al.* 2008: fig. 9e). The carapace structure closely resembles that of Palaeocorystidae.

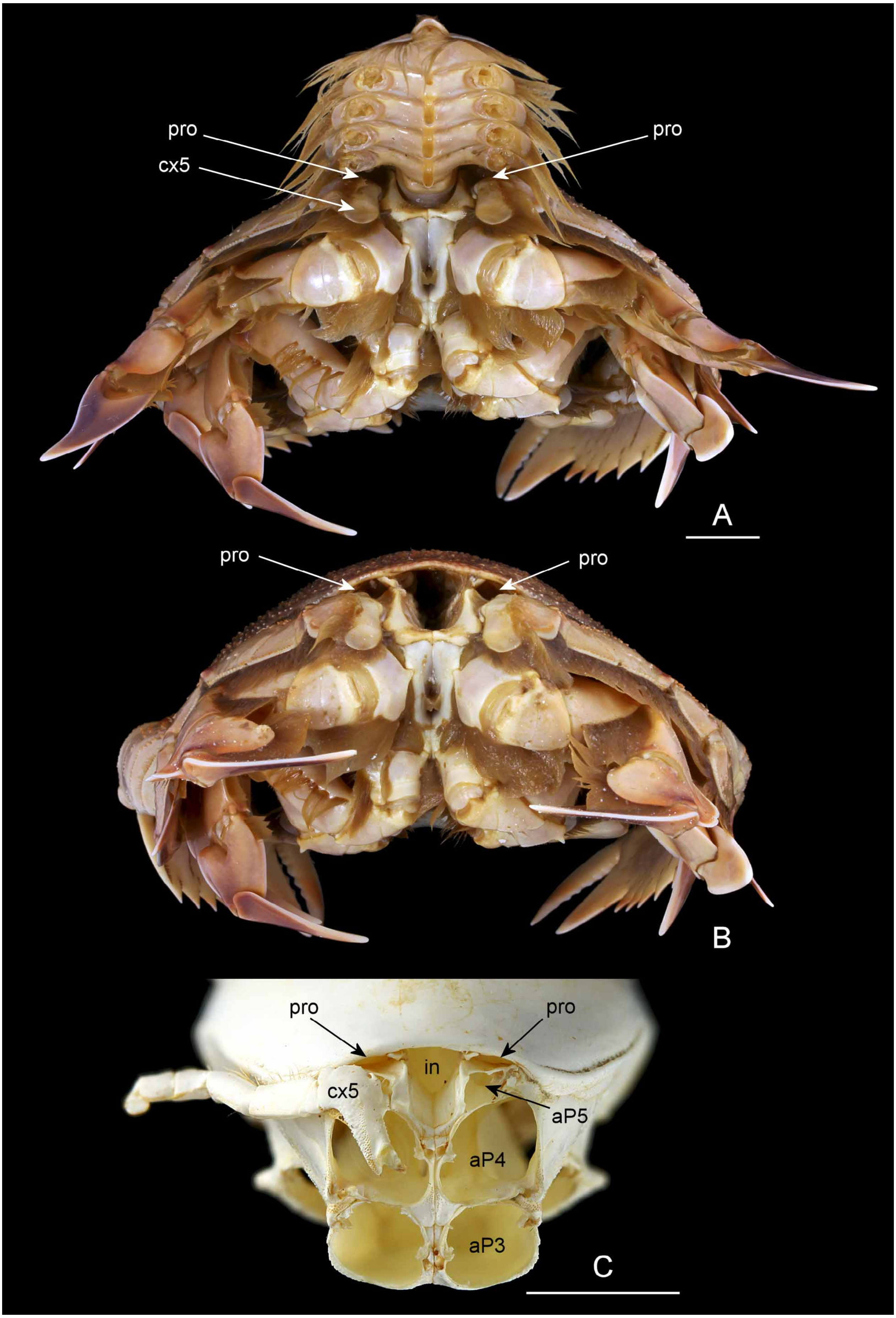
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FIGURE 53. Posterior respiratory openings in selected raninids; A, *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), NCB-RGM unregistered (female), Recent, Sulawesi, Indonesia; posterior view, abdomen pulled upwards to reveal posterior respiratory openings; B, same view, abdomen removed; C, *Raninoides bouvieri* Capart, 1951 (Raninidae, Raninoidinae), MAB k. 2919 (male), Recent, provenance unknown; posterior view showing posterior respiratory openings. **aP3, aP4,** arthrodial cavities of P3, P4; **cx5,** P5 coxa; **in,** intestinal canal; **pro,** posterior respiratory opening. Scale bars: A, B: 10mm; C: 5mm.

The Camarocarcinidae is characterised by having rather blunt lateral margins. The anterolateral carapace margin bears one spine in all members so far known (note that *Cretacocarcinus* Feldmann, Li & Schweitzer, 2008 is here transferred to Necrocarcinidae).

Different modifications of the chelae can be seen among palaeocorystoids. The upper margin of the palm of *Necrocarcinus* is strongly inclined inwards and bears four wide teeth (Jagt *et al*. 2010: fig. 4b), the lower margin being tuberculate. Paranecrocarcinines have chelipeds in which the upper margin bears triangular flattened teeth (Fig. 54A), similar to those seen in most calappids. The proximal part of the upper margin of the dactylus of *Paranecrocarcinus quadriscissus* (Noetling, 1881) bears several larger tubercles (Jagt *et al*. 2010: fig. 3e–g). All palaeocorystid claws examined (*Cretacoranina schloenbachi*, *Ferroranina dichrous* **n. comb.**, *Joeranina broderippii* **n. comb.,** and *Notopocorystes stokesii*) have spines on both upper and lower margins of the cheliped. The upper margin of the propodus of *N. stokesii* is slightly inclined and lined with four strong, triangular teeth. The proximal part of the upper margin of the dactylus bears strong, inwardly directed spines; the lower margin of the cheliped shows slender, evenly distributed spines (Fig. 54D, E).

Spinose upper and lower margins of chelipeds also characterise Cenomanocarcinidae (*Cenomanocarcinus vanstraeleni*, *Campylostoma matutiforme*) and Orithopsidae (*Cherpiocarcinus rostratus*; see Marangon & De Angeli 1997: fig. 2.2). The spines on the upper margin of the propodus are long and thin in both families. The chelae of *Camarocarcinus arnesoni* were described as 'the upper surface of the manus bears a row of tubercles and spinules on its inner margin' (Holland & Cvancara 1958: 501, text-fig. 2). The lower cheliped margin has small spines (Holland & Cvancara 1958: pl. 74, figs. 1–5; Feldmann *et al.* 2007: fig. 5.4). In addition to the upper and lower margins, the inner surfaces of the palaeocorystoid P1 merus, carpus and propodus are modified, being smooth and flat or concave, as a whole closely fitting the pterygostome. The condition has been verified here in Cenomanocarcinidae, Necrocarcinidae and Palaeocorystidae. Holland & Cvancara (1958: 501) described the chelae with, 'all surfaces granular and pitted except inner surface which is commonly quite polished.'

Garstang (1897a, b) explained in detail the function of the brachyuran anterolateral carapace spines in collaboration with spines on the upper margin of the cheliped. The chelipeds are held in close approximation to the body when individuals are buried. The flat or concave, 'polished' inner surface of the cheliped matches the altitude of the pterygostome, between which a narrow exostegal channel is formed. Water can flow between them in order to reach the Milne-Edwards openings and enter the branchial chamber. The orifice of this channel is formed between the anterolateral margin of the carapace and the upper margin of the propodus. This narrow opening is overhung by spines or teeth of the carapace and propodus as a coarse filtering mechanism to prevent larger sediment particles from entering the respiratory flow.

In addition to filtering off larger particles, Garstang (1897a: 399, 400) hypothesised that a strong epibranchial spine might be a mechanical solution to place the cheliped in exactly the right position for a respiratory function. A strongly developed anterolateral or epibranchial spine is present in camarocarcinids, cenomanocarcinids as well as in many raninoids. It is here assumed that in the Palaeocorystoidea the anterolateral carapace spines and the upper margin of the cheliped were functional within the respiratory process. Palaeocorystoids were likely shallow buriers because their anterolateral margins would need to have been in contact with the sediment to create the exostegal waterways. The shallow depth of burial may also indicate why nearly all palaeocorystoids have areolated, tuberculate carapaces; they gathered sediment on their anterior carapace, which was buried under a weak angle in the sediment. Many palaeocorystids (i.e., *Notopocorystes*, *Eucorystes*) and orithopsids (i.e., *Cherpiocarcinus, Orithopsis*) have anterior areolation or ornamentation. The trend towards a carapace without tuberculation or areolation, as documented for Palaeocorystidae, is interpreted as a progressive adaptation to a more sophisticated burying.

The respiratory adaptations in Necrocarcinidae and Cenomanocarcinidae are considered basal. The wide, straight orbitofrontal margin of Orithopsidae, with flattened orbital spines and deep open notches, may be involved in the respiratory system. A possible mechanism was to draw water through the orbital notches and through the wide orbital cavities into the exostegal channel.

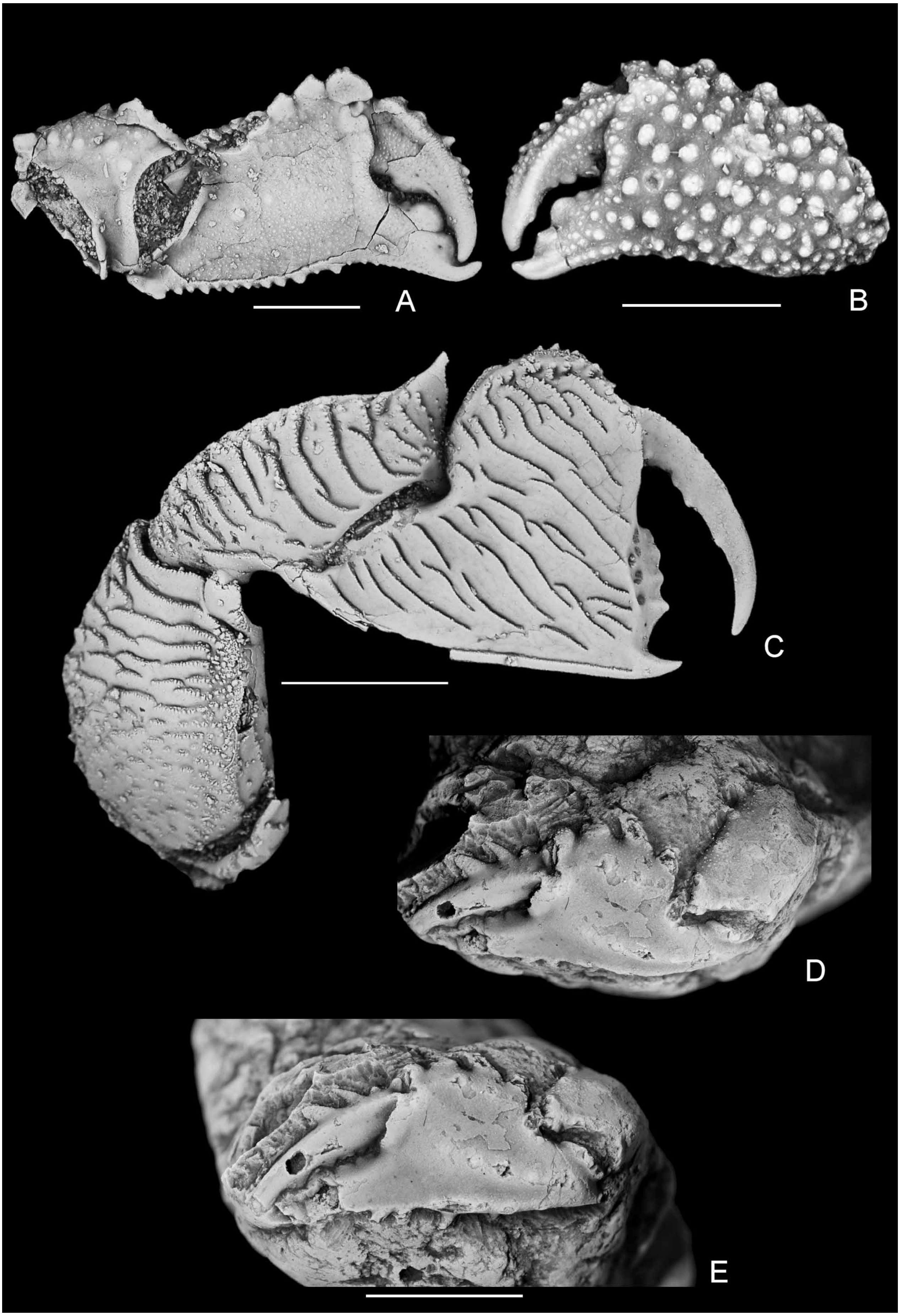
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FIGURE 54. Chelipeds of raninoidian crabs; A, B, *Paranecrocarcinus quadriscissus* (Noetling, 1881) (Necrocarcinidae, Paranecrocarcininae), upper Maastrichtian, Maastricht, the Netherlands, left chelae, NHMM JJ 6737 (A, inner view) and MAB k. 0720 (B, outer view); C, *Eumorphocorystes sculptus* van Binkhorst, 1857 (Raninidae, Notopodinae), MAB k. 2905 (right chela, outer view), upper Maastrichtian, Bemelen, the Netherlands; D, E, *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), IRScNB unregistered [Van Straelen Collection], left cheliped, upper Albian Cambridge Greensand, Cambridge (southern England), oblique dorsal view showing upper margin of propodus and dactylus and outer view showing spinose lower margin. Scale bars: 5mm.

The spinose anterolateral margin of Palaeocorystoidea, functional in respiration, contrasts with that of Raninoidea, in which one spine (rarely two) may be present, which more likely functioned in limiting cheliped flexion. The lateral carapace margin presents an obvious difference between Palaeocorystoidea and Raninoidea, which can be explained by modifications of the exostegal channel. A secondary loss of anterolateral spines thus occurred in Raninoidea as a result of a modification of the respiratory system. Nearly all raninoids also have non-areolated carapaces in order to deeply and rapidly penetrate the sediment. Surface structures are applied to prevent the animal being pulled out of the sediment (Schmalfuss 1978a, b; Savazzi 1981, 1982, 1985) rather than to gather sediment on the carapace to camouflage the shallowly buried body.

The palaeocorystoid pterygostome shows a constant condition morphology, the surface being tumid, a broad oblique groove separating two long, blunt crests, of which the outer (lateral) extends into the prominent subantennary lobe of the pterygostome. The inner blunt crest may be parallel to the outer crest, or they may diverge. The crest's surface is invariably granular, and the grooves may be smooth or having pits. It may be hypothesised that this constant arrangement is related to the exostegal waterway, thus the inhalant respiratory flow of water between the pterygostome and chelipeds. The crests on the pterygostome are parallel in Necrocarcinidae and Camarocarcinidae, the inner crest extending onto the branchiostegite. The crest becomes obsolete on the branchiostegite of *Necrocarcinus*, the surface between this crest and the pereiopods being flattened (see Wright & Collins 1972: pl. 11, fig. 8a, b), whereas the crest is more pronounced in *Cretacocarcinus*, the flat surface along the pereiopods being more obvious (see Feldmann *et al.* 2008: fig. 4.1); In *Camarocarcinus*, the inner crest is distinct and sharp, the surface between the crest and the pereiopods concave and excavated (Fig. 15C, D). This was described as a 'pterygostomian rim' by Holland & Cvancara (1958: 501) (see also under Camarocarcinidae).

This excavated surface on the branchiostegite may have facilitated the flow of water between the bases of the pereiopods and the branchiostegite in order to enter the branchial chambers through the inhalant openings at the bases of the pereiopods. Such endostegal system was regarded as 'primitive' by Garstang (1897b: 215).

Setal pits are observed on the mouthparts and pterygostome and frontal region in all palaeocorystoids, but the most distinct setation is found in Palaeocorystidae. In this family especially the mxp3 exopod, the flabelliform mxp3 coxa, along the broad buccal collar, the groove between the crests on the pterygostome and the basal elements (coxa, basis-ischium) of the P1 are covered with setal pits. The setation on the mxp3 coxa and the P1 coxa most likely served a filtering function; when these setae interlock in front of the Milne-Edwards opening they could have prevented particles from entering the branchial chamber. Such dense setation may indicate that fine particles, such as mud, must be filtered from the inhalant current (see also Garstang 1897b: 219). On the other hand, setation on the mxp3 exopod and in the depression along the broad buccal collar of the buccal frame, appears to be homologous to setation in these regions in extant raninids, serving to limit the exostegal waterway.

The endostome is preserved in several palaeocorystoids. The endostome of *Necrocarcinus* is clearly modified, being elongated, anteriorly projected and with the lateral sides forming deep channels (Fig. 50E, G). It is wide and excavated into two broad, concave surfaces in *Cenomanocarcinus vanstraeleni*. *Joeranina broderipii* **n. comb.**, *Notopocorystes stokesii* and *Eucorystes iserbyti* **n. sp.**, have strongly elongated endostomes, their tips projected and rounded (Fig. 55A, D); the lateral surfaces are deeply excavated posteriorly and extend under the pterygostome (Fig. 55B, C). Without exception, the mxp3 are distinctly elongated in Palaeocorystoidea. The mxp3 of Orithopsidae was not examined. The exopod of palaeocorystoids is typically elongated, weakly curved and acutely tipped; the endopod basis-ischium and merus are slender, axially sulcate and nearly equal in length, closing medially. In camarocarcinids and necrocarcinids, both groups having tumid bodies and pterygostomes, the endopod basis-ischium and merus are positioned in two different planes (see Feldmann *et al.* 2008: 1743). These elements are in about the same plane in the other palaeocorystoid families. Anteriorly, the pterygostome terminates in a distinct, pointed process, the subantennary lobe of the pterygostome (Fig. 50F; for *Cretacocarcinus smithi* see Feldmann *et* *al.* 2008: figs. 6.3, 7.3). These pointed processes are parallel to the elongated endostome, and in the same plane as the mxp3 endopod merus. Together these three elements (subantennary lobe of the pterygostome, elongated endostome and tips of mxp3 endopods) are projected, and they form the oxystomian mouth, whichs form the exhalant orifice (and, in case of flow reversal, the inhalant opening) in the normal respiratory mode.

Two specimens of *Ferroranina dichrous* retain the basal articles (element 3) of the antenna (Fig. 8C, D). These elements are enlarged, strongly flabelliform, and, when opposed, form a funnel. There is a remarkable similarity to the structure seen in extant raninoids, and it may be assumed they had a similar function correlated to the oxystomian condition.

All palaeocorystoids have a similar configuration of the mxp3 coxae, not being close to each other, but separated by sternite 3; they are large, flabelliform, with many setal pits and intercalated between the thoracic sternum and the pterygostome, and in front of the P1. The posterior surface of the mxp3 coxa is curved inwards, which represents the Milne-Edwards openings. The distal margin of the coxa coincides with the posterior margin of the pterygostome, in contrast to the raninoid disposition where they do so with the lateral (buccal) margin of the pterygostome. A similar shape of the mxp3 coxa was described for *Calappa* by Bellwood (2002a: 118). The densely setose coxae 'appear to have the ability to regulate, and filter, the water entering the branchial chamber'. The same function is suggested here for the palaeocorystoid mxp3 coxae.

It may be concluded that the palaeocorystoid respiratory system is more basal than the raninoid respiratory system, with *Marylyreidus* **n. gen.,** showing an intermediate condition. The reduced P5 in Palaeocorystoidea most probably had no role in the respiratory process; implementation of the P5 in the respiratory process in Raninoidea (*pro parte*) is considered a subsequent innovation associated with innovation of posterior respiratory openings.

It is hypothesised that the respiratory function in Cenomanocarcinidae, Camarocarcinidae and Necrocarcinidae illustrates the most basal condition. The primitive modifications of *Necrocarcinus* rapidly evolved into the more specialised condition of *Notopocorystes*. The spinose anterolateral margins, areolated pterygostome and large, flabelliform mxp3 coxae, all efficient in respiration, are features that distinguish Palaeocorystoidea from Raninoidea. The Palaeocorystoidea flourished during the mid-Cretaceous (Albian–early Turonian). A global change in sediment type may have subsequently triggered their replacement by raninoid crabs, with the specialised stock (Palaeocorystidae) going extinct first.

Spermathecae and spermathecal apertures

The thoracic sternum is strongly modified in suture 7/8 of females in Podotremata. The interosternites between sternite 7 and 8 are altered by having its two component sheets separated (all thoracic sternites consisting of two sheets at the level of the sutures, the interosternites, at least in sutures 4/5–7/8) on both sides of the body to form internalised sperm chambers, the spermathecae. The podotreme spermatheca is thus derived from two adjacent thoracic somites, basically a split between the two sheets of the intersegmental phragma 7/8, one derived from sternite 7, the other from sternite 8 (Gordon 1950, 1963, 1966; Hartnoll 1975, 1979; Tavares & Secretan 1993; Guinot & Quenette 2005). The apertures of these paired spermathecae are located at the distal end of the suture 7/8. The chambers may be in direct contact with the aperture, or, in several cases (see below)**,** a tube is formed to accomplish sperm transfer from the aperture to the chamber. The shape, size and location of the podotreme spermathecal apertures vary (see Guinot & Tavares (2001: fig. 10).

The process of fertilisation in podotremes still is far from clear. Eggs are released from the female gonopores on P3 coxae and must be fertilised by sperm stored in the spermathecae. It is not known how this is achieved in the different groups.

Paired spermathecae are an apomorphy of Podotremata, in contrast to the unpaired spermathecae of e.g. Nephropidae Dana, 1852, and Cambaridae Hobbs, 1942. It is not homologous to the paired vulva on thoracic sternite 6 of Eubrachyura, in which the region for the sperm storage should be referred to as seminal receptacle (Tavares & Secretan 1993; Guinot & Quenette 2005).

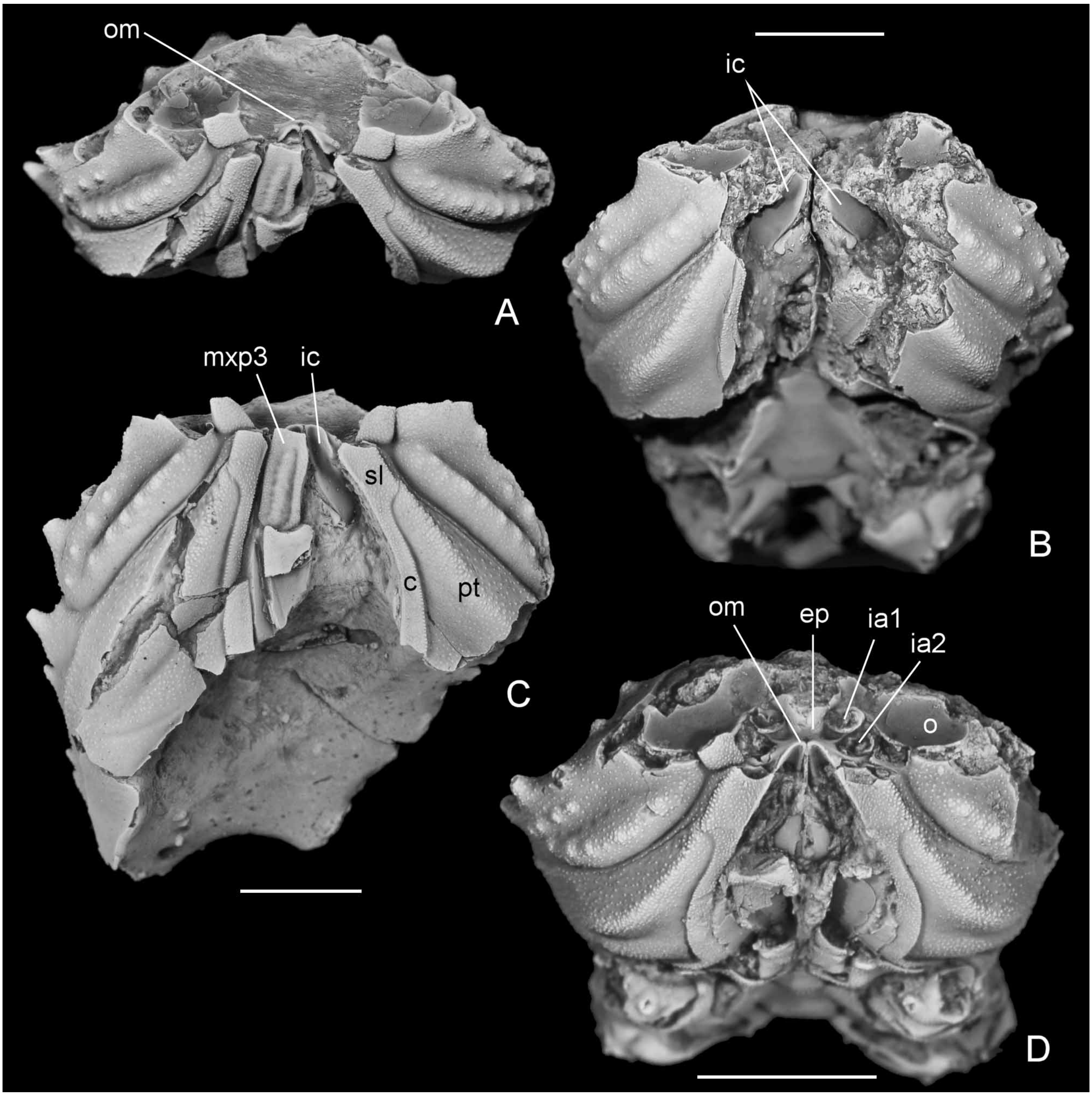

FIGURE 55. Oxystomian condition in *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), Albian, Escalles (Calais, northern France); A, C, MAB k. 2906 (indeterminate sex); frontal and ventral views; B, MAB k. 2873 (female), oblique frontal view; D, MAB k. 2907 (female), oblique frontal view. **c,** buccal collar of pterygostome; **ia1,** insertion of antennule; **ia2,** insertion of antenna; **ic,** inhalant channel; **ep,** epistome; **mxp3,** third maxilliped; **o,** orbit; **om,** oxystomian mouth; **sl,** subantennary lobe of pterygostome; **pt,** pterygostome. Scale bars: 5mm.

