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Systematics of the Raninidae (Crustacea: Decapoda: Brachyura), with accounts of three new genera and two new species

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Abstract.—Reexamination of the Raninidae reveals revised relationships of raninid genera, both fossil and Recent. *Symethis* Weber is removed from the Raninidae and placed in the newly erected Symethidae under the Raninoidea. One subfamily is reestablished, Palaeocorystinae, and several subgenera are elevated to generic status: *Notopocorystes* McCoy, *Eucorystes* Bell, and *Cretacoranina* Mertin within the Palaeocorystinae. *Lysirude* Goeke, within the Lyreidinae, is distinguished as a discrete genus rather than as a subgenus of *Lyreidus* De Haan. Additionally, three new genera are described: *Macroacaena,* within the Lyreidinae and *Carinaranina* and *Quasilaeviranina* within the Raninoidinae. Two new raninid species, *Laeviranina goedertorum* and *Carinaranina marionae,* from the Eocene Hoko River Formation of Washington, U.S.A., are established. Descriptions of three species previously described by Rathbun are emended based upon new fossil material: *Carinaranina willapensis* (Rathbun) new combination, *Laeviranina lewisanus* (Rathbun) and *L. vaderensis* (Rathbun). The description of *Eumorphocorystes sculptus* Binkhorst is emended.

Phylogenetic relationships within the Raninidae are explored using parsimony analyses. A hypothetical phylogeny is established for the Raninidae, including fossil and extant genera. One result of these analyses is the importance of using character states from the oldest recognized species for fossil genera, while continuing to use character states of the type for extant genera.

Reexamination of the Raninidae was initiated as a result of an investigation of fossil decapods recovered from the Eocene Hoko River Formation, Olympic Peninsula, Washington, U.S.A. Two new species of raninids were discovered and are described from this locality. In addition, many new specimens of fossil raninids described by Rathbun (1926) also were collected, adding greatly to the understanding of those species. Three of Rathbun's descriptions are emended herein, those of *Carinaranina willapensis* (Rathbun, 1926) new combination, *Laeviranina lewisanus* (Rathbun, 1926), and *L. vaderensis* (Rathbun, 1926). It has been recognized for some time that specimens from the Pacific coast of North American, which Rathbun (1926, 1932) referred to *Eumorphocorystes* Binkhorst, 1857, were incorrectly placed. In order to resolve this problem, it was necessary to reexamine *Eumorphocorystes* and emend the original description.

In order to make complete comparisons of fossil raninids from Washington State, it was found essential to examine many other extant and fossil forms. That effort demonstrated the need to provide an arrangement that would include fossil and Recent species. To accomplish this, species were studied employing traditional systematic procedures, and were arranged in genera defined by mutually exclusive characteristics. The generic-level and subfamily-level arrangements were tested using cladistic methods.

J. Martin

The Raninidae was subdivided into six subfamilies by Guinot (1993): Ranininae De Haan, 1841; Notopodinae Serène & Umali, 1972; Symethinae Goeke, 1981; Raninoidinae De Haan, 1841; Lyreidinae Guinot, 1993; and Cyrtorhininae Guinot, 1993. The present work agrees with five of these designations, and suggests (as did Guinot 1993) that the Symethinae should be elevated to family rank within the Superfamily Raninoidea. The Cyrtorhininae should be retained within the Raninidae and not be placed as a subfamily of the Symethidae, as suggested by Guinot (1993).

The systematic treatment of the Raninidae that follows includes descriptions of subfamilies that contain genera or species that are newly recognized, or genera that were elevated from subgeneric rank. In cases where no noteworthy changes within a subfamily were made, that subfamily was not described. In addition, Palaeocorystinae is re-established to embrace three of the earliest fossil members of the Raninidae.

Methods.—When possible, specimens representing each species were borrowed for study. When it was not possible to borrow specimens, photographs were used to determine pertinent characteristics for those species. As a last resort, drawings were used.

All specimens in this paper are identified by collection or museum numbers. Institutions and their acronyms are: California Academy of Science, San Francisco, California (CAS); Institut Royal des Sciences Naturelles de Belgique (IG); Museum für Naturkunde Zentralinstitut der Humboldt-Universität zu Berlin, Institut für Paläontologie (MNZH); Kent State University (KSU); New Zealand Geological Survey, Lower Hutt (NZGS AR); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Localities for the specimens from the Hoko River Formation are identified by numbers assigned by Ross Berglund (RB) who collected most of those specimens.

Systematic Paleontology

Order Decapoda Latreille, 1803
Superfamily Raninoidea De Haan, 1841
Family Raninidae De Haan, 1841

Raninoidea De Haan, 1841:136–137.

Key to subfamilies of the Raninidae

1. Carapace with distinct cervical and branchiocardiac grooves; 2 or more anterolateral spines; longitudinal carina present, often centrally nodose; rostrum bifid; carapace anterior of cervical groove often tuberculate or lingulate . . . . . Palaeocorystinae Lörenthey (*in* Lörenthey & Beurlen 1929)

1′. Carapace rarely bearing cervical groove, branchiocardiac groove faint, rarely complete; usually no more than 2 anterolateral spines; longitudinal carina sometimes present, never nodose; rostrum variable, never bifid; carapace anterior of cervical groove variable, never tuberculate or lingulate 2

2. Carapace often quite rounded, broad, ovate in outline; surface of dorsal carapace variable; front margin variable . . 3

2′. Carapace elongate oval; surface of dorsal carapace almost always smooth; front margin always toothed 4

3. Orbits straight, directed forward; outer margin of extraorbital spines often quite convex; chelipeds with elongate propodus, tip of dactylus sometimes extending beyond margin of propodus; rostrum extending as triangular process, sometimes trifid 5

3′. Orbits often oblique, directed obliquely downward; outer margin of extraorbital spines never very convex; chelipeds with short flattened propodus, dactylus very short and bent against margin of propodus; rostrum present as triangular process, or absent . . . . . Notopodinae Serène & Umali, 1972

4. Fronto-orbital margin equal to or more than ½ extreme width of carapace; 2 orbital fissures; medial supraorbital tooth always present, though not always produced beyond orbital rim; never more than 1 anterolateral spine . . . . . Raninoidinae De Haan, 1841

4'. Fronto-orbital margin somewhat narrow, often less than ½ extreme width of carapace; 1 or 2 orbital fissures; medial supraorbital tooth sometimes absent; 1 or 2 anterolateral spines, though often reduced in size . . Lyreidinae Guinot, 1993

5. Dorsal surface of carapace either scabrous or terraced; front margin of carapace wide; rostrum often trifid, base with sides parallel, or produced triangle; chelipeds with short, flattened propodus, dactylus very short and bent against margin of fixed finger; sternal thoracic shield quite broad, especially between first pereiopods . . Raninidae De Haan, 1841

5'. Dorsal surface of carapace granulate in front and anteriorly, smoother medially; front margin of carapace narrow; rostrum never trifid, short produced triangle; chelipeds with elongate swollen or subcircular propodus, dactylus long so that tip often crosses propodus; sternal thoracic shield narrow, nearly linear between first pereiopods . . . . . Cyrtorhininae Guinot, 1993

Subfamily Lyreidinae Guinot, 1993

Lyreidinae Guinot, 1993:1325.

Key to *Lyreidus, Lysirude* and *Macroacaena*

The three genera included within Lyreidinae, *Lyreidus, Lysirude,* and *Macroacaena,* are often difficult to distinguish from one another. The following key is provided only as an aid in identification, and should be used with caution.

1. Tridentate fronto-orbital margin with 2 pairs orbital fissures; 2 pairs orbital teeth, outer teeth as long, or longer than the rostrum; inner teeth small, barely protruding; carapace typically with distinct longitudinal ridge; 1 pair of hypertrophied anterolateral spines, and additional obsolete anterolateral spine often present at midpoint of anterolateral border; no spines on abdominal somites; no spine or lobe on lancelate propodus of fourth pereiopods . . . . . *Macroacaena,* new genus

1'. Tridentate fronto-orbital margin with single pair orbital fissures; single pair extraorbital teeth, no inner orbital teeth; carapace sometimes with indistinct longitudinal ridge; carapace with 1 or 2 pairs anterolateral spines; spine on abdominal somites 3 and/or 4; sternite 4 about as wide anteriorly as posteriorly; fourth pereiopods with spine or lobe on propodus of fourth pereiopods 2

2. Carapace with not more than 1 pair of anterolateral spines; anterolateral spines sometimes reduced or absent; anterolateral margins smooth or beaded; extraorbital teeth typically as long as wide, about as long as rostrum; sternal plate about as wide at anterior sternite 4 as process between sternites 4 and 5; propodus of fourth pereiopods with spine carrying a spine . . . *Lyreidus* De Haan, 1841

2'. Carapace with 2 pairs of anterolateral spines or anterolateral margin coarsely corrugated; anterolateral spines often hypertrophied; anterolateral margins typically bearing an obsolete spine; extraorbital teeth as long as rostrum, often elongated; sternal plate distinctly widest between sternites 4 and 5; propodus of fourth pereiopods with expanded lobe . . . . . *Lysirude* Goeke, 1985

Lyreidus De Haan, 1841

Lyreidus De Haan, 1841:138
Figs. 1(1–2), 2(10–13)

Type species.—*Lyreidus tridentatus* De Haan, 1841:140, by monotypy. Gender: Masculine.

Diagnosis (modified from Feldmann 1992:943).—Carapace fusiform, much longer than wide, fronto-orbital region narrow, between ¼ to ½ maximum width of carapace; extraorbital spines about equal in length to rostrum; orbits with single, diminutive fissure; marginal spines, if present, at anterolateral corner; anterolateral margin straight, smooth or slightly granulate; surface of carapace smooth or very finely pitted, regions not clearly defined.

Remarks.—There has been some difficulty placing certain species referred to *Lyr-*

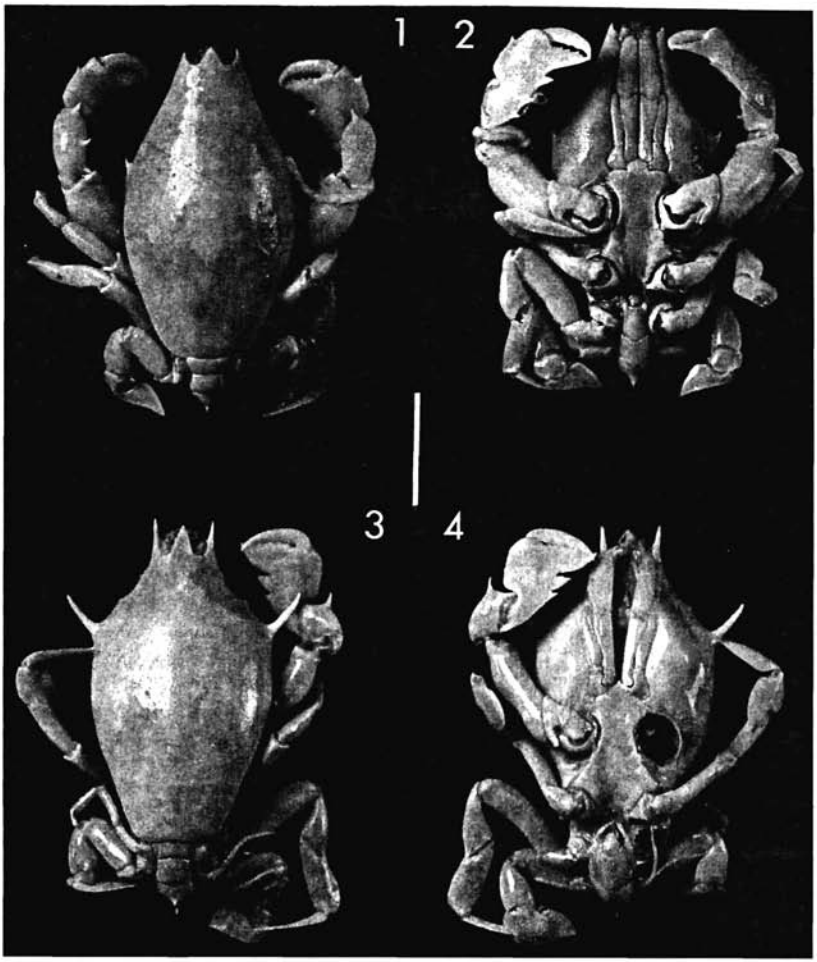

Fig. 1. *Lyreidus tridentatus* De Haan, 1841, USNM 18848: 1, dorsal view; 2, ventral view showing sternites. *Lysirude channeri* (Wood-Mason, 1885), USNM 216686: 3, dorsal view; 4, ventral view. Scale bar equals 1 cm.

eidus De Haan, 1841, and *Lysirude* Goeke, 1985, into their proper systematic positions. Among the most problematic are *Lyreidus succedanus* Collins & Rasmussen, 1992; *Lyreidus rosenkrantzi* Collins & Rasmussen, 1992; *Lyreidus bispinulatus* Collins & Rasmussen, 1992; and *Lyreidus alseanus* (Rathbun, 1932). These four species are placed in a new genus (see *Macroacaena*, new genus). There are several characteristics that are useful taxonomic indicators for species within *Lyreidus*; these were expressed in some detail by Feldmann (1992).

Generic differences between *Lyreidus* and *Lysirude* species often are quite subtle. Goeke (1985) erected the genus *Lysirude* for two species formerly assigned to *Lyreidus*, based upon the lobate nature of the

Table 1.—Distributions and geologic ages of recognized species of *Lyreidus*.

Taxon	Age	Locality
Lyreidus tridentatus De Haan, 1841	Recent	Indopacific
Lyreidus antarcticus Feldmann & Zinsmeister, 1984	early to late Eocene	Antarctica
Lyreidus bennetti Feldmann & Maxwell, 1990	late Eocene	New Zealand
Lyreidus brevifrons Sakai, 1937	Recent	Indian Ocean; Philippines; Japan
Lyreidus elegans Glaessner, 1960	Micoene	New Zealand
Lyreidus lebuensis Feldmann & Chirono-Gálvez, 1992 in Feldmann, 1992	Eocene	Chile
Lyreidus stenops Wood-Mason, 1887	Recent	S. China Sea; Philippines; Japan
Lyreidus sp. Karasawa, 1993	early Pliocene	Japan

dactylus and propodus of fourth pereiopods and the rudimentary spine on the anterolateral margin of *Lysirude*. Feldmann (1992) subsequently united the two groups as subgenera of *Lyreidus*. Further observations yielded additional characters, which can be used to differentiate these two genera. The fronto-orbital margins of *Lyreidus* species in all cases are very narrow, much narrower than one-half the maximum width of the carapaces. *Lysirude* species typically have a fronto-orbital margin that is relatively wider than those of *Lyreidus*. Typically, the rostrum and orbital spines of *Lysirude* species are more produced than those of *Lyreidus*. These additional observations, when coupled with those provided by Goeke (1985:214), serve to distinguish members of *Lysirude* as a separate generic group. Table 1 provides a list of the geographic and stratigraphic positions of recognized species of *Lyreidus*.

Lysirude Goeke, 1985
Figs. 1(3–4), 2(6–9)

Lysirude Goeke, 1985:205–228.
Lyreidus (*Lysirude*) Feldmann, 1992:943–957.

Type species.—*Raninoides nitidus* A. Milne Edwards, 1880:34, by original designation. Gender: Masculine.

Diagnosis.—Fronto-orbital margin tridentate, equal to or slightly wider than posterior margin or ½ maximum width of carapace; rostrum and extraorbital spines often elongate; anterolateral margin typically not straight, usually corrugated, granular, or with rudimentary anterolateral spine at midlength; spine at anterolateral corner often hypertrophied.

Remarks.—Species of *Lysirude* (Table 2) share many traits with species of *Lyreidus*, including a narrow, tridentate fronto-orbital margin, a single orbital furrow, an abdominal spine on the third somite, and "ptery-

Table 2.—Distributions and geologic ages of recognized species of *Lysirude*.