Gordon (1963, 1966) gave an account of the spermathecae in Raninidae. She externally examined specimens of *Ranina ranina*, and dissected individuals of *Notopoides latus*, suggesting that there was but a single, unpaired spermatheca. Hartnoll (1979) observed that there were paired apertures, and he put forward a hypothesis on the modified position of the spermathecal aperture in Raninoidea. Guinot (1993b) briefly mentioned the peculiar nature of the spermathecal aperture in raninoids and illustrated the paired apertures, which are mostly situated in a sunken pit in the different subfamilies. Guinot & Quenette (2005) studied and reviewed the spermathecae in podotremes and illustrated (Guinot & Quenette 2005: fig. 25) different patterns amongst the diverse subfamilies. Despite these accounts, and Hartnoll's (1979) well-argumented discussion in particular, the construction of the spermathecae in Raninoidea has never been well understood.

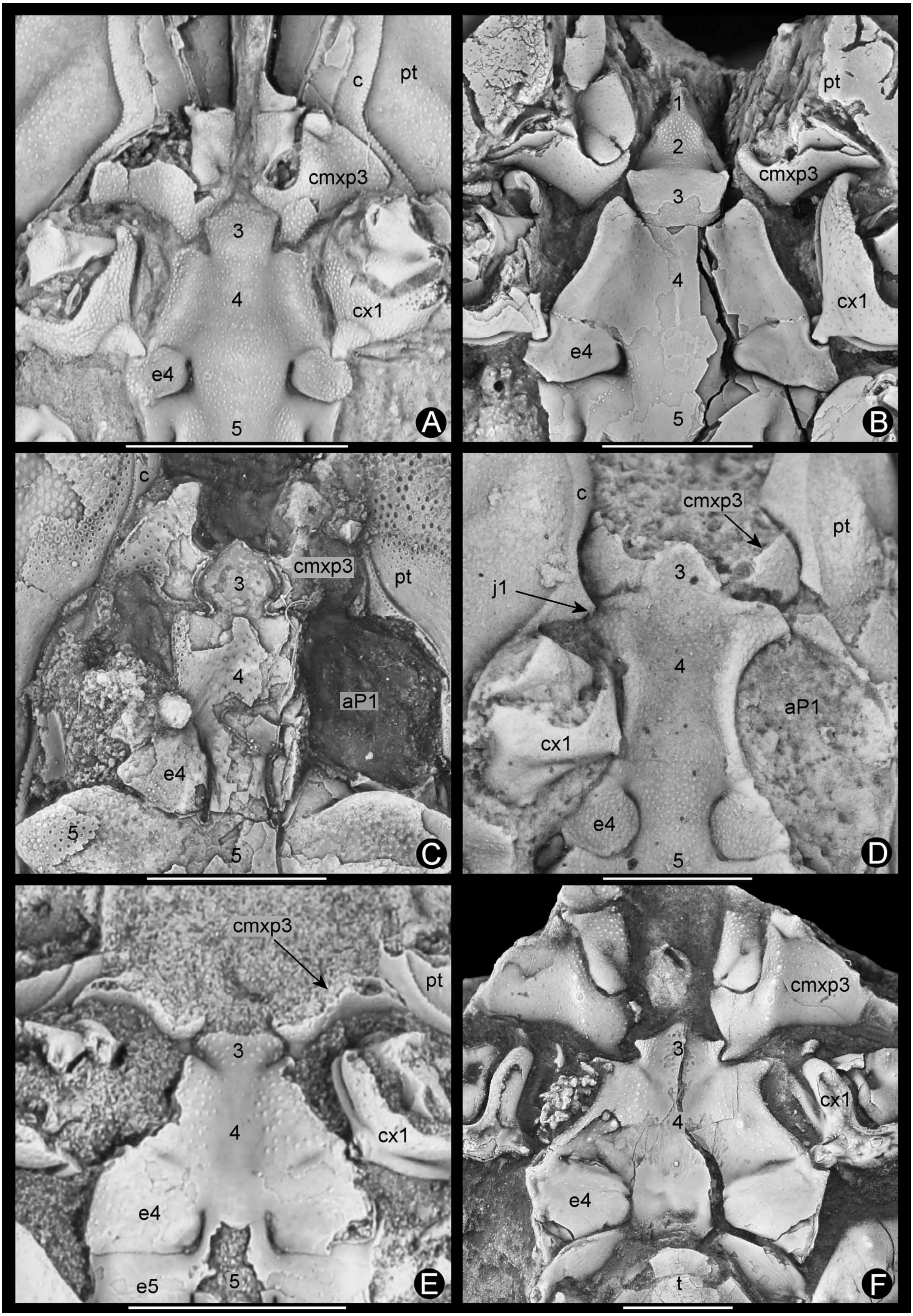
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FIGURE 56. Configuration of sternum-pterygostome and details of thoracic sternum in fossil Raninoidia; A, *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), MAB k. 2889 (female), Albian, Escalles (Calais, northern France); B, *Joeranina broderipii* (Mantell, 1844) **n. comb.** (Palaeocorystidae), MAB k. 2896 (indeterminate sex), Albian, Folkestone (Kent, southeastern England); C, *Marylyreidus punctatus* (Rathbun, 1935b) **n. comb.** (Lyreididae, Marylyreidinae **n. subfam.**), MAB k. 2884 (male), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County (Texas, U.S.A); D, *Bournelyreidus tridens* (Roberts, 1962) **n. comb.** (Lyreididae, Lyreidinae), MAB k. 0214 (cast of GAB 37-832, ?adult female), lower Maastrichtian, Mississippi (U.S.A); E, *Silvacarcinus laurae* Collins & Smith, 1993 (Orithopsidae), IRScNB TCCI 6115 (**holotype**; indeterminate sex), lower Eocene (Ypresian), Brussels (Belgium); F, *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Cenomanocarcinidae), MAB k. 2895 (female), upper Albian-lower Cenomanian (Pawpaw Formation), Tarrant County (Texas, U.S.A). **1, 2, 3, 4, 5,** thoracic sternites 1, 2, 3, 4, 5; **aP1,** arthrodial cavity of P1; **c,** buccal collar of pterygostome; **cmxp3,** coxa of mxp3; **cx1,** P1 coxa; **e4, e5,** episternites 4, 5; **j1,** junction thoracic sternum/pterygostome; **pt,** pterygostome; **t,** telson. Scale bars: A-B, E-F: 5mm; C-D: 2mm.

Fossil record of spermathecae. The spermathecal apertures of fossil Podotremata have only been rarely noted. As recent examples have shown, however, dedicated research and delicate preparation has resulted in the discovery of spermathecal apertures in extinct podotremes, which invariably involve thoracic sternal suture 7/8 and which are often accompanied by a well-visible female gonopore on the P3 coxa.

Amongst Dromioidea, a spermathecal aperture was illustrated for *Dromilites simplex* Quayle and Collins, 1981 from the lower Eocene (Ypresian) of Kent, southeastern England (see Schweitzer & Feldmann 2010d: figs. 4h, 5). *Dromilites* was assigned to Sphaerodromiinae, which they considered to be of family rank. Previously, Van Bakel *et al.* (2009: 49) had observed that *Basinotopus tricornis* Collins & Jakobsen, 2004 from the middle Eocene of Jylland (northern Denmark) revealed spermathecal apertures (see Collins & Jakobsen 2004: pl. 2, fig. 1b). The specimen illustrated is a female and the gonopore on the P3 coxa is clearly seen. Sternal suture 7/8 is rather short, the small spermathecal apertures being situated at about the same level as the gonopore (see also Guinot *et al.* in press). Spermathecal apertures (sometimes well-preserved) have also been documented in Dakoticancroidea, in particular for *Dakoticancer overana* Rathbun, 1917 (see Guinot 1993a: fig. 7; Guinot & Tavares 2001: fig. 7; Artal *et al*. 2008: fig. 3D) and for *Tetracarcinus subquadratus* Roberts (1962: pl. 87, fig. 3). Spermathecal apertures of *Ibericancer sanchoi* Artal, Guinot, Van Bakel & Castillo, 2008, are fairly large, ovate and oblique.

Amongst the Etyoidea Guinot & Tavares, 2001, spermathecal apertures in *Etyus martini* Mantell, 1844, were demonstrated by Guinot & Tavares (2001: figs. 2, 3) in a specimen figured by Wright & Collins (1972: pl. 21, fig. 6a-e) from the Albian of southern England. Newly collected material of this species is currently under study.

Spermathecae in the Palaeocorystoidea. Only one example of spermathecal apertures for Cenomanocarcinidae and several instances for Palaeocorystidae exist in the material examined. As to the former family, a specimen of *Cenomanocarcinus beardi* with a partially preserved thoracic sternum reveals a spermathecal aperture on the left-hand side (Fig. 58A–D). Although the cuticle of this specimen is not particularly well-preserved, the spermathecal aperture can be clearly observed; it is elongated, slightly raised and its position at the extremity of sternal suture 7/8 is plesiomorphic for Podotremata. There is no median line on the thoracic sternum. Better-preserved material needs to be examined. Spermathecal apertures in Palaeocorystidae are documented for *Notopocorystes* and *Joeranina* **n. gen.** (Figs. 57A–D; 59A, B; 61A). The fairly large and elongated apertures have slightly raised or thickened margins and are situated at the extremities of sternal sutures 7/8. The spermathecal apertures are exposed at the surface of the thoracic sternum, thus not located in a pit or depression. There is a median line along thoracic sternite 8 in both genera. The cuticle in the great majority of specimens of *Notopocorystes* and *Joeranina* **n. gen.** is well-preserved, so that the presence and nature of the spermathecal aperture are proved unambiguously.

Spermathecae in the Raninoidea. Spermathecal apertures in Raninoidea are known only in extant material, their position being modified as they appear to open anteriorly on thoracic sternite 7 in proximity of the female gonopore on the P3 coxa. Various modes may be recognised.

Lyreididae: The small spermathecal apertures face each other on opposite sides of a depression (‘sunken pit’) of thoracic sternite 7, and are separated by a median line. Spermathecal apertures have not been recognised in the available Marylyreidinae **n. subfam.** material, but a depression is seen (Haj & Feldmann 2002: figs. 3.2, 4.2, 4.5).

Ranininae: The anterior part of thoracic sternite 7 shows a deep, elongated median depression; the apertures of the spermathecae are at the bottom of this depression (see Figs. 60C; 61B).

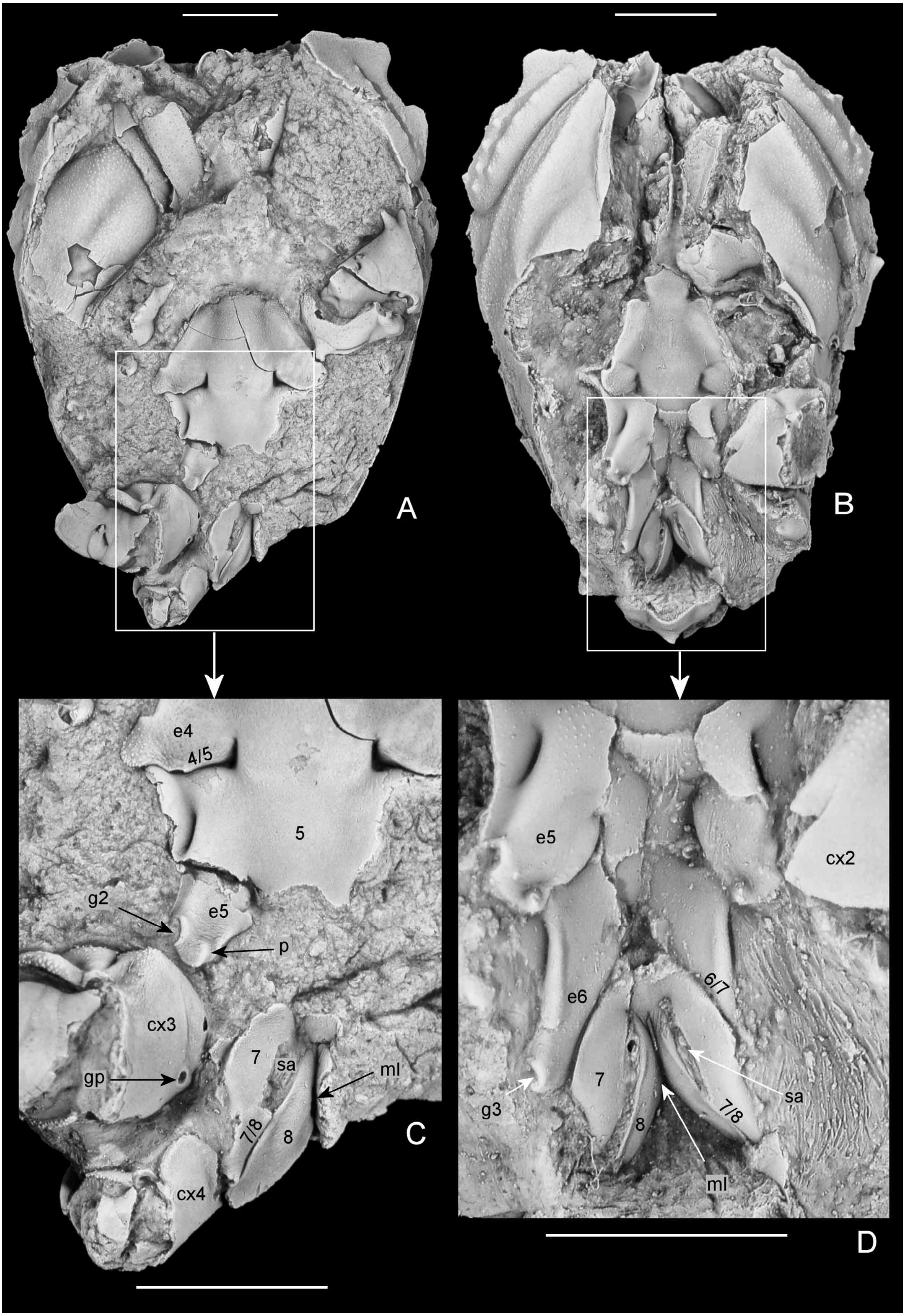
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FIGURE 57. Spermathecal aperture in palaeocorystids; A, C, *Joeranina broderipii* (Mantell, 1844) **n. comb.**, MAB k. 2913 (female), Albian, Escalles (Calais, northern France), ventral view showing thoracic sternum and detail of posterior thoracic sternum showing spermathecal aperture; B, D, *Notopocorystes stokesii* (Mantell, 1844), MAB k. 2873 (female), Albian, Escalles (Calais, northern France); ventral view showing thoracic sternum and detail of posterior thoracic sternites showing spermathecal apertures. **5, 7, 8,** thoracic sternites 5, 7, 8; **4/5, 6/7, 7/8,** thoracic sternal sutures 4/5, 6/7, 7/8; **cx2, cx3, cx4,** P2, P3, P4 coxae; **e4, e5, e6,** episternites 4, 5, 6; **g2, g3,** gynglymes for P2, P3 coxa; **gp,** female gonopore; **ml,** median line; **p,** peg (undifferentiated); **sa,** spermathecal aperture. Scale bars: 5mm.

Raninoidinae: Small spermathecal apertures situated on the tilted posterior part of the sternal plate and lying at the bottom of a deep, pit-like depression.

Notopodinae: The anterior part of sternite 7 shows a deep, elongated median depression with two small spermathecal apertures.

Symethinae: The spermathecal apertures are peculiar, neither situated in a median pit nor recessed. They are large, widely separated, horizontal in position and overhung by two calcified hoods.

Cyrtorhininae: The spermathecal apertures are small, contiguous and are recessed in a rather deep depression.

We agree with Hartnoll (1979: 80) and Goeke (1981: 975) that on the basis of spermathecal structure Lyreididae and Symethinae are the most basal, whereas Cyrtorhininae, Notopodinae, Raninoidinae and Ranininae, with more recessed spermathecal apertures, are derived.

Evolution of the raninoidian spermathecae. The plesiomorphic state of the spermathecal aperture is clearly seen in Palaeocorystoidea. The posterior thoracic sternum is relatively wide in Cenomanocarcinidae, yet narrower in Palaeocorystidae (Figs. 37A; 58A, B). Through specialisation towards burying, the raninoidian body has become extremely narrowed, inclusive of the thoracic sternum. When in an evolutionary series the thoracic sternum narrows, the sternites initially will not drastically decrease in size, but their surfaces become steeper and the coxae closer together (Fig. 61C). At first, narrowing the body will not strongly affect the width of sternite 4 (i.e., the chelipedal sternite), but does have an impact on the posterior sternites (Fig. 61A). The steep angle of the posterior sternites is clearly seen in specimens of *Notopocorystes* spp. (Figs. 11D, 57D, 59B). The steep surfaces of the sternites on both sides of the thoracic sternum abut. A median plate is initiated when the sternites on both sides of the thoracic sternum do so, a process that may be refered to as ‘infolding’ (Fig. 61C). The narrowing process starts posteriorly, hence the median line originates posteriorly, along thoracic sternite 8. If in an evolutionary polarity the sternum becomes narrower, the posterior sternites become increasingly narrower, and the median line will expand forwards. If the sternal sutures are situated laterally, their extremities will come closer to the median line.

The median line (see Pearson 1908: 35, fig. 6; pl. 3, fig. 18) forms an internal, median septum called the ‘median plate’. This is formed by the invaginated surfaces of the thoracic sternites. According to H. Milne Edwards (1851: 57, pl. 9, figs. 9, 10), the endosternites of the axial skeleton are medially connected by a ‘mesosternal plate’. Pearson (1908: 35) observed that the median plate was composed of two closely applied laminae in *Cancer pagurus* (Linnaeus, 1758). According to Drach (1939: 370, pl. 6, fig. 27; pl. 7, figs. 31, 32; in the cancrid *Cancer pagurus*), the somites were divided into two symmetrical parts by a vertical median partition (*lame*, *plaque médiane*) issued from an invagination of the sternal floor.

Various terminologies for the median line and median plate have been used: ‘deep longitudinal mid-ventral apodeme’ (Bourne 1922: 39), ‘median infolding of sternal apodeme’ (Gordon 1966: 348, 350), ‘median apodeme’ (Hartnoll 1979: 76), ‘*ligne médiane*’ and ‘*plaque médiane*’ (Guinot 1979a: 253) and ‘median line’ and ‘median plate’ (Guinot *et al.* in press).

That the median plate is situated mainly at the posterior sternites is clearly seen in the longitudinal sections of *Notopoides latus* of Gordon (1966: figs. 2b, 3b). The median plate is prominent at sternites 6 and 7, but weakly developed at sternite 5. When the sternum is so narrow that the sutures reach the median line, the internal phragmae corresponding to the sternal sutures are connected to the internal plate of the median line. This forms a very strong, grating-like structure, much stronger than the initial state; a favourable body construction for a burying crab. A similar modification is seen in other (unrelated) specialised burying species such as *Corystes cassivelaunus* (see Gordon 1966: figs. 5, 6). Burying crabs in general have a long median line (sutures 5/7–7/8 complete or only the first weakly interrupted) and a well-developed median plate. It appears that raninoids have the highest median plate amongst all brachyurans.

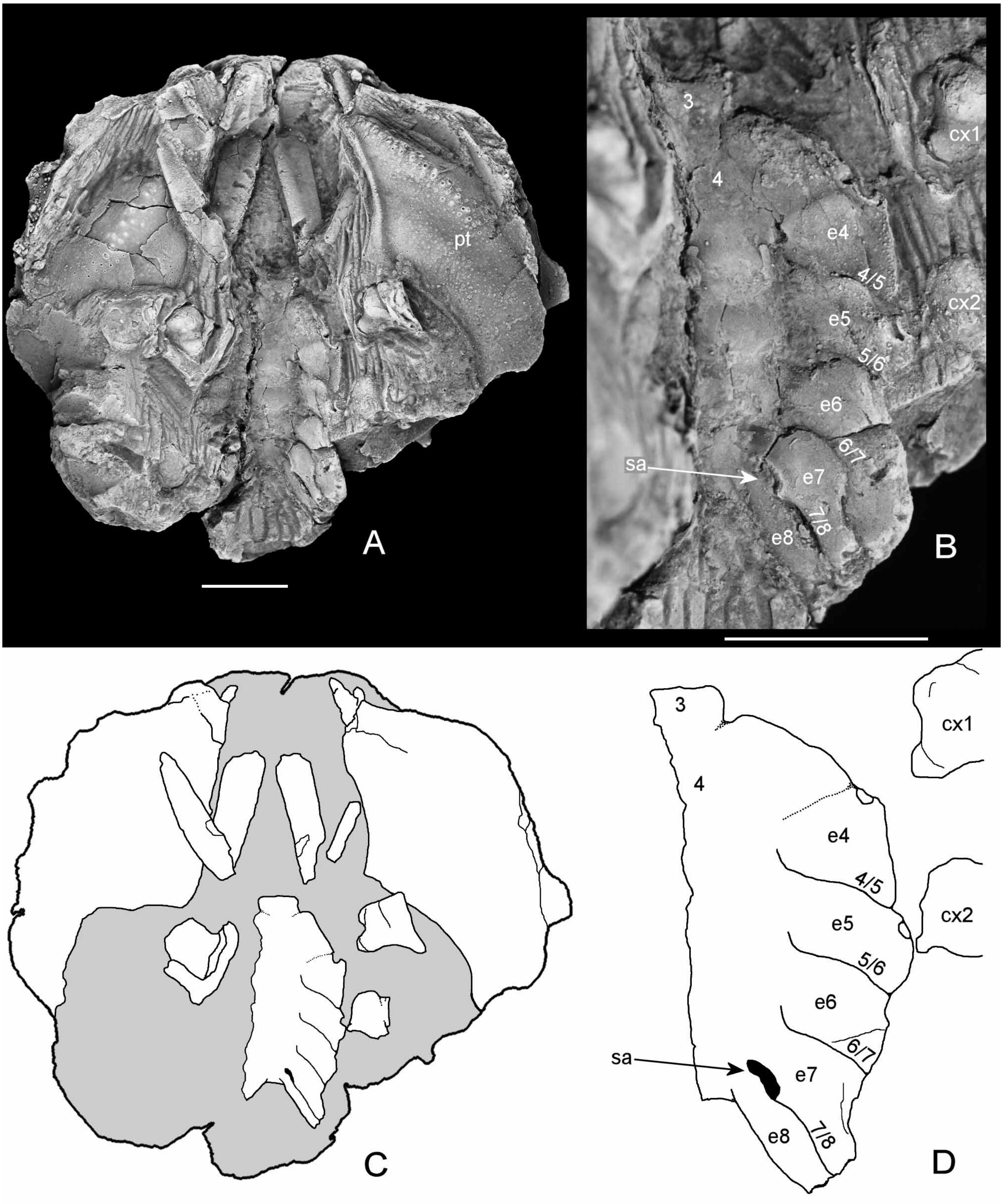

FIGURE 58. Spermathecal aperture in cenomanocarcinids; A, B, *Cenomanocarcinus beardi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003a, MAB k. 2544 (female), Cenomanian (Woodbine Formation), Wagner Park, Texas (U.S.A); ventral view showing thoracic sternum, mxp3 and detail of thoracic sternum showing spermathecal aperture; C, D, Interpretative line drawings of A and B. **3, 4,** thoracic sternites 3, 4; **4/5, 5/6, 6/7, 7/8,** thoracic sternal sutures 4/5, 5/6, 6/7, 7/8; **cx1, cx2,** P1, P2 coxae; **e4, e5, e6, e7, e8,** episternites 4, 5, 6, 7, 8; **pt,** pterygostome; **sa,** spermathecal aperture. Scale bars: 5mm.