Taxon	Age	Locality
Lysirude nitidus (A. Milne Edwards, 1880)	Recent	western N. Atlantic; Caribbean
Lysirude channeri (Wood-Mason, 1885)	Recent	Bay of Bengal; Philippines
Lysirude griffini Goeke, 1985	Recent	Philippines
Lysirude hookeri (Feldmann, 1992)	late early Eocene	Antarctica
Lysirude hungaricus (Beurlen, 1939)	middle Oligocene	Hungary
Lysirude paronae (Crèma, 1895)	Miocene	Italy
Lysirude waitakiensis (Glaessner, 1980)	middle Eocene	New Zealand

goid processes" (Bourne 1922) along the margin of the sternum between the fifth and sixth somites. These processes are used to lock the abdomen into the sternum, and they do not occur on any other known raninid except *Rogueus* Berglund and Feldmann 1989 and, possibly, *Macroacaena* new genus. In contrast, members of *Lysirude* typically have a much longer rostrum and orbital spines than do species of *Lyreidus*. Variations in the fronto-orbital width within some species of *Lysirude* (for example, *Lysirude nitidus* (A. Milne Edwards 1880)) can be attributed to ontogenetic changes, with juveniles exhibiting a relatively wider fronto-orbital margin (Goeke 1980) than adults. The anterolateral spine generally is hypertrophied in *Lysirude* species, and most species bear some evidence of an extra pair of smaller, rudimentary anterolateral spines at the midlength of the anterolateral margin. Typically, species of *Lysirude* also have a flattened dactylus and a propodus with a flattened flap, which is extended, along the outer margin. Finally, the sterna of *Lysirude* have a broad alate process separating the first and second pereiopods. These differences are significant enough to justify elevation of the subgenus *Lysirude* to generic status.

The earliest records of *Lysirude* are from rocks in high southern latitudes in Antarctica. Table 2 documents the occurrences of species of *Lysirude*.

Macroacaena, new genus
Fig. 2(1–5)

Type species.—*Lyreidus succedanus* Collins & Rasmussen, 1992:23, figs. 11A, B, C, 12, by present designation.

Diagnosis.—Fronto-orbital margin tridentate, wider than posterior margin with orbits bearing 2 fissures; anterolateral margin with or without small tubercle at midlength; spine at anterolateral corner typically hypertrophied; distinct, median, longitudinal ridge typically extending through cardiac region to posterior margin. Abdominal somites (where observed) smooth. Fourth pereiopods (where observed) without spine or extended propodus (Fig. 2).

Etymology.—"Macra", from Greek μακροζ (makros) = long + "acaena" from Greek ακαιγα (akaina) thorn or spine. Gender: Feminine.

Remarks.—Members of this genus appear superficially similar to *Lyreidus* and *Lysirudae*. The fronto-orbital margins of some species of *Lysirude* are just slightly wider than the posterior margins. This also is true of three taxa from Greenland assigned by Collins & Rasmussen (1992:23–30) to *Lyreidus*. However, the three species from Greenland have two orbital fissures, while members of *Lyreidus* and *Lysirude* typically bear only a single orbital fissure. This is a very important taxonomic character, based upon cladistic character analysis (see section on Phylogenetic Analysis and Fig. 22). The additional orbital fissure demarks a rudimentary mid-orbital tooth not observed in species within *Lyreidus* or *Lysirude*. Furthermore, the pronounced longitudinal ridge observed on *L. succedanus* and *L. alseanus* does not appear to be as prominent on species of *Lyreidus* or *Lysirude*. Two of the three species described by Collins & Rasmussen (1992), *Lyreidus rosenkrantzi* and *L. succedanus*, have portions of the abdomen preserved; no specimens appear to bear any abdominal spines, a character typical of species of *Lyreidus* and *Lysirude* (Fig. 2). Moreover, three species from Greenland have a lancelet dactylus on the fourth pereiopods, and show no protuberance, spine or flap on the propodus of the fourth pereiopods, as exhibited on *Lyreidus* species and *Lysirude* species. These species should be united within a distinct genus. Additionally, *Lyreidus alseanus* Rathbun, 1932, appear to have these same characteristics; thus, they also must be united under the new genus (Table 3). All four species referred to *Macroacaena* are discussed below.

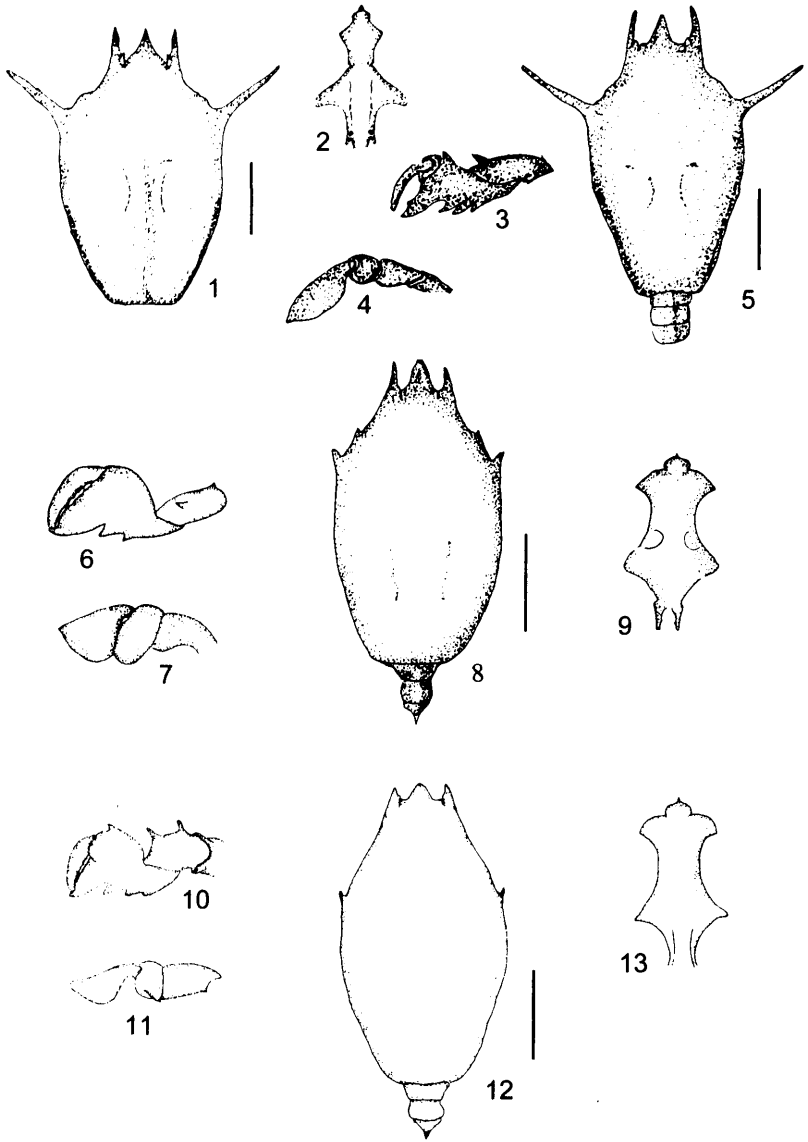

Fig. 2. *Macroacaena alseana* (Rathbun, 1932): 1, View of dorsal carapace; 2, sternum. *M. rosenkrantzi* (Collins & Rasmussen, 1992): 3, cheliped; 4, fourth pereiopod; 5, dorsal carapace. *Lysirude nitidus* (A. Milne Edwards, 1880): 6, cheliped; 7, fourth pereiopod; 8, dorsal carapace; 9, sternum. *Lyreidus tridentatus* De Haan, 1841: 10, Cheliped; 11, fourth pereiopod; 12, dorsal carapace; 13, sternum. Scale bar equals 1 cm.

Macroacaena succedana (Collins & Rasmussen, 1992), new combination

Lyreidus succedanus Collins & Rasmussen 1992:23, figs. 11A–C, 12.

Material examined.—Plastotype kindly supplied by J. H. S. Collins, Jr., supplemented with photographs and drawings by Collins & Rasmussen (1992).

Remarks.—The carapace is somewhat fusiform in outline; the fronto-orbital region is slightly wider than the posterior margin and bears two closed fissures and a medial tooth; the anterolateral margin is armed with two spines, one hypertrophied and positioned at the anterolateral corner, the other rudimentary tubercle and positioned at about the midlength of the anterolateral margin; the fourth pereiopod has a lancelet dactylus; and there is no spine observable on any abdominal somite such as occurs on species of both *Lyreidus* and *Lysirude.*

Occurrence.—Lyreidus succedana is represented by 192 carapaces from many localities ranging in age from Campanian to Maastrichtian, along the central western shores of Greenland (Collins & Rasmussen 1992).

Macroacaena alseana (Rathbun, 1932), new combination

Lyreidus alseanus Rathbun, 1932:239, 240, 242, figs. 3–4; Glaessner, 1960:17; Bennett, 1964:24; Feldmann, 1989:63–69, figs. 1.1–2, 3.1–8; text fig. 4.1–3.

Ranidina teshimai Fujiyama & Takeda, 1980:339–342, pl. 39, figs. 1–5, pl. 40, figs. 1–4.

Lyreidus (Lysirude) alseanus. Feldmann, 1992:951, figs. 4.10–11.

Material examined.—Fifteen specimens (USNM 431289–431303); 4 specimens, coll. R. Berglund (private collector affiliated with Burke Museum).

Remarks.—Specimens previously referred to *Macroacaena alseana* bear a mid-orbital tooth that protrudes just beyond the orbital rim, thus allowing this taxon to be distinguished from members of *Lyreidus* or *Lysirude.* The fronto-orbital margin is just slightly wider than the posterior margin, or one-half the extreme width of the carapace. Specimens of *M. alseana* have a very distinctive longitudinal carina, a character that is shared with some species of *Carinaranina,* a new genus assigned herein to the Raninoidinae. However, the three prominent frontal teeth, two extraorbital teeth and the rostrum, serve to distinguish this taxon from any other described from the Pacific northwest of North America. *Macroacaena alseana* also bears a rudimentary second anterolateral tooth or nubbin, which is not observed on any species of *Carinaranina* new genus. This last character also serves to distinguish *M. alseana* from species of *Carinaranina* when the fronto-orbital region is not well preserved.

Macroacaena alseana is most similar to *M. succedana,* but differs in the possession of a relatively wider carapace and a more well defined longitudinal ridge. The medial tooth is positioned a little closer to the extraorbital spine than in *M. succedana.*

As noted by Feldmann (1989:68, 1992: 951), *Ranidina teshimai,* recognized from the Oligocene Poronae Formation of Hokkaido, Japan, is a junior synonym of *Lyreidus alseanus* Rathbun. Photographs (Fujiyama & Takeda 1980, plates 39 & 40) indicate that specimens of *R. teshimai* have the same broad carapace as seen in specimens of *M. alseana,* and the anterolateral spines are positioned similarly and at a similar angle as specimens from Washington and Oregon.

Occurrence.—Macroacaena alseana is known from several localities in Washington and Oregon, U.S.A., in rocks that range in age from late Eocene to Oligocene (Feldmann 1989:951).

Macroacaena bispinulata (Collins & Rasmussen, 1992), new combination

Lyreidus bispinulatus Collins & Rasmussen, 1992:27, fig. 16A–D.

Material examined.—Several plastotypes supplied by J. S. H. Collins.

Remarks.—Upon inspection of photographs as well as several plastotypes, I agree with Collins & Rasmussen (1992) that this species should not be referred to *Hemioon* Bell, 1863, which it superficially resembles. Even though there is no extra anterolateral tooth or tubercle, this species is more correctly placed within *Macroacaena*, since the occurrence of a rudimentary anterolateral tooth seems to be quite variable within this genus. The front of *M. bispinulata*, however, appears to be exceptionally wide and the extraorbital tooth exceptionally short, when compared with other members of *Macroacaena*. In the description by Collins & Rasmussen (1992:28–29), the species is defined as possessing a medial orbital tooth and two orbital fissures, two very important characters for uniting *Macroacaena* species. The front margin is described as being rather narrow, and as possessing a rostrum that is broadly triangular with no median furrow. This observation serves to differentiate this species from those referred to *Hemioon* Bell, with which it could easily be confused.

Occurrence.—*Macroacaena bispinulata* is known from six incomplete carapaces collected from Paleocene age rocks on the western coast of Greenland.

Macroacaena rosenkrantzi (Collins & Rasmussen, 1992), new combination

Lyreidus rosenkrantzi Collins & Rasmussen (1992):23, figs. 11A–C, 12.

Material examined.—Plastotype supplied by J. S. H. Collins.

Remarks.—*Macroacaena rosenkrantzi* possesses all the characteristics of the genus, and is distinguished from *M. succedana* and *M. alseana* primarily by the lack of a longitudinal median ridge. *Macroacaena rosenkrantzi* is further distinguished from *M. succedana* by the possession of less deeply impressed cardiac furrows and by anterolateral spines that are positioned at a more acute angle with the carapace midline than those of *M. succedana*.

Occurrence.—*Macroacaena rosenkrantzi* is represented by 1240 carapaces from many localities, Maastrichtian in age, along the central western shores of Greenland.

Subfamily Notopodinae Serène & Umali, 1972

Notopinae [sic] Serène & Umali 1972:25, 29.—Notopodinae Goeke 1986:224, 226.—Notopodinae Guinot 1993:1324–1325, 1327–1329.

Diagnosis.—Carapace either elongate or quite rounded; front margin variable, often directed forward but sloping obliquely downward; median dorsal carina sometimes present; chelipeds, where known, with short flattened propodus, dactylus very short and bent against margin of propodus; rostrum present as triangular process, or absent.

Remarks.—Serène & Umali (1972:29) first erected the Notopinae [sic] and designated *Notopus* De Haan 1841 as the type genus. Subsequently, Manning & Holthuis (1981:7) corrected the name to Notopodinae. The genera that Serène & Umali referred to the Notopodinae included *Notopus* De Haan, *Cosmonotus* White, 1847, and *Ranilia* H. Milne Edwards, 1837. Eight additional genera are included within this subfamily: *Eumorphocorystes* Binkhorst, 1857, *Lianira* Beschin et al., 1991, *Lovarina*, Beschin et al., 1991, *Notopella* Lörenthey (*in* Lörenthey & Beurlen, 1929), *Pseudoraninella* Lörenthey (*in* Lörenthey & Beurlen, 1929), *Raniliformis* Jagt et al., 1993, and *Umalia* Guinot, 1993. *Umalia* is the only extant taxon; seven of the eight are fossil.

Genus *Eumorphocorystes* Binkhorst, 1857 Fig. 3

Type species.—*Eumorphocorystes sculptus* Binkhorst 1857, by monotypy:108, pl. VI, figs. 1–2. Gender: Masculine.

Diagnosis.—Carapace obovate, with anteriorly directed anterolateral spines. Ros-

Fig. 3. *Eumorphocorystes sculptus* Binkhorst, 1857, IG 6521-9.7: dorsal view of carapace. Scale bar equals 1 cm.

trum long, very narrow. Dorsal surface of carapace with narrow, raised median ridge extending entire length of carapace; surface covered with longitudinal and oblique raised, beaded ridges which are irregular in pattern, but somewhat symmetrical on each side of midline of carapace; surface very finely punctate.

Remarks.—See discussion under *Carinaranina,* new genus.

Eumorphocorystes sculptus Binkhorst, 1857
Fig. 3

Eumorphocorystes sculptus Binkhorst, 1857:108, pl. VI, figs. 1–2.–Binkhorst, 1861, pl. 9, fig. 2.—Straelen, 1923: 119.—Glaessner, 1929:170.—Lörenthey (*in* Lörenthey & Beurlen, 1929).—Tucker & Feldmann, 1990.

Raninella sculpta A. Milne Edwards, 1862: 493.—Pelseneer, 1886:174.

Diagnosis.—Same as for genus.

Description (emending E. sculptus*).*—Carapace longer than broad; widest at or just slightly posteriad anterolateral spines; extreme width, excluding anterolateral spines, about 75% length. Carapace slightly convex transversely, less so longitudinally; dorsal surface of carapace evenly covered by minute punctae. Dorsal surface with raised, almost bilaterally symmetrical longitudinal and oblique ridges with flattened tops lying on either side of raised median carina which extends entire length of carapace including rostrum. Median carina and ridges steep-sided and irregularly beaded along both margins.

Width of fronto-orbital margin about 66% extreme width; front about 33% extreme width of carapace, with median narrow triangular rostrum bordered on either side by broad inner orbital regions. Orbits ovate, moderately oblique; dorsal margin of each orbit beaded and bearing 2 closed fissures.

Anterolateral margins sinuous, terminating at anterolateral angle with short, acicular spine directed anteriorly. Posterolateral margins only slightly convergent to posterolateral angle, then strongly convergent to posterior corners, and narrow posterior margin.

Most prominent transverse raised ridges on dorsal surface of carapace originating at anterolateral tooth, and extending medially marking position of cervical groove. Another prominent transverse groove parallel to cervical ridge marking position of branchial furrow. Protogastric regions with raised ridges in h-shaped pattern on either side of median carina; these attach at their base to transverse Y-shaped ridges. Branchial regions with irregular ridges in irregular pattern of loops.