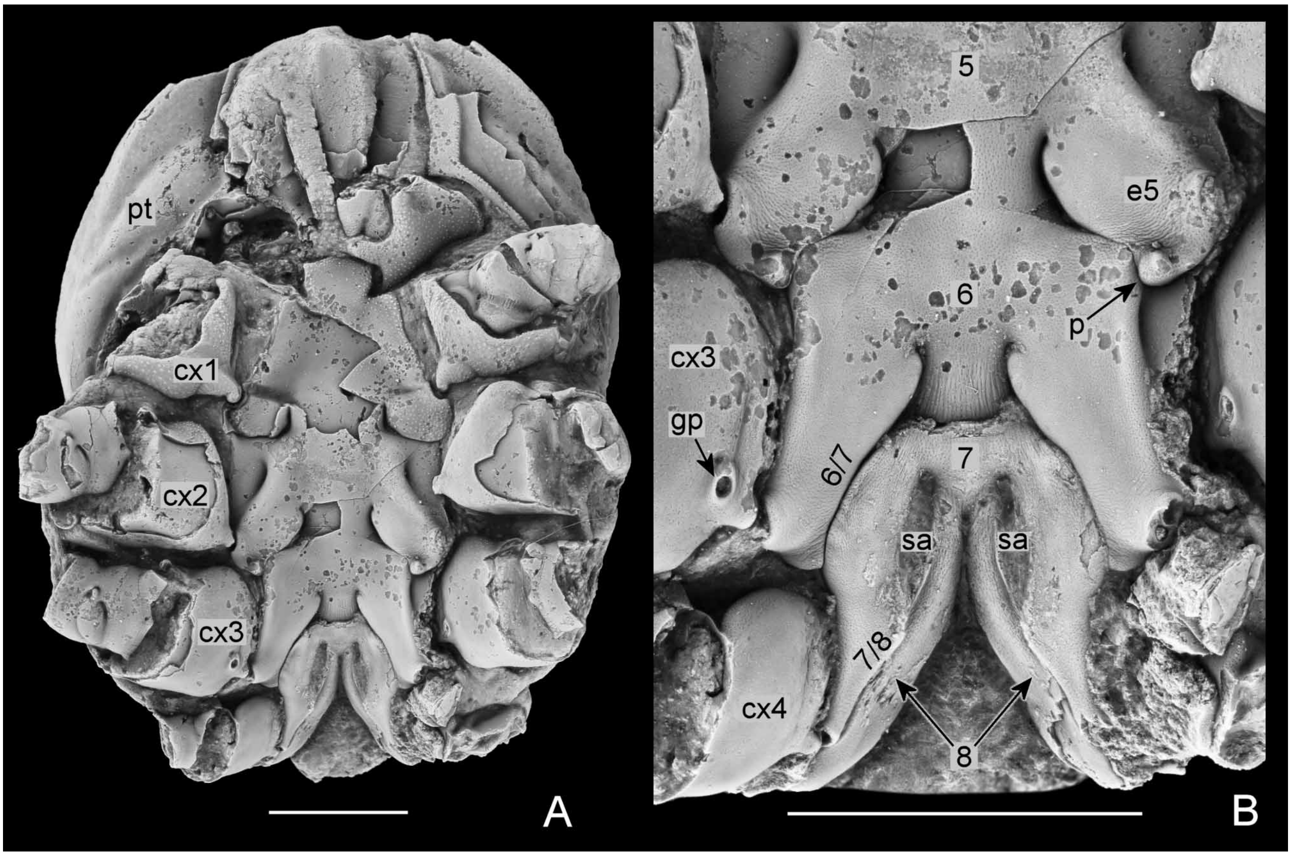

FIGURE 59. Spermathecal apertures in *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae); MAB k. 2924 (*ex* Guy van den Eeckhaut Collection; female), middle Albian, Lac du Der (northern France); A, ventral view showing well-preserved thoracic sternum, pterygostome and bases of appendages; B, detail of posterior thoracic sternites, showing spermathecal apertures. **5, 6, 7, 8,** thoracic sternites 5, 6, 7, 8; **6/7, 7/8,** thoracic sternal sutures 6/7, 7/8; **cx1, cx2, cx3, cx4,** P1, P2, P3, P4 coxae; **e5,** episternite 5; **gp,** female gonopore; **p,** peg (undifferentiated); **pt,** pterygostome; **sa,** spermathecal aperture. Scale bars: 5mm.

Extreme narrowing and infolding of the posterior thoracic sternites nevertheless leads to biomechanical difficulties. The spermathecal apertures are situated at the extremity of sternal suture 7/8 in females. In a gradual evolutionary process of infolding, the area which becomes internalised has gradually increased. The spermathecal apertures may migrate forwards (as in Dromiinae, see Tavares & Franco 2004), but this possibility is finite. Through infolding of sternite 7, the spermathecal apertures become 'trapped' within sternite 7. Despite the displaced position and cryptic construction, the spermathecal aperture is plesiomorphically situated at the extremity of suture 7/8, thus does not represent a secondarily acquired opening. It illustrates the normal configuration of Podotremata. This observation contrasts with Hartnoll (1979: 82, fig. 5), who discussed the possibility that 'the present raninid spermathecal openings are not the original ones.' The spermathecal aperture is thus still in connection with the spermathecal chamber, formed by separation of the two laminae composing endosternite 7/8. In other words, suture 7/8 has become partially internalised. Suture 7/8 is not short *per se*, but long, continuing 'within' the median plate (Fig. 61D), a condition verified by dissecting the thoracic sternum of a female *Ranina ranina* (Fig. 60A, B). The fact that suture 7/8 continues within the median plate demonstrates that the 'walls' of the infolding are actually the internalised exterior surfaces of somites 7 and 8. Through this cryptic construction, suture 7/8 is visible between the narrowly interspaced spermathecal apertures, as seen in Hartnoll (1979: fig, 1).

The potential survival value of narrowing the body must be substantial in view of the complex modification of the thoracic sternum, and it may be stated that the absolute limit of sternal narrowing has been achieved amongst raninoideans. The raninoid male gonopods are modified, coherent with the modified condition of the female spermathecal apertures (axial placement, paired but approximate) and the posterior/dorsal orientation of the abdomen. Gordon (1966: 348, 349, fig. 4a-c) described how the proximal segments of male pleopods 1 and 2 were extended backwards and the distal segments positioned at right angles to the proximal segments. The tips of the first pair of pleopods are closely apposed so they can enter the spermathecal pit.

Phylogeny of the Raninoidia

The status of subsection Raninoidia ranks amongst the most important issues in discussions on brachyuran systematics, not only as far as their early differentiation is concerned, but also from the viewpoint of understanding brachyuran macroevolutionary patterns. The inability to determine what the fundamental characters of extant Raninoidea are and how to interpret their organisation have been the major reasons behind this impediment for taxonomy. The strange, frog-like shape, plus various unusual features displayed by modern representatives have led to a number of hypotheses on their affiliation, either with anomurans, macrurans or brachyurans. The uniqueness of the Raninoidea was recognised on a number of occasions, which explains their assignment to distinct tribes: the Notopterygia within the 'Macruri' (see *The name* Notopterygia *Latreille, 1831* above), or the Notopoda and Gymnopleura within Brachyura. The last-named epithet refers to a unique raninoid characteristic, the partial exposure and calcification of several pleurites ('gymnopleure'), the gymnopleurity being a trait that has been insufficiently studied by neontologists following publication of Bourne's seminal paper (Bourne 1922b), and has even been largely ignored in palaeontological studies. The brachyuran nature of Raninoidea is presently widely accepted, but its precise placement amongst the true crabs remains controversial, with substantial debate during the last decade (Martin & Davis 2001; Ahyong *et al*. 2007, 2009; De Grave *et al.* 2009; Ng *et al.* 2009; Schweitzer *et al*. 2010). A decisive key is to determine whether or not this gymnopleurity, combined with other unique features, suffices to grant Raninoidea a distinct, high-level phylogenetic position within Brachyura. Carcinologists have recently favoured either: (1) a subsection Raninoida (containing the Raninoidea and Cyclodorippoidea) within the Eubrachyura, next to two other subsections, Heterotremata and Thoracotremata, as proposed by Martin & Davis (2001) and adopted by, for example, by Feldmann (2003), De Angeli & Garassino (2006b) and Schweitzer *et al.* (2010); (2) a separate section, Raninoida, next to two other sections, Dromiacea and Cyclodorippoida, alongside the section Eubrachyura (Ahyong *et al.* 2007, 2009; Ng *et al.* 2009; De Grave *et al.* 2009; Karasawa *et al*. 2011). This second scheme questions the monophyly of Podotremata, a status that has not been supported by most molecular studies and has been considered 'untenable' (Ahyong *et al.* 2007: 576, 581) (see below).

An alternative scheme is proposed here, the placement of Raninoidea within Podotremata together with four other main podotreme taxa, Homolodromioidea, Dromioidea, Homoloidea and Cyclodorippoidea (see Table 2), all of equivalent rank. The section Podotremata should be the sister group of the section Eubrachyura, which includes two subsections, Heterotremata and Thoracotremata (see Table 2; Guinot 1977, 1978, 1993a, b; Guinot & Tavares 2001; Guinot & Quenette 2005; Števčić 2005; Guinot *et al.* 2008; Ng *et al*. 2008; Guinot *et al*. in press).

This study of Palaeocorystoidea and Raninoidea does not support the opinion that raninoid crabs are eubrachyurans (see also Guinot *et al.* in press). The Raninoidia shows the presence of an internalised paired spermatheca formed by phragma 7/8 (synapomorphy of Podotremata) (Fig. 57A–D), and the podotreme condition of the female gonopore on the P3 coxa (Fig. 39A, D). Furthermore, despite its distinctive characters, the raninoid thoracic sternum (e.g., Figs. 31C; 34B) is not eubrachyuran in nature. Inclusion of the podotreme Raninoidea and Cyclodorippoidea in Eubrachyura conflicts with the major eubrachyuran synapomorphy; presence of sternal vulvae. Such a placement was considered 'counterproductive', rendering the 'eubrachyuran clade meaningless with respect to the degree of structural organisation of the heterotreme-thoracotreme assemblage' (Ahyong *et al.* 2007: 584).

The only alternative is to accept the podotrematous nature of Raninoidea together with that of Cyclodorippoidea. The taxonomic placement of both groups is intimately linked, even if a wide thoracic sternum characterises the latter (Fig. 47B). Brösing (2008: 277) assumed that, 'a common ancestor for Raninidae and Cymonomidae occurred in the middle of the Cretaceous'. Karasawa *et al.* (2009: 80) concluded that Podotremata consisted of 10 major subclades (but was clearly paraphyletic); this is a step in the good direction in recognising that a podotreme clade does exist, in opposition to the eubrachyuran crabs (with heterotremes and thoracotremes).

The Raninoidea, as previously noted above, exhibits unique, morphological characters. The study of well-preserved fossils which led to the establishment of Cenomanocarcinidae (Guinot *et al.* 2008) and the present results based on a range of new palaeontological data now permit a more comprehensive view of the evolutionary history of the group in a phylogenetic context. The extinct Palaeocorystoidea is here considered to be the sister group of Raninoidea, and the two superfamilies are grouped in subsection Raninoidia alongside the three other podotreme subsections, Dromioidia, Homoloidia and Cyclodorippoidia (Table 2).

Karasawa *et al*. (2011: 550) considered the assignment of Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae, Orithopsidae and Palaeocorystidae in a separate superfamily to be 'unwarranted'. Their analysis

(Karasawa *et al*. 2011: 533) rejects the opinion of Guinot *et al*. (2008) that a subsection Raninoidia could be divided into two superfamilies. However, theirs is based on a character matrix with several incorrect observations, a lack both of thorough examination of material available and understanding of extant raninoids; in consequence, there is no sound interpretation of evolutionary polarities. Karasawa *et al*. (2011: table 2) used a data matrix with several erroneous interpretations. For example, they stated that Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae and Palaeocorystidae (Orithopsidae not included in their analysis) do not have a socket ventrally at abdominal somite 6 (2011: 529, character 52; erroneously termed 'socket on sternite 6'); that Cenomanocarcinidae, Necrocarcinidae and Palaeocorystidae have a complete sternal suture 6/7 (character 33); and that Raninidae and Symethidae have the spermatheca 'united' (character 42). In addition, key characters of the raninoid clade were not studied and used in their consideration (i.e., exposure of pleurites, respiratory system, Milne-Edwards openings, junction of sternum with pterygostome). Therefore, we here consider their conclusions unsubstantiated.

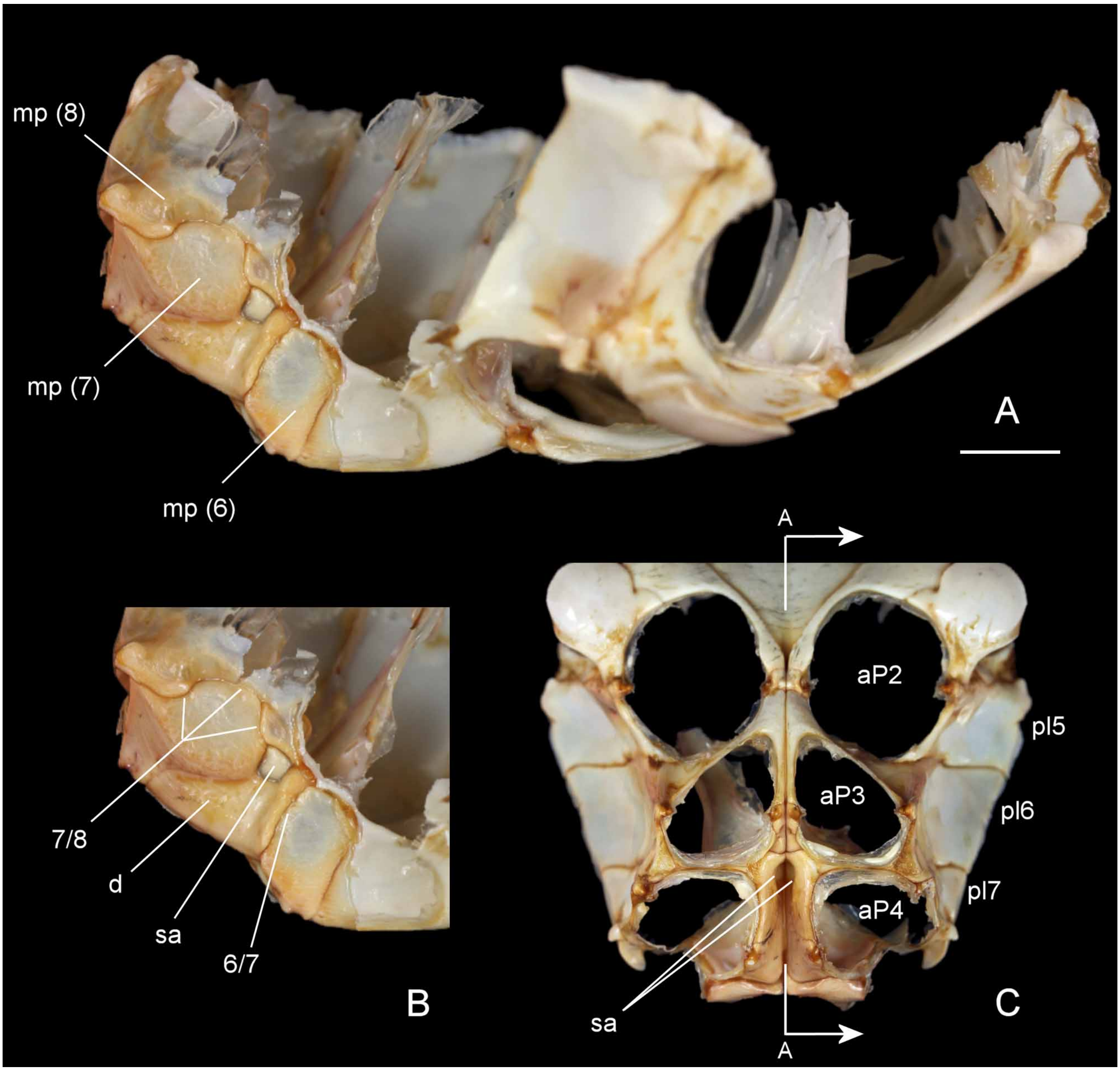

FIGURE 60. Thoracic sternum of *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae); MNHN unregistered (female), Recent, provenance unknown, prepared by S. Secretan; A, right lateral view showing partial internal view (axial section, for direction see Fig. C) of median plate; B, detail of internal view (axial section) of median plate showing long, sinuous suture 7/8 and spermathecal aperture; C, ventral view showing posterior thoracic sternites and spermathecal apertures in depression. **6/7, 7/8,** thoracic sternal sutures 6/7, 7/8; **aP2, aP3, aP4,** arthrodial cavities of P2, P3, P4; **d,** depression; **mp(6), mp(7), mp(8),** median plate (thoracic sternites 6, 7, 8); **pl5, pl6, pl7,** exposed pleurites 5, 6, 7; **sa,** spermathecal aperture. Scale bars: 5mm.

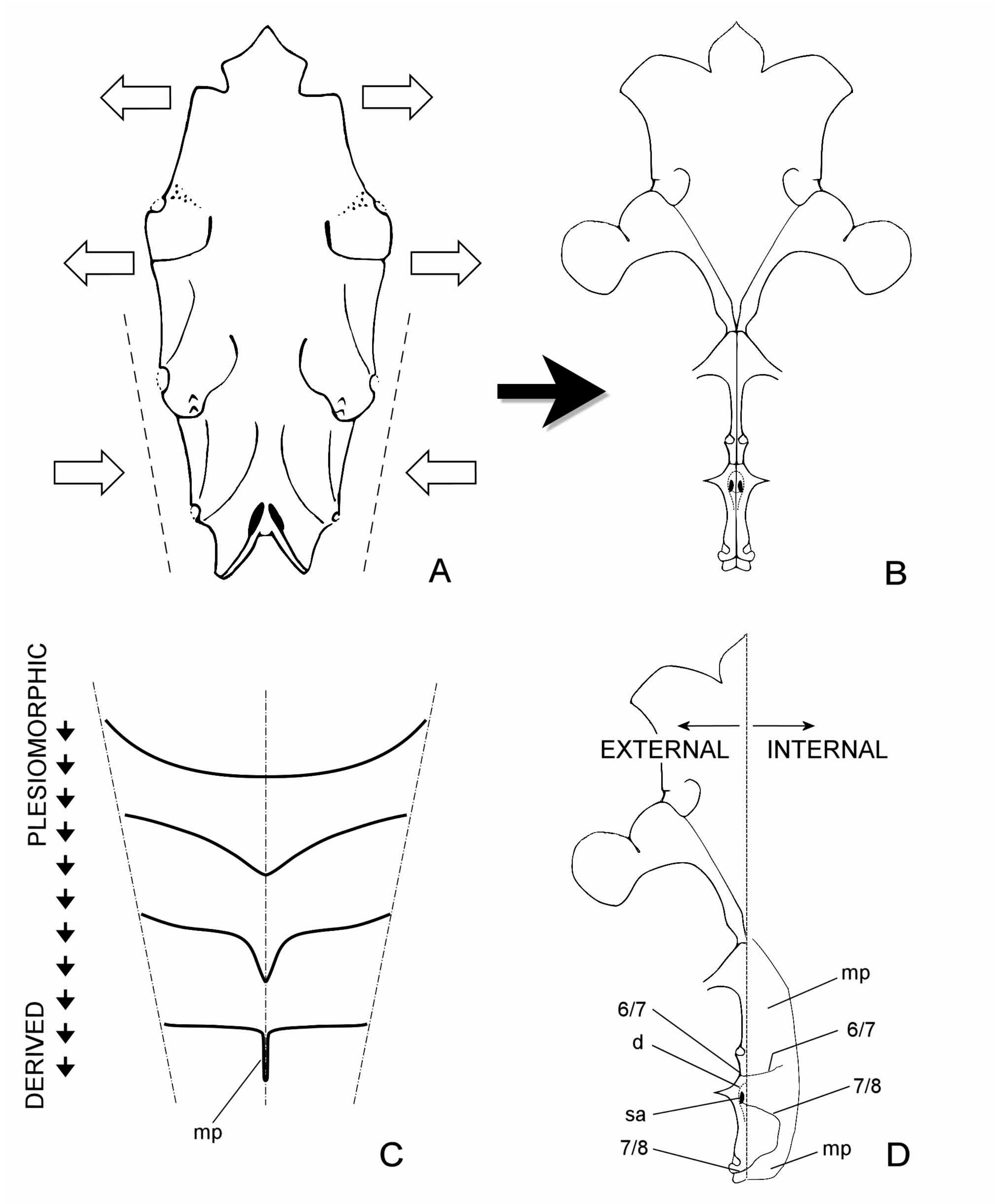

FIGURE 61. Narrowing of thoracic sternum in Raninoidia. A**,** thoracic sternum of *Notopocorystes stokesii* (Mantell, 1844) (Palaeocorystidae), reconstructed after several specimens; B, thoracic sternum of *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae); C, hypothetical narrowing of thoracic sternum: transverse cross-section; D, thoracic sternum of *Ranina ranina* (Linnaeus, 1758) (Raninidae, Ranininae), left-hand side showing ventral (external) view, right-hand side showing section (internal) view of median plate. **6/7, 7/8,** thoracic sternal sutures 6/7, 7/8; **d,** depression; **mp,** median plate; **sa,** spermathecal aperture.

The Podotremata is very diverse. Morphological patterns shared by podotremes are: the paired and internalised spermatheca depending of phragma 7/8 (see *Spermatheca and spermathecal apertures*), the male abdomen filling entirely in width the space between the pereiopods (but there are exceptions: Cyclodorippoidea, Dakoticancroidea), the shape of the intertagmal phragma that do not form a sella turcica similar to that of Eubrachyura (Guinot *et al.* in press), the shape of suture 4/5. A comparison of Palaeocorystoidea with the other extant and extinct podotreme superfamilies is an important prerequisite to unambiguously clarify the various morphological patterns of Podotremata.

Comparison of the superfamily Palaeocorystoidea with other podotreme superfamilies

Palaeocorystoidea versus Glaessneropsoidea Patrulius, 1959

This comparison considers Glaessneropsoidea *sensu* Schweitzer & Feldmann (2009, 2010b–c) and Schweitzer *et al*. (2010). This assemblage comprises five families: Glaessneropsidae Patrulius, 1959, Lecythocaridae Schweitzer & Feldmann, 2009, Longodromitidae Schweitzer & Feldmann, 2009, Nodoprosopidae Schweitzer & Feldmann, 2009, and Konidromitidae Schweitzer & Feldmann, 2010c. Only carapace material is so far known, and both the composition and diagnosis of the superfamily (Schweitzer & Feldmann 2009: 82) are far from stable at the moment, exemplified by the various rigorous changes recently proposed by Karasawa *et al*. (2011); additional studies are needed to elaborate its status.

Carapace.
- Carapace gently convex in transverse direction in Palaeocorystoidea (strongly convex in Glaessneropsoidea).
- Front as wide as or narrower than orbits in Palaeocorystoidea (much broader, more prominent in Glaessneropsoidea).
- Groove system shallow and subtle in Palaeocorystoidea (acute and prominent in Glaessneropsoidea).
- Cervical groove generally much more strongly incised in Glaessneropsoidea than in Palaeocorystoidea.
- Branchial groove weak, not notching the carapace margins in Palaeocorystoidea (always clearly defined, notching margins in Glaessneropsoidea).

Palaeocorystoidea versus Homolodromioidea Alcock, 1900

Extant Homolodromioidea are discussed and listed by e.g. Baéz & Martin (1989), Martin (1990, 1992, 1994), Guinot (1995), Guinot & Bouchard (1998), Ho & Ng (1999), Martin *et al.* (2001), Dawson (2002), Tavares & Young (2004), Guinot & Quenette (2005), Ng & Naruse (2007), Ahyong *et al.* (2009) and Guinot *et al*. (in press). The fossil record of Homolodromioidea (*sensu* Schweitzer & Feldmann 2009; Schweitzer *et al*. 2010) comprises four families: Bucculentidae Schweitzer & Feldmann, 2009, Goniodromitidae Beurlen, 1932, Prosopidae von Meyer, 1860, and Tanidromitidae Schweitzer & Feldmann, 2009. So far, all four are known solely from carapaces, which demonstrate a highly diverse pattern of carapace bauplan; their suprafamilial assignment remains doubtful. Discovery of ventral morphology may change the taxonomic composition of the extinct portion of this superfamily.

Carapace.
- Carapace varying from elongated (Palaeocorystidae) to subcircular or subhexagonal (Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae and Orithopsidae), always narrowing posteriorly in Palaeocorystoidea (always longer than wide, and generally constant in width or wider posteriorly in Homolodromioidea).
- Front subtriangular to subtrapezoidal in Palaeocorystoidea (two strong triangular teeth in Homolodromioidea).
- Branchial groove not notching the carapace margins in Palaeocorystoidea (notching margins in Homolodromioidea).

Pterygostome, endostome and mxp3.
- Endostome elongated (‘oxystomian mouth’) in Palaeocorystoidea (normal condition in Homolodromioidea).
- Mxp3 with oxystomian condition in Palaeocorystoidea (pediform, never oxystomian in Homolodromioidea).

Appendages.

- – Only P5 dorsal and reduced in Palaeocorystoidea (P4 and P5 reduced in Homolodromioidea).
- – P2–P4 with flattened articles in Palaeocorystoidea (cylindrical articles in Homolodromioidea).
- – Chelae with spiny lower margin in Palaeocorystoidea, an adaptation to burying (smooth in Homolodromioidea).

Thoracic sternum.

- – Sterno-abdominal depression wide, weak in Palaeocorystoidea (Cenomanocarcinidae, Orithopsidae and Palaeocorystidae) or strongly excavated (Camarocarcinidae and Necrocarcinidae) (long, wide and well excavated in Homolodromioidea).
- – Spermathecal apertures large, oval in Palaeocorystoidea (small, circular in Homolodromioidea).
- – Thoracic sternum with crescent-shaped (horizontal outer part, and deep, vertical inner part) sutures 4/5 and 5/6 in Palaeocorystoidea (anterior sutures hidden in sterno-coxal depressions in Homolodromioidea).
- – Sterno-coxal depressions absent in Palaeocorystoidea (present in Homolodromioidea).

Abdomen.

- – Male abdomen not longitudinally filling sterno-abdominal depression with telson partially covering sternite 4, leaving anterior portion of sternites 3 and 4 exposed in Palaeocorystoidea (entirely filling sterno-abdominal depression, with long telson reaching mxp3 in Homolodromioidea, so thoracic sternum not exposed at all).
- – Male abdomen without distinct pleura in Palaeocorystoidea (distinct pleura in Homolodromioidea).
- – Abdominal somite 6 long in both sexes of Palaeocorystoidea (normal in length in Homolodromioidea).
- – Telson rounded in Palaeocorystoidea (elongated, distinctly triangular in Homolodromioidea).

Abdominal holding.

- – Paired tooth on episternite 5 to hold the abdomen in Palaeocorystoidea (only coxal locking structures in Homolodromioidea).
- – Male abdomen in contact with coxae, but no locking by appendages in Palaeocorystoidea (structures on P1 and P2 to hold the abdomen in Homolodromioidea).