Affinities.—(See discussion under *Carinaranina,* new genus, for affinities of *Eumorphocorystes* sensu Binkhorst, and *Eu-*

morphocorystes sensu Rathbun. Species referred by Rathbun to *Eumorphocorystes* are herein included in *Carinaranina.*)

Material examined.—4 specimens, Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.; 11 specimens, Institut Royal des Sciences Naturelles de Belgique (IG 6521, 9.1–9.9; IG 4285, and IG 5185); 5 specimens, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany.

Remarks.—Cuticular terraces have been the focus of research regarding the burrowing habits of crabs (Savazzi 1981, 1985). However, little attention has been paid to terraces that are irregular in pattern, and that are not transverse. The raised ridges on *Eumorphocorystes sculptus* van Binkhorst, are probably not analogous to the terraces on *Lophoranina* species, because they do not demonstrate an anchoring capability. That is, they are not perpendicular to the borrowing direction of the crab, nor is the anterior side of the terrace raised to prevent withdrawal of the crab from its burrow. On the other hand, the roughened surface may have had some gripping capability, and it is possible that the beading along the margins carried spines, although none has been observed to date on any specimens.

Pelseneer (1886:14) suggested that *Notopocorystes Mülleri* [sic] and *Eumorphocorystes sculptus* might be congeneric and quite similar to *Raninella* species; thus, he placed both species within *Raninella.* He believed that the slight sculpting along the postfrontal region of *N. muelleri* was analogous to the raised ridges on the dorsal surface of *E. sculptus.* However, there are several major differences between the species that are sufficient to require placement within separate genera. *Pseudoraninella muelleri,* reassigned by Lörenthey (*in* Lörenthey & Beurlen 1929), is extremely vaulted transversely, while *E. sculptus* is nearly flat. This is an important distinction that often reflects the positioning of the gills. The fronto-orbital margins of *Eumorphocorystes* are beaded, but without spines; the margins of *Pseudoraninella* species bear orbital spines.

Occurrence.—Late Cretaceous (Maastrichtian) Maastricht Formation, Belgium.

Subfamily Palaeocorystinae Lörenthey (*in* Lörenthey & Beurlen, 1929)

Palaeocorystinae Lörenthey (*in* Lörenthey & Beurlen, 1929):299.

Diagnosis.—Carapace with distinct cervical and branchiocardiac grooves; two or more anterolateral spines; longitudinal carina present, often centrally nodose; rostrum bifid; carapace anterior of cervical groove often tuberculate or lingulate.

Description.—Elongated, somewhat flat to moderately inflated crabs with small projecting bifid rostrum, straight orbitofrontal margin, large oval orbits with 2 fissures above and 1 below. Distinct longitudinal carina may or may not be present. Cervical furrow directed anteriorly from margin, then posteriorly, forming 3 forwardly concave arcs; epibranchial lobes delimited by short furrows; branchiocardiac furrows weak to absent. Upper surface may bear sharp tubercles, or be bare, or have straplike ornament, or transverse lobed line posterior to depressed frontal area. Pterygostomial regions strongly ridged. [modified from Wright & Collins 1972:73]

Remarks.—Wright & Collins (1972:73) interpreted *Notopocorystes, Eucorystes,* and *Cretacoranina* as subgenera of *Notopocorystes* because of the many features they have in common. Any distinctions that separated the three were considered by Wright & Collins to be of subgeneric importance. For example, they considered that widening of the front and size of the orbits was not an important enough distinction to warrant separation at the level of genus. Features of the fronto-orbital margin are interpreted by this author to be of greater significance than numbers of tubercles. Additionally, the carapace of *Notopocorystes* has a deep cervical groove and many robust tubercles. *Eucorystes* retains the cervical groove, but there

is already a loss of tubercles and a unique pattern of raised ridges. *Cretacoranina* has a much fainter cervical groove and is much smoother on the dorsal surface than either Notopocorystes or Eucorystes. Raninids demonstrate a general trend, then, from the tuberculate dorsal surface of *Notopocorystes* with a well defined cervical groove, to the smooth dorsal surface of Recent raninids which, with few exceptions, bear no cervical groove. Wright & Collins (1972:73) also pointed out that these three taxa could be treated equally well as three distinct genera, and this arrangement has been followed in the cladistic analysis.

Wright & Collins (1972:75) used subspecies to distinguish successive populations recovered from many Albian horizons in England. They stated that "Although the differences between them are greater than those sometimes used to distinguish species . . .", but that they preferred to treat them as subspecies. Indeed, other workers have used several of the same characteristics to describe species within one or more of these genera (Secretan 1964:155). Using the same characters to describe species-level taxa one time, and subspecies-level taxa another, contributes to a certain amount of confusion when considering all the species assigned to all three genera. I prefer to structure the descriptions of genera and species within the Raninidae so that there is a sense of uniformity throughout. At the same time, it is important to recognize the remarkable collection of specimens that demonstrates the evolution of several species.

The Palaeocorystinae, comprised of three genera, ranged from the lower Albian to the Cenomanian, and are recognized from Europe, Japan, North America, New Zealand, and Madagascar. The Palaeocorystinae are interpreted to represent the rootstock of the Raninidae.

Key to genera of Palaeocorystinae

1. Dorsal surface decorated with tubercles or vermiform ridges (=strap ornament). Carapace moderately to strongly vaulted. Cervical furrow deep, complete; branchiocardiac furrow complete, but feeble; anterolateral margins straight to slightly convex 2

1′. Dorsal surface finely granulate or smooth. Carapace only weakly vaulted, if at all. Cervical and branchiocardiac furrows shallow, incomplete, often reduced to medial portions only; anterolateral margins distinctly convex . . . . . *Cretacoranina* Martin, 1941

2. Distinct, sharp tubercles on anterior dorsal surface of carapace with no vermiform ridges; median carina present, tuberculate or smooth . . . . . *Notopocorystes* McCoy, 1849

2′. Anterior dorsal carapace with distinct system of vermiform, steep-sided, flat-topped ridges (=strap ornament) and no tubercles; long ridges parallel to longitudinal axis of carapace may, or may not, be present posteriorly . . . . . *Eucorystes* Bell, 1863

Genus *Notopocorystes* McCoy, 1849
Fig. 4(1–2)

Notopocorystes McCoy, 1849:169.
Palaeocorystes Bell, 1863:11, pl. II, figs. 8–13.

Type species.—Subsequent designation by Withers (1928), *Corystes stokesii* Mantell, 1844:533. Gender: Masculine.

Diagnosis.—Distinct sharp tubercles on anterior portion of upper surface of carapace and smooth or dentate median carina or row of tubercles (Wright & Collins 1972: 73). Carapace elongate oval in outline; vaulted transversely, less so longitudinally. Dorsal surface of carapace with distinct, longitudinal, median keel for almost entire length of carapace, often bearing row of tubercles; surface of carapace finely punctate; regions marked by grooves and tubercles or ridges. Fronto-orbital margin broad, greater than 40% extreme width of carapace; supraorbital ridges bearing 2 distinct fissures; rostrum bifid. Cervical furrow distinct; epibranchial region often delimited by furrow. Posterolateral margins straight.

Fig. 4. *Notopocorystes serotinus* Wright & Collins, 1972, KSU 4940 (a plastotype of B22902): 1, dorsal view; 2, ventral view. Scale bar equals 1 cm.

Remarks.—Species in this genus are easily distinguished from other Cretaceous raninids by several characters. *Notopocorystes* species generally are quite tuberculate and almost always bear a tuberculate median keel for their entire length. *Eucorystes* species, on the other hand, do not bear tubercles; rather, they are adorned with steep-sided vermiform ridges, referred to as "strap ornament", especially anterior to the cervical furrow. *Cretacoranina* species generally have a much smoother dorsal surface, and are much less vaulted than *Notopocorystes* species. Additionally, *Cretacoranina* species often have a somewhat concave aspect to the posterolateral margins, not observed on species of either of the other two genera.

See Table 3 for species assigned to this genus.

Genus *Cretacoranina* Mertin, 1941
Fig. 5(1–2)

Cretacoranina Mertin, 1941:237, pl. 8, fig. 9; as subgenus.

Type species.—By original designation, *Raninella schloenbachi* Schlüter, 1879. Gender: Feminine.

Diagnosis.—Carapace oval to oblong; surface finely granulate or smooth; distinct, longitudinal, median keel for almost entire length of carapace not tuberculate. Front slightly produced, rostrum bifid; postfrontal area sometimes depressed. Supraorbital margin bearing 2 distinct fissures. Anterolateral margins toothed.

Remarks.—Characters that distinguish *Cretacoranina* from other Palaeocorystinae include the smooth, nontuberculate dorsal carapace and the often-depressed postfrontal area. Taxa referred to this genus (see Table 4) retain the well-impressed cervical and branchial furrows, although often the furrows are reduced to the median portions of the dorsal carapace. Species of the genus are distinguished upon the basis of the shape of the anterolateral margin and the

Table 3.—Distribution and geologic ages of recognized species of *Notopocorystes*.

Taxon	Age	Locality
Notopocorystes stokesii (Mantell, 1844)	Albian	England
N. praecox Wright & Collins, 1972	Albian	England
N. serotinus Wright & Collins, 1972	Albian	England
N. normani (Bell, 1863)	Cenomanian	England; Germany
N. bitubericulatus (Secretan, 1964)	Albian	Madagascar
N. japonicus (Jimbô, 1894)	late Turonian or early Coniacian	Japan
N. xizangensis Wang, 1981	Albian	China

Fig. 5. *Cretacoranina testacea* (Rathbun, 1926): paratype USNM 327238: 1, dorsal view of anterior; 2, ventral view showing buccal frame. Scale bar equals 1 cm.

number of anterolateral spines, the presence or absence of a depressed frontal area, and the smoothness of the dorsal carapace. The dorsal median keel is faint to absent on some species.

Genus *Eucorystes* Bell, 1863
Fig. 6(1–2)

Eucorystes Bell, 1863:17, pl. II, figs. 14–17.

Type species.—Subsequent designation by Bell (1863), *Notopocorystes carteri* McCoy, 1854. Gender: Masculine.

Diagnosis.—Carapace rectangular in outline; only slightly vaulted transversely, nearly flat longitudinally. Dorsal surface of carapace with longitudinal median keel for almost entire length of carapace; surface of carapace possessing many granulate, flattened ridges; anteriormost ridges linear and arrayed longitudinally and symmetrically on either side of longitudinal axis of carapace; surface of carapace between ridges finely punctate. Fronto-orbital margin representing extreme width of carapace; supraorbital ridges bearing 2 distinct fissures; rostrum small, bifid or trifid. Cervical furrow distinct; epibranchial region often delimited by furrow. Posterolateral margins straight; converging only slightly posteriorly.

Remarks.—Bell (1863) distinguished this genus based primarily upon the shape of the carapace as more square than *Notopocorystes* species, the shape and greater size of the orbits of *Eucorystes* species, and the "strap" ornament found on the anterior

Table 4. Distributions and geologic ages of recognized species of *Cretacoranina* Mertin, 1941.

Taxon	Age	Locality
Cretacoranina schloenbachi (Schlüter, 1879)	Coniacian	England; Germany
C. australis Secretan, 1964	late Santonian–early Campanian	Madagascar
C. broderipii (Mantell, 1844)	Albian–Cenomanian	England; France
C. denisae Secretan, 1964	Campanian	Madagascar
C. dichrous Stenzel, 1944	Turonian	Texas
C. exiquus Glaessner, 1980	Cretaceous	Bathhurst Is., Australia
C. fritschi Glaessner, 1930	Turonian	Germany
C. harveyi (Woodward, 1896)	Cenomanian	Vancouver Is., B. C.
C. ornatus Wright & Collins, 1972	Cenomanian	England
C. pattutensis Collins & Rasmussen, 1992	late Santonian–early Campanian	Greenland
C. syriacus Withers, 1928	Cenomanian	Syria
C. cf. *syriacus* Withers, 1928	Cenomanian	England
C. testacea (Rathbun, 1926)	Late Cretaceous	Delaware; New Jersey

portions of the carapace. Bell (1863:18) suggested that characteristics of the fronto-orbital region were extremely important at the level of genus. *Eucorystes* species (see Table 5) can be separated on the basis of the shape of the anterolateral borders, the sharpness of anterolateral and orbital spines, the relative width of the fronto-orbital margin, the amount of vaulting, the character of the grooves, and the character of the 'strap' ornamentation.

Subfamily Raninoidinae De Haan, 1841

Raninoidea De Haan, 1841:136–137.

Diagnosis (emending Raninoidinae).—Carapace elongate oval; fronto-orbital margin equal to or more than ½ extreme width of carapace; 2 orbital fissures; medial orbital tooth always present, though not always produced beyond supraorbital rim; never more than 1 anterolateral spine. Sternal shield between third pereiopods at base of sternite 5 relatively wide, sternite 6 relatively broad. Chelipeds with propodus flattened and somewhat elongate, long fixed finger; anterolateral spine, when present, often hypertrophied.

Remarks.—The cladistic analysis (see Phylogenetic Analysis and Fig. 22) suggests that this subfamily consists of two clades. One clade includes *Raninoides, Laeviranina,* and *Carinaranina,* new genus; another includes *Quasilaeviranina,* new genus, *Notopoides,* and *Notosceles.* Characters which unite these two clades and distinguish the Raninoidinae from other raninids include their elongate, ovate outline, the shape of the chelipeds, the shape of sternites, the presence of only a single pair of anterolateral spines (although these are sometimes reduced to absent), and the general conformation of the toothed fronto-orbital region. The *Quasilaeviranina* group is distinguished by the more rounded appearance of the outline of the carapace, and by a fronto-orbital margin that tends to converge anteriorly and often bears closed rather than open orbital fissures. The two groups are so closely related to one another that they should remain united as a single subfamily.

Genus *Carinaranina,* new genus

Type species.—*Eumorphocorystes naselensis* (Rathbun, 1926), by present designation. Gender: Masculine.

Diagnosis.—Carapace elongate, greatest width posteriad to antero-lateral spines; outline of carapace often egg-shaped; fronto-orbital region narrow, orbits marked by fissures; rostrum produced. Anterolateral spines often hypertrophied. Branchial regions usually depressed. Surface of carapace coarsely punctate, often with dorsal

Fig. 6. *Eucorystes carteri* (McCoy, 1854): dorsal view of plastotype 1, KSU 4967; 2, CU 319f. Scale bar equals 1 cm.

ridge extending entire length of carapace, including rostrum.

Remarks.—Rathbun (1926) described a new species of crab from Washington that she referred to *Eumorphocorystes* Binkhorst (1857) because of the egg-shaped body, the dorsal ridge, and the narrow orbital fissures. Apparently, from her comments (Rathbun 1926:100), this decision was based entirely upon written description of the genus by Binkhorst (1857). Rathbun (1932) later referred two more species to *Eumorphocorystes, E. schencki* and *E.* (?) *leucosiae.* Since that time, others (Lörenthey, *in* Lörenthey & Beurlen 1929:297; Glaessner 1969:R2–498) have questioned these assignments; however, none of the species have been reassigned to other genera. Some workers have doubted the accuracy of the lithographic illustration of the type with regard to the rostrum (Pelseneer 1886:174, Lörenthey, *in* Lörenthey & Beurlen 1929:297; Glaessner 1969:R–495), pointing out that the rostrum should have been depicted as quite narrow, carrying a median ridge with furrows on either side, and about 4 mm long for a carapace 36 mm in length (translated from Pelseneer 1886: 174). Indeed, a photograph of a specimen identified as belonging to *Eumorphocorystes sculptus,* but not the holotype, shows the rostrum as described by Pelseneer (1886) (see Fig. 3).

It is necessary, then, to place the species of *Eumorphocorystes* sensu Rathbun (1926, 1932) in a newly erected genus reflecting their close relationships. It is clear that the species Rathbun described are not related at the generic level with the monotypic genus *Eumorphocorystes* sensu Binkhorst (1857). None of the *Eumorphocorystes* species sensu Rathbun bear the strap ornamentation of *Eumorphocorystes sculptus* Binkhorst, but, instead, are covered with evenly spaced, relatively coarse punctae (Fig. 7). Even more fundamental is the fact that the orbits of *Eumorphocorystes* species sensu Rathbun face forward, while those of *E. sculptus* are directed somewhat obliquely away from the longitudinal axis of the animal. The extreme width of the carapace on *Eumorphocorystes* species sensu Rathbun is posterior to the anterolateral spines, rather than at the anterolateral spines as with *E. sculptus.* In-

Table 5. Distributions and geologic ages of recognized species of *Eucorystes* Bell.