Palaeocorystoidea versus Dromioidea De Haan, 1833

Extant Dromioidea are discussed and listed by e.g. Gordon (1950, 1963), Lewinsohn (1977, 1984), McLay & Crosnier (1991), Crosnier (1994), McLay (1991, 1993, 1999, 2001a–c, 2002, 2009), Guinot & Bouchard (1998), Ng *et al.* (2000), Chen & Sun (2002), Guinot & Tavares (2003), Tavares & Franco (2004), Guinot & Quenette (2005), McLay & Ng (2007), Ahyong *et al.* (2009), Ng & McLay (2010) and Guinot *et al*. (in press).

Carapace.

- – Branchial grooves present as scars, or absent in Palaeocorystoidea (carapace mostly with well-defined branchial grooves in Dromioidea).

Pterygostome, endostome and mxp3.

- – Mxp3 oxystomian: distinctly elongated in Palaeocorystoidea (normal/operculiform in Dromioidea).
- – Endostome elongated (‘oxystomian mouth’) in Palaeocorystoidea (normal condition in Dromioidea).

Appendages.

- – Only P5 (sub)dorsal and reduced in Palaeocorystoidea (dorsal P4 and P5 in Dromiidae; only P5 in Dynomenidae).
- – P2–P4 with flattened articles in Palaeocorystoidea (cylindrical in Dromioidea).
- – Chelae always with spiny lower margin in Palaeocorystoidea, an adaptation to burying (non-spinose margins in dromioids).

Thoracic sternum.

- – Sternite 3 visible in Palaeocorystoidea (sternite 3 either dorsally visible at the same level as preceding ones or sternites 1–3 at a lower level in Dromiidae; anterior sternites crown shaped, sternite 3 variable in Dynomenidae).
- – Female suture 7/8 rather long, but not forming a tube in Palaeocorystoidea (forming a spermathecal tube of variable length in Dromioidea, usually conspicuously long in Dromiinae, short in Sphaerodromiinae and Dynomenidae).
- – Thoracic sternum with crescent-shaped sutures 4/5 and 5/6 (sutures short, hidden in sterno-coxal depressions in

Dromiidae and Dynomenidae).

Abdomen.

– Dorsal uropods absent in Palaeocorystoidea (present as dorsal plates in most Dromiidae, in some as ventral lobes, and all Dynomenidae).

Abdominal holding.

– Male abdomen in contact with coxae but no locking by appendages in Palaeocorystoidea (locking by appendages, acting often with uropods, in Dromioidea, except for Dynomeninae, which shows a sternal structure beside the uropod).

– Paired sternal tooth (double peg), on episternite 5 in Palaeocorystoidea (no sternal locking structures in Dromioidea, except in Dynomeninae, where the impaired sternal 'button' is not covered by abdomen, nor by uropod, thus no abdominal socket, the small sternal structure being located aside the abdomen and not facing any abdominal complementary part; e.g., *Dynomene hispida* (Latreille, *in* Milbert 1812)).

Palaeocorystoidea versus Homoloidea De Haan, 1839

Extant Homoloidea are discussed and listed by e.g. Gordon (1950), Serène & Lohavanijaya (1973), Guinot & Richer de Forges (1981, 1995), Wicksten (1985), Guinot & Bouchard (1998), Castro *et al*. (2003), Guinot & Quenette (2005), Richer de Forges & Ng (2007, 2008), Garassino (2009), Ahyong *et al.* (2009), Naruse & Richer de Forges (2010) and Guinot *et al*. (in press).

Carapace.

– Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (invariably elongated or pyriform in Homoloidea).

– Orbits well protected in Palaeocorystoidea (cornea often external: 'false orbit' *sensu* Wright & Collins 1972: 44; 'plage orbitaire' *sensu* Guinot & Richer de Forges 1995: 303, in Homoloidea).

Pterygostome, endostome and mxp3.

– Endostome elongated ('oxystomian mouth') in Palaeocorystoidea (normal condition in Homoloidea).

– Mxp3 oxystomian condition in Palaeocorystoidea (mxp3 pediform to almost operculiform, never oxystomian in Homoloidea).

Appendages.

– Chelae in Palaeocorystoidea with spiny lower margin (adaptation to burying) (margins smooth, granular, or with small spines on the whole surface but never with row of long spines in Homoloidea).

Thoracic sternum.

– Sternite 2 concealed in Palaeocorystoidea (sternites 1–3 forming a triangle, well visible between mxp3 in Homoloidea).

– Suture 6/7 only lateral in Palaeocorystoidea (complete in Homoloidea).

– Sterno-abdominal depression regularly excavated in Palaeocorystoidea (floor of sterno-abdominal depression with distinctive flat surface in Homoloidea).

Abdomen.

– Male abdomen not longitudinally filling sterno-abdominal depression; telson partially covering sternite 4, leaving anterior portion of sternites 3 and 4 exposed in Palaeocorystoidea (male abdomen entirely covering sterno-abdominal depression, so thoracic sternum not exposed in Homoloidea, except for sternites 1–3 visible between mxp3).

– Telson in Palaeocorystoidea not reaching mxp3 (reaching mxp3 in Homoloidea).

Abdominal holding.

– Paired tooth (double peg) on episternite 5 in Palaeocorystoidea for holding the abdomen (coxal holding by mxp3, P1–P3 in Homoloidea (except in Latreilliidae); presence of 'homoloid press-button' on sternite 4 acting with a socket on abdominal somite 6).

– Mxp3 never involved in abdominal holding in Palaeocorystoidea (base of mxp3 may be used in Homoloidea).

Palaeocorystoidea versus Raninoidea De Haan, 1839

Extant Raninoidea are discussed and listed by e.g. Bourne (1922b), Monod (1956), Gordon (1963, 1966), Gomes Corrêa (1970), Griffin (1970), Serène & Umali (1972), Hartnoll (1979), Goeke (1980, 1981, 1984, 1986), Davie (1989), Werding & Müller (1990), Guinot (1993b), Guinot & Bouchard (1998), Dawson & Yaldwyn (1994, 2000, 2002), Guinot & Quenette (2005), Ahyong *et al.* (2009) and Guinot *et al*. (in press).

Carapace.

– Carapace areolated and generally with cervical groove in Palaeocorystoidea, indistinct in Camarocarcinidae (not areolated, obsolete cervical groove in Raninoidea).

– Anterolateral margin of carapace with multiple teeth or tubercles in Palaeocorystoidea, fewer, however, in Camarocarcinidae (unarmed or with a single tooth or two teeth in Raninoidea).

Pterygostome, endostome and mxp3.

– Coxa of mxp3 large, flabelliform in Palaeocorystoidea (small and flat in Raninoidea).

– Antero-lateral corner of sternite 4 not in contact with pterygostome in Palaeocorystoidea, large coxa of mxp3 intercalated between thoracic sternum and pterygostome, presence of Milne-Edwards openings (sternum/pterygostome junction present, absence of Milne-Edwards openings in Raninoidea, except Marylyreidinae **n. subfam.**).

– Pterygostome with groove and blunt crest in Palaeocorystoidea (groove or crest absent in Raninoidea).

Appendages.

– Pereiopods equally spaced, putatively not separated by sternal extensions in Palaeocorystoidea (sterno-pleural extensions separating P1 and P2, and P2 and P3, thus pereiopods unequally spaced, in Raninoidea).

Thoracic sternum.

– No exposed pleurites in Palaeocorystoidea (pleurites 5–7 partially exposed (‘gymnopleurity’) and calcified in Raninoidea).

– Sterno-pleural extensions absent (present between P1 and P2 and between P2 and P3 in Raninoidea).

– Spermathecal apertures large, oval, separate, thus normal podotreme condition in Palaeocorystoidea (embedded in sternite 7, small, close to each other, deeply recessed in Raninoidea, rarely otherwise).

Abdomen.

– Male abdomen rather long, telson reaching sternite 4, completely flexed under the body and locked in Palaeocorystoidea (short and posterior, telson only reaching sternite 6, not completely flexed and not locked in Raninoidea, except Lyreididae).

Abdominal holding.

– Paired sternal tooth (double peg) on episternite 5 in Palaeocorystoidea (absent in Raninoidea, except in Lyreididae, with two teeth at tip of a short or long hook-like projection formed by extended episternite 5).

Palaeocorystoidea versus Cyclodorippoidea Ortmann, 1892

Extant Cyclodorippoidea are discussed and listed by e.g. Tavares (1991, 1992a, b, 1993a, b, 1994, 1996, 1997, 1998, 1999, 2006), Guinot & Bouchard (1998), Guinot & Quenette (2005), Ahyong *et al.* (2009) and Guinot *et al.* (in press).

Carapace.

– Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (varying from longer than wide but never markedly elongated, to subcircular, wider than long, occasionally expanded posteriorly in Cyclodorippoidea).

Pterygostome, endostome and mxp3.

– Epistome normally visible in Palaeocorystoidea (covered by extended endostome in Cyclodorippoidea, having a complete oxystomian condition in most Cyclodorippidae, but epistome present in Phyllotymolinidae).

– Endostome elongated in Palaeocorystoidea (long, extended and reaching the front, sometimes visible dorsally, except in Phyllotymolinidae, Cymonomidae and some Cyclodorippinae).

– No sternum/pterygostome junction and 'normal' Milne-Edwards openings in Palaeocorystoidea (a sternum/pterygostome junction and absence of Milne-Edwards openings in Cyclodorippidae, which has a complete oxystomian condition, but no junction in Phyllotymolinidae and Cymonomidae).

Appendages.

– Only P5 dorsal and reduced in Palaeocorystoidea (P4 and P5 reduced, usually subchelate, mobile, may be placed on dorsal carapace in Cyclodorippoidea; carrying behaviour described in some species, P4 and P5 are vestigial, reduced to an article in *Elassopodus*).

Thoracic sternum.

– Thoracic sternum rather narrow, not exposed laterally in Palaeocorystoidea (thoracic sternum wide, largely exposed laterally in Cyclodorippoidea).

– No sternal extensions in Palaeocorystoidea (a sternum/branchiostegite junction in Cyclodorippoidea due to extension of episternites between P1 and P2, P2 and P3, variable between P3 and P4).

– Presence of a sterno-abdominal depression in Palaeocorystoidea (usually short, posterior sterno-abdominal cavity, occupying only sternites 5–8 or 6–8, in Cyclodorippoidea).

Abdomen.

– All (6 + telson) abdominal somites free in Palaeocorystoidea (a variable number of abdominal somites fused in Cyclodorippoidea, often with a pleotelson, i.e., somite 6 fused to telson).

– Abdomen with continuous margin in Palaeocorystoidea (various arrangements, often with elongated pleura, in Cyclodorippoidea).

Abdominal holding.

– Sternal paired tooth (double peg) on episternite 5 in Palaeocorystoidea ('sliding system' (Cyclodorippidae) or 'block system' (Phyllotymolinidae) to hold the abdomen; no system known in Cymonomidae; absence of sockets in Cyclodorippoidea).

Palaeocorystoidea versus Etyoidea Guinot & Tavares, 2001

Extinct Etyoidea are discussed and listed by e.g. Carter (1898), Rathbun (1935b), Wright & Collins (1972), Schweitzer Hopkins *et al*. (1999), Guinot & Tavares (2001), Van Bakel *et al.* (2005), Fraaije *et al.* (2008b), Karasawa *et al*. (2008a), Collins & Breton (2009) and Klompmaker *et al*. (2011).

Carapace.

– Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (exceptionally wide in Etyoidea).

– Areolation of dorsal carapace weak in Palaeocorystoidea (marked areolation in Etyoidea).

– Orbits medially uninterrupted in Palaeocorystoidea (widely separated through intercalation of antennular fossae in Etyoidea).

– Front narrow in Palaeocorystoidea (wide in Etyoidea).

– No antennular fossa in Palaeocorystoidea (distinct and large fossa for large basal antennular article in Etyoidea).

Pterygostome, endostome and mxp3.

– Endostome elongated (oxystomian condition) in Palaeocorystoidea (normal condition in Etyoidea).

– Mxp3 oxystomian in Palaeocorystoidea (entirely operculiform in Etyoidea).

Appendages.

– Chelae with spiny lower margin in Palaeocorystoidea for burying (chelae long and slender, without spinose lower margin in Etyoidea).

– Pereiopods 2–4 with flattened articles in Palaeocorystoidea (cylindrical articles in Etyoidea).

Thoracic sternum.

– Shallow, lateral sterno-coxal depressions in Palaeocorystoidea (deep, complete sterno-coxal depressions in Etyoidea).

Abdomen.

– Female abdomen not reaching mxp3 in Palaeocorystoidea (reaching mxp3 in female Etyoidea).

Abdominal holding.

– Male abdomen in contact with coxae but no locking by appendages in Palaeocorystoidea (distinct structures on several pereiopods, P1–P3 may be involved, to hold the abdomen in Etyoidea).

Palaeocorystoidea versus Dakoticancroidea Rathbun, 1917

The extinct Dakoticancroidea are discussed and listed by e.g. Weller (1905), Rathbun (1917, 1923), Kesling & Reimann (1957), Roberts (1962), Bishop (1981, 1988), Vega & Feldmann (1991), Guinot (1993b), Bishop *et al.* (1998) and Artal *et al.* (2008).

Carapace.
– Carapace varying from elongated to subcircular or subhexagonal in Palaeocorystoidea (subquadrate to subrectangular in Dakoticancroidea).
Pterygostome, endostome and mxp3.
– Endostome elongated ('oxystomian mouth') in Palaeocorystoidea (normal condition in Dakoticancroidea).
– Mxp3 oxystomian in condition: distinctly elongated in Palaeocorystoidea (operculiform in Dakoticancroidea).
Appendages.
– Only P5 reduced in Palaeocorystoidea, as in Dakoticancridae (P4 and P5 reduced in Ibericancridae).
– Articles of P2–P4 modified (propodus, dactylus flattened) in Palaeocorystoidea (Cenomanocarcinidae, Palaeocorystidae, unknown condition in others) (pereiopods stronger developed, distal articles not modified in Dakoticancroidea).
Thoracic sternum.
– Thoracic sternum narrow in Palaeocorystoidea (wide in Dakoticancroidea, in which sutures are much longer).
– Thoracic sternum entirely covered in width by abdomen in both sexes in Palaeocorystoidea (laterally exposed in male and even in female Dakoticancroidea).
– Sterno-abdominal depression in Palaeocorystoidea (distinct, rather deep sterno-abdominal cavity in male Dakoticancridae; sterno-abdominal depression towards a cavity in male Ibericancridae).
– Spermathecal apertures elongated, oval in Palaeocorystoidea (circular in Dakoticancroidea).
Abdomen.
– Sexual dimorphism indistinct in Palaeocorystoidea (well-defined, i.e., abdomen much wider in female Dakoticancroidea).
– First abdominal somites in prolongation with the carapace, thus visible in dorsal view, in Palaeocorystoidea (completely folded in Dakoticancroidea).
– Telson as wide as abdominal somite 6 in both sexes of Palaeocorystoidea (telson narrower than abdominal somite 6 in females, but as wide as abdominal somite 6 in males in Dakoticancroidea).
Abdominal holding.
– Sternal paired teeth on episternite 5 near outer lateral margin of thoracic sternum in Palaeocorystoidea (one or more tubercles in the medial part of thoracic sternum, thus at the margin of the sterno-abdominal cavity in Dakoticancroidea).

Monophyly of the Raninoidia

The above comparisons place more emphasis on the considerable diversity displayed by podotremes rather than highlighting the homologous features that they share. With the addition of fossil taxa, both palaeocorystoid and raninoid, the subsection Raninoidia appears to be a diversified, major podotreme subclade which represents a relict fauna, which dates back at least to the Early Cretaceous (Hauterivian, 136.4–130.0 Ma). Modern raninoid faunas comprise merely twelve genera and forty-six species, in contrast with the 196 exclusively fossil species listed by De Grave *et al.* (2009: table 1). The 37 genera listed by Schweitzer *et al.* (2010: 70–78) are, in fact, inaccurate since several podotreme taxa (Necrocarcinidae and Orithopsidae) were included by those authors in Dorippoidea (Eubrachyura; see Schweitzer *et al.* 2010: 80) and therefore not counted. Here counted are 48 extinct genera (see Tables 3 and 6) and 251 nominal extinct species (see Appendix) of Raninoidia; *incertae sedis* are excluded for both.

The Palaeocorystoidea first appears in the Hauterivian with the Necrocarcinidae; the oldest known occurrence of Orithopsidae is late Aptian, that of Palaeocorystidae early Albian, and Cenomanocarcinidae late Albian (Fig. 62). The Palaeocorystidae is assumed to have gone extinct during the late Maastrichtian (Late Cretaceous), whereas Orithopsidae extends into the Oligocene.

Raninoidian diversity is illustrated by the number of new fossil genera (eight) and species (nine) that are erected herein. Moreover, the extinct subfamily Marylyreidinae **n. subfam.** constitutes a transitional form which fills a gap in exhibiting the gymnopleurity of Raninoidea, yet not revealing the junction sternum-pterygostome (and hence exhibiting a different respiratory system from all other raninoids). The Lyreididae is here considered a separate lineage, having retained a relatively long abdomen inserted in the sterno-abdominal depression and held in place by a hook matching a conspicuously long and deep socket (Fig. 36C, D). The socket matching the double peg of Palaeocorystoidea is not exposed in any of the available material.

The interrelationships of the extant Raninoidea have not been studied here but a single family is recognised, as opposed to Lyreididae, namely Raninidae, which comprises Ranininae, Notopodinae, Raninoidinae, Cyrtorhininae and Symethinae. The Cyrtorhininae and Symethinae, which show a number of similarities, are the more basal taxa, and may represent separate sublineages within Raninoidea.

The very long stratigraphic range and diversity of Raninoidia could explain the difficulties encountered when interpreting their morphological organisation and genetics of representatives in nature; many possess derived characters that have evolved since the time of the lineage’s divergence and successive radiations.

The paired spermathecae formed by phragma 7/8, the synapomorphy that supports the monophyly of Podotremata (see below), is a trait shared by all raninoidian taxa, both fossil and extant. Tavares & Franco (2004: 132) recognised two additional synapomorphies: (1) the development in a forward direction of the thoracic sternal suture 7/8, leading to the forward displacement of the spermathecae; (2) the intersegmental phragma 7/8 modified to form the spermathecal bulb. A spermathecal bulb is found only in Dromioidia, so it would be better to describe the chamber, which is found in all Podotremata.

The podotreme spermatheca displays several modalities in shape, size and precise location of its apertures on the sternal surface (Guinot & Tavares 2001: fig. 10). That it invariably involves the same two somites and same skeletal parts has not been contradicted so far. The spermathecal apertures that have been found and examined in several fossil podotreme families are no exceptions: Etyidae (Guinot & Tavares 2001: figs. 2, 3, 10J), Dakoticancridae (Guinot 1993a: figs. 7, 8; Guinot & Tavares 2001: fig. 10H; Artal *et al*. 2008: fig. 3D), Ibericancridae (Artal *et al*. 2008: 17), Cenomanocarcinidae and Palaeocorystidae (present paper; Guinot *et al.* 2008: 719). The same is true for the spermathecal apertures recently discovered in several other podotreme taxa (unpublished data).

The spermathecal apertures observed in Palaeocorystoidea are separate, not recessed, normally located at the extremities of sutures 7/8, as usual in Podotremata. They become displaced and cryptic in the more derived Raninoidea, a primitive condition being supplied by archaic forms such as Lyreididae and Symethinae (Goeke 1981: fig. 2A; Davie 1989: fig. 1c). The key problem, the determination of the evolution of the raninoidian spermathecal structure, has been solved by identifying the polarity of the transformation series: from the plesiomorphic palaeocorystoid character-state (Figs. 57, 58, 59) to the apomorphic character-state of Raninoidea (Fig. 53). The evolution of the peculiar raninoid spermathecae beyond the condition found in the other Podotremata, i.e., how the basal condition of the spermatheca could have evolved into the raninoid one, was discussed by Hartnoll (1979: 82, fig. 5). We agree with Hartnoll (1979: 82) who argued for, ‘a common spermathecal structure for all early Brachyura’, namely Podotremata, including Raninoidea, and concluded that most likely ‘the raninids are not on the direct line leading to the higher Brachyura, and that their spermathecal structure is not relevant to the origin of that of the higher forms’. The raninoid spermathecal apertures, however, are not secondarily acquired openings (see *Spermatheca and spermathecal apertures*). Only their apertures are displaced (Fig. 53) and became cryptic as a result of the strong modifications that affected the whole body; the same major transformation that led to the numerous original features of Raninoidea, exemplified by the gymopleurity (Fig. 42B), a unique brachyuran trait.

The acquisition of particular features in the derived Raninoidea, e.g., the lift of the carapace, the narrowing of the carapace and the thoracic sternum, the shortening and unfolding of the abdomen, the modified respiratory structures with a progressive excavation of the plate formed by the exposed and calcified pleurites 5–7, and the increasing implementation of functional cuticle microstructures, may be followed in the transformation series Palaeocorystoidea–Raninoidea. These transformations are considered adaptations to a highly specialised burying mode of life (see *Modifications for a burying mode of life* above). The survival of the raninoidian clade was dependent of its ability to exploit different environments through geological times, and the implementation of novel features permitted its diversification and increased the number of available ecological areas. Such adaptations have evidently involved a more successful reproduction. An oxystomian condition was already present in all families of Palaeocorystoidea, with the endostome only weakly modified in Necrocarcinidae, here considered the most primitive Palaeocorystoidea (see *Respiration in the Brachyura* above). The general morphology of cenomanocarcinids and orithopsids suggests they were able both to bury and swim, whereas palaeocorystidae were the back-burying specialists, in an evolutionary path leading to Raninoidea.

The monophyly of Raninoidia is supported by: (1) the modification of the distal articles of the P2–P4, the propodi and dactyli being flattened and/or enlarged, constantly with a special shape of the P2–P5 dactyli; (2) the crown-shaped anterior sternites; (3) the abdominal-locking system consisting of a double structure on sternite 5, consisting either of a double peg (Palaeocorystoidea) or a hook-like projection ending in two teeth (Lyreididae), or lost (Raninoidea, except Lyreididae) (see *Diagnosis of the Raninoidia* above).

The male abdomen of Raninoidia is either rather long, folded and locked, filling entirely in width the sterno-abdominal depression (Palaeocorystoidea) or moderately elongated, narrow, filling the total width of the sternal plate and locked (Lyreididae), or short, incompletely flexed, not held, virtually not leaving any sternal space exposed laterally (Raninidae). The characters of Raninidae are in fact plesiomorphic, but a strong specialisation has given rise to a considerable modification. It is hoped that the perennial uncertainty about the nature of Raninoidia is now solved thanks to the study of its extinct component, Palaeocorystoidea, in context of their extant representatives.

Glaessner (1960: 46) suggested that *Notopocorystes*, closer to *Necrocarcinus* than to its known descendants, was the most primitive palaeocorystid, with a common ancestor for *Notopocorystes* and *Necrocarcinus* during Early Cretaceous or even Jurassic times (see also Collins 1997). The oldest Lyreididae (Marylyreidinae **n. subfam.**) and Raninidae are known from about the same date, the late Albian.

Carcinisation and secondary elongation

Carcinisation, which is the phenomenon leading to the evolution to a crab-like body form in the higher Decapoda (von Sternberg 1996; McLaughlin & Lemaitre 1997; McLaughlin *et al.* 2004, 2007; Lemaitre & McLaughlin 2009; Guinot *et al.* in press), is a notion not yet addressed in Raninoidia. Carcinisation in Brachyura involves several anatomical readjustments, mainly the reduction of the relative length of the cephalothorax, flattening of the carapace, broadening of the thoracic sternum and its transformation into a wide plastron, cephalic condensation with folding of sensorial organs (antennules and antennae), modification of orbits and eyestalks with formation and closure of the orbits, excavation of a cavity to receive the abdomen, lateral opening of the arthrodial cavities, expansion of sternite 4 linked with increased strength for the chelipeds and expansion of posterior sternites. The female and male gonopores of Podotremata are located on the appendages (P3 and P5 coxae, respectively), thus the widening of the thoracic sternum in Eubrachyura, which increases the distance between the pereopods coxae and the gonopods, is a determining factor in the evolution of the genital region in both sexes. The female gonopore is no longer located on the appendage (P3 coxa); instead, there is formation of a vulva on sternite 6, whereas the broadening of the posterior half (sternites 7 and 8) in males determines the change of the male gonopore, from the P5 coxa (Heterotremata) to sternite 8 (Thoracotremata). It is clear that there are only two different anatomical arrangements in the female and male Brachyura, without a known continuum between the appendicular and sternal positions, respectively (Guinot *et al.* in press).

It is hypothesised here that a different process of carcinisation occurred in Raninoidia. The evolution in Raninoidea led to a narrowing of the body, including a ventral opening of the arthrodial cavities. This contrasts with the broadening of the body in the usual process of carcinisation of Brachyura, a change in polarity. This phenomenon could be regarded as a secondary elongation. An elongated body often characterises burying crabs, podotremes or eubrachyurans such as Corystidae (see *Modifications for a burying mode of life* above).

Evolution induced also a loss of the anterolateral teeth, often developed in Palaeocorystoidea (e.g., Fig. 7C), and changes in cuticle microstructure roughly varying from upright nodes and/or fungiform nodes (Palaeocorystoidea, Symethinae), pits and upright nodes (Lyreididae) to inclined nodes (other Raninoidea) (Waugh *et al.* 2009; see *Respiration in the Brachyura* and *Modifications for a burying mode of life* above).