Taxon	Age	Locality
Eucorystes carteri (McCoy, 1854)	Albian	England
E. eichhorni Bishop, 1983	Campanian	Montana
E. intermedius Nagao, 1931	Cenomanian	Japan
E. oxtedensis Wright & Collins, 1972	Albian	England

deed, the only unifying characters are the median ridge and characters which reflect the fact that both groups of organisms belong to the Raninidae. Each of the species of *Eumorphocorystes* sensu Rathbun clearly reflects certain unifying characteristics. In each, the carapace is coarsely punctate and the greatest width is posterior to the anterolateral spines. Each has a relatively narrow fronto-orbital margin, and has a median ridge extending the entire length of the dorsal carapace, including at least part of the rostrum. The three species described by Rathbun, *E. naselensis, E. schencki,* and *E.* (?) *leucosiae,* are herein assigned to *Carinaranina,* new genus.

There are five recognized species included in this genus and described below. In addition, *Carinaranina* was recognized from the ?Aldwell Formation (Squires et al. 1992) at Pulali Point, Washington. Another undescribed species of this genus is recognized from the Oligocene-aged Quimper Sandstone, Port Townsand, Washington.

Etymology.—From Latin *carina* = keel (of a ship), in reference to the dorsal median ridge + *Ranina,* type genus of the family, from Latin *rana* = frog, hence the name "frog crabs" for members of this family. Gender: Feminine.

Carinaranina naselensis (Rathbun, 1926), new combination
Fig. 7(1 & 4)

Eumorphocorystes naselensis Rathbun, 1926:100, pl. 24, figs. 9–10; Lörenthey (*in* Lörenthey & Beurlen), 1929:297; Jeletzky, 1973:339, figs. 3A–D, 4 A–C; Tucker & Feldmann, 1990:412, fig. 4.1–4.2.

Description [emending Rathbun (1926) and Tucker & Feldmann (1990)].—Carapace broadly ovate in outline, widest behind anterolateral teeth; greatest width about 60% total length; carapace convex longitudinally, very convex transversely; lateral margins turned slightly under, taper posteriorly to anterolateral teeth, becoming straight.

Width of fronto-orbital region slightly less than ½ greatest width; fronto-orbital region widest posteriorly, tapering slightly anteriorly; orbits directed forward. Dorsal margin of each orbit marked by 2 U-shaped open fissures, wider than deep, directed posteriorly; approximately parallel to longitudinal axis of animal; outer tooth of orbit longest; 2 inner teeth progressively shorter, second tooth bifid. Frontal margin of carapace produced to form rostrum, not extending beyond orbits, not downturned. Rostrum long, triangular, margins slightly convex, inflated; rostrum keeled medially; keel subtle, extending posteriorly into well-defined medial ridge that extends entire length of carapace; keel bounded laterally by shallow sulci.

Anterolateral margins of carapace convex in outline, turned under at lateral angle, becoming straight and tapering posteriad lateral angle; 1 pair of long, stout lateral spines; spines directed outward and very slightly forward; posterolateral margin convex, converging posteriorly to blunt posterolateral corner; posterior margin slightly concave.

Midline of carapace strongly keeled for entire axial region; urn-shaped cardiac region gently and broadly swollen, tapering, merging into keeled axial region posteriorly; 2 deeply etched branchiocardiac grooves as arcuate impressions; remainder of cardiac groove subtle; 2 arcuate muscle scars, di-

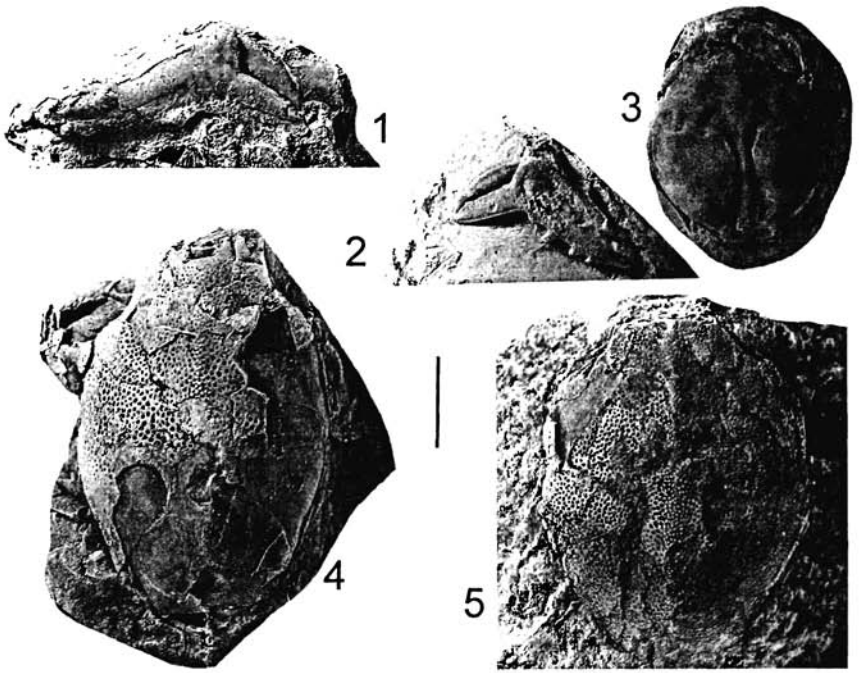

Fig. 7.' *Carinaranina naselensis* (Rathbun, 1926), GSC 32066: 1, right major cheliped; 4, GSC32067, dorsal view. *C. leucosiae* (Rathbun, 1932), USNM 371902: 2, dorsal view; 3, left major cheliped. *C. schencki* (Rathbun, 1932), USNM 336007: 5, dorsal view. Scale bars equal 1 cm.

rected toward axis of carapace, lying just anteriad cardiac grooves; pair of gastric pits either side of midline at anterior termini of muscle scars; metabranchial region slightly less inflated than remaining branchial region; dorsal carapace covered by large punctae or pits.

Sternum narrow, elongate; sternites 1–3 narrow anteriorly, broadening at midlength to form rounded, triangular termination separated from sternite 4 by narrower, parallel-sided part; sternite 4 with narrow anterior processes directed anterolaterally, forming widest part of sternum, narrowing at midpoint, wider posteriorly; axis of sternum slightly concave anteriorly, becoming deeply depressed posterior to sternite 4.

Abdominal somites uniformly narrow, somites 3–5 bear median, anteriorly directed spines; telson longer than wide, tapering posteriorly, axial region raised.

Appendages unknown.

Material studied.—USNM 431254, USNM 431255, USNM 431256, USNM 431257, and CAS 29180 (each number represents a single specimen).

Occurrence.—*Carinaranina naselensis* was recovered from "Washington: shale bluffs along Nasel River near mouth of Salmon Creek, Nasel; middle Oligocene" (Rathbun, 1926:100).

Carinaranina leucosiae (Rathbun, 1932), new combination
Fig. 7(2–3)

Eumorphocorystes (?) *leucosiae* Rathbun, 1932:242, fig. 7, fig. 8.

Remarks.—Rathbun (1932:242) expressed reservations about assigning this species to *Eumorphocorystes,* stating that it bore close resemblance to species belonging to the Leucosidae. Although the branchial regions are much more inflated than is typical for species of the *Carinaranina,* new genus, the median carina and the configuration of the claws, which are typically raninid-like and not as in the Leucosidae, suggest that this species can be retained in the *Carinaranina.*

Material examined.—Holotype USNM 371902, paratype USNM 336004.

Occurrence.—*Carinaranina schencki* (Rathbun, 1932:242) and *C.? leucosiae* (Rathbun, 1932:242) were collected from the Upper Eocene Keasey Formation, "*Cardium weaveri*" zone, Polk County, which was thought at the time to be Oligocene in age. However, Snavely (1987: 310) placed the Keasey Formation in the latest Eocene.

Carinaranina marionae, new species
Fig. 8(1–4)

Diagnosis.—Carapace rather slender for genus; outer, lateral margins of orbits diverge anteriorly. Rostrum not extending beyond orbital spines. Anterolateral margin short, concave; anterolateral spines about 25% total length. Fronto-orbital margin not quite 66% extreme width. Posterior margin concave. Surface coarsely punctate; median ridge covering entire length of carapace, including rostrum.

Description.—Carapace obovate in outline, anterior ⅔ widest, greatest width 66–70% total length; entire surface punctate, punctae more coarse anteriorly; carapace vaulted longitudinally, more so transversely. Width of fronto-orbital region about 60% extreme width; fronto-orbital region widest anteriorly, tapering slightly posteriorly; orbits directed forward. Dorsal margin of each orbit marked by 2 fissures; inner fissure open U-shape, deeper than wide, directed posteriorly, approximately parallel to longitudinal axis of animal; outer fissure open, shallow, asymmetric V-shape, wider than deep, directed posteriorly toward longitudinal axis of animal; outer tooth of orbit longest; 2 inner teeth progressively shorter. Frontal margin of carapace produced to form rostrum, not extending beyond orbits; not downturned. Rostrum long, triangular, margins straight; rostrum keeled medially; keel subtle, extending from posterior ½ of rostrum into well-defined medial ridge that extends entire length of carapace.

Anterolateral margins concave in outline; 1 pair of elongate, slender lateral spines; spines directed outward and very slightly forward; posterolateral margin convex, converging posteriorly to posterolateral corner; posterior margin concave. Midline of carapace strongly keeled for entire axial region; urn-shaped cardiac region gently and broadly swollen, merging into keeled axial region posteriorly; 2 shallow branchiocardiac grooves as arcuate impressions; remainder of cardiac groove not obvious; cardiac region bearing pair of nodes on either side of distinct boss on midline of carapace on a transverse line posteriad termini of cardiac grooves; metabranchial region less inflated than remaining branchial region; dorsal carapace covered by large punctae or pits.

Abdomen, pterygostomial region, sternum, buccal cavity unknown.

Merus of major appendage compressed, bearing transverse ridges. Upper margin of propodus bears four distinct spines, the second proximal spine reduced in size relative to remaining spines. Remaining appendages unknown.

Measurements.—(See Table 6, and Fig. 9).

Types.—Holotype, T 408 (RB32–302), and paratypes, T433 (RB32–114), T530 (RB33–173), T417 (RB32–301), T411 (RB34–3), T407 (RB30–1), and T531 (RB32–113).

Type locality.—The type locality is the shoreline encompassing RB 30, 31, 32, and 34 (RB refers to the localities noted by

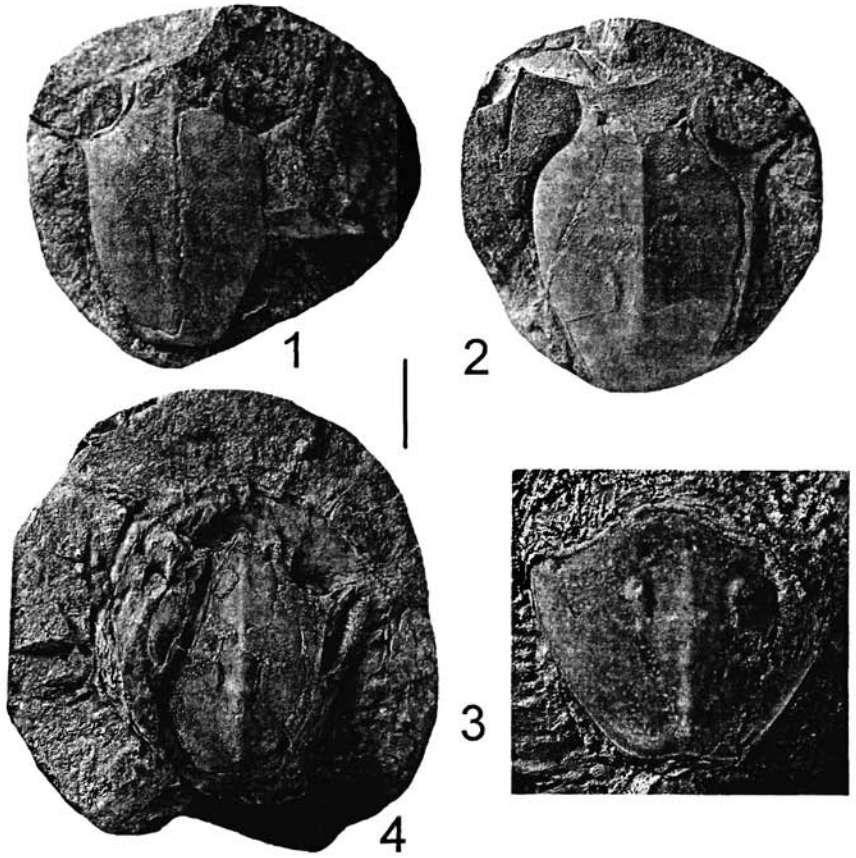

Fig. 8. *Carinaranina marionae*, new species: 1, holotype USNM 494628, dorsal view; 2, paratype USNM 494629, dorsal view, preservation showing two phases of concretion formation; 3, paratype USNM 494631, dorsal view; 4, paratype USNM 494630, dorsal view of posterior, by comparison shows variation in size. Scale bars equal 1 cm.

Table 6.—Representative measurements (mm) of *Carinaranina marionae* new species. L = length, W = width (for definition of measurements see Fig. 9).

Specimen number	L1	L2	L3	L4	W1	W2	W3	W4	W5	W6
USNM 494628*	31.6	7.5	23.8	21.0	24.8	11.6	5.9	4.0	4.9	10.8
USNM 494629	27.9	5.1	20.1	16.7	25.2	13.8	—	3.4	4.3	8.4
USNM 494630	—	—	—	—	—	—	—	—	—	13.2
USNM 494631	—	7.3?	20.2	—	24.2	13.3	—	—	—	—
USNM 494632	—	7.9	—	—	20.4	—	—	—	—	—

* Holotype.

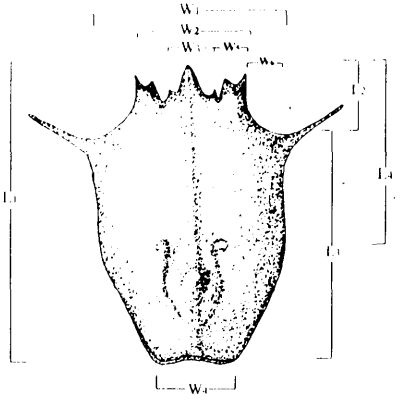

Fig. 9. *Carinaranina marionae*, new species; line drawing of dorsal view of carapace, showing measurements given in Table 6. L = length, and W = width. Scale bar equals 1 cm.

Ross Berglund who collected most of the specimens), from Warmhouse beach east to Kydaka Point, along the Strait of Juan de Fuca, Cape Flattery Quadrangle, 15 min series, Clallam, Washington (Fig. 10).

Etymology.—The specific name honors Marion Berglund who has spent many hours devoted to helping her husband Ross Berglund collect fossil crabs in Washington and Oregon. Without Marion's assistance, sharp eyes, encouragement, and constant companionship, Ross's collecting likely would have been at least slightly less inspired. Gender: Feminine.

Material.—The five specimens referable to this taxon were preserved within concretions. All were preserved as partially exfoliated molds of the interior, with some integument preserved by replacement. One specimen, USNM 494628, is stained red-brown by an iron oxide, others have manganese dioxide dendrites on the surface.

Another specimen, USNM 494629 has a very obvious inner rind around the crab, and a much thicker outer layer. This multiple layering probably implies reworking of some of the concretions. Indeed, many of the concretions have an inner rind with a weathered outer surface.

The range in size (see Fig. 8) suggests some of the smaller specimens may be juveniles. Alternatively, this range in size may be the result of sexual dimorphism. It is not possible, based upon the number of specimens and degree of preservation, to distinguish with certainty which is the case. The range seems to be gradual rather than bimodal, which would suggest that the interpretation of a range in age is more likely than sexual dimorphism.

Stratigraphic and geographic ranges.—Specimens belonging to this taxon were recovered from the Eocene Hoko River Formation at localities RB30, RB32, RB33, and RB34 (Fig. 10).

Remarks.—Representatives of this taxon exhibit several characters compatible with placement within the Raninidae. The essential character is an elongate carapace that does not cover the proximal abdominal terga, and flattened chelipeds. The combination of characters including the greatest width of carapace posterior to the anterolateral spines, narrow fronto-orbital region, orbits marked by fissures, rostrum produced, anterolateral spines often quite long and well-developed, dorsal ridge extending entire length of carapace, and coarsely punctate dorsal surface of the carapace clearly demonstrates this taxon's relationship to the other species within *Carinaranina,* new genus.