The monophyly of the Podotremata

Any interpretation of Raninoidea, like that of other podotremes, must take into account that it belongs to the basal brachyuran group, inherently complex, with a long evolutionary history and a high degree of specialisation leading to major changes of many structures. A number of podotreme subclades are extinct, and the surviving ones are most often in decline. The complexity of Podotremata necessarily increases when extinct taxa are added. The Recent Podotremata, with fewer than 400 species in a hundred genera, represents a small percentage of the whole living brachyuran group (approximately 7,000 valid species and more than 1,300 genera), thus only about 13 % of genera and 18 % of the species (Ng *et al*. 2008, updated; Ng *et al*. 2010; Guinot *et al*. in press). Extant podotremes may be regarded as survivors of a once large and widely distributed group, as demonstrated by the fossil record, with a great number of extinct families, and known since the Jurassic. Moreover, the brachyuran plesion is much more diversified than presently assumed, many taxa having not yet been described, consisting of several major clades. The Recent Raninoidea embraces twelve genera and 46 species, currently assigned to two families, Raninidae and Lyreididae, the latter comprising the subfamilies Lyreidinae and Marylyreidinae **n. subfam.** (Table 1).

Assignment of Raninoidea to the group that includes Dromioidia and Homoloidia is contradicted by molecular data (Spears *et al.* 1993; Ahyong *et al.* 2007; Chu *et al.* 2009), and because the paired spermathecae are ignored as synapomorphy, phylogenetic position of the Raninoidea has become one of the core issues of the monophyly of Podotremata. While the monophyly of the section Eubrachyura and of each of its subsections, Heterotremata and Thoracotremata, is supported by most morphological, larval and molecular data, Podotremata is recovered either as polyphyletic or paraphyletic in molecular studies. Molecular data have been used by many workers, both neontologists and palaeontologists, sometimes leading to suppression of the taxon Podotremata. While the first genetic studies (Spears *et al.* 1993) were largely incomplete, more recent ones were based on several different genes and on a wider taxon sampling. Ahyong *et al*. (2007), who sequenced three raninoids (*Ranina ranina*, *Raninoides louisianensis* and *Symethis corallica*), plus three genera of Cyclodorippoidea, provided a similar paraphyletic Podotremata interpretation. The protein-coding gene tree obtained by Chu *et al.* (2009: 95, figs. 1, 3) similarly supported monophyletic Heterotremata and Thoracotremata, but paraphyletic Podotremata. In the first application of two combined nuclear protein-coding genes (Tsang *et al.* 2008), Podotremata was recovered as basal, monophyletic and inclusive of Raninoidea. This monophyly was, however, weakly supported, the tree being based on only one of the two genes and the taxonomic sampling being limited, with only *Ranina* sequenced and Cyclodorippoidea missing.

Morphologists are unable to comprehend or even measure the root underlying the discordance between the diverse molecular phylogenies (Mooi & Gill 2010). The recently proposed molecular classifications of Brachyura suffer (in comparison to a wealth of accurate morphological data) from relying on a too small a number of genes and too few sequenced taxa, and often lack the most significant representatives. A notable example is the incomprehensible absence of Lyreididae from molecular analyses. Its genetic study would be expected to be the most revealing in exploring raninoid relationships, the family Lyreididae retaining the most ancestral features. Lyreidids are abundant in extant faunas, thus their sequencing should not present any problems. In addition, the very diverse, and possibly paraphyletic, Cyclodorippoidea needs to be tested more comprehensively. The ‘accumulating evidence increasingly’ suggestive of a paraphyletic Podotremata (Ng *et al.* 2009: 16, fig. 4) will need to be substantiated by new genetic sequencing efforts. A new molecular estimation including more raninoid taxa and focused on this clade could show its extreme diversification, and would be a beneficial addition to morphological data for reliable phylogenies.

Numerous authors have recently preferred phylogenies based on molecular analyses, including palaeontologists who are experienced morphologists. It is, nevertheless, a challenge to reconstruct the phylogeny by using the morphology of a wealth of completely preserved fossils at our disposal because fossils turn out to be more informative than previously thought. It is evident that Dromioidia and Homoloidia are basal (although their close common ancestor remains unknown) and that Cyclodorippoidia, which combines a wide thoracic sternum with primitive characters, may appear more similar to Eubrachyura. It should be noted that a developed thoracic sternal plate already evolved in the Cretaceous podotremes, for instance in the extinct Dakoticancroidea, in particular Dakoticancridae (Artal *et al.* 2008), which are indisputably true podotremes (see below).

There are additional views against the monophyly of Podotremata. Some authors, e.g., Rice (1980) and von Sternberg & Cumberlidge (2001), refuted the monophyletic status of the Podotremata by arguing that the initial grouping of Guinot (1977) was based on a symplesiomorphy, the possession of both appendicular female and male gonopores being shared by other Malacostraca. The use of a character at a wrong level of generality (Podotremata, instead of Malacostraca) does not deny the monophyletic status of the group, which is supported by a strong synapomorphy, the paired spermathecae (Guinot 1978; de Saint Laurent 1980; Tavares & Secretan 1993; Guinot & Bouchard 1998; Guinot & Tavares 2001, 2003; Tavares 2003; Guinot & Quenette 2005). Additionally Rice (1980) argued for a closer relationship between Anomura and Podotremata based on larval characters. However, the characters put forward to advocate for a closer relationship between Anomura and Podotremata (partially or collectively) should be discarded on the ground that they are shared plesiomorphies (see Tavares & Franco 2004)

Another serious counterargument to a monophyletic Podotremata is that the podotreme spermatheca is considered unsuitable for phylogenetic purposes (e.g., Ahyong & O'Meally 2004; Scholtz & McLay 2009; Ng *et al.* 2009). The data matrix of Ahyong & O'Meally (2004: 691) included the character 'seminal receptacle' as 'medial', 'absent' or 'paired'. 'Paired seminal receptacles' were considered a synapomorphy of Brachyura, whereas 'in other reptants, the seminal receptacle lies on the sternal midline'. The term 'paired spermatheca' was avoided because of 'its specific reference to the podotreme seminal receptacles' and, consequently, the rather different structures, namely the vulvae and spermathecae, have been confused. This leads to an interpretation of all brachyurans as having the same kind of seminal receptacle, which is not correct.

The phylogenetic 'tree' of Scholtz & McLay (2009: 419) was obtained 'by hand and brain following a Hennigian approach', a method that is perhaps too subjective and based too much on *a priori* decisions. Their discussion (Scholtz & McLay 2009: 418, 431, 432) is far from clear, as exemplified by diverse startling assertions: the spermatheca 'is restricted to podotrematan representatives, but it suffers from a problematic polarization because nothing comparable exists in other reptant groups' and 'the seminal receptacle and spermathecae may not be homologous structures, so the derivation of one from other is difficult'. The opinion that the eubrachyuran condition (sternal vulvae) might be derived from that found in podotremate groups (with coxal female gonopores and spermatheca) was discussed and rejected by Hartnoll (1979). We share Hartnoll's conclusion and assume that the separation of Podotremata and Eubrachyura is based on the fact that the female vulva and the spermatheca are not homologous. The region for sperm storage in Brachyura indiscriminately referred to as 'spermatheca' by many authors actually concerns two anatomically different organs. It creates a false homology to group under the same term the two structures for storage of sperm, the spermatheca and seminal receptacle, which only have a similar function. We appeal for restriction of the use of 'spermatheca' to the independent structure of the podotremes, always formed by phragma 7/8 and with its aperture located at the extremity of the sternal suture 7/8. We thus disagree with the statement 'spermathecae connected to the oviducts and internal fertilization' employed for Eubrachyura by Scholtz & McLay (2009: 431). 'Seminal receptacle' must be applied only to the eubrachyuran structure, directly connected to, and thus part of, the female gonad.

To support the molecular results of Ahyong *et al.* (2007) and Chu *et al.* (2009), Ng *et al.* (2009: 16, fig. 5) suggested that the podotreme spermatheca was only 'a feature retained by successive podotreme clades and then lost with derivation of the eubrachyuran synapomorphies' and that 'internalization of the spermatheca is therefore an innovation in the stem brachyuran [*sic*], but not a synapomorphy supporting Podotremata'. The assertion by Ng *et al.* (2009) is insufficient and requires a more detailed explanation. What Ng *et al.* (2009) were referring to were probably the various patterns of the podotreme spermathecae figured by Guinot & Tavares (2001: fig. 10; see also Gordon 1950; Guinot & Quenette 2005), not detracting its homology but only underlining four main patterns: a basal one in Dromioidia, more primitive in Dynomenidae and Sphaerodromiinae than in Dromiinae (see Tavares & Franco 2004); another one, also basal, in Homoloidia (Gordon 1950; Garassino 2009); another one in Raninoidia; and more than one in the poorly known Cyclodorippoidia. All these patterns are variations of the same basic architecture, which is a secondary specialisation of the intersegmental phragma 7/8, a split between its two skeletal plates, one derived from sternite 8 and the other one from sternite 7, leading to sternal modifications at the limit of the two adjacent somites 7 and 8 in females.

Claims that Podotremata is paraphyletic (Ahyong *et al.* 2007; Brösing *et al.* 2007; Ng *et al.* 2009; Scholtz & McLay 2009; Bracken *et al.* 2009; De Grave *et al.* 2009; Karasawa *et al.* 2011), or even polyphyletic (Spears *et al.* 1993) do not provide new information and are not supported by strong data. The conclusion of Scholtz & McLay (2009: 431, 432) that, 'the Cyclodorippoidea is the sister group to the Eubrachyura', is supported only by weak data. The cladistic analysis of Karasawa *et al.* (2011), which includes extinct and extant brachyuran taxa, is based on a data matrix with a great number of unknown character states and several characters that are insufficiently informative since many fossil crabs do not preserve all ventral characters. In addition, several erroneous observations are found in their character matrix. Combined morphological and molecular studies which demonstrate that the podotreme spermatheca is not a synapomorphy have not yet been conducted.

The deliberate use of restricted morphological sources (as opposed to the integration of all characters, i.e., the holomorphology) for phylogenetic inference, such as the foregut-ossicle system (Brösing *et al.* 2007; Brösing 2008), imposes too many limitations (as in some molecular analyses) in attempts to recover monophyly. Despite providing interesting data on foregut ossicles, this interpretation of Podotremata as paraphyletic does not come as a surprise. Some other conclusions concerning Eubrachyura, e.g., the interpretation of Palicidae as a basal taxon of Thoracotremata (Brösing *et al*. 2007: 28; Brösing 2008: 281), are inconsistent with a substantial body of adult and larval morphology and even with recent molecular data, so that some doubt is cast upon the interpretation of the foregut ossicle data, mainly for other higher-level taxa (see Guinot *et al*. in press).

Taxonomic levels

The proposed suppression of Podotremata (Ahyong *et al.* 2007, 2009; Ng *et al.* 2009: 16, figs. 4, 5; see also De Grave *et al.* 2009: 5, 7, 8, table 1; Schweitzer *et al.* 2010: 57) is not only unjustified (see above), but also implies giving a similar rank to the section Eubrachyura and their three podotreme 'sections', Dromiacea, Raninoida and Cyclodorippoida. We do not agree with such a classification structure. From a conceptual and nomenclatural point of view, these three podotreme 'sections', to which a fourth, representing the homoloid clade, must be added, are not equivalent to section Eubrachyura. It is true that the International Code of Zoological Nomenclature (ICZN 1999) does not regulate the 'Section' and 'Subsection' categories, and only mentions five ranks in the 'family-group', from superfamily to subtribe, for which it provides standardised endings (Art. 29, 35.1). For higher-level taxa above the superfamily (suffix -oidea) within the infraorder Brachyura, we use 'subsection' as an additional podotreme rank, as did Guinot *et al*. (2008), to which we apply the oldest available family group name, thus meeting the Principle of Priority of the Code (Art. 23). The same suffix -oidia, applied to these subsections, constituted a mandatory change in spelling (Art. 34.1). It is particularly appropriate to designate as subsections the taxa above the superfamilies within the highly diversified podotreme crabs, and especially when new higher-level taxa, based on a wealth of fossil material, are included.

Proposed scheme

An alternative scheme is therefore proposed herein: a section Podotremata comprising four subsections (Dromioidia, Cyclodorippoidia, Raninoidia, and Homoloidia), alongside a section Eubrachyura, its sister group (Table 2). We consider indispensable the separation of a distinct clade, Homoloidia, distinct from Dromioidia, contrary to recent classifications by Martin & Davis (2001), Ahyong *et al*. (2007, 2009), Ng *et al*. (2009), De Grave *et al*. (2009) and Schweitzer *et al.* (2010), both which were accepted by Števčić (2005), Karasawa *et al*. (2009, 2011) and Scholtz & McLay (2009). A number of morphological characters, as well as spermatological and larval traits, support a homoloidian clade (see *Comparison of the superfamily Palaeocorystoidea with other podotreme superfamilies, Palaeocorystoidea* versus *Homoloidea De Haan, 1839* above). According to Rice (1980: 293, fig. 8), the Homoloidea diverged from the primitive brachyuran line at an early stage, the phylogenetic tree showing 'a close alliance between the raninids and the homolids'. Interestingly, according to Williamson (1965: 394), the short antennal spine of the raninid zoeae resembled that found in most anomurans and dromiids, representing a more primitive state than that of homolids and eubrachyurans, in contrast with many other raninid zoeal characters that indicated a more derived level than the homolids. Other larval characters, however, are in favour of an alliance of Raninidae and Homolidae (Rice 1980: 291, 295). These conflicting traits are indicative of the complex situation of extant Raninoidea, albeit in favour of its podotreme affinities.

Only the future discovery of two or more origins for Podotremata could demonstrate its polyphyly. To determine if Podotremata is paraphyletic, we need to know if Eubrachyura is nested within the podotremes, thus having evolved from within the podotremes, as supported by several molecular studies, but not yet resolved by recent histological and morphological studies (see McLay & López Greco 2011). It should be noted that Linnean classification without paraphyletic taxa is practically impossible. It is well known that paraphyletic taxa are inevitable for classifying earlier representatives of a large group, the early Decapoda, that would evolve into the Brachyura cannot be easily placed in any monophyletically defined podotreme clades. Paraphyletic taxa also provide information on significant changes in morphology, ecology and other aspects of the biology of organisms. A paraphyletic Podotremata is therefore a valuable hypothesis and will continue to generate interesting studies of the most primitive crabs.

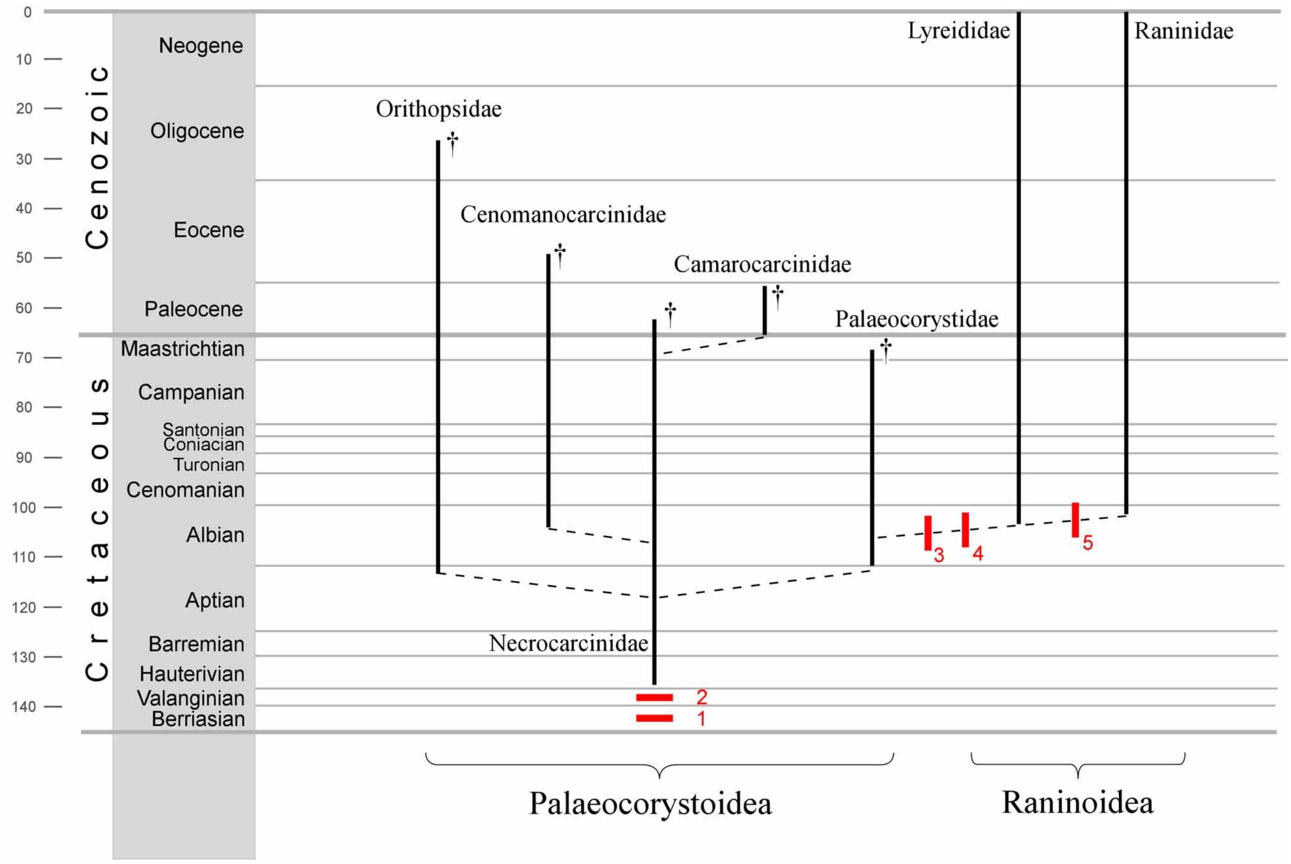

FIGURE 62. Hypothetical phylogeny of Raninoidia, with the various characters numbered as follows: 1. Paired spermathecae dependent of phragma 7/8 (symplesiomorphy of Raninoidia with Podotremata); 2. Paired structure (double peg or hook with two spines) on episternite 5 involved in abdominal holding (preserved in Lyreididae, lost in all other Raninoidea) (synapomorphy of Raninoidia); 3. Gymnopleurity (synapomorphy of Raninoidea); 4. Modified position of spermathecal apertures (synapomorphy of Raninoidea); 5. Abdomen not held against body (synapomorphy of Raninidae).

Podotreme clades

The section Podotremata embraces a number of clades in extant faunas, at least four main large ones, here considered subsection rank: Dromioidia, Homoloidia, Cyclodorippoidia and Raninoidia (Table 2). These subsections are very diverse, Cyclodorippoidia being the least well known and with a very meagre fossil record. Raninoidia consists of two superfamilies, the extinct Palaeocorystoidea (Fig. 56) and Raninoidea, both extinct and extant (Table 1).

The Podotremata had its origins in the Jurassic, and Homolodromioidea, Glaessneropsoidea (Schweitzer & Feldmann 2010c) and Homoloidia (Collins 1998) all have a robust fossil record. Uncertainties nevertheless remain, the ventral surface being largely unknown for these groups. The Dynomenidae is supposed to have appeared during the Late Jurassic (McLay 1999; Guinot 2008; Jagt *et al*. 2010). Despite recent progress, the traits of most fossil Dromiidae remain too poorly known for an accurate placement. This is exemplified by the case of *Basinotopus* McCoy, 1849, traditionally assigned to Dromiidae (McCoy 1849; Bell 1858; Collins 2003; Collins & Jakobsen 2004; Beschin *et al.* 2005), but recently referred to Dynomenidae (De Grave *et al*. 2009; Schweitzer *et al*. 2010) and even to a separate family, Basinotopidae Karasawa, Schweitzer & Feldmann, 2011. The reduced and dorsal P4 and P5 as well as the uropods on the male and female abdomens (McCoy 1849; Bell 1858; see Guinot & Tavares 2001) of the type species, *B. lamarckii* (Desmarest, 1822), could actually belong to a typical dromiid. However, recent discoveries of more complete specimens of the Eocene *B. tricornis* Collins & Jakobsen, 2004, reveal particular sternal characters (Collins & Jakobsen 2004: 69, text-fig. 3, pl. 2, figs. 1–7), so a new interpretation based on all known data is required. It is true that dromiids, with their developed and specialised uropods that are often used for the abdominal holding, are less 'primitive' than supposed. However, the Eocene as the earliest occurrence of dromiids suggested by Glaessner (1969) appears too late. The Sphaerodromiinae Guinot & Tavares, 2003 is considered the most ancient; Hypoconchinae Guinot & Tavares, 2003 are hitherto absent in the fossil record.

Schweitzer & Feldmann (2010d) elevated Sphaerodromiinae to family level. These authors nevertheless listed the same plesiomorphic morphological characters of Sphaerodromiidae, which Guinot & Tavares (2003) had defined in establishing the subfamily, and did not recognise any synapomorphies. The hierarchical rank of Sphaerodromiinae must be determined in conformity with the level of generality of characters in the related groups, thus Homolodromiidae, Dromiidae and Dynomenidae. For the time being, we prefer to treat Sphaerodromiinae as a dromiid subfamily.

The relationships between the podotreme clades are poorly understood. The Dromioidia and Homoloidia may be considered as basal, having a long abdomen entirely filling the sterno-abdominal depression transversely (only a narrow exposed space may be present in Dynomeninae and Latreilliidae), and completely in length (Homolodromioidea, Homoloidia, Dromiidae *pro parte*) or nearly so (Dromiidae *pro parte).* The fossil record of podotreme crabs certainly holds the key to clarification of the phylogeny of Podotremata.

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APPENDIX. Systematic list of the subsection Raninoidia.

Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Subsection Raninoidia De Haan, 1839 emend.
Superfamily Palaeocorystoidea† Lőrenthey *in* Lőrenthey & Beurlen, 1929 new status

Family Palaeocorystidae† Lőrenthey *in* Lőrenthey & Beurlen, 1929 new status

Genus *Cenocorystes*† Collins & Breton, 2009

Cenocorystes bretoni† **n. sp.** [lower Cenomanian, northwestern France]
Cenocorystes fournieri† Collins & Breton, 2009 [Collins & Breton 2009: 46, figs. 5–7, lower Cenomanian, northwestern France]

Genus *Cretacoranina* Mertin, 1941

Cretacoranina fritschi† (Glaessner, 1929) [Glaessner 1929a: 155, pl. 10, fig. 5 (as *Notopocorystes*), middle Turonian, Bohemia (Czech Republic), Germany]
Cretacoranina schloenbachi† (Schlüter, 1879) [Schlüter 1879: 612, pl. 18, fig. 2, 2a (as *Raninella*), upper Coniacian–lower upper Maastrichtian; northern Germany, ?southern England, northeastern Belgium, northern Spain]
Cretacoranina cf. *schloenbachi*† sensu Förster 1970 [Förster 1970: 139, text-fig. 4A, pl. 17, fig. 3 (as *Notopocorystes* (*Cretacoranina*)), ?lower Santonian, southern Germany]
Cretacoranina testacea† (Rathbun, 1926) [Rathbun 1926b: 190, pl. 68, figs. 1–4 (as *Raninella*), upper Campanian–Maastrichtian, Delaware, New Jersey, Tennessee, USA, lower Maastrichtian, Mississippi, USA (see Bishop, 1983b)]
Cretacoranina trechmanni† (Withers, 1927) [Withers 1927: 12, text-fig. 1, pl. 7, figs. 1, 2. (as *Ranina*), ?Campanian (Maastrichtian according to Morris 1993), Jamaica (*Raninella trechmanni* in Tucker 1995)]

Genus *Eucorystes* Bell, 1863

Eucorystes carteri† (McCoy, 1854) [McCoy 1854: 118, pl. 4, fig. 3 (as *Notopocorystes*), upper Albian, southern England, France, Switzerland]
Eucorystes eichhorni† (Bishop, 1983) [Bishop 1983a: 905, figs. 5, 6 (as *Notopocorystes* (*Eucorystes*)), upper Campanian, Montana, USA]
Eucorystes intermedius† Nagao, 1931 [Nagao 1931: 207, pl. 14, fig. 4, 4a (as *Notopocorystes* (*Eucorystes*)), Cenomanian–Santonian, Japan]
Eucorystes exiguus† (Glaessner, 1980) [Glaessner 1980: 175, fig. 4, 4a (as *Notopocorystes* (*Cretacoranina*)), Cretaceous (= lower Cenomanian; see Collins 1997), Northern Territory, Australia]
Eucorystes ligulatus† Wright & Collins, 1972 [Wright & Collins 1972: 82, pl. 16, fig. 4 (as *Notopocorystes* (*Eucorystes*) *carteri ligulatus*), uppermost Albian, England [stated to have been overlooked by Tucker (1998) [see Collins, 2003: 84], but synonymised with *E. carteri* by Tucker (1995)]
Eucorystes mangyshlakensis† Ilyin & Pistshikova *in* Ilyin, 2005 [Ilyin 2005: 210, text-fig. 39B, pl. 10, figs. 1, 2 (as *Notopocorystes* (*Eucorystes*)), lower Albian, Kazakhstan]
Eucorystes oxtedensis† Wright & Collins, 1972 [Wright & Collins 1972: 79, text-fig. 11c, pl. 16, figs. 1, 2 (as *Notopocorystes* (*Eucorystes*)), lower Albian, southern England]
Eucorystes iserbyti† **n. sp.** [middle Albian, northern France]
Eucorystes navarrensis† **n. sp.** [Albian, northern Spain]

Genus *Ferroranina*† n. gen.

Ferroranina australis† (Secretan, 1964) [Secretan 1964: 158, text-figs. 90, 91, 92 (right), 97 (left), pl. 18, figs. 1–3 (as *Notopocorystes*), upper Santonian–lower Campanian, Madagascar]
Ferroranina denisae† (Secretan, 1964) [Secretan 1964: 162, text-figs. 93–96, 97 (right), pl. 18, figs. 4–7 (as *Notopocorystes*), lower–upper Campanian, Madagascar]
Ferroranina dichrous† (Stenzel, 1945) [Stenzel 1945: 438, text-fig. 13, pl. 43, figs. 5–7 (as *Notopocorystes*), Turonian, Texas, USA]
Ferroranina cf. *dichrous*† sensu Vega *et al*. 2007 [Vega *et al*. 2007a: 418, figs. 9.6–9.8 (as *Cretacoranina*), lower–middle Turonian, Mexico]

Ferroranina tamilnadu† **n. sp.** [middle Cenomanian, India; see Guinot *et al*. 2008: 712, fig. 9C (as *Cretacoranina* cf. *dichrous*)]

Genus *Joeranina*† n. gen.

Joeranina broderipii† (Mantell, 1844) [Mantell 1844: 532, 534, text-fig. 115/3 (as *Corystes*), middle–upper Albian–?Cenomanian, southern England, northern and central France, Switzerland]

Joeranina gaspari† **n. sp.** [Albian, northern Spain]

Joeranina harveyi† (Woodward, 1896) [Woodward 1896: 225, fig. 4 (as *Palaeocorystes*), Cenomanian, British Columbia, USA (upper Santonian/lower Campanian according to Collins 1997) (Schweitzer *et al*. 2003a: 24, as *Eucorystes harveyi*)]

Joeranina japonica† (Jimbô, 1894) [Jimbô 1894: 101, pl. 9, fig. 7 (as *Eucorystes*), Cenomanian–Santonian, Japan (Collins *et al*. 1993: 300, as *Notopocorystes* (*Notopocorystes*) *japonica*)]

Joeranina paututensis† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 30, fig. 17a, b (as *Notopocorystes* (*Cretacoranina*)), upper Santonian or lower Campanian, West Greenland]

Joeranina platys† (Schweitzer & Feldmann, 2002) [Schweitzer & Feldmann 2002b: 199, figs. 15, 16 (as *Eucorystes*), Albian, Oregon, USA]

Joeranina syriaca† (Withers, 1928) [Withers 1928: 459, pl. 13, figs. 1, 2 (as *Notopocorystes*), Cenomanian, Syria]

Joeranina cf. *syriaca*† sensu Wright & Collins, 1972 [Wright & Collins 1972: 84 (as *Notopocorystes* (*Cretacoranina*)), lower Cenomanian, southern England]

Joeranina sp.† sensu Van Straelen, 1931 [Van Straelen 1931: 56, pl. 2, fig. 39 (as *Notopocorystes* sp.), Cenomanian, Madagascar]

Genus *Notopocorystes*† McCoy, 1849 (= *Palaeocorystes*† Bell, 1863)

Notopocorystes bituberculatus† Secretan, 1964 [Secretan 1964: 155, text-fig. 86; pl. 18, figs. 8, 9, Albian, Madagascar]

Notopocorystes normani† (Bell, 1863) [Bell 1863: 16, pl. 3, figs. 10–12 (as *Palaeocorystes*), Cenomanian, southern England, northern Germany, northern France, Kazakhstan]

Notopocorystes praecox† Wright & Collins, 1972 [Wright & Collins 1972: 75, pl. 13, fig. 4a–c (as *Notopocorystes* (*Notopocorystes*) *stokesii praecox*), lower Albian, southern England]

Notopocorystes serotinus† Wright & Collins, 1972 [Wright & Collins 1972: 76, pl. 14, figs. 3–6, pl. 22, fig. 7 (as *Notopocorystes* (*Notopocorystes*) *stokesii serotinus*), uppermost middle–upper Albian, southern and eastern England]

Notopocorystes stokesii† (Mantell, 1844) [Mantell 1844: 533, text-fig. 115/2 (as *Corystes*), middle Albian, southern England, France, Switzerland]

Notopocorystes xizangensis† Wang, 1981 [Wang 1981: 352, text-fig. 4, pl. 2, fig. 1a–c, upper Lower Cretaceous, Xizang, China; ?lower/middle Albian, central Iran (Yazdi *et al*. 2009: 73, pl. 2, figs. 6–11)]

Family Camarocarcinidae† Feldmann, Li & Schweitzer, 2008

Genus *Camarocarcinus*† Holland & Cvancara, 1958

Camarocarcinus arnesoni† Holland & Cvancara, 1958 [Holland & Cvancara 1958: 499, text-figs. 2, 3a, b, pl. 74, figs. 1–14, Paleocene, North Dakota, USA]

Camarocarcinus obtusus† Jakobsen & Collins, 1979 [Jakobsen & Collins 1979: 63, pl. 1, figs. 3–5, upper Paleocene, eastern Denmark]

Camarocarcinus quinquetuberculatus† Collins & Wienberg Rasmussen, 1992 [Collins & Wienberg Rasmussen 1992: 33, fig. 19a–e, middle Paleocene, West Greenland]

Family Cenomanocarcinidae† Guinot, Vega & Van Bakel, 2008

Genus *Campylostoma*† Bell, 1858

Campylostoma matutiforme† Bell, 1858 [Bell 1858: 23, pl. 3, figs. 8–10, lower Eocene, southern England; Eocene, northern Germany]

Genus *Cenomanocarcinus*† Van Straelen, 1936 (= *Sagittiformosus*† Bishop, 1988)

Cenomanocarcinus beardi† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 [Schweitzer *et al.*

2003a: 38, figs. 12.1–12.4, Cenomanian, Texas, USA; upper Turonian–Santonian, British Columbia, Canada]

Cenomanocarcinus cantabricus† **n. sp.** [Albian, northern Spain]

Cenomanocarcinus dissimilis† Collins, 2010 [Collins 2010: 15, fig. 1.4, lower Cenomanian, southeastern Nigeria]

Cenomanocarcinus inflatus† (A. Milne-Edwards MS *in* Guillier 1886) [Van Straelen 1936: 37, pl. 4, fig. 8, upper Cenomanian–Turonian, northern France (= *Cenomanocarcinus hierosolymitanus*† Avnimelech, 1961 [Avnimelech, 1961: 1, figs. 3, 4, upper Cenomanian, Israel; as *Cenomanocarcinus* cf. *vanstraeleni*† by Remy & Avnimelech, 1955: 314)]

Cenomanocarcinus multituberculatus† (Joleaud & Hsu, 1935) [Joleaud & Hsu 1935: 107, fig. 10 (as *Campylostoma*), 'Senonian', Niger]

Cenomanocarcinus oklahomensis† (Rathbun, 1935) [Rathbun 1935b: 44, pl. 11, fig. 9 (as *Necrocarcinus*), upper Albian, Oklahoma and Texas, USA]

Cenomanocarcinus pierrensis† (Rathbun, 1917) [Rathbun 1917: 389, pl. 33, figs. 4, 5 (as *Campylostoma pierrense*), upper Campanian–lower Maastrichtian, South Dakota, USA (as *Necrocarcinus* by some authors; compare Guinot *et al*. 2008)]

Cenomanocarcinus tenuicarinatus† Collins, 2010 [Collins 2010: 15, fig. 1.3, lower Turonian, southeastern Nigeria]

Cenomanocarcinus vanstraeleni† Stenzel, 1945 [Stenzel 1945: 447, text-fig. 15, pl. 44, figs. 1–6, Cenomanian–lower Turonian, Texas, USA (= *Ophthalmoplax spinosus*† Feldmann, Villamil & Kauffman, 1999 [Feldmann, Villamil & Kauffman, 1999: 96, figs. 3.1, 3.2, 4.1, 4.2, middle Turonian, New Mexico (see Bishop 1986a: 135; Toolson & Kues 1996); lower–middle Turonian, Mexico; upper Albian, Colombia; lower Turonian, Colombia (see Vega *et al*. 2010: 270)]

Cenomanocarcinus aff. *vanstraeleni*† sensu Guinot *et al*. 2008 [Guinot *et al*. 2008: 694, fig. 6, Coniacian, Colombia]

Cenomanocarcinus† sp. sensu Vega *et al*. 2010 [Vega *et al*. 2010: 274, fig. 8.16, Campanian, Mexico]

Genus *Hasaracancer*† Jux, 1971

Hasaracancer cristata† Jux, 1971 [Jux 1971: 158, text-fig. 2, pl. 17, figs. 1–7, upper Campanian, Afghanistan]

Hasaracancer merijaensis† Ossó-Morales, Artal & Vega, 2011 [Ossó-Morales *et al.* 2011: 2, figs. 5, 6, upper Campanian, Morocco]

Hasaracancer renfroae† (Stenzel, 1945) [Stenzel 1945: 443, text-fig. 15, pl. 41, fig. 13 (as *Necrocarcinus*), upper Albian, Texas, USA, Colombia (see Guinot *et al.* 2008: 698, fig. 8A–D; Vega *et al*. 2010: 272, figs. 8.6–8.12)]

Family Necrocarcinidae† Förster, 1968

Subfamily Necrocarcininae† Förster, 1968

Genus *Cretacocarcinus*† Feldmann, Li & Schweitzer, 2008

Cretacocarcinus smithi† Feldmann, Li & Schweitzer, 2008 [Feldmann *et al.* 2008: 1747, figs. 4.1, 4.6, 4.7, Campanian, Manitoba, Canada]

Genus *Marycarcinus*† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

Marycarcinus hannae† (Rathbun, 1926) [Rathbun 1926: 84, pl. 18, figs. 1, 2 (as *Necrocarcinus*), Eocene, Oregon and California, USA (Schweitzer & Feldmann 2000: 242, figs. 11, 12)]

Genus *Necrocarcinus*† Bell, 1863

Necrocarcinus? *bispinosus*† Segerberg, 1900 [Segerberg 1900: 26 (372), pl. 3, fig. 7, lower Paleocene, southern Sweden]

Necrocarcinus davisi† Bishop, 1985 [Bishop 1985: 619, figs. 3.6, 3.10–3.12, lower Campanian, South Dakota, USA]

Necrocarcinus inornatus† Breton & Collins, 2011 [Breton & Collins 2011: 147, fig. 6, lower Cenomanian, northern France]

Necrocarcinus labeschii† (J.A. Deslongchamps, 1835) [J.A. [Eudes-] Deslongchamps 1835: 40, pl. 1, figs. 7, 8 (as *Orythia*, incorrect spelling), (?upper Aptian) lowermost Albian–middle Cenomanian, southern England, northern France; upper Albian, southwestern Crimea, Ukraine (= *N. bodrakensis*† Levitskyi, 1974: 115, pl. 2, fig. 4, pl. 3, fig. 3; see Ilyin 2005: 199]

Necrocarcinus oklahomensis† Rathbun, 1935 [Rathbun 1935b: 44, pl. 11, fig. 9, upper Albian, Texas, USA]

Necrocarcinus olsonorum† Bishop & Williams, 1991 [Bishop & Williams 1991: 452, figs. 1–5, 6B, Turonian, South Dakota and Wyoming, USA]

Necrocarcinus rathbunae† Roberts, 1962 [Roberts 1962: 181, pl. 85, fig. 12, pl. 87, figs. 1, 2, lower Campanian, New Jersey and Delaware, USA]

Necrocarcinus senonensis† Schlüter *in* von der Marck & Schlüter, 1868 [von der Marck & Schlüter 1868: 297, pl. 44, fig. 3, Santonian–upper Campanian, northern Germany; lower Paleocene, central Poland, Denmark (= *N. insignis*† Segerberg, 1900: 26 (372), pl. 3, figs. 1, 6)]

Necrocarcinus cf. *senoniensis*† [*sic*] sensu Mertin 1941 [Mertin 1941: 239, text-fig. 27b, pl. 8, figs. 13, 14, 'Untersenon', northern Germany]

Necrocarcinus tauricus† Ilyin & Alekseev, 1998 [Ilyin & Alekseev 1998: 46, figs. 1a, 2b, upper Albian, southwestern Crimea (see Ilyin 2005: 201–203)]

Necrocarcinus texensis† Rathbun, 1935 [Rathbun 1935b: 45, pl. 11, figs. 20–22 uppermost Albian–?lowermost Cenomanian, Texas, USA]

Necrocarcinus undecimtuberculatus† Takeda & Fujiyama, 1983 [Takeda & Fujiyama 1983: 133, text-fig. 3, pl. 1, figs. 1, 2, upper Aptian, northern Japan]

Necrocarcinus woodwardii† Bell, 1863 [Bell 1863: 20, pl. 4, figs. 1–3 (*non* pl. 5, figs. 4–7), upper Albian–lower Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Necrocarcinus wrighti† Feldmann, Tshudy & Thomson, 1993 [Feldmann *et al.* 1993: 35, figs. 29.1–5, 30, lower Campanian–?lowermost Maastrichtian, James Ross Basin, Antarctica]

Genus *Protonecrocarcinus*† Förster, 1968

Protonecrocarcinus ovalis† (Stenzel, 1945) [Stenzel 1945: 442, text-figs. 14, 15, pl. 41, figs. 7–9 (as *Necrocarcinus*?), upper Cenomanian, Texas, USA; upper Turonian, New Mexico, USA]

Subfamily Paranecrocarcininae† Fraaije, Van Bakel, Jagt & Artal, 2008

Genus *Glyptodynomene*† Van Straelen, 1944

Glyptodynomene alsasuensis† Van Straelen, 1944 [Van Straelen 1944: 10, pl. 1, fig. 4, 4a, upper Albian–lower Cenomanian, northern Spain]

Genus *Paranecrocarcinus*† Van Straelen, 1936 (= *Pseudonecrocarcinus*† Förster, 1968)

Paranecrocarcinus balla† **n. sp.** [Cenomanian, France; see A. Milne-Edwards *in* Guillier 1886: 244, as *Necrocarcinus minutus*† (*nomen nudum*)]

Paranecrocarcinus biscissus† Wright & Collins, 1972 [Wright & Collins 1972: 71, text-fig. 10b, pl. 22, fig. 6 (as *Paranecrocarcinus* (*Pseudonecrocarcinus*)); lower–middle/upper Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Paranecrocarcinus digitatus† Wright & Collins, 1972 [Wright & Collins 1972: 69, text-fig. 10a, pl. 12, fig. 7a–c, lower Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Paranecrocarcinus foersteri† Wright & Collins, 1972 [Wright & Collins 1972: 70, pl. 22, fig. 5a–c, lower–middle Cenomanian, southern England, northern France (see Breton & Collins 2011)]

Paranecrocarcinus gamma† Roberts, 1962 [Roberts 1962: 182, pl. 85, figs. 7, 8, 11, lower Campanian, New Jersey, USA]

Paranecrocarcinus graysonensis† (Rathbun, 1935) [Rathbun 1935b: 45, pl. 11, figs. 23–25 (as *Necrocarcinus*), upper Albian, Texas, USA (= *Necrocarcinus scotti*† Stenzel, 1945: 445, text-fig. 15, pl. 41, figs. 10, 11; see Förster 1968: 173)]

Paranecrocarcinus hexagonalis† Van Straelen, 1936 [Van Straelen 1936: 36, pl. 4, figs. 6, 7, Hauterivian, northern France (see Förster 1970: figs. 2A, 3A)]

Paranecrocarcinus libanoticus† Förster, 1968 [Förster 1968: 171, pl. 13, fig. 1, Cenomanian, Lebanon, northern France, southern England (see Breton & Collins 2011)]

Paranecrocarcinus milbournei† Collins, 2010 [Collins 2010: 16, figs. 1.5–1.8, Cenomanian, southeastern Nigeria]

Paranecrocarcinus moseleyi† (Stenzel, 1945) [Stenzel 1945: 441, text-fig. 15, pl. 41, fig. 12 (as *Necrocarcinus*), uppermost Albian–lowermost Cenomanian, Texas, USA]

Paranecrocarcinus mozambiquensis† Förster, 1970 [Förster 1970: 135, text-figs. 2B, 3B, pl. 17, fig. 4, lower Cenomanian, southern Mozambique]

Paranecrocarcinus olssoni† (Rathbun, 1937) [Rathbun 1937b: 26, pl. 5, fig. 6 (as *Dakoticancer*), Barremian, Colombia (in Feldmann *et al*. 1999: 91 as *Necrocarcinus olssoni*; in Vega *et al.* 2010: 276 as *Orithopsis tricarinata*, age indicated as upper Aptian and upper Albian)]

Paranecrocarcinus pulchellus† (Secretan, 1964) [Secretan 1964: 169, figs. 98, 99, pl. 19, fig. 7 (as *Dromiopsis*), Cenomanian, Madagascar]

Paranecrocarcinus pusillus† Breton & Collins, 2011 [Breton & Collins 2011: 150, figs. 10, 11, lower Cenomanian, northern France, southern England]

Paranecrocarcinus quadriscissus† (Noetling, 1881) [Noetling 1881: 368, pl. 20, fig. 4a, b (as *Necrocarcinus*), upper Maastrichtian, southeastern Netherlands, northeastern Belgium (= *Dromiopsis ubaghsi* Forir, 1889: 452, pl. 14, fig. 3)

Paranecrocarcinus stenzeli† (Bishop, 1983) [Bishop 1983c: 49, text-fig. 8B, pl. 1, figs. 3–5 (as *Pseudonecrocarcinus*), lower Albian, Texas, USA (see Bishop 1986a: 136)]

Paranecrocarcinus vanbirgeleni† Fraaije, 2002 [Fraaije 2002: 916, figs. 1.3, 3.1, 3.2, upper Maastrichtian, southeastern Netherlands]

Genus *Shazella*† Collins & Williams, 2005

Shazella abbotsensis† Collins & Williams, 2005 [Collins & Williams, 2005: 33, fig. 1, ?middle/upper Turonian, southern England]

Family Orithopsidae† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

Genus *Cherpiocarcinus*† Marangon & De Angeli, 1997

Cherpiocarcinus rostratus† Marangon & De Angeli, 1997 [Marangon & De Angeli 1997 : 102, text-fig. 2, pl. 1, figs. 1, 2, middle Oligocene, northern Italy]

Genus *Orithopsis*† Carter, 1872

Orithopsis angelica† (Fraaije, 2002) [Fraaije 2002: 914, figs. 1.1, 1.2 (as *Necrocarcinus*), upper Maastrichtian, southeastern Netherlands]

Orithopsis carinata† (Feldmann, Tshudy & Thomson, 1993) [Feldmann *et al.* 1993: 36, fig. 29.6, lower Campanian, James Ross Basin, Antarctica

Orithopsis? *iserica*† (Fritsch *in* Fritsch & Kafka, 1887) [Fritsch & Kafka 1887: 46, pl. 10, figs. 5, 6 (as *Palaeocorystes*), upper Turonian, Bohemia (Czech Republic) (see Van Straelen 1923a: 118; Collins 1997: table 1; Glaessner 1929a: 156, pl. 10, fig. 7, as *Necrocarcinus isericus*)]

Orithopsis siouxensis† (Feldmann, Awotua & Welshenbaugh, 1976) [Feldmann *et al.* 1976: 986, pl. 1, figs. 1–5 (as '*Necrocarcinus*'), Maastrichtian, North Dakota, USA (as *Cenomanocarcinus* by Schweitzer *et al*. 2003a: 36)]

Orithopsis? *transiens*† (Fritsch *in* Fritsch & Kafka, 1887) [Fritsch & Kafka 1887: 48, pl. 10, fig. 7 (as *Lissopsis*), upper Turonian, Bohemia (Czech Republic)]

Orithopsis tricarinata† (Bell, 1863) [Bell 1863: 21, pl. 4, figs. 9–11, upper Aptian–lower Cenomanian, southern England, northern Spain; lower Cenomanian, Mangyshlak, Kazakhstan (see Ilyin 2005, as *Necrocarcinus tricarinatus*); ?upper Albian, Angola; upper Aptian, Colombia; upper Albian, Oregon (see Vega *et al*. 2010: 275, figs. 8.18–8.23) (= *O. bonneyi*† Carter, 1872, upper Aptian, lower Cenomanian, southern England)]

Orithopsis? *youngi*† (Bishop, 1983) [Bishop 1983c: 46, pl. 1, figs. 8–11 (as *Hillius*), lower Albian, Texas, USA]

Genus *Paradoxicarcinus*† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

Paradoxicarcinus nimonoides† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 [Schweitzer *et al.* 2003a: 43, fig. 14, Santonian, British Columbia, Canada]

Genus *Silvacarcinus*† Collins & Smith, 1993

Silvacarcinus laurae† Collins & Smith, 1993 [Collins & Smith 1993: 263, text-fig. 2 (*non* fig. 3a, b), pl. 2, figs. 1, 2, 4–6 (*non* fig. 3), lower Eocene, central Belgium]

Superfamily Raninoidea De Haan, 1839
Family Lyreididae Guinot, 1993
Subfamily Lyreidinae Guinot, 1993

Genus *Bournelyreidus*† n. gen.

Bournelyreidus carlilensis† (Feldmann & Maxey, 1980) [Feldmann & Maxey 1980: 858, fig. 1a–e (as *Raninella*), upper middle Turonian, Kansas]

Bournelyreidus eysunesensis† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 19, fig. 10a–c (as *Hemioon*), upper Campanian, West Greenland]

Bournelyreidus laevis† (Schlüter *in* von der Marck & Schlüter, 1868) [von der Marck & Schlüter 1868: 298, pl. 44, fig. 2 (as *Palaeocorystes*), upper Turonian, northern Germany (cited after Van Straelen 1923a: 117, 118; Collins 1997: table 1)]

Bournelyreidus manningi† (Bishop & Williams, 2000) [Bishop & Williams 2000: 292, fig. 5 (as *Raninella*), upper Campanian, South Dakota and Colorado, USA]

Bournelyreidus? *oaheensis*† (Bishop, 1978) [Bishop 1978: 615, fig. 5 (as *Raninella*), lower Campanian, South Dakota, USA; ?upper Campanian–Maastrichtian, South Dakota and North Dakota, USA]

Bourneylyreidus teodorii† **n. sp.** [upper Maastrichtian, southwestern France]

Bournelyreidus tridens† (Roberts, 1962) [Roberts 1962: 187, pl. 88, figs. 5, 6 (as *Raninella*), Campanian, New Jersey, Delaware; lower Maastrichtian, Mississippi, USA (see Bishop 1983b)]

Bournelyreidus sp.† sensu Collins & Jakobsen 1995 [Collins & Jakobsen 1995: 39, pl. 10, fig. 10 (as *Lyreidus*), Danian, Denmark]

Genus *Heus*† Bishop & Williams, 2000

Heus foersteri† Bishop & Williams, 2000 [Bishop & Williams 2000: 290, fig. 4, upper Campanian, South Dakota and Colorado, USA]

Genus *Lyreidus* De Haan, 1841

Lyreidus antarcticus† Feldmann & Zinsmeister, 1984 [Feldmann & Zinsmeister 1984: 1048, figs. 3a–k, 4a–i, 5, 6b, 7, lower/upper Eocene, Seymour Island, Antarctica]

Lyreidus bennetti† Feldmann & Maxwell, 1990 [Feldmann & Maxwell 1990: 787, figs. 7.1–7.5, 8, upper Eocene, New Zealand]

Lyreidus brevifrons Sakai, 1937 [Sakai 1937: 171, text-figs. 38b, 41b, 42a, b, pl. 16, fig. 6, Recent, western Indian Ocean, Philippines, Japan, Taiwan, South China Sea]

Lyreidus elegans† Glaessner, 1960 [Glaessner 1960: 16, text-fig. 5, pl. 2, figs. 15, 16 (? = *L. tridentatus*; see Griffin 1970), lower Miocene, New Zealand]

Lyreidus fastigatus† Rathbun, 1919 [Rathbun 1919: 168; Oligocene, Anguilla, West Indies]

Lyreidus hungaricus† Beurlen, 1939 [Beurlen 1939: 146, text-fig. 4, pl. 7, fig. 7, middle Oligocene, Hungary (Feldmann 1992: 954 placed it in *Lyreidus* (*Lysirude*); Tucker 1998: 324 in *Lysirude*)]

Lyreidus lebuensis† Feldmann & Chirono-Gálvez *in* Feldmann, 1992 [Feldmann 1992: 948, fig. 6, Eocene, Chile]

Lyreidus stenops Wood-Mason, 1887 [Wood-Mason 1887: 209, pl. 1, figs. 7, 8 (= *L. integra* Terazaki, 1902: 217, unnumbered figure; *L. politus* Parisi, 1914: 311, pl. 13, fig. 5), Recent, Indo-West Pacific (South China Sea, Philippines, Japan)]

Lyreidus tridentatus† De Haan, 1841 [De Haan 1841: 140, pl. 35, fig. 6, middle Oligocene–Recent, Indo-West Pacific (Japan, South China Sea, Nansha Is., Philippines, eastern and western Australia, New Zealand, Hawaiian Is. (= *L. elongatus* Miers, 1879: 46, as conditional name; *L. australiensis* Ward, 1933: 377; *L. fossor* Bennett, 1964: 24, figs. 5–9; see Griffin 1970, Feldmann 1992, Ng *et al*. 2008)]

Lyreidus waitakiensis† Glaessner, 1980 [Glaessner 1980: 178, fig. 7, 7a, upper middle Eocene, New Zealand (Feldmann 1992: 954 assigned it to *Lyreidus* (*Lysirude*); Tucker 1998: 324 to *Lysirude*)]

Lyreidus† sp. sensu Karasawa 1993 [Karasawa 1993: 42, pl. 7, fig. 4, lower Pliocene, Japan]

Genus *Lysirude* Goeke, 1986

Lysirude channeri (Wood-Mason, 1885) [Wood-Mason 1885: 104 (as *Lyreidus*), see Wood-Mason 1887: 206, pl. 1, figs. 1–6; 1888: 376, Recent, Indo-West Pacific (Arabian Sea, northern Indian Ocean, Bay of Bengal, Philippines, South China Sea) (= *Lyreidus gracilis* Wood-Mason, 1888: 376)]

Lysirude griffini Goeke, 1986 [Goeke 1986: 215, figs. 4, 5, Recent, Philippines]