Carinaranina marionae is smaller than its congeners; the dorsal ridge is more obvious than on *C. schencki* or *C. leucosiae,* but is similar to that of *C. naselensis.* The outer margins of the orbits of *C. marionae* diverge in an anterior direction, whereas *C. naselensis* have outer orbital margins that are parallel to the longitudinal axis of the animal. The orbital margins on *C. schencki* and *C. leucosiae* were not preserved. The anterolateral spines are similar in shape and attitude to those of *C. naselensis,* but are placed slightly more forward on *C. marion-*

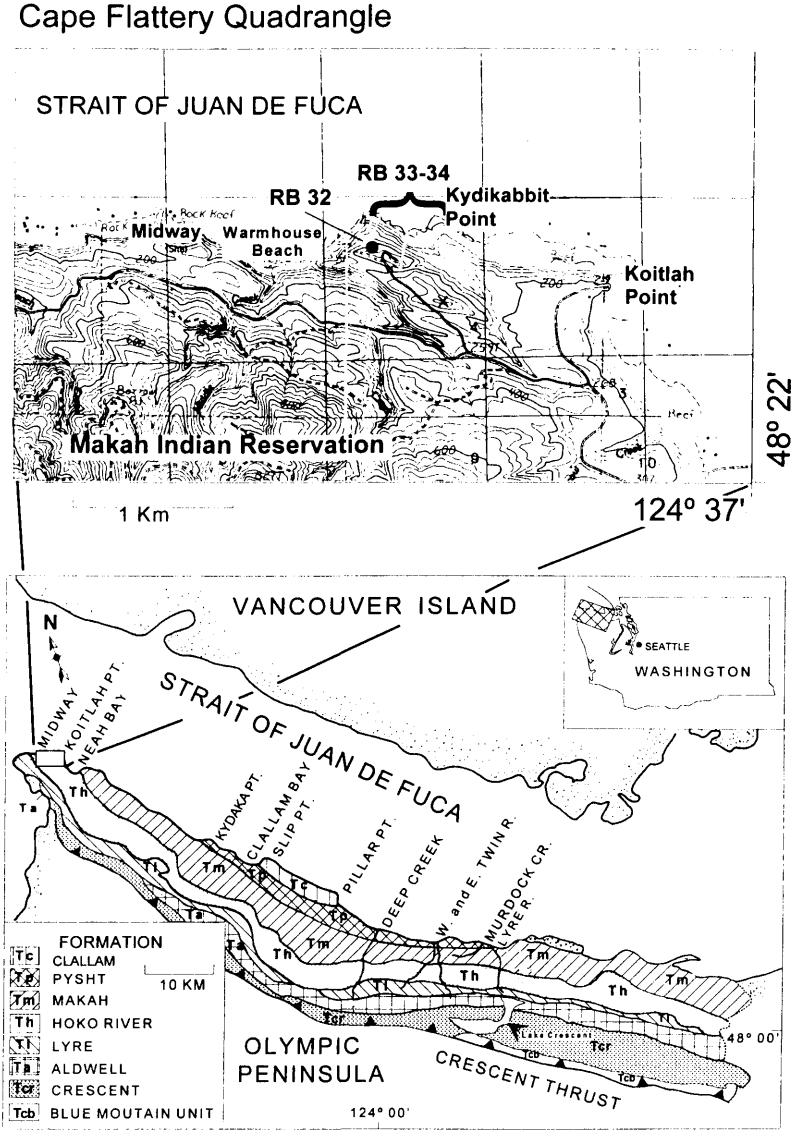

Fig. 10. Geology of the Twin River Group on the Olympic Peninsula, Washington (revised after Snavely 1983:8–9) with inset illustrating approximate position of Hoko River Formation localities RB 32–34.

ae. The anterolateral spines of *C. schencki* and *C. leucosiae* are unknown. This combination of unique characters clearly distinguishes this taxon from its congeners.

Even though *C. schencki* and *C. leucosiae* are known from the latest Eocene age rocks of the Keaseay Formation, it is quite likely that *Carinaranina marionae*, new species represents one of the earliest occurrences for the genus. This is implied as the result of earlier formation of the crab-bearing concretions with subsequent reworking and downslope movement interpreted for the Hoko River Formation (Feldmann et al. 1991).

Carinaranina willapensis (Rathbun, 1926), new combination
Fig. 11(1–11)

Ranidina willapensis Rathbun, 1926:99, pl. 21, figs. 4–5.

Diagnosis.—Carapace elongate, greatest width at midlength; fronto-orbital region narrow, outer extraorbital margins concave, diverging anteriorly; orbits marked by fissures; rostrum produced. Anterolateral spines often quite long and well developed. Posterolateral margin slightly sigmoidal, converging rapidly toward posterior. Posterior margin concave. Surface of carapace coarsely punctate; subtle medial ridge on anterior half of dorsal carapace.

Description emending R. willapensis.—Carapace obovate in outline, widest at or just slightly anteriad mid-length; greatest width about 66% total length; carapace only slightly convex longitudinally, much more so transversely; anterolateral flanks turned under; entire surface coarsely and evenly punctate.

Width of fronto-orbital region about 60% extreme width; fronto-orbital region widest anteriorly, tapering posteriorly; orbits directed slightly away from longitudinal axis of carapace. Ventral margin of each orbit concave, bearing single, open, U-shaped fissure near proximal edge; dorsal margin of each orbit marked by 2 deeply grooved, open fissures, distalmost fissure V-shaped, about twice as deep as wide, directed away from longitudinal axis of animal; interior fissure U-shaped, wider than lateral fissure, approximately parallel to lateral margin of orbit. Extra-orbital tooth wide, bifid, outer margin produced into long spine, inner portion of tooth blunt, anterior margin serrated; second tooth a triangle, extending forward about ¾ as far as extra-orbital spine; inner tooth a short triangle directs anteriorly away from longitudinal axis. Frontal margin of carapace produced to form rostrum that extends just beyond extra-orbital tooth, very slightly downturned; rostrum long, narrow triangle, with straight, beaded margins. Anterolateral margin of carapace slightly concave in outline, bearing 1 pair of very elongate, slender hepatic spines directed forward and outward; posterolateral margin weakly sigmoid, tapering to posterolateral corner, with narrow, beaded marginal rim. Posterior margin narrower than fronto-orbital margin, concave, with narrow, beaded rim.

Midline of carapace smooth, subtly carinate on anterior ½; cardiac region poorly defined, just slightly elevated, marked by 2 subtle arcuate cardiac grooves; cephalic groove slightly indicated; other regions undefined.

Buccal frame longer than wide; pterygostomian regions with sharp ridge originating at about mid-point of buccal cavity and diverging posteriorly. Sternum, narrow, elongate, and smooth, fused through sternites 1–6; sternites 1–3 separated from sternite 4 by narrow extension with margins diverging posteriorly; slender alate processes at anterior sternite 4, directed slightly anteriorly, quite broad; margins of sternite 4 concave, but not converging posteriorly; processes between sternites 4 and 5 wider, but not broader than sternites 3–4; sternite 6 narrower than 5; processes between 6 and 7 narrower than 4–5.

Abdomen unknown.

Chelipeds unknown. Manus of major cheliped compressed, surface granulate. Other appendages unknown.

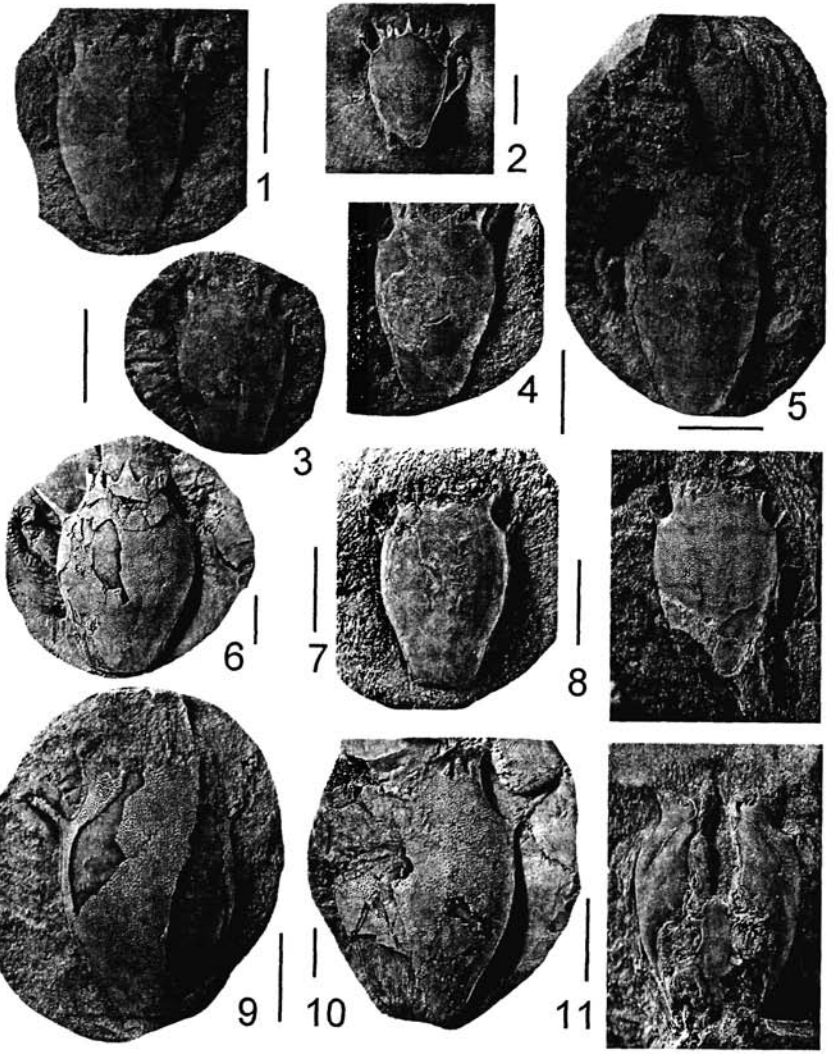

Fig. 11. *Carinaranina willapensis*, new combination: dorsal views of 1, USNM 494637; 2, USNM 494635; 3, USNM 494639; 4, USNM 494642; 5, USNM 494640; 6, USNM 494641, 7, USNM 494636; 8, USNM 494634; 9, USNM 494638; 10, USNM 494633; 11, ventral view of USNM 494643. Scale bars equal 1 cm.

Measurements.—(See Table 7, Fig. 12).

Localities.—Hoko River Formation localities include the shoreline encompassing RB 32–33, from Warmhouse beach east to Kydaka Point, along the Strait of Juan de Fuca, Cape Flattery Quadrangle, Clallam, Washington.

Material.—12 specimens: all but 1 pre-

Table 7.—Representative measurements (mm) of *Carinaranina willapensis*, new combination. L = length, W = width, ? = uncertain measurement (for definitions of measurements see Fig. 12).

Specimen number	L1	L2	L3	L4	W1	W2	W3	W4	W5	W6
USNM 494633	?47.9	12.6	37.1	24.1	?20.4	—	—	6.9	4.6	13.6
USNM 494634	23.1	4.9	18.3	8.3	14.4	11.4	4.8	4.0	1.3	?6.9
USNM 494635	23.3	5.1	18.2	12.3	14.4	12.1	5.1	4.5	1.7	6.4
USNM 494636	24.3	5.3	18.7	10.0	14.8	12.0	4.7	4.2	1.2	5.6
USNM 494637	?22.9	5.2	?18.6	11.7	13.9	11.8	5.2	4.9	1.0	7.3
USNM 494638	?31.1	8.7	23.2	12.1	19.9	13.1	—	—	—	7.8
USNM 494639	22.0	4.3	16.8	10.2	12.8	10.9	4.7	4.2	1.3	?6.1
USNM 494640	25.5	6.1	19.1	10.6	15.6	13.5	5.6	4.7	1.4	6.9
USNM 494641	38.4	10.1	28.7	21.4	25.2	19.0	7.1	6.1	3.3	10.7
USNM 494642	?22.4	4.3	18.2	8.4	13.9	11.3	—	4.0	1.1	6.0
USNM 494643	—	5.8	—	—	17.5	14.0	—	—	—	—

served in concretions as partially exfoliated molds of the interior of the dorsal carapace with replacement of the preserved integument; 1 (USNM 494643) preserved as a mold of the interior of the venter with the sternum well preserved; 2 of the concretions (USNM 494637 and USNM 494642) show concentric layering as seen on *C. marionae*, new species.

Location and stratigraphic position.— The specimens in this study were collected primarily from localities RB32 and RB33. Rocks from these localities are late Eocene in age, based upon benthic foraminiferans recovered from the matrix (Rau 1964:G6; Snavely et al. 1978:A115; Snavely 1987: 310). Many of the specimens were preserved in concretions which were collected as float that was weathered out of the matrix by wave action along a wave-cut platform on the southern shore of the Strait of Juan de Fuca. Some specimens were collected as float from the upper cliffs above Warmhouse Beach. As suggested above, some of the concretions were reworked and possibly were formed sometime prior to the downslope movement. The same genus also was recognized from the ?Aldwell Formation (Squires & Demetrion 1992; Tucker, unpublished data) at Pulali Point, Washington. In addition, another undescribed species of this genus is recognized from the Oligocene-aged Quimper Sandstone, Port Townsand, Washington.

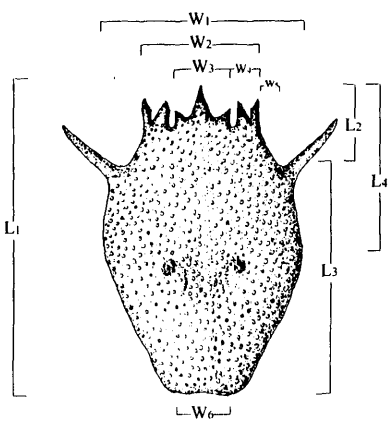

Fig. 12. *Carinaranina willapensis*, new combination: line drawing of dorsal view showing measurements given in Table 7. L = length and W = width. Scale bar equals 1 cm.

Remarks.—Representatives of this taxon exhibit characters compatible with placement within *Carinaranina*. The greatest width of the carapace is posterior to the anterolateral corner, the fronto-orbital margin is narrow relative to the greatest width of the carapace, the rostrum is produced, the orbits bear two fissures, the anterior spines are quite long, and the surface of the carapace is punctate.

Carinaranina willapensis is not as egg-shaped as *C. nasselensis, C. schencki,* or *C. leucosiae. Carinaranina willapensis* most closely resembles *C. marionae.* Both have orbital margins with two fissures; however, the fissures are deeper and more closed on *C. willapensis.* The extreme width of the carapace of *C. willapensis* is more anterior than that of *C. marionae.* In addition, the outer orbital tooth of *C. willapensis* is broader and bifid, unlike the more acicular, narrower outer tooth of *C. marionae.* The anterolateral spines are quite similar in size for both taxa, but the spines of *C. willapensis* are directed more toward the anterior. This taxon, however, bears a dorsal ridge that is much less pronounced than any of its congeners. Although this last character is an important one for establishing a relationship with *Carinaranina* species, the unique shape of the sternum of *C. willapensis* supersedes it. The sterna of *Carinaranina naselensis* (Rathbun 1926), as described by Tucker & Feldmann (1990:413), have a very similar parallel-sided posterior extension between sternites 3 and 4, and alar processes on the anterior portion of sternite 4. This unusual sternal configuration is sufficiently unique that the two taxa are deemed to be congeneric, notwithstanding the inconspicuous dorsal ridge of *C. willapensis.* Sterna from the remaining members of *Carinaranina* species are unknown.

Carinaranina schencki (Rathbun 1932), new combination
Fig. 7(5)

Eumorphocorystes schencki Rathbun, 1932: 242, figs. 5–6.

Remarks.—The surface of the dorsal carapace is coarsely punctate, and there is a distinct dorsal median carina typical for the genus. The position and configuration of the anterolateral spine also is typical for the genus. This taxon is most like *C. naselensis,* but is relatively wider and more egg-shaped.

Material examined.—Holotype USNM 371921; paratype USNM 336007.

Occurrence.—Upper Eocene Keasey Formation, "*Cardium weaveri*" zone, Polk County, Oregon.

Genus *Laeviranina* Lörenthey (*in* Lörenthey & Beurlen 1929)

Laeviranina Lörenthey (*in* Lörenthey & Beurlen 1929):105, pl. 4, figs. 10–12.

Type species.—*Ranina budapestinensis* Lörenthey, 1898:23, by original designation. Gender: Feminine.

Diagnosis.—Carapace elongate oval, lateral margins convex; fronto-orbital margin directed anteriorly, bearing 2 fissures on upper border and medial orbital tooth. Anterolateral spines near fronto-orbital region. Postfrontal ridge present.