Lysirude hookeri† Feldmann, 1992 [Feldmann 1992: 953, figs. 12.1–12.5, 13, upper lower Eocene, Seymour I., Antarctica]

Lysirude nitidus (A. Milne-Edwards, 1880) [A. Milne-Edwards 1880: 34, western North Atlantic, from Maine, USA to Caribbean, Venezuela]

Lysirude paronae† (Crema, 1895) [Crema 1895: 671, text-fig. 11, middle Miocene–Pliocene; northern Italy (Feldmann 1992: 954 assigned it to *Lyreidus* (*Lysirude*); see Garassino *et al*. 2004; De Angeli *et al*. 2009b)]

Genus *Macroacaena*† Tucker, 1998 (= *Carinaranina*† Tucker, 1998)

Macroacaena alseana† (Rathbun, 1932) [Rathbun 1932: 239, figs. 3, 4 (as *Lyreidus*), upper Eocene–lower Oligocene, Washington, Oregon, Pacific Northwest of North America (assigned by Feldmann 1992: 951 to *Lyreidus* (*Lysirude*)) (? = *Ranidina teshimai*† Fujiyama & Takeda, 1980 339, pl. 39, figs. 1–5, pl. 40, figs. 1–4, Oligocene, Hokkaido)]

Macroacaena bispinulata† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 27, fig. 16a–d (as *Lyreidus*), middle Paleocene, West Greenland]

Macroacaena chica† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 [Schweitzer *et al.* 2003a: 30, figs. 10.3–10.5, upper Eocene, British Columbia, Canada]

Macroacaena franconica† Schweigert, Feldmann & Wulf, 2004 [Schweigert *et al.* 2004: 62, fig. 2, lower Turonian, southern Germany]

Macroacaena cf. *franconica*† sensu Schweigert *et al*. 2004 [see Gripp 1969; Kümmel 1972; Schweigert *et al*. 2004: fig. 3; ?lower Paleocene, northern Germany (erratic boulders)]

Macroacaena fudoujii† (Karasawa, 2000) [Karasawa 2000b: 806, figs. 2, 3 (as *Carinaranina*), lower Miocene, southern Japan]

Macroacaena johnsoni† (Rathbun, 1935) [Rathbun 1935b: 83, pl. 17, figs 12–17 (as *Symethis*), Paleocene, Alabama; see Armstrong *et al*. 2009: 752, figs. 4.1, 4.2, upper lower Paleocene, central Texas, USA)]

Macroacaena leucosiae† (Rathbun, 1932) [Rathbun 1932: 242, figs. 7, 8 (as *Eumorphocorystes*?), upper Eocene (?Oligocene), Oregon]

Macroacaena marionae† (Tucker, 1998) [Tucker 1998: 338, figs. 8.1–8.4 (as *Carinaranina*), Eocene, Washington]

Macroacaena naselensis† (Rathbun, 1926) [Rathbun 1926a: 100, pl. 24, figs. 9, 10 (as *Eumorphocorystes*), ?middle Oligocene, Washington, Alaska (Waugh *et al*. 2009: 20, table 1, in upper Eocene–Oligocene)]

Macroacaena rosenkrantzi† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 24, figs. 13, 14a–c, 15a, b (as *Lyreidus*), Maastrichtian, West Greenland]

Macroacaena schencki† (Rathbun, 1932) [Rathbun 1932: 242, figs. 5, 6 (as *Eumorphocorystes*), upper Eocene (?Oligocene), Oregon]

Macroacaena succedana† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 23, figs. 11a–c, 12, Campanian–Maastrichtian, West Greenland]

Macroacaena venturai† Vega, Nyborg, Fraaye & Espinosa, 2007 [Vega *et al.* 2007b: 1436, fig. 5.2, Paleocene, northeastern Mexico]

Genus *Rogueus*† Berglund & Feldmann, 1989

Rogueus orri† Berglund & Feldmann, 1989 [Berglund & Feldmann 1989: 70, figs. 2.1–2.6, 3.1, 3.2, lower middle Eocene, Oregon, USA]

Rogueus robustus† Collins & Jakobsen, 1996 [Collins & Jakobsen 1996: 63, fig. 1a, b, middle Paleocene, eastern Denmark]

Subfamily Marylyreidinae† n. subfam.

Genus *Marylyreidus*† n. gen.

Marylyreidus punctatus† (Rathbun, 1935) [Rathbun 1935b: 48, pl. 12, figs. 14–16 (as *Notopocorystes*) (= *Notopocorystes parvus*† Rathbun, 1935, see Rathbun 1935b: 48, pl. 12, figs. 11–13, *Raninella mucronata*† Rathbun, 1935, see Rathbun, 1935b: 50, pl. 14, figs. 32, 33; synonymy after Haj & Feldmann 2002), upper Albian–lower Cenomanian, Texas, USA]

Family Raninidae De Haan, 1839

Subfamily Ranininae De Haan, 1839 emend.

Genus *Lophoranina*† Fabiani, 1910 (= *Palaeonotopus*† Brocchi, 1877)

Lophoranina aculeata† (A. Milne-Edwards, 1881) [A. Milne-Edwards 1881: 7, pl. 22, fig. 4, upper Eocene, southwestern France; lower Oligocene, northern Italy (see Marangon & De Angeli 2007)]

Lophoranina albeshtensis† Schweitzer, Feldmann & Lazăr, 2009 [Schweitzer *et al.* 2009: 7, fig. 4, lower–middle Eocene, Romania]

Lophoranina aldrovandii† (Ranzani, 1818) [Ranzani 1818: 344, pl. 14 (as *Ranina*), ?Eocene, ?northern Italy]

Lophoranina bakerti† (A. Milne-Edwards, 1872) [A. Milne-Edwards 1872: 4 (as *Ranina*), middle Eocene, 'India' (see Withers 1932: 468, pl. 13, figs. 3–5, as *Lophoranina bakeri*), middle Eocene, Pakistan]

Lophoranina barroisii† (Brocchi, 1877) [Brocchi 1877: 4, pl. 29, figs. 6–8 (as *Palaeonotopus*), Eocene, central France]

Lophoranina bishopi† Squires & Demetrion, 1992 [Squires & Demetrion 1992: 44, fig. 130, lower Eocene, Baja California, Mexico]

Lophoranina bittneri† (Lőrenthey, 1902) [Lőrenthey 1902: 104 (809), pl. 1, figs. 1, 2 (as *Ranina*), middle–upper Eocene, northern Italy; Eocene, Sicily, Hungary, Spain]

Lophoranina cf. *bittneri*† sensu Wank 1983 [Wank 1983: 147, figs. 1, 2, lower Eocene, Austria]

Lophoranina cristaspina† Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer & Waugh, 2001 [Vega *et al.* 2001: 933, figs. 4, 5, middle Eocene, southern Mexico]

Lophoranina georgiana† (Rathbun, 1935) [Rathbun 1935b: 97, text-fig. 2, pl. 21, figs. 7, 8 (as *Ranina*), lower Oligocene, Alabama, USA]

Lophoranina aff. *georgiana*† sensu Portell 2004 [Portell 2004: 2, pl. 2, figs. A, B, Eocene, Florida]

Lophoranina kemmerlingi† Van Straelen, 1923 [Van Straelen 1923b: 489 (1), figs. 1, 2a, b, Eocene, Borneo]

Lophoranina laevifrons† (Bittner, 1875) [Bittner 1875: 68, pl. 1, fig. 4 (as *Ranina*), middle Eocene, northern Italy]

Lophoranina levantina† Lewy, 1977 [Lewy 1977: 98, text-figs. 1, 2, pl. 1, figs. 2–9 (as *Ranina* (*Lophoranina*)), middle Eocene, Israel]

Lophoranina marestiana† (König, 1825) [König 1825: 2, pl. 1, fig. 15 (*non* fig. 14) (as *Ranina maresiana* and *R. Maretiana*), lower/upper Eocene, northern Italy, Spain, Israel, Croatia, Egypt, ?Sicily, Kazakhstan]

Lophoranina cf. *marestiana*† sensu Wank 1986 [Wank, 1986: 61, figs. 1–3 (as *Ranina* (*Lophoranina*)), Eocene, Austria]

Lophoranina marestiana var. *avesana*† Bittner, 1883 [Bittner 1883: 301, pl. 2, fig. 2, middle Eocene, northern Italy]

Lophoranina maxima† Beschin, Busulini, De Angeli & Tessier, 2004 [Beschin *et al.* 2004: 110, text-figs. 1, 2, pl. 1, figs. 1–3, pl. 2, figs. 1, 2, middle Eocene, northern Italy]

Lophoranina persica† (Withers, 1932) [Withers 1932: 469, pl. 13, fig. 1 (as *Ranina* (*Lophoranina*)), Eocene, Iran]

Lophoranina porifera† (Woodward *in* Guppy, 1886) [Guppy 1886: 591, pl. 26, fig. 18 (as *Ranina*), lower Oligocene, Trinidad]

Lophoranina? *quinquespinosa*† (Rathbun, 1945) [Rathbun 1945: 375, pl. 55B–E (as *Ranina*), Neogene, Fiji]

Lophoranina raynorae† Blow & Manning, 1996 [Blow & Manning 1996: 7, pl. 2, fig. 3, middle Eocene, North Carolina, USA]

Lophoranina reussi † (Woodward, 1866) [Woodward 1866: 592; middle/upper Eocene, Spain, Italy, Hungary, Slovakia]

Lophoranina rossi† Blow & Manning, 1996 [Blow & Manning 1996: 8, pl. 2, fig. 4 middle Eocene, South Carolina, USA]

Lophoranina soembaensis† (Van Straelen, 1938) [Van Straelen 1938: 95, pl. 1, fig. 3, lower Eocene, Sumba, Indonesia]

Lophoranina straeleni† Vía, 1959 [Vía 1959: 366, text-fig. 7, lower/middle Eocene, Spain, northern Italy]

Lophoranina tchihatcheffi† [d'Archiac MS] (A. Milne-Edwards, 1866) [A. Milne-Edwards 1866: 105, pl. 1, fig. 7 (as *Ranina*), Eocene, Greece (incorrect spelling in Reuss 1859, *tschichatscheffi*; see A. Milne Edwards 1872: 4, 8)]

Lophoranina toyosimai† (Yabe & Sugiyama, 1935) [Yabe & Sugiyama 1935: 2, text-figs. 1, 2, pl. 1, figs. 1-11 (as *Ranina* (*Lophoranina*)); Eocene, Japan

Genus *Lophoraninella*† Glaessner, 1945

Lophoraninella cretacea† (Dames, 1886) [Dames 1886: 553 (Schweitzer *et al*. 2003b: 890, 'as 'likely' in Galatheoidea'), Cenomanian, Lebanon]

Genus *Ranina* Lamarck, 1801 (= *Ranina* (*Eteroranina*)† Fabiani, 1910)

Ranina americana† Withers, 1924 [Withers 1924: 125, pl. 4, figs. 1–3, upper Eocene (Oligocene?), Washington (Waugh *et al*. 2009: 20, table 1, shown as Miocene)]

Ranina bavarica† Ebert, 1887 [Ebert 1887: 264, pl. 8, figs. 5–9, Eocene, southern Germany]

Ranina berglundi† Squires & Demetrion, 1992 [Squires & Demetrion 1992: 43, figs. 128, 129, Eocene, northern and southern Mexico]

Ranina bouilleana† A. Milne Edwards, 1872 [A. Milne Edwards 1872: 6, 9, pl. 8, figs. 2, 2a–c, Oligocene, southwestern France, northern Italy]

Ranina brevispina† Lőrenthey, 1898 [Lőrenthey 1898b: 135, pl. 10, figs. 2, 3, pl. 11, fig. 1, Miocene, Algeria]

Ranina cf. *brevispina*† [= *R. adamsi*† Woodward, *nomen nudum*, lower Miocene, Malta]

Ranina cuspidata† Guppy, 1909 [Guppy 1909: 6, lower Miocene, Trinidad (see Collins *et al*. 2009: 75)]

Ranina elegans† Rathbun, 1945 [Rathbun 1945: 375, pl. 55F, G, Neogene, Fiji]

Ranina granulosa† A. Milne Edwards, 1872 [A. Milne Edwards, 1872: 5, pl. 8, fig. 1, Eocene–?Oligocene, southwestern France (as '*granulata*' on p. 9 and caption to pl. 8)]

Ranina haszlinskyi† Reuss, 1859 [Reuss 1859: 23, pl. 4, figs. 4, 5, Oligocene (?upper Eocene), Hungary]

Ranina hirsuta† Schafhäutl, 1863 [Schafhäutl 1863, middle Eocene, southern Germany]

Ranina lamiensis† (Rathbun *in* Ladd, 1934) [Ladd 1934: 239, pl. 44, fig. 9 (as *Montezumella*) (see Rathbun 1945: 374, pls. 55A, 56A, B), Neogene, Fiji]

Ranina libyca† (Van Straelen, 1935) [Van Straelen 1935: 113, text-figs. A-D (as *Raninella*), Danian, Kurkur Oasis, Egypt]

Ranina molengraaffi† Van Straelen, 1924 [Van Straelen 1924: 777, fig. 1a, b (as *Ranina* (*Hela*)), Miocene, Borneo]

Ranina oblonga† (von Münster, 1840) [von Münster, 1840: 24, pl. 2, fig. 4, Oligocene, Germany]

Ranina palmea† Sismonda, 1846 [Sismonda 1846: 64, pl. 3, figs. 3, 4, lower Miocene, northern Italy]

Ranina propinqua† Ristori, 1891 [Ristori 1891: 11, pl. 1, figs. 4–7, Pliocene, central Italy]

Ranina ranina† (Linnaeus, 1758) [Linnaeus, 1758: 625 (as *Cancer raninus*), middle Pleistocene–Recent, South Africa to Japan, Australia, Norfolk I., New Caledonia, Hawaiian Is.) (= *Ranina dentata* Latreille, 1802; *R. serrata* Lamarck, 1801; ?*Ranina cristata* Desjardins, 1835); some of these names might refer to distinct species]

Ranina speciosa† (von Münster, 1840) [von Münster 1840: 24, pl. 2, figs. 1–3 (as *Hela*), Oligocene (–?Miocene), northern and eastern Germany, northern Italy]

Ranina tejoniana† Rathbun, 1926a [Rathbun 1926a: 90, text-fig. 1, pl. 22, figs. 1, 2, Eocene, California]

Ranina sp.† sensu Hyžný 2007 [Hyžný 2007: 59, fig. 1A–C, lower Oligocene, Slovakia]

Ranina sp.† sensu Remy 1960 [Remy 1960: 58, fig. 3, pl. 1, fig. 12 (as *Ranina* (*Laeviranina*)? sp. indet.), Eocene (probably), Ivory Coast]

Ranina sp.† sensu De Angeli *et al*. 2009 [De Angeli *et al*. 2009a: 120, fig. 2, upper Eocene, northern Italy]

Genus *Raninella*† A. Milne Edwards, 1862 (= *Hemioon*† Bell, 1863)

Raninella? *bidentata*† (Rathbun, 1935) [Rathbun 1935b: 85, pl. 18, figs. 9–12 (as *Symnista bidentata*), lower Paleocene, Alabama, USA]

Raninella circumviator† (Wright & Collins, 1972) [Wright & Collins 1972: 89, text-fig. 12d, pl. 19, fig. 3 (as *Hemioon*), upper Turonian, southern England]

Raninella elongata† A. Milne Edwards, 1862 [A. Milne Edwards 1862: 493 (= *Palaeocorystes callianassarum*† Fritsch *in* Fritsch & Kafka, 1887: 46, text-fig. 69, pl. 10, fig. 9) (see Brocchi 1877: 4, figs. 4, 5, upper Albian–Coniacian, southern England, Czech Republic, northern France, Germany (see Glaessner 1929a: 155, fig. 1a, b); = *Hemioon cunningtonii*† Bell, 1863: 10; = *Raninella atava*† Carter, 1898: 24, pl. 1, fig. 7 [as *Ranina* (*Raninella*?)], ?Cenomanian, England]

Raninella eocenica† Rathbun, 1935 [Rathbun 1935b: 82, pl. 18, figs. 13–16, Eocene, Alabama, USA]

Raninella griesbachi† (Noetling, 1897) [Noetling 1897: 78, pl. 22, fig. 4, Maastrichtian, India]

Raninella novozelandica† (Glaessner, 1980) [Glaessner 1980: 177, fig. 5, 5a (as *Hemioon*), upper Albian, New Zealand (see Feldmann 1993)]

Raninella quadrispinosa† (Collins, Fraaye & Jagt, 1995) [Collins *et al.* 1995: 188, fig. 9a–d (as *Raninoides*?), upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Raninella trigeri† A. Milne Edwards, 1862 [A. Milne Edwards 1862: 493 (compare Brocchi 1877: 2), Cenomanian, southern France]

Raninella yanini† (Ilyin & Alekseev, 1998) [Ilyin & Alekseev 1998: 48, figs. 1b–c, 2d (as *Hemioon*), upper Albian, Crimea (see Ilyin 2005)]

Raninella? n. sp.† sensu Lehmann 2004 [Lehmann 2004, ?Upper Cretaceous/Paleogene, northern Germany (erratics)]

Raninella? *ornata*† (Wright & Collins, 1972) [Wright & Collins 1972: 85, pl. 18, figs. 4, 5 (as *Notopocorystes* (*Cretacoranina*)), lower Cenomanian, southern England (Wright & Collins 1972: pl. 18, fig. 5b, can be attributed to Ranininae but "untraced specimen" and may not be conspecific with fragmentary holotype)]

Genus *Remyranina*† Schweitzer & Feldmann, 2010

Remyranina ornata† (Remy, 1960) [Remy 1960: 57, fig. 2, unnumbered plate, figs. 8, 9, ?Eocene, Ivory Coast (see Schweitzer & Feldmann 2010a: 401, 402)]

Genus *Vegaranina*† n. gen.

Vegaranina precocia† (Feldmann, Vega, Tucker, García-Barrera & Avendaño, 1996) **n. comb.** [Feldmann *et al.* 1996: 297, figs. 3.1–3.3, 4.1, 4.2 [as *Lophoranina precocious*], lower Maastrichtian, southeastern Mexico; Campanian–Maastrichtian, Cuba (see Varela & Rojas-Consuegra 2009), Schweitzer *et al*. (2009c: 7) amended epithet to *precocia*]

Vegaranina cf. *precocia*† sensu Schweitzer *et al*. 2008 [Schweitzer *et al.* 2008: 5, fig. 3 (as *Lophoranina*), lower upper Maastrichtian, Puerto Rico]

Vegaranina sp.† [herein]

Subfamily Raninoidinae Lőrenthey *in* Lőrenthey & Beurlen, 1929

Genus *Bicornisranina*† Nyborg & Fam, 2008

Bicornisranina bocki† Nyborg & Fam, 2008 [Nyborg & Fam 2008: 689, figs. 1–6, Upper Cretaceous, British Columbia, Canada (= *Raninoides bocki* Fam & Nyborg, 2003: 57 (*nomen nudum*)]

Genus *Cristafrons*† Feldmann, Tshudy & Thomson, 1993

Cristafrons praescientis† Feldmann, Tshudy & Thomson, 1993 [Feldmann *et al.* 1993: 33, figs. 25, 26, lower Campanian–?lower Maastrichtian, James Ross Basin, Antarctica (type is contained in the collections of the British Antarctic Survey, Cambridge, listed erroneously as a cirripede, under *Cretiscalpellum*)]

Genus *Notopoides* Henderson, 1888

Notopoides exiguus† Beschin, Busulini, De Angeli & Tessier, 1988 [Beschin *et al.* 1998: 188, text-fig. 9, pl. 9, figs. 2, 3, lower–middle Eocene, northern Italy; Eocene, southern Mexico (= *Notopus minutus*† Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer & Waugh, 2001: 936, figs. 6.1, 8, Eocene, southern Mexico)]

Notopoides latus Henderson, 1888 [Henderson 1888: 29, pl. 3, fig. 1, Recent, Indo-West Pacific (Kenya, Somalia ,Indonesia, Philippines, Kei Is., Norfolk I., Hawaiian Is. (see correction of Henderson's original figure by Dawson & Yaldwyn 2002: 202, figs. 1–3)]

Notopoides? *pflugervillensis*† Beikirch & Feldmann, 1980 [Beikirch & Feldmann 1980: 322, text-figs. 5a, b, 11, lower Campanian, Texas, USA]

Notopoides verbeeki† J. Böhm *in* Martin, 1922 [Martin 1922: 527, pl. 63, fig. 11a, b, Miocene, Java]

Genus *Notosceles* Bourne, 1922

Notosceles acanthocolus† (Schweitzer, Feldmann, Gonzáles-Barba & Ćosović, 2007) [Schweitzer *et al.* 2007a: 29, fig. 2.7 (as *Raninoides*), Eocene, Baja California Sur, Mexico]

Notosceles bournei† Rathbun, 1928 [Rathbun 1928: 1, pl. 1, figs. 1–4, Paleocene/Eocene, Texas, Arkansas and Alabama, USA (Rathbun 1935b: 51, pl. 28, fig. 5, recorded 'Navarro Group, Upper Cretaceous'; Bishop 1986a: 136 recorded upper Campanian or lower Maastrichtian of Texas, USA; Armstong *et al.* 2009: 752, figs. 4.3, 4.4 recorded material from the upper lower Paleocene of central Texas, USA)]

Notosceles chimmonis Bourne, 1922 [Bourne 1922b: 74, pl. 4, figs. 2, 3, 24, 40, 41a, 43, pl. 7, figs. 44–47, 57 (= *Raninoides fossor* A. Milne-Edwards & Bouvier, 1923: 300, pl. 1, fig. 10, pl. 2, figs. 2, 3), Recent, Indo-West Pacific (Réunion, India, Philippines, Indonesia, French Polynesia]

Notosceles ecuadorensis (Rathbun, 1935) [Rathbun 1935a: 1 (as *Raninoides*), Recent, Gulf of California, Perú, Galápagos Is.]

Notosceles pepeke Dawson & Yaldwyn, 2000 [Dawson & Yaldwyn 2000: 54, figs. 1–6, Recent, northern New Zealand, Norfolk I., Norfolk Ridge, Kermadec Is.]