Remarks.—There has been much disagreement about the placement of species referred to the genera *Raninoides* H. Milne Edwards (1837), *Laeviranina* Lörenthey (*in* Lörenthey & Beurlen 1929), and *Notosceles* Bourne (1922). The following review illustrates the confusion about the systematic position of species referred to these three genera. Glaessner & Withers (1931:489) recognized the problems in distinguishing among these genera; ultimately, they (1931: 490) regarded *Laeviranina* and *Raninoides* as distinct genera, and distinguished *Laeviranina* species as having relatively narrower fronto-orbital margins, relative to the extreme width of the carapace, than did *Raninoides* species. In addition, the distance between the extraorbital spine and the anterolateral spine was observed to be shorter in *Laeviranina* species, and more importantly, *Laeviranina* species bore a postfrontal ridge. Although Glaessner & Withers differentiated between these two genera, they did so with reservations, "There is no clearly marked division between the forms included in *Laeviranina* and *Raninoides,* but the Eocene forms have a common character, namely, the greater

comparative width of the carapace" (Glaessner & Withers 1931:491).

Förster & Mundlos (1982:156) not only agreed with the conclusions of Glaessner & Withers (1931), but they thought *Raninoides* species and *Laeviranina* species should be united within a single genus, with *Raninoides* the senior subjective synonym. Förster & Mundlos (1982:156) based their conclusions on comparisons of *Laeviranina* species and their specimens with *Raninoides serratifrons* Henderson (1893). Bourne (1922:75) had proposed that *R. serratifrons* should be placed within a newly erected genus, *Notosceles.* Serène & Umali (1972:35) and Goeke (1985:219) concurred with Bourne's proposal by placing *R. serratifrons* with *Notosceles,* and they suggested that separation of *Raninoides* species and *Notosceles* species remained uncertain.

Feldmann & Maxwell (1990:785) recognized several characters, based upon the orbital fissures and the postfrontal ridge, which could be used to differentiate between *Raninoides* and *Laeviranina.* They indicated that the orbital fissures had a tendency to be open and distinct, and the postfrontal ridge was reduced or absent in *Raninoides* species. On the other hand, the orbital fissures of *Laeviranina* species appeared to be smaller and more closed, and the postfrontal ridge more pronounced. Examination of all species referred to each group suggests otherwise. There are at least two species referred to *Raninoides, R. crosnieri* and *R. personatus,* which have closed orbital fissures. Also, there are many species referred to *Laeviranina* that have open orbital fissures, including the type *L. budapestiniensis.* Feldmann (1991:20) further suggested that two points of distinction might be made with regard to the sterna of *Laeviranina* and *Raninoides.* He indicated that the anterior alation of sternite 4 of the sternum of *L. perarmata* appeared to project laterally farther than the posterior termination of the same sternite, whereas the anterior and posterior terminations of sternite 4 on many species of *Raninoides* were more equal. Additionally, Feldmann (1991: 20) suggested that the cleft exhibited along the midline of sternite 5 of the sternum of *Laeviranina* species was narrow and well defined, and typically terminated anteriorly at the level of the chelipeds; whereas a similar cleft on *Raninoides* species was less pronounced and did not extend as far anteriorly. Collins & Rasmussen (1992:33) agreed with these distinctions. However, examination of many specimens of Recent *Raninoides* species, as well as sterna from specimens confidently referred to *Laeviranina* (see Table 9), suggests that these characteristics are mixed within each genus. Furthermore, inspection of Recent *Raninoides* species seems to eliminate the possibility of sexual dimorphism for both the width of the sternum and the extent of the medial cleft due to the variability among both sexes. Sterna from *Laeviranina* species present another problem typical of fossil taxa; that is, often both the sternum and the dorsal carapace are not present for the same specimen, so that one is not always confident of the true identity of the specimen.

Upon further inspection of examples of all three genera, the following observations are offered. Distinguishing *Notosceles* species from *Laeviranina* species and *Raninoides* species is, in most cases, rather straightforward. *Notosceles* species have a serrated or trifid rostrum a granulated postfrontal region, a converging fronto-orbital margin, a first abdominal somite which is equal in width to the posterior margin of the cephalothorax, a narrow obliquely-directed anterior process on the sternite 4, and a very restricted sternum between the third pereiopods.

In contrast, distinguishing between *Laeviranina* species and *Raninoides* species is more difficult. There appears to be a mixture within each genus with regard to the nature of the sternum, especially the sternal cleft; thus, although not enough is known about the sterna of *Laeviranina* species to draw firm conclusions, this seems to be a character best suited for discrimination

among species within each group. It seems, so far, that this is somewhat true for the conformation of the orbits. Finally, although not many specimens of *Laeviranina* bear preserved abdominal somites, observation of those that do suggests that the anterior border of the first somite is more narrow than the posterior margin of the carapace, as is true with *Raninoides* species (Feldmann & Duncan 1992:458, Glaessner & Withers 1931:487–488).

Upon careful inspection of a combination of borrowed material, and published photographs and interpretive drawings, the nature of the postfrontal region seems to offer an excellent way to distinguish between *Raninoides* and *Laeviranina,* as well as the new genus herein, *Quasilaeviranina,* with *Laeviranina* sensu stricto and *Quasilaeviranina* bearing a postfrontal escarpment or ridge, and *Raninoides* having a smooth postfrontal region. The position of the anterolateral spines also appears to indicate a separation among the three groups. A new genus is necessary to distinguish those species previously referred to *Laeviranina* that possess a combination of characters that set them apart from *Raninoides* or *Laeviranina.* As more material representing the sterna of *Quasilaeviranina* species and *Laeviranina* species becomes available, it is possible that other discriminating characters for all three genera might become more obvious. At this point, observations suggest that species referred to *Raninoides* and *Laeviranina* sensu stricto more strongly resemble each other than species referred to either *Quasilaeviranina* or *Notosceles* (see key below).

Key to *Raninoides, Notosceles, Quasilaeviranina,* new genus, and *Laeviranina*

[This key is to be used as an aid in identification of the three most problematic genera of seven assigned to this subfamily (see Fig. 22). The key is based upon personal observations and characters recognized by Serène & Umali, 1972:35].

1. Rostrum trifid or serrated; carapace granulate at postfrontal region; width of first abdominal somite equal to width of posterior margin; anterior border of sternite 4 of sternum narrow, somewhat narrowly alate, directed obliquely forward; sternum between third pereiopods quite narrow; sternal processes between pereiopods 1 and 2 with blunt termination; no spine on ischium of first pereiopods ..... *Notosceles* Bourne, 1922

1′. Rostrum not trifid, but triangular, blunt or acutely pointed at termination; carapace either smooth or bearing postfrontal ridge; width of first abdominal somite narrower than posterior margin of carapace, or unknown; anterior borders of fourth sternite convex forward, not oblique or narrowly alate sternum between third pereiopods often wide where known; sternal lateral processes, where known, between pereiopods 1 and 2 not blunt; spine sometimes present on ischium of first pereiopods 2

2. Carapace without postfrontal ridge; orbital teeth often long, usually delimited by open, deep orbital fissures; anterior border of sternite 4 of sternum convex forward, but perpendicular to longitudinal axis of cephalothorax; sternum between third pereiopods usually quite wide; sternal process between pereiopods 1 and 2 broad, with acute termination; spine present on ischium of first pereiopods ..... *Raninoides* H. Milne Edwards, 1837

2′. Carapace with postfrontal ridge; orbital teeth often short, often delimited by shallow, closed fissures; anterior border of sternite 4 of sternum perpendicular to longitudinal axis of cephalothorax, often straight, sometimes moderately convex; sternum between third pereiopods moderately narrow; sternal processes between pereiopods 1 and 2 generally blunt, not well known; occurrence of spine on ischium of first pereiopods unknown 3

3. Carapace ovate with convex lateral margins, sometimes rounded in outline; anterolateral spines reduced, positioned at

posterior of the fronto-orbital region, or absent; orbital fissures narrowed or entirely closed; orbital spines weak with medial orbital tooth truncated, not extending beyond orbital margin; fronto-orbital region convergent anteriorly . . . . . *Quasilaeviranina*, new genus

3'. Carapace elongate oval with somewhat straight lateral margins, sometimes rectangular in outline; anterolateral spines quite well developed, set just posteriad to fronto-orbital region; orbital fissures open or closed; orbital spines robust; external margins of orbits straight or divergent . . . . . *Laeviranina* sensu stricto

Laeviranina goedertorum, new species
Fig. 13.1–13.7

Types.—Holotype, USNM 494657, and 21 paratypes (see Table 8).

Diagnosis.—Carapace elongate hexagonal, widest at anterior ⅓, covered with fine setal pits; orbit interrupted by 2 well-developed U-shaped fissures; rostrum extending very slightly beyond extraorbital teeth; postfrontal escarpment obvious; posterior margin fairly wide.

Description.—Moderately sized raninid, carapace elongate hexagonal in outline, bearing sinuous postfrontal escarpment; vaulted transversely, only slightly so longitudinally. Fronto-orbital region broad, about 62% maximum width; maximum width at about anterior one-third. Rostrum triangular, bounded on each side by short, broad, acicular innerorbital tooth directed away from longitudinal axis of carapace. Rostrum about as long as broad, width of base about ¼ total width of front; midline only slightly depressed. Orbits not quite as deep as wide, 2 pairs deeply impressed, open supraorbital fissures; inner fissures about ½ as wide as deep, directed very slightly toward midline of carapace; outer fissures not quite as deep, parallel to inner fissures. Orbital teeth somewhat shorter than rostrum inner teeth directed anteriorly, bifid, with outer projections shorter than inner; extraorbital teeth directed anteriorly just slightly farther than inner teeth, bifid, with inner projections shorter than outer, external tooth long and slender; extraorbital teeth forming lateral margins of front, converging only slightly toward anterior. Anterolateral margins short, slightly concave; bounded by short, acicular anterolateral spine directed more forward than out. Lateral margins comprised of 2 straight segments; anterior segments short, diverging posteriorly to extreme width; posterior segments much longer, converging from extreme width to posterolateral corners. Lateral margin bearing furrow and narrow, beaded rim, extending from point of maximum width, continuous with finely beaded posterior margin; flanks turned under. Posterolateral corners smoothly and tightly curved. Posterior margin relatively broad, about 50% extreme width, convex across entire posterior width, with slight medial concavity.

Carapace surface smooth, except for very fine setal pits, subtle cardiac grooves, and an unornamented postfrontal escarpment arising at level between postorbital region and anterolateral spines, traversing entire width of carapace.

Width of first abdominal somite about 70% width of posterior margin. Venter unknown.

Merus of cheliped obovate in cross section; transverse shallow furrows evenly distributed on upper surface. Carpus bearing a single spine on distal outer margin; tubercle on anterior upper surface. Chelipeds with single spine on distal upper margin of hand, lower margin toothed, number of teeth unknown. Hand compressed; fixed finger quite bent, compressed, spines unknown. Dactylus quite slender.

Remarks.—*Laeviranina* embraces fifteen species, all fossil (see Table 9). *Laeviranina goedertorum*, new species shares several characters with its congeners that serve to confirm their relationships: the carapace tends to be smooth, with the exception of very fine setal pits; the orbits are interrupted by two open fissures; the postfrontal re-

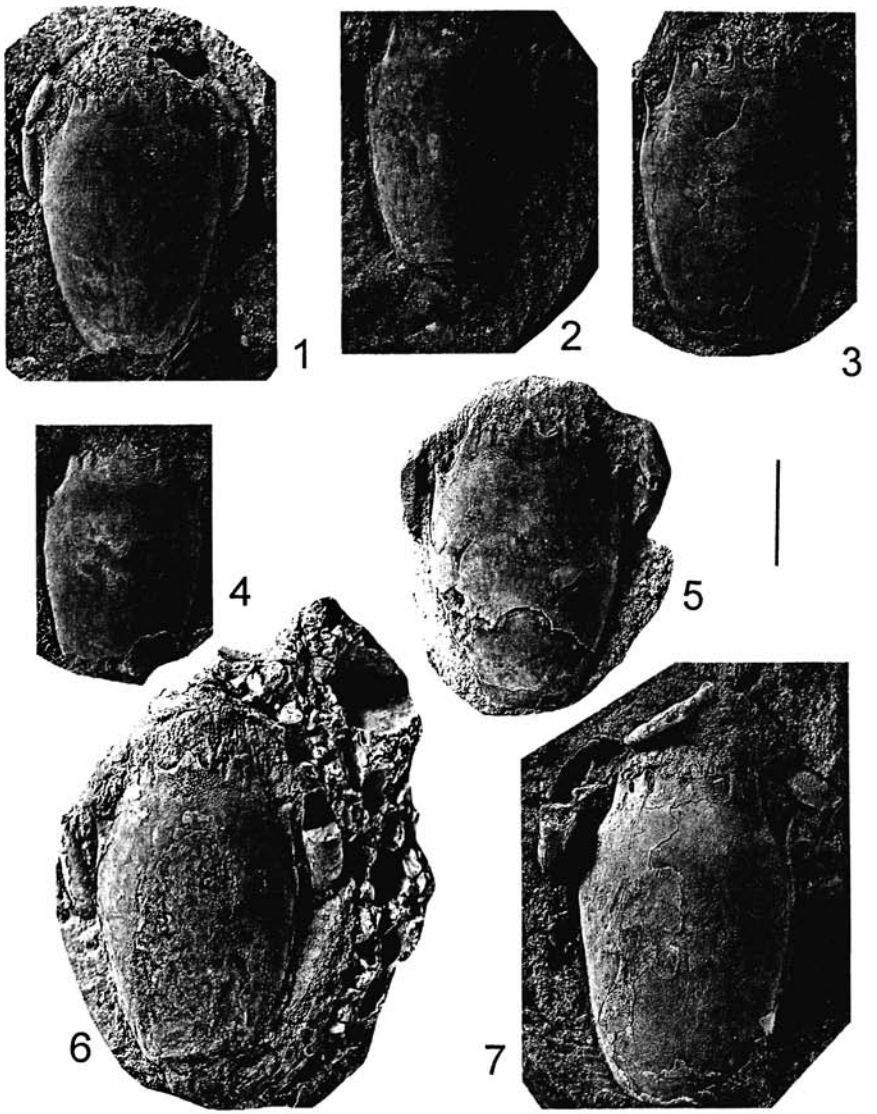

Fig. 13. *Laeviranina goedertorum*, new species, dorsal views: 1, USNM 494663; 2, USNM 494649; 3, USNM 494647; 4, USNM 494651; 5, holotype USNM 494657; 6, USNM 494656; 7, USNM 494662. Scale bar equals 1 cm.

Table 8.—Representative measurements (mm) of *Laeviranina goedertorum*, new species. L = length, W = width, ? = uncertain measurement (for definitions of measurements see Fig. 14).

Specimen number	L1	L2	W1	W2	W3
USNM 494646	31.9	4.6	20.9	17.1	9.3
USNM 494647	30.8	4.2	20.5	16.1	10.3
USNM 494648	28.6	—	—	—	—
USNM 494649	31.7	3.7	21.6	15.6	9.1
USNM 494650	32.3	4.0	20.7	17.6	8.3
USNM 494651	—	3.5	16.9	14.7	0.0
USNM 494652	33.1	4.7	21.5	17.3	8.4
USNM 494653	24.3	2.8	15.3	13.1	6.7
USNM 494654	—	4.4	19.4	16.2	8.9
USNM 494655	30.0	4.8	19.5	16.7	—
USNM 494656	35.8	5.5	22.4	18.5	9.4
USNM 494657*	34.0	5.5	23.4	18.5	12.4
USNM 494658	31.9	4.0	21.0	16.5	9.3
USNM 494659	31.7	3.8	19.2	15.9	7.6
USNM 494660	23.8	3.4	14.6	12.2	7.1
USNM 494661	?27.0	5.0	—	—	8.1
USNM 494662	36.3	5.7	23.5	18.6	12.9
USNM 494663	28.8	4.3	19.7	16.6	7.4
USNM 494664	—	4.4	19.9	17.4	—
USNM 494665	23.9	3.4	16.1	14.7	9.2
USNM 494666	34.9	4.6	23.3	19.4	10.1

* Holotype.

gion is set off by an escarpment or ridge; and the anterolateral teeth are set quite far forward, with the extreme width of the carapace posterior to these. The presence of these characters serves to distinguish species of *Laeviranina* from species of other raninid genera.

Laeviranina goedertorum appears most like *L. gottschei* in the shape of the outline of the carapace; however, the orbital fissures of *L. goedertorum* are more open, the postfrontal escarpment more pronounced, the cephalothorax relatively shorter, and the lateral margins slightly more convex. The tip of the rostrum of *L. vaderensis* extends somewhat beyond the extraorbital spines; the tip of the rostrum and the extraorbital spines of *L. goedertorum* are about equidistant. The posterior margin of *L. lewisanus* is more narrow relative to the maximum width of the carapace.

Measurements.—(See Table 8, Fig. 14).