Notosceles serratifrons (Henderson, 1893) [Henderson 1893: 408, pl. 38, figs. 10–12 (as *Raninoides*), Recent, Indo-West Pacific (Sri Lanka, Andaman Sea, Japan, Philippines, Nansha Islands, northwestern Australia (Hu & Tao 1999: 219, text-fig. 3, pl. 1, figs. 8, 11, fossil members from Taiwan as *Raninoides serratifrons*†)]

Notosceles viaderi Ward, 1942 [Ward 1942: 47, pl. 4, figs. 5, 6, Recent, Indo-West Pacific, from Réunion and Mauritius to the Hawaiian Is. and French Polynesia]

Genus *Pseudorogueus*† Fraaye, 1995

Pseudorogueus rangiferus† Fraaye, 1995 [Fraaye 1995: 66, figs. 1, 2, lower Eocene, northern Spain]

Genus *Quasilaeviranina*† Tucker, 1998

Quasilaeviranina arzignanensis† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 194, text-fig. 11, pl. 10, figs. 2, 3 (as *Notosceles*), middle Eocene, northern Italy]

Quasilaeviranina keyesi† (Feldmann & Maxwell, 1990) [Feldmann & Maxwell 1990: 784, figs. 3.1, 3.2, 4 (as *Laeviranina*), upper Eocene, New Zealand]

Quasilaeviranina ombonii† (Fabiani, 1910) [Fabiani 1910a: 30, pl. 2, fig. 1 (as *Ranina*), lower Eocene, northern Italy]

Quasilaeviranina ovalis† (Rathbun, 1935) [Rathbun 1935b: 81, pl. 18, figs. 1–8 (as *Raninoides*), Eocene, Alabama, USA]

Quasilaeviranina pororariensis† (Glaessner, 1980) [Glaessner 1980: 177, fig. 6, 6a (as *Ranilia*), upper Eocene, New Zealand]

Quasilaeviranina simplicissima† (Bittner, 1883) [Bittner 1883: 305, pl. 1, fig. 4a, b (as *Ranina*), middle Eocene, northern Italy; upper Eocene, Hungary]

Genus *Raninoides* H. Milne Edwards, 1837 (= *Symnista* Philippi, 1887; *Raninellopsis*† J. Böhm, 1922; *Laeviranina* Lőrenthey *in* Lőrenthey & Beurlen, 1929; ?*Porcellanoidea*† Hu & Tao, 1996)

Raninoides araucana† (Philippi, 1887) [Philippi 1887: 222, pl. 50, fig. 6 (as *Symnista*), lower Eocene, Chile]

Raninoides asper† Rathbun, 1926 [Rathbun 1926a: 98, pl. 23, fig. 5, Oligocene, Oregon, USA]

Raninoides barnardi Sakai, 1974 [Sakai 1974: 87; 1976: 51, text-fig. 24a–d, Recent, Japan and probably South Africa; see *R. serratifrons* sensu Barnard 1950: 399, text-fig. 75e–g, *non* Henderson 1893, which is a species of *Notosceles*; Hu & Tao 1999: 219, text-fig. 2, pl. 1, figs. 2, 4, recorded fossil members from Taiwan]

Raninoides benedicti Rathbun 1935 [Rathbun 1935a: 1; 1937a: 9, text-figs. 4, 5, pl. 1, figs. 7, 8, Recent, Gulf of California, Ecuador]

Raninoides cf. *benedicti*† sensu Todd & Collins 2006 [Todd & Collins 2006: 68, pl. 2, fig. 5, upper Miocene–?lower Pleistocene, Panama]

Raninoides borealis† (Collins & Wienberg Rasmussen, 1992) [Collins & Wienberg Rasmussen 1992: 31, fig. 18a–c (as *Laeviranina*), middle Paleocene, West Greenland]

Raninoides bouvieri Capart, 1951 [Capart 1951: 59, fig. 17, Recent, eastern Atlantic (Senegal to Angola)]

Raninoides budapestiniensis† (Lőrenthey, 1897) [Lőrenthey 1897: 153, 166 (as *Ranina*), middle/upper Eocene, northern Italy; upper Eocene, Hungary]

Raninoides crosnieri Ribes, 1990 [Ribes 1990: 908, text-fig. 1a–h, pl. 2, figs. A–D, Recent, Madagascar]

Raninoides dickersoni† Rathbun, 1926a [Rathbun 1926a: 94, text-fig. 3, pl. 20, fig. 5 (= *Cancer* sp. sensu Dickerson 1916: 427, 434, pl. 42, fig. 12), middle Eocene, California (see Schweitzer & Feldmann 2002a: 949, fig. 9)]

Raninoides eugenensis† Rathbun, 1926 [Rathbun 1926a: 96, pl. 24, fig. 4, upper Oligocene, Oregon, USA]

Raninoides fabianii† (Lőrenthey & Beurlen, 1929) [Lőrenthey & Beurlen 1929: 106, pl. 4, fig. 10 (as *Ranina* (*Laeviranina*)), upper Eocene, northern Italy; middle–upper Eocene, Hungary, Germany]

Raninoides cf. *fabianii*† [see Beschin, Busulini, De Angeli, Tessier & Ungaro 1998: 18, text-figs. 7, 9, middle Eocene, northern Italy; see Förster & Mundlos 1982: 156, text-figs. 7, 8, 9B, 10B, pl. 1, figs. 4–6; Lienau 1984, upper Eocene, northern Germany]

Raninoides fulgidus† Rathbun, 1926 [Rathbun 1926a: 96, text-fig. 4, pl. 23, fig. 6, upper Eocene–Oligocene, Washington, Oregon, USA]

Raninoides fulungensis† Hu & Tao, 1999 [Hu & Tao 1999: 218, text-fig. 1, pl. 1, fig. 3, Oligocene–Miocene, Taiwan]

Raninoides glabra† (Woodward, 1871) [Woodward 1871: 90, fig. 1a, b (as *Palaeocorystes*; see *Laeviranina*), lower Eocene, Belgium, southern England]

Raninoides goedertorum† (Tucker, 1998) [Tucker 1998: 348, figs. 13.1–13.7, 14 (as *Laeviranina*), upper Eocene, Washington, USA]

Raninoides gottschei† (J. Böhm, 1928) [Böhm 1928: 563, figs. 1, 2 (as *Raninellopsis*), lower Eocene, northern Germany, southern England]

Raninoides hendersoni Chopra, 1933 [Chopra 1933: 81, text-fig. 1b, pl. 3, fig. 1, 1a, Recent, Indo-West Pacific (Andaman Sea, Philippines, Nansha Is)]

Raninoides hollandica† (Collins, Fraaye, Jagt & van Knippenberg, 1997) [Collins *et al.* 1997: 2, pl. 1, fig. A–D (as *Laeviranina*), ?upper Oligocene, eastern Netherlands]

Raninoides intermedius Dai & Xu, 1991 [Dai & Xu 1991: 1, fig. 1, Recent, South China Sea]

Raninoides javanus† (J. Böhm, 1922) [Böhm 1922: 526, pl. 63, fig. 12a–c (as *Raninellopsis*), lower Miocene, Java]

Raninoides lamarcki A. Milne-Edwards & Bouvier, 1923 [A. Milne-Edwards & Bouvier 1923: 299, pl. 1, figs. 8, 9, pl. 2, figs. 4, 5 (as *Raninoides laevis lamarckii*), Recent, western Atlantic (Gulf of Mexico, Venezuela, Brazil)]

Raninoides laevis (Latreille, 1825) [Latreille 1825: 268 (as *Ranina*), Recent, western Atlantic (eastern USA to Brazil) (= *R. schmitti* Sawaya, 1944: 137)]

Raninoides longifrons Chen & Türkay, 2001 [Chen & Türkay 2001: 332, fig. 1, Recent, western Pacific (Hainan, Nansha Is.)]

Raninoides louisianensis† Rathbun, 1933 [Rathbun, 1933: 186, upper Pleistocene, Jamaica; Recent, Gulf of Mexico, Caribbean, Suriname]

Raninoides madurensis† (Beets, 1950) [Beets 1950: 350, pl. 1, figs. 4–6 (as *Raninellopsis*), lower Miocene, Madura, Indonesia]

Raninoides mexicanus† Rathbun, 1930 [Rathbun, 1930: 8, pl. 4, fig. 1, Miocene, Mexico]

Raninoides morrisi† Collins *in* Collins, Lee & Noad, 2003 [Collins, Lee & Noad 2003: 198, pl. 1, fig. 4, Miocene, Sabah, Brunei]

Raninoides nodai† Karasawa, 1992 [*nodai* Karasawa 1992: 1252, figs. 4.2–4.8, upper middle Eocene, southern Japan]

Raninoides notopoides† (Bittner, 1883) [Bittner 1883: 304, pl. 1, fig. 3 (as *Ranina*), middle Eocene, northern Italy; lower Eocene, England]

Raninoides oregonensis† Rathbun, 1932 [Rathbun 1932: 239, figs. 1, 2, Eocene, Oregon]

Raninoides perarmatus† (Glaessner, 1960) [Glaessner 1960: 15, text-fig. 4, pl. 2, figs. 13, 14 (as *Laeviranina*), upper middle Eocene, New Zealand]

Raninoides personatus (White MS) Henderson, 1888 [Henderson 1888: 27, pl. 2, fig. 5, Recent, Indo-West Pacific (Bay of Bengal, Philippines, Western Australia, Japan, Nansha)]

Raninoides pliocenicus† De Angeli, Garassino & Pasini, 2009 [De Angeli *et al.* 2009b: 171, fig. 5a–d, Pliocene (*s. lat.*), Toscane, Italy]

Raninoides proracanthus† Schweitzer, Feldmann, Gonzáles-Barba & Ćosović, 2007 [Schweitzer *et al.* 2007a: 29, fig. 2.8, Eocene, Baja California, Mexico]

Raninoides pulchrus† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 171, text-fig. 5, pl. 4, figs. 1–3 (as *Laeviranina*), middle Eocene, northern Italy]

Raninoides rathbunae† Van Straelen, 1933 [Van Straelen 1933: 3, fig. 2a, b, lower Miocene, Venezuela (not upper Eocene; see Feldmann & Schweitzer 2004)]

Raninoides sinuosus† (Collins & Morris, 1978) [Collins & Morris 1978: 964, pl. 116, figs. 4–6 (as *Laeviranina*), lower Eocene, Pakistan]

Raninoides slaki† Squires, 2001 [Squires 2001: 22, figs. 47–55, Eocene, California]

Raninoides? *taiwanicus*† (Hu & Tao, 1996) [Hu & Tao 1996: 152, figs. 1, 12 (as *Porcellanoidea*), Miocene, Taiwan]

Raninoides toehoepae† (Van Straelen, 1924) [Van Straelen 1924: 780, fig. 2a–c (as *Raninella*), Miocene, Borneo]

Raninoides treldenaesensis† (Collins & Jakobsen, 2004) [Collins & Jakobsen 2004: 71, text-fig. 4, pl. 3, fig. 5 (as *Laeviranina*), middle Eocene, northern Denmark; Eocene, southern Mexico; upper lower Paleocene, central Texas, USA (see Armstrong *et al*. 2009: 752, figs. 4.5–4.8)]

Raninoides vaderensis† Rathbun, 1926 [Rathbun 1926a: 93, pl. 22, fig. 5 (= *R. lewisanus* Rathbun, 1926a: 94, pl. 22, fig. 4), middle–upper Eocene, Pacific Northwest, North America]

Raninoides washburnei† Rathbun, 1926a [Rathbun 1926a: 95, pl. 22, fig. 6, upper Oligocene, Oregon (Waugh *et al.* 2009: 20, table, indicated as Eocene)]

Raninoides willapensis† (Rathbun, 1926) [Rathbun 1926a: 99, pl. 21, figs. 4, 5 (as *Ranidina*), Eocene (?middle Oligocene), Washington (Tucker 1998: 342 assigned to *Carinaranina*; Waugh *et al.* 2009: 20, table 1, assigned to *Macroacaena*)]

Raninoides sp.† sensu Vega *et al*. 2001 [Vega *et al*. 2001: 935, figs. 6.2, 7 (as *Laeviranina*), Eocene, southern Mexico]

Raninoides sp.† sensu Morris & Collins, 1991 [Morris & Collins 1991: 4, fig. 39, ?upper middle Pleistocene, Brunei (= *R. morrisi*)]

Raninoides sp.† sensu Bachmayer & Mundlos, 1968 [Bachmayer & Mundlos 1968: 670, ?upper Oligocene, northern Germany]

Raninoides sp.† sensu Karasawa *et al*. 2008 [Karasawa *et al*. 2008b: 57, fig. 3S, Pleistocene, Philippines]

Subfamily Notopodinae Serène & Umali, 1972

Genus *Cosmonotus* Adams & White *in* White, 1848 (= *Engonionotus* Rathbun, 1897; *Paralbunea* Hu & Tao, 1996, *non Paralbunea* Serène, 1977)

Cosmonotus chevrona† (Fraaye & Van Bakel, 1998) [Fraaye & Van Bakel 1998: 296, figs. 1d–g, 2c, 3c (as *Raniliformis*), upper Maastrichtian, southeastern Netherlands]

Cosmonotus genkaiae Takeda & Miyake, 1970 [Takeda & Miyake 1970: 199, text-figs. 1b, 2a–f, 3a, b, Recent, East China Sea]

Cosmonotus grayii White, 1847 [White 1847: 129 (*nomen nudum*), 1848: 227, two unnumbered figures (see Adams & White 1849: 60, pl. 13, fig. 3, for publication dates of Adam White's papers, see Clark & Presswell 2001), Recent, Indo-West Pacific (Réunion, East Africa, Persian Gulf, India, Philippines, Nansha Is., Japan, Taiwan, Borneo, Australia)]

Cosmonotus mclaughlinae Tavares, 2006 [Tavares 2006: 534, fig. 1, Recent, Indo-West Pacific (Réunion, Philippines, Indonesia, Solomon Islands, Futuna I., Vanuatu, Loyalty Is., Fiji, Tonga)]

Genus *Eumorphocorystes*† van Binkhorst, 1857

Eumorphocorystes sculptus† van Binkhorst, 1857 [van Binkhorst 1857: 108, pl. 6 (2), figs. 1a, b, 2a, 3a, 5a, *non* 4a, upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Genus *Lianira*† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991

Lianira beschini† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991 [Beschin *et al.* 1991: 197, text-fig. 4, pl. 1, fig. 1a–e, pl. 2, figs. 1, 2a–c, pl. 3, fig. 1a–d, middle Eocene, northern Italy]

Lianira convexa† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991 [Beschin *et al.* 1991: 199, text-fig. 5, pl. 4, figs. 1a, b, 3a–c, middle Eocene, northern Italy]

Lianira isidoroi† Beschin, De Angeli & Checchi, 2007 [Beschin *et al.* 2007: 14, text-fig. 3, pl. 1, figs. 1a–d, 2–4, lower–middle Eocene, northern Italy]

Genus *Lovarina*† Beschin, Busulini, De Angeli, Tessier & Ungaro, 1991

Lovarina cristata† Beschin, Busulini, De Angel, Tessier & Ungaro, 1991 [Beschin *et al.* 1991: 202, text-fig. 6, pl. 5, figs. 1a, b, 2, 3, middle Eocene, northern Italy]

Genus *Notopella*† Lőrenthey *in* Lőrenthey & Beurlen, 1929

Notopella vareolata† Lőrenthey *in* Lőrenthey & Beurlen, 1929 [Lőrenthey & Beurlen 1929: 119, pl. 5, fig. 7, middle–upper Eocene, Hungary, northern Spain, northern Italy]

Genus *Notopus* de Haan, 1841 (= *Pseudoraninella*† Lőrenthey *in* Lőrenthey & Beurlen, 1929)

Notopus beyrichi† Bittner, 1875 [Bittner 1875: 72, pl. 1, fig. 6, middle–upper Eocene to lower Oligocene, northern Italy; upper Eocene, Hungary]

Notopus dorsipes (Linnaeus, 1758) [Linnaeus, 1758: 630 (as *Cancer*), Recent, Indo-West Pacific (from Red Sea to Japan, Western Australia) (= *N. rumphii* Rathbun, 1937a: 17)]

Notopus mulleri† (van Binkhorst, 1857) [van Binkhorst 1857: 107, pl. 1, fig. 1a, b (as *Notopocorystes muelleri*), upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Notopus novemdentatus Ortmann, 1892 [Ortmann 1892: 573, pl. 26, fig. 11a, b, k, Recent, New Caledonia]

Notopus vahldieki† (Förster & Mundlos, 1982) [Förster & Mundlos 1982: 159, text-fig. unnumbered (between figs. 10 and 11) (as *Pseudoraninella?*), upper Eocene, northeastern Germany (Waugh *et al.* 2009: 20, table 1, retained this species in *Pseudoraninella*)]

Notopus sp.† sensu Förster & Mundlos 1982 [Förster & Mundlos 1982: 160, text-figs. 9A, 10A, 11, pl. 1, fig. 7a, b (as *Pseudoraninella*), upper Eocene, northeastern Germany]

Genus *Ponotus*† Karasawa & Ohara, 2009

Ponotus shirahamensis† Karasawa & Ohara, 2009 [Karasawa & Ohara 2009: 200, fig. 1, lowermost mid-Miocene, central Japan]

Genus *Ranidina*† Bittner, 1893

Ranidina rosaliae† Bittner, 1893 [Bittner 1893: 33, pl. 2, fig. 2, Miocene, Austria, Bulgaria (see Müller 1984: 71)]

Genus *Ranilia* H. Milne Edwards, 1837 (=*Raninops* A. Milne-Edwards, 1880; *Paralbunea*† Hu & Tao, 1996, pars [*non Paralbunea* Serène, 1977]; *Erroranilia*† Boyko, 2004)

Ranilia angustata Stimpson, 1860 [Stimpson 1860: 240 (112), Recent, eastern Pacific (Gulf of California)]

Ranilia constricta (A. Milne-Edwards, 1880) [A. Milne-Edwards, 1880: 35 (as *Raninops*), Recent, western (Florida to Brazil), central (Ascension I.) and eastern Atlantic (Senegal to Congo) (= *Notopus* (*Raninoides*?) *atlanticus*† Studer, 1883: 17, pl. 1, fig. 5a, b, upper Pleistocene, southern Italy)]

Ranilia fornicata (Faxon, 1893) [Faxon 1893: 162 (as *Raninops*), Recent, eastern Pacific (Gulf of California to Ecuador, Galápagos)]

Ranilia guinotae de Melo & Campos, 1994 [de Melo & Campos 1994: 69, figs. 16–22, Recent, Brazil]

Ranilia muricata H. Milne Edwards, 1837 [H. Milne Edwards 1837: 196, Recent, western Atlantic (from North Carolina, USA, Gulf of Mexico to Colombia and Brazil) (= *Raninops stimpsoni* A. Milne-Edwards, 1880: 35; *R. saldanhai* Rodrigues da Costa, 1970: 33, fig. 1)]

Ranilia punctulata† Beschin, Busulini, De Angeli & Tessier, 1988 [Beschin *et al.* 1988: 196, text-fig. 12, pl. 11, figs. 1, 2, lower middle Eocene, northern Italy]

Ranilia taipeiensis† (Hu & Tao, 1996) [Hu & Tao 1996: 62, pl. 11, figs. 2, 4, 6 (as *Paralbunea*), lower Miocene, Taiwan (see Boyko 2004)]

Ranilia sp.† sensu Portell & Agnew 2004 [Portell & Agnew 2004: 2, pl. 4, fig. E–G, Pliocene, Florida]

Genus *Raniliformis*† Jagt, Collins & Fraaye, 1993

Raniliformis baltica† (Segerberg, 1900) [Segerberg 1900: 22 (368), pl. 2, figs. 9–11 (as *Raninella*), lower Paleocene, eastern Denmark, southeastern Netherlands]

Raniliformis bellini† De Angeli, 2011 [De Angeli 2011: 103, fig. 2/1–5, middle Eocene, northern Italy]

Raniliformis eocenica† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 160, text-fig. 2, pl. 1, figs. 1–4 (as *Cosmonotus*), middle Eocene, northern Italy (Waugh *et al.* 2009: 20, table 1, retain this species in *Cosmonotus*)

Raniliformis occlusa† Collins, Fraaye & Jagt, 1995 [Collins *et al.* 1995: 194, fig. 10d, e, upper Maastrichtian, southeastern Netherlands, northeastern Belgium]

Raniliformis ornata† De Angeli & Beschin, 2007 [De Angeli & Beschin 2007: 34, text-fig. 4(3a, b), pl. 2, fig. 3a–c, lower middle Eocene, northern Italy]

Raniliformis prebaltica† Fraaye & Van Bakel, 1998 [Fraaye & Van Bakel 1998: 295, figs. 1b, c, 2b, 3b, upper Maastrichtian, southeastern Netherlands]

Raniliformis rugosa† De Angeli & Beschin, 2007 [De Angeli & Beschin, 2007: 35, text-fig. 4(2a, b), pl. 2, figs. 1a, b, 2, lower middle Eocene, northern Italy]

Genus *Umalia* Guinot, 1993

Umalia chinensis (Chen & Sun, 2002) [Chen & Sun 2002: 184, fig. 78 (1–10), 560 (as *Ranilia*), Recent, South China Sea]

Umalia guinotae† De Angeli & Beschin, 2007 [De Angeli & Beschin 2007: 36, text-fig. 4(4a, b), pl. 3, figs. 2a, b, 3a–c, middle Eocene, northern Italy]

Umalia horikoshii (Takeda, 1975) [Takeda 1975: 139, text-figs. 2, 3, pl. 1, fig. 1 (as *Ranilia*), Recent, East China Sea]

Umalia misakiensis (Sakai, 1937) [Sakai 1937: 176, text-fig. 44 (as *Notopus*), Recent, Indian Ocean (Réunion), Japan]

Umalia orientalis (Sakai, 1963) [Sakai 1963: 226, text-fig. 6 (as *Ranilia*), Recent, Japan]

Umalia ovalis (Henderson, 1888) [Henderson 1888: 31, pl. 2, fig. 6 (as *Notopus*), Recent, Indo-West Pacific (Japan to Indonesia)]

Umalia tenuiocellus (Davie & Short, 1989) [Davie & Short 1989: 165, 171, figs. 5a–g, 7b, 8d–f (as *Ranilia*), Recent, Australia]

Umalia trirufomaculata (Davie & Short, 1989) [Davie & Short 1989: 167, 172, figs. 6a–h, 7a, 8a–c (as *Ranilia*), Recent, Australia]

Subfamily Symethinae Goeke, 1981

Genus *Eosymethis*† n. gen.

Eosymethis aragonensis† **n. sp.** [lower Eocene, northern Spain]

Genus *Symethis* Weber, 1795 (= *Zanclifer* Henderson, 1888)

Symethis corallica Davie, 1989 [Davie 1989: 426, text-fig. 1, pl. 1 (as '*Smethis*', typographical error), Recent, Indo-West Pacific (Australia, New Caledonia, Philippines)]

Symethis garthi Goeke, 1981 [Goeke 1981: 972, text-figs. 1–3, Recent, eastern Pacific (Gulf of California, western Panama)]

Symethis variolosa (Fabricius, 1793) [Fabricius, 1793: 476 (as *Hippa*), Recent, North Carolina, USA to Gulf of Mexico and Brazil (= *Eryon caribensis* de Fréminville, 1832: 273, pl. 8B, figs. 1, 2)]

Genus *Symethoides*† n. gen.
Symethoides monmouthorum† **n. sp.** [lower Danian, New Jersey]

Subfamily Cyrtorhininae Guinot, 1993 emend.
Genus *Antonioranina*† n. gen.
Antonioranina fusseli† (Blow & Manning, 1996) [Blow & Manning 1996: 7, pl. 2, fig. 1 (as *Cyrtorhina*), middle Eocene, North Carolina, USA]
Antonioranina globosa† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 163, text-fig. 3, pl. 2, fig. 1a–d (as *Cyrtorhina*), lower/middle Eocene, northern Italy, Croatia]
Antonioranina? *oblonga*† (Beschin, Busulini, De Angeli & Tessier, 1988) [Beschin *et al.* 1988: 166, text-fig. 4, pl. 3, figs. 1–3 (as *Cyrtorhina*), middle Eocene, northern Italy]
Antonioranina ripacurtae† (Artal & Castillo, 2005) [Artal & Castillo 2005: 34, figs. 2, 3 (as *Cyrtorhina*), lower Ypresian (middle Ilerdian), northeast Spain]

Genus *Cyrtorhina* Monod, 1956
Cyrtorhina balabacensis Serène, 1971 [Serène 1971: 904, pl. 1A, Recent, Indo-West Pacific (South China Sea)]
Cyrtorhina granulosa Monod, 1956 [Monod 1956: 49, figs. 19–31, Recent, Gulf of Guinea from Ghana to Principe I.]

Incertae sedis

Genus *Araripecarcinus*† Martins Neto, 1987
Araripecarcinus ferreirai† Martins Neto, 1987 [Martins Neto 1987: 407, figs. 1, 2, Lower Cretaceous (?Aptian, ?Albian), Brazil (Karasawa *et al*. 2008b noted that this represents a 'raninid' sternum; see Schweitzer *et al.* 2010: 71). The holotype represents a raninoidian, but a palaeocorystoid rather than a raninoidean]

Genus *Corazzatocarcinus*† Larghi, 2004
Corazzatocarcinus hadjoulae† (Roger, 1946) [Roger 1946: 43, text-figs. 32, 33, pl. 8, fig. 1 (as *Geryon*), Cenomanian, Lebanon (interpretation of P4 in text-fig. 32 ('very small and narrow') and P5 (long, 'normal') is inaccurate, as shown by Larghi (2004), P5 being more dorsal and thus easily misinterpreted)]
Corazzatocarcinus cf. *hadjoulae*† sensu Garassino *et al*. 2008 [Garassino *et al*. 2008: 60 (not illustrated), Cenomanian–Turonian, Morocco]

Genus *Cristella*† Collins & Wienberg Rasmussen, 1992
Cristella hastata† Collins & Wienberg Rasmussen, 1992 [Collins & Wienberg Rasmussen 1992: 36, fig. 20a, b, lower Paleocene, West Greenland]

Genus *Lyreidina*† Fraaye & Van Bakel, 1998
Lyreidina pyriformis† Fraaye & Van Bakel, 1998 [Fraaye & Van Bakel 1998: 294, figs. 1a, 2a, upper Maastrichtian, southeastern Netherlands, northeastern Belgium (Waugh *et al*. 2009: 20, table 1, in Lyreidinae)]

Genus *Neoraninella*† Hu & Tao, 1996
Neoraninella tyranna† Hu & Tao, 1996 [Hu & Tao 1996: 64, pl. 11, fig. 13, Oligocene, Taiwan (Hu & Tao 1996: 63 placed in Porcellanidae; see Ng 1999 for comments on the status of new taxa erected therein)]

Genus *Sabahranina*† Collins *in* Collins, Lee & Noad, 2003
Sabahranina trushidupensis† Collins *in* Collins, Lee & Noad, 2003 [Collins, Lee & Noad 2003: 200, pl. 1, fig. 3, Miocene, Sabah, Indonesia]

Genus *Tribolocephalus*† Ristori, 1886
Tribolocephalus laevis† Ristori, 1886 [Ristori, 1886: 128, pl. 2, fig. 19, Pliocene, central Italy (see De Angeli & Garassino 2006b: 39)]

Uncertain placement

'*Cenomanocarcinus*' sp.† sensu Neumann & Jagt 2003 [Neumann & Jagt 2003: 162, fig. 1 (as *Carcineretes* sp.), lower Turonian, northern Germany; probably referable to Cenomanocarcinidae]

'*Necrocarcinus*' *franconicus*† Lehner, 1937 [Lehner 1937: 214, pl. 19, figs. 21, 22, lower Turonian, southern Germany; probably referable to Dynomenidae (Jagt *et al*. 2010)]

Notopocorystes sp.† *sensu* Bishop 1986 [Bishop 1986b: 1099, fig. 2.4, lower Campanian, Montana, USA]

Paranecrocarcinus kennedyi† Wright, 1997 [Wright 1997: 135, figs. 7a, b, 13, Barremian, Zululand, South Africa (removed from Necrocarcinidae and Palaeocorystoidea, see Guinot *et al*. 2008: 707)]

Notopocorystes? *ripleyensis*† Rathbun, 1935 [Rathbun 1935b: 49, pl. 12, figs. 6–10, lower Campanian, Mississippi, USA (see Collins 1997: table 1)]

Necrocarcinidae gen. et sp. indeterminate† sensu Schweitzer *et al*. 2003 [Schweitzer *et al*. 2003b: 890, fig. 1, Cenomanian, Egypt]

Raninella? *armata*† Rathbun, 1935 [Rathbun 1935b: 50, pl. 11, figs. 32, 33, upper Albian, Texas, USA (= *Raninella*? *starkvillensis*† Rathbun, 1935b: 51, pl. 9, figs. 4, 5) (possibly synonymous with *Ferroranina dichrous*†) (Schweitzer *et al*. 2010: 70 as *Cenomanocarcinus armatus*)]

Ranina? *burleighensis*† Holland *in* Holland & Cvancara, 1958 [Holland & Cvancara 1958: 504, text-fig. 3c, pl. 74, fig. 15, Paleocene, North Dakota, USA (indeterminate fragment of chela)]