Etymology.—The specific name honors James Goedert, and his wife Gail, of Gig Harbor, Washington and Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County. Jim and Gail have spent countless hours in the field collecting decapods, as well as vertebrate material for their own endeavors.

Laeviranina lewisana (Rathbun, 1926)
Figs. 15.1–15.4, 17.3

Raninoides lewisanus Rathbun, 1926:94, pl. 22, fig. 4; Glaessner, 1929:372; Förster & Mundlos, 1982:158.

Laeviranina lewisana.—Glaessner & Withers, 1931:490, 491.—Vía Boada, 1965: 263.—Vía Boada, 1969:125.

Diagnosis.—Postfrontal escarpment subtle and concave forward axially, less subtle abaxially; carapace marked by granules on margins anterior to anterolateral teeth. Rostrum relatively long, about equal in length to orbital spines. Posterior margin narrow, almost straight.

Description emending L. lewisana.—Carapace ovate, egg-shaped, widest posterior to anterolateral teeth; greatest width about 57% total length; carapace slightly convex longitudinally, quite vaulted transversely. Width of fronto-orbital margin about 72% extreme width of carapace; orbital region widest posteriorly, tapering slightly anteriorly; orbits directed anteriorly. Dorsal margin of each orbit marked by 2 U-shaped fissures; exterior fissure almost as wide as deep, inner fissure deeper than wide. Outer tooth of orbit bifurcate with exterior spine produced almost to tip of rostrum, separated from inner spine by broad, shallow concave margin, inner spine short, blunt. Medial orbital tooth bifurcate, with inner spine longest, produced approximately equal to extraorbital tooth. Inner orbital spine acute, separated from base of rostrum by U-shaped margin, narrower and deeper than outer tooth; spine directed more forward than outward. Rostrum with base about ⅔ length, not downturned; extending somewhat beyond orbital teeth.

Table 9.—Distributions and geologic ages of recognized species of *Laeviranina* (Lörenthey *in* Lörenthey & Beurlen, 1929).

Taxon	Age	Locality
Laeviranina budapestiniensis (Lörenthey, 1897)	late Eocene	Hungary
L. araucana (Philippi, 1887a, b)	early Eocene	Chile
L. borealis Collins & Rasmussen, 1992	middle Paleocene	Greenland
L. bournei (Rathbun, 1928)	Paleocene	Alabama
L. fabianii (Lörenthey *in* Lörenthey & Beurlen, 1929)	middle to late Eocene	N. Germany
		Hungary
L. goedertorum new species	late Eocene	Washington
L. glabra (Woodward, 1871)	early Eocene	England
L. gottschei (Böhm, 1927)	early Eocene	England
L. lewisanus (Rathbun, 1926)	late Eocene	Washington
L. nodai (Karasawa, 1992)	middle Eocene	Japan
L. notopoides (Bittner, 1883)	early Eocene	England
L. perarmata Glaessner, 1960	middle Eocene	New Zealand
L. pulchra Beschin et al., 1988	middle Eocene	Italy
L. sinuosus Collins & Morris, 1978	early Eocene	Pakistan
L. vaderensis (Rathbun, 1926)	middle to late Eocene	Washington, Alaska

Postfrontal ridge subtle, but distinct; originating just anteriad anterolateral spines and extending across entire carapace, slightly concave at midpoint. Anterolateral spines directed outward and forward, forming V-shaped angle with carapace. Anterolateral margin gently convex in outline, merging into gently convex posterolateral margins; lateral margins terminating posteriorly in blunt corner that joins convex posterior margin.

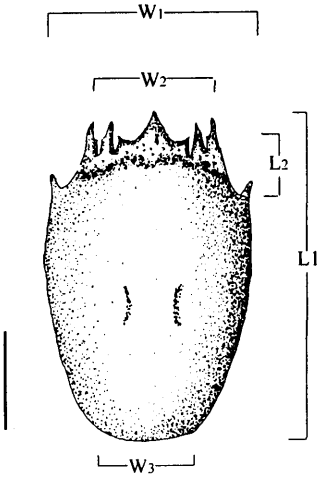

Fig. 14. *Laeviranina goedertorum*, new species: dorsal view showing measurements given in Table 8. L = length and W = width. Scale bar equals 1 cm.

Surface of carapace finely punctate, more coarsely so at postfrontal ridge and on orbital teeth. Adductor epimeralis scars marking lateral positions of cardiac region, about ⅔ toward posterior.

Sternum narrow, elongate; sternites 1–3 narrow anteriorly, broadening at midlength to form rounded, triangular termination, separated from sternite 4 by slight lateral emargination; base of sternite 4 more narrow than anterior; sternite 5 expanding laterally to broadened alate processes which extend slightly beyond anterior width of sternite 4, then converging toward posterior and juncture with sternite 6. Juncture of sternites 5 and 6 marked by deep pit. Axial cleft on sternites 5 and 6.

First abdominal somite not quite as wide as posterior margin; somites progressively more narrow. Somites 1–4 visible dorsally, raised medially on somites 2 and 3, 4 less so, 1 not at all.

Appendages unknown.

Remarks.—Laeviranina lewisana is most like *L. vaderensis*, but is distinguished by a

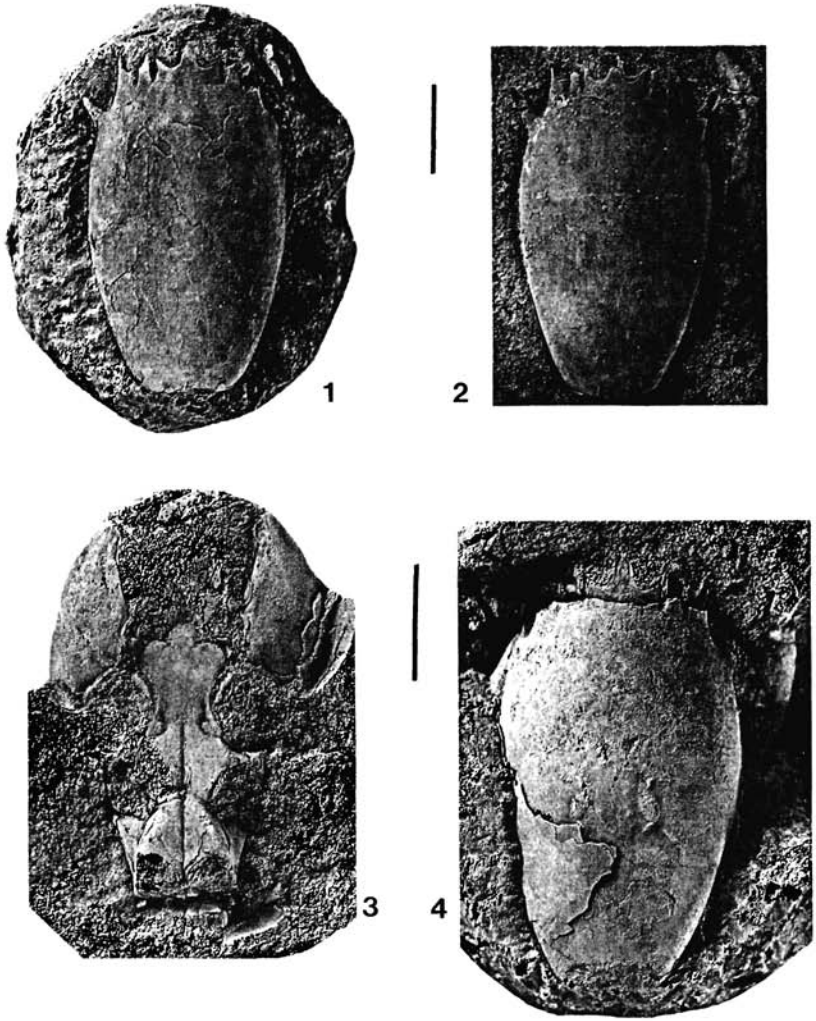

Fig. 15. *Laevivramina lewisana* (Rathbun, 1926), dorsal views: 1, USNM 494676; 2, USNM 494670; 4, USNM 494675; 3, ventral view. Scale bars equal 1 cm.

less produced front, by the greater width of the fronto-orbital margin, by a slightly wider posterior margin, and by the more convex lateral margins, giving it a more egg-shaped appearance.

Material examined.—10 specimens, preserved in concretions primarily as partially exfoliated molds of the interior of the dorsal surface of the carapace.

Measurements.—(See Table 10, Fig. 16).

Table 10.—Representative measurements (mm) of *Laeviranina lewisana* (Rathbun, 1926). L = length, W = width (for definitions of measurements see Fig. 16).

Specimen number	L1	L2	L3	W1	W2	W3
USNM 494668	35.3	11.0	5.2	21.1	14.6	7.8
USNM 494669	36.4	10.7	4.5	20.8	12.6	8.2
USNM 494670	35.8	12.4	3.7	20.8	13.7	8.4
USNM 494671	—	11.1	4.4	19.2	12.9	—
USNM 494672	—	9.7	4.6	18.3	12.4	—
USNM 494673	35.6	9.5	5.1	18.8	13.8	—
USNM 494674	35.8	12.0	5.5	20.3	14.4	8.5
USNM 494675	35.3	11.9	3.5	20.3	13.3	8.6
USNM 494676	34.2	12.2	4.1	19.2	11.9	7.6
USNM 494644	33.0	12.6	3.3	20.6	13.4	8.7

Occurrence.—Until now, *L. lewisana* was recognized only from Lewis County, Washington. This study extends the geographic range northward to include the Hoko River Formation of the Olympic Peninsula, Washington, U.S.A.

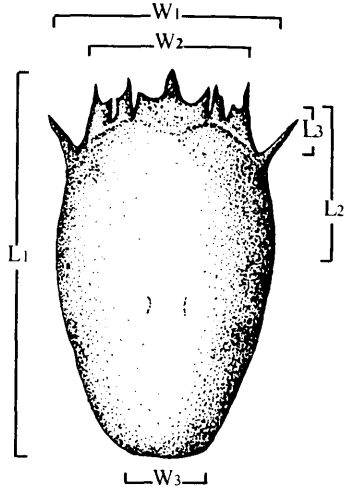

Fig. 16. *Laeviranina lewisana* (Rathbun, 1926): dorsal view showing measurements given in Table 10. L = length and W = width. Scale bar equals 1 cm.

Laeviranina vaderensis (Rathbun, 1926)
Fig. 17.1–17.2, 17.4–17.5

Raninoides vaderensis Rathbun, 1926:93. pl. 22, fig. 5.—Glaessner, 1929:372.—Tucker & Feldmann, 1990:412, figs. 3.1–2.—Karasawa, 1992:1252.

Laeviranina vaderensis.—Glaessner & Withers, 1931:490, 491.—Vìa Boada, 1965:263.—Vìa Boada, 1969:125.

Diagnosis.—Postfrontal escarpment quite subtle axially, less so abaxially. Rostrum produced well beyond orbital margin. Carapace widest near midpoint Posterior margin narrow.

Description emending R. vaderensis.—Carapace oblong oval in outline, widest posterior to anterolateral spines; greatest width about 56% total length; carapace slightly convex longitudinally, more so transversely.

Width of fronto-orbital margin about 70% extreme width; fronto-orbital margin widest at midlength, tapering slightly posteriorly; orbits directed forward, dorsal margin of each orbit marked by two narrow, U-shaped, open fissures, inner deeper than exterior, both deeper than wide, directed posteriorly and toward longitudinal axis of carapace. Extraorbital tooth bifurcate, outer margin of tooth convex abaxially, tip directed toward rostrum; inner portion of extraorbital tooth short and blunt. Medial orbital tooth bifurcate, not as long or wide as extraorbital, inner spine longest. Inner orbital tooth directed more outward than forward, connected to base of rostrum by broad, shallow margin. Front produced to form rostrum a little longer than width of base, extending well beyond orbital rim.

Postfrontal ridge subtle, more obvious laterally, forming steep arc directed anteriorly. Anterolateral spines close to front, tip arched toward axis, of medium length; spines form U-shaped angle with anterolateral margin. Posterolateral margins slightly concave, beaded rim for entire margin. Posterior margin straight or just slightly convex. Carapace punctate, except posterior branchial region; feeble, widely separated attractor epimeralis scars delimit cardiac region.

Remarks.—The postfrontal ridge of *L.*

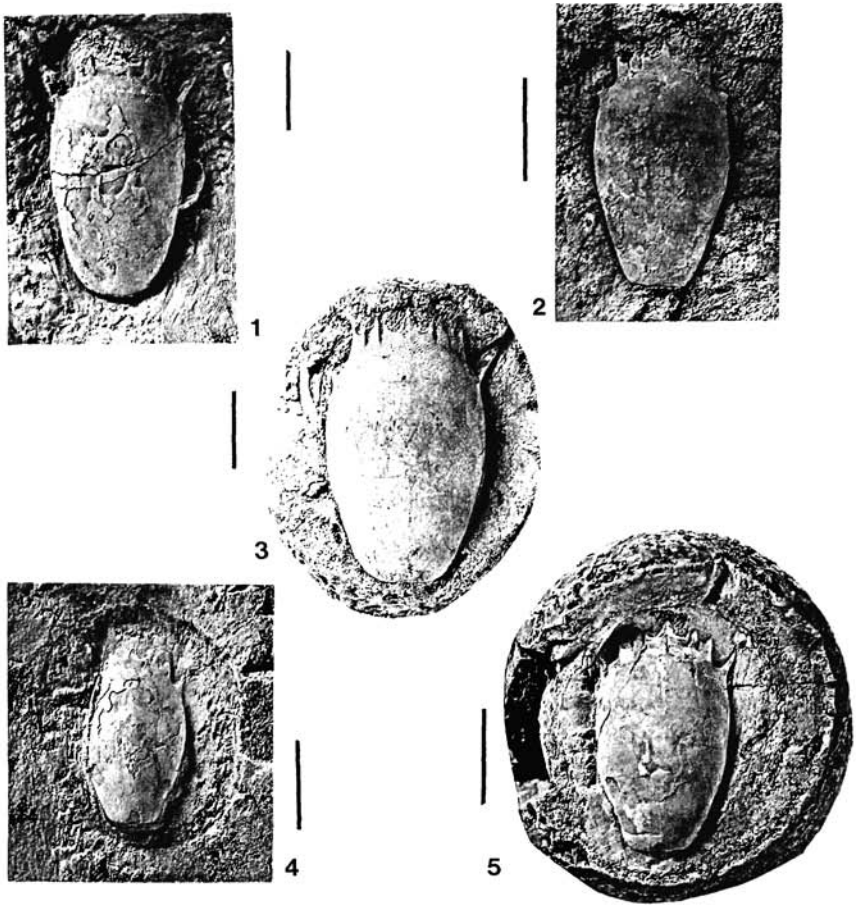

Fig. 17 *Laeviranina vaderensis* (Rathbun, 1926), dorsal views: 1, USNM 494679; 2, USNM 494678; 4, USNM 494680; 5, USNM 494677; *Laeviranina lewisana* (Rathbun, 1926): 3, USNM 494644, for comparison. Scale bars equal 1 cm.

vaderensis and the anterior placement of the anterolateral spines, clearly places this species within *Laeviranina*. *Laeviranina vaderensis* is most like *L. lewisana*; however, the two species are distinguished by several characters. *Laeviranina vaderensis* has a less distinct and extensive postfrontal ridge that is steeply and tightly arched, while that of *L. lewisana* is less arched and has a median concavity; the front of *L. vaderensis* is more produced; the posterolateral margins are straighter, so that the carapace is less egg-shaped in outline; the posterior is narrower; and the anterolateral spines form a U-shaped connection with the anterolateral margin, rather than the V-shaped angle observed on *L. lewisana*.

Laeviranina vaderensis is easily distinguished from other raninids found along the northwest coast of North America. *Rani-*

Table 11.—Representative measurements (mm) of *Laeviranina vaderensis* (Rathbun, 1926). L = length, W = width (for definitions of measurements see Fig. 18).

Specimen number	L1	L2	L3	W1	W2	W3
USNM 494677	24.8	3.5	10.5	14.0	9.8	6.2
USNM 494678	22.7	3.5	9.2	12.8	8.7	5.7
USNM 494679	28.1	4.1	10.9	15.5	10.8	7.5
USNM 494680	20.9	2.8	7.2	—	—	4.9

noides fulgidus has much longer orbital spines and a narrower carapace and *Carinaranina* species are more egg-shaped, bear much larger punctae that cover most of the carapace and a median ridge.

Material examined.—10 specimens: 2 (USNM 494677 and USNM 494680) show concentric rings in the matrix surrounding the specimen as result of reworking of the concretions. The holotype is deposited in the Burke Memorial Washington State Museum, University of Washington (not seen). 4 additional specimens (USNM 6649414, USNM 431250, USNM 431251, and USNM 431253) were studied.

Measurements.—(See Table 11, Fig. 18).

Occurrence.—*Laeviranina vaderensis* is known from the middle Eocene Orca Group of Valdez, Alaska; the upper Eocene Tejon Formation in Lewis County, Washington; the middle Eocene of Oregon, and the upper Eocene Hoko River Formation of Washington.

Genus *Quasilaeviranina*, new genus

Type species.—*Ranina simplicissima* Bittner, 1883, by present designation.

Diagnosis.—Carapace elongate oval in outline, greatest width posteriad anterolateral spines; convex transversely, less so longitudinally; surface often covered with very fine setal pits; cardiac grooves sometimes present; postfrontal region bearing raised transverse escarpment between anterolateral spines. Fronto-orbital margin weakly dentate with shallow, closed orbital fissures. Anterolateral spines directly posterior to fronto-orbital region.

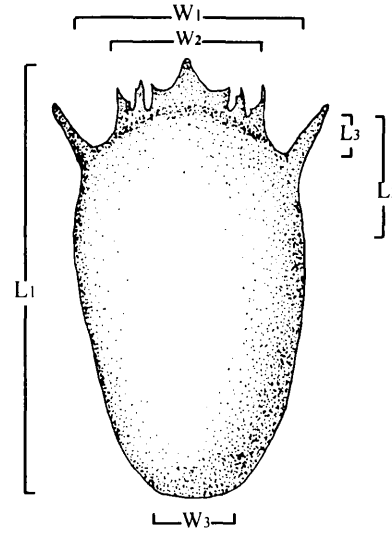

Fig. 18. *Laeviranina vaderensis* (Rathbun, 1926): dorsal view showing measurements as given in Table 11. L = length and W = width. Scale bar equals 1 cm.

Etymology.—From Latin *quasi* = appearing like, in reference to *Laeviranina*. Gender: Feminine.

Remarks.—All 6 species referred to this genus are treated below. *Laeviranina* sensu stricto is distinguished by the wider fronto-orbital margin, open orbital fissures, the more rectangular outline of the cephalothorax, and the slight migration of the anterolateral spines to a more posterior position. *Quasilaeviranina* is distinguished by the convergent fronto-orbital region, the closed orbital fissures, the reduced size of the medial orbital tooth, the more anterior position of the anterolateral spines as well as their diminutive size, and by the broadened appearance of the dorsal carapace resulting from the more convex lateral margins.

The oldest species assigned to the genus, *Q. ovalis* (Fig. 19), used in the cladistic analyses, was recovered from Paleocene age rocks in Alabama. Based upon the cladistic analysis (see Phylogenetic Analysis

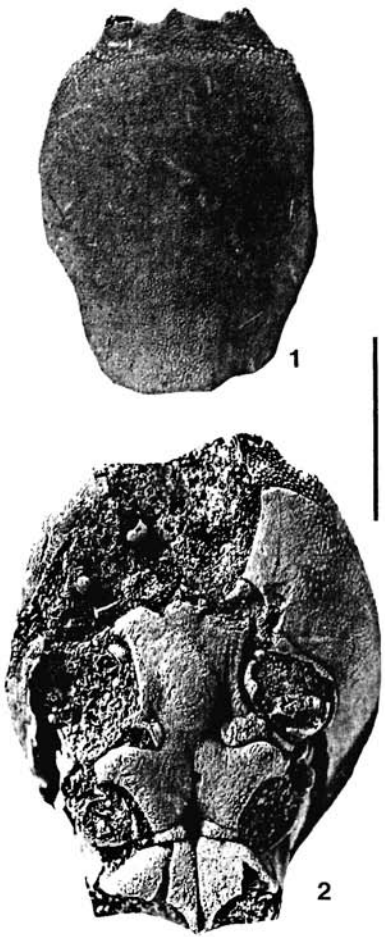

Fig. 19. *Quasilaeviranina ovalis* (Rathbun, 1935), USNM 371689 (2 of 32 syntypes): 1, dorsal view; 2, ventral view showing swollen area on sternite 4. Scale bar equals 1 cm.

and Fig. 22), *Quasilaeviranina* is most closely related to *Notosceles* and *Notopoides*.

Quasilaeviranina simplicissima (Bittner, 1883), new combination

Ranina simplicissima Bittner, 1883:305, pl. 1, fig. 4.

Laeviranina simplicissima.—Lörenthey (*in* Lörenthey & Beurlen), 1929:106, pl. 4, fig. 11.

Laeviranina cf. *simplicissima*.—Busulini et al., 1983:59, pl. 1, fig. 3.—Beschin et al., 1988:173, fig. 5-1, pl. 4, figs. 4–5.—Beschin et al., 1994:173, pl. 3, fig. 2.

Remarks.—*Quasilaeviranina simplicissima* has a fronto-orbital region that is convergent anteriorly and displays shallow, closed orbital fissures and truncated medial orbital teeth. The diminutive anterolateral spines are placed just posterior to the post-orbital teeth and are joined by a distinct postfrontal escarpment. Although the cephalothorax is somewhat elongated, the lateral margins are convex. The taxon is differentiated from its congeners by granulation along the escarpment and by the more narrow carapace.

Material examined.—Line drawings and photographs, especially those of Beschin et al. (1988).

Occurrence.—*Quasilaeviranina simplicissima* is recognized from the middle Eocene of Italy.

Quasilaeviranina arzignanensis (Beschin, Busulini, de Angeli, & Tessier, 1988), new combination

Notosceles arzignanensis Beschin et al., 1988:193–196, pl. 10, figs. 2–3, fig. 11.

Remarks.—*Quasilaeviranina arzignanensis* has all the characters which distinguish *Quasilaeviranina* species from *Notosceles* species (see key). Furthermore, the sternum, which is well preserved for *Q. arzignanensis*, is much more typical of *Quasilaeviranina* species than of *Notosceles* species. On Recent *Notosceles* species, the anterior of sternite 4 is quite alate and directed anteriorly, and is distinctly narrower than the alation between the first and second pereiopods. This taxon has a sternum that is more robust at the anterior of sternite 4 and is about equal in width at the anterior of sternite 4 and the alation between the

first and second pereiopods, characters more typical of *Quasilaeviranina* species. Therefore, it seems best to include this species with *Quasilaeviranina.*

Material examined.—Figures and plates from Beschin et al. (1988, fig. 11, and pl. 10, figs. 2–3).

Occurrence.—*Quasilaeviranina arzignanensis* is known from the middle Eocene of Italy.

Quasilaeviranina keyesi (Feldmann & Maxwell, 1990), new combination

Laeviranina keyesi Feldmann & Maxwell, 1990:784–786, figs. 3–4.

Remarks.—The closed orbital fissures, reduced and truncated medial orbital tooth, convergent fronto-orbital region, and anteriorly positioned, diminutive anterolateral spines clearly indicate that this taxon should be moved to *Quasilaeviranina.*

Material examined.—Holotype, NZGS AR 958, and 2 paratypes, NZGS AR 962 and AR 1931, deposited in the New Zealand Geological Survey, Lower Hutt, New Zealand.

Occurrence.—*Quasilaeviranina keyesi* is known from the Eocene of South Island, New Zealand.

Quasilaeviranina ombonii (Fabiani, 1910), new combination

Ranina ombonii Fabiani, 1910:2, pl. 2, Fig. 1.
Ranina (*Laeviranina*) *ombonii.*—Lörenthey (*in* Lörenthey & Beurlen), 1929:105, 106, 107.
Laeviranina ombonii.—Beschin et al., 1988:169, pl. 3, figs. 4–6, Text fig. 5.3.

Remarks.—Examination of illustrations and drawings by Beschin et al. (1988) confirms that this species should be placed within *Quasilaeviranina.* The fronto-orbital margin is convergent, the anterolateral spines are quite diminutive, the medial orbital tooth is reduced and truncated, and the lateral margins are convex. Interestingly, Glaessner & Withers (1931:490—footnote) recognized that both *Q. ombonii* and *Q. simplissima* differed from descriptions of many of the species referred to *Laeviranina,* primarily because of the diminutive size of the anterolateral spines. *Quasilaeviranina ombonii* is differentiated from its European congeners by possessing anterolateral spines that are placed a little farther forward and by its more convex lateral margins.

Material examined.—None.

Occurrence.—*Quasilaeviranina ombonii* is known from the Eocene of Italy.

Quasilaeviranina ovalis (Rathbun, 1935) Fig. 19.1–19.2

Raninoides ovalis Rathbun, 1935:5, 11, 81, 143, pl. 18, figs. 1–8.
Laeviranina ovalis.—Glaessner, 1960:16.

Remarks.—The postfrontal ridge and the overall configuration of the carapace confirm the placement of this taxon with *Quasilaeviranina.* The diminutive anterolateral spines are placed well forward and the fronto-orbital region is convergent. The orbits bear two closed, shallow fissures, which is typical for the genus. Several specimens have a venter with a unique swollen region at the midpoint of sternite 4; otherwise, the general character of the sternum is typical for the genus.

Material examined.—Syntypes, 32 carapaces, USNM 371689 and USNM 371692

Occurrence.—*Quasilaeviranina ovalis* is known from the Eocene of Alabama.

Quasilaeviranina pororariensis (Glaessner, 1980)

Ranilia pororariensis Glaessner, 1980, by monotypy:177, figs. 6, 6A.
Laeviranina pororariensis.—Feldmann & Maxwell, 1990:786, figs. 5.1–2, 6.

Remarks.—At first glance, the outline of the carapace of *Quasilaeviranina pororariensis* does not appear to agree with the outline typical for the genus; that is, it appears to be much wider across the front than is

typical. Glaessner (1980:177), however, described the single specimen as slightly distorted by preservational flattening of the carapace. This certainly could account for the observed differences. Feldmann & Maxwell (1990:786) pointed out that the morphology of the claws precluded an assignment of the species to *Ranilia*. Placement within *Quasilaeviranina* appears to be reasonable based upon the configuration of the fronto-orbital region, the diminutive anterolateral spines, and the postfrontal ridge.

Material examined.—None.

Occurrence.—A single specimen of *Quasilaeviranina pororariensis*, the holotype, was recognized from the Eocene of New Zealand and is maintained at the Canterbury Museum, Christchurch, South Island, New Zealand.

Phylogenetic Analysis

Previous work on raninid classification and phylogeny.—As put forth earlier in this work, much confusion remains about the phylogenetic position of the Raninidae among the Decapoda, although their position as specialized members of the Brachyura is no longer in dispute. Spears et al. (1992) used a molecular approach to test hypotheses about the phylogeny of selected brachyuran crabs. Results from their study suggest that the Raninidae form a distinct lineage, at the lower limit of the Brachyura, which diverged early from an unknown ancestral lineage.

Not much work has been done on the phylogenetic relationships within the Raninidae. Most discussions have revolved around how to subdivide the family into related groups. Lörenthey (*in* Lörenthey & Beurlen 1929), in a review of the primarily fossil Raninidae, recognized three subfamilies based upon the front margin of the carapace: the Palaeocorystinae (*Palaeocorystes, Eucorystes, Eumorphocorystes, Raninella, Notopocorystes,* and *Hemioon*), the Raninidae (*Ranina, Laeviranina, Lophoranina, Hela,* and *Notoporanina*) and the Raninoidinae (*Pseudoraninella, Raninoides, Notopella, Ranidina, Raninellopsis, Tribolocephalus,* and *Lyreidus*). Serène & Umali (1972:25), who considered only extant genera, recognized two subfamilies defined by the type and relative position of male pleopods and the resting position of the eye peduncles: the Notopodinae (*Cosmonotus, Notopus,* and *Ranilia*) and the Raninidae sensu Serène & Umali (*Ranina, Lyreidus, Notopoides, Raninoides, Notosceles, Symethis,* and *Cyrtorhina*). Work by Hartnoll (1979), following earlier works by Gordon (1963, 1966) which centered on the structure of the spermathecal pits of female raninids, indicated some uncertainty about the validity of the two subfamilies recognized by Serène & Umali.

Goeke (1981) accepted the divisions of Serène & Umali (1972) and distinguished a third subfamily, the Symethinae, for a single genus, *Symethis*. Goeke (1981:978) established the uniqueness of the Symethinae based upon possession of seven gills instead of eight, and the unornamented terminus of the first male pleopod. In addition, three more characteristics set the Symethinae apart: the form of the chelipeds which is unique among all Raninidae, the greatly reduced eye peduncles, and the very narrow, but extremely produced fronto-orbital region. The present study supports the significance of these characters, and in the interest of maintaining the Raninidae as a monophyletic group, *Symethis* is removed from the Raninidae.

Based upon the sternum and the paired spermathecae, Guinot (1993:1325) organized the Raninidae into six subfamilies: Raninae (*Ranina*), Notopodinae (*Notopus, Ranilia, Cosmonotus, Umalia*), Symethinae (*Symethis*), Raninoidinae (*Raninoides, Notosceles, Notopoides*), Lyreidinae (*Lyreidus, Lysirude*), and Cyrtorhininae (*Cyrtorhina*). Serène & Umali (1972:49) had suggested that *Cyrtorhina* and *Symethis* were closely related. Monod (1956:49), on the other hand, indicated that *Cyrtorhina* and *Ranina* might be closely related, based

upon the 1st male pleopods; Goeke (1980: 976) agreed with Monod, recognizing the similarity of the spermathecae. Guinot (1993:1325) suggested that *Symethis* and *Cyrtorhina* should each form a separate monotypic subfamily. She further suggested that *Symethis* was sufficiently unique to be elevated to the rank of family and that the Cyrtorhininae could then be removed from the Raninidae and placed as a monotypic subfamily under the Symethidae. This study supports the observations made by Goeke (1980) and Guinot (1993); thus, the Symethidae, under the Raninoidea, is erected to receive *Symethis*. However, the present study does not agree with the removal of Cyrtorhininae from the Raninidae as suggested by Guinot (1993:1329).

Fraaye (1995) described a new genus, *Pseudorogueus*, based upon a single specimen from the lower Eocene of Catalunya, Spanish Pyrenees. Fraaye (1995) distinguished *Pseudorogueus* based upon its unique anterolateral spines, which bear extra smaller spines along the forward borders. This gives Pseudorogueus a superficial resemblance to *Rogueus*. A cladistic analysis, which included *Pseudorogueus*, was run. This test confirmed that the specimen described by Fraaye (1995) is more closely related to the Raninoidinae clade, not the Lyreidinae which includes *Rogueus*. Indeed, when *Pseudorogueus* was inserted into the data matrix, a new analysis resulted with *Pseudorogueus* and *Raninoides* unresolved. Therefore, *Pseudorogueus rangiferus* should be moved to *Raninoides*. The multibranched anterolateral spines observed on both *Pseudorogueus* and *Rogueus* are not unlike those observed on adult members of *Ranina*; therefore, this character probably is homoplasic (reversal) within the Raninidae and should not be used to name a new genus. Furthermore, the fronto-orbital region is most like species of *Raninoides* and there is no obvious postfrontal escarpment as is found in species of *Laeviranina*, a genus very similar to, and often confused with, *Raninoides*. Because *Pseudorogueus rangiferus* is removed to *Raninoides*, *Pseudorogueus* was not included in the phylogenetic analyses described below.

Methods.—Fossils present a special problem in phylogenetic analysis. Wiley (1981) suggested three distinct problems associated with classifications incorporating fossils and Recent organisms: fossil organisms are intrinsically incomplete; whenever a fossil taxon is classified with Recent taxa, there is a very real risk that the fossil may indeed be the ancestral "stem group" for one of the Recent taxa; and it becomes increasingly difficult to incorporate fossil groups into a Linnaean classification without the addition of more and more categories with fewer and fewer specimens. Though these problems cannot be ignored, there are methods to deal with the problems and still provide valid phylogenetic conclusions that permit stable rank designations. Furthermore, fossils offer the most direct historical evidence available to researchers and allow speculation about character transformations and evolutionary scenarios.

The objective of this study was to reconstruct the phylogeny of the Raninidae, and to include within the phylogenetic analysis all genera of the family, both fossil and living. Fossil taxa, heretofore unassigned to the various subfamilies designated by Guinot (1993), were placed within the appropriate subfamily based upon the results of the phylogenetic analyses. The construction of a hypothetical phylogeny for the entire family, using cladistic analysis as a tool, was compared to the prevailing taxonomic subfamilial classification of living genera (Guinot 1993) as a means of congruence testing of the present analysis. As a result of fossil placements, descriptions of each of the subfamilies were emended to reflect important characteristics of their fossil members, as well as the characters already in use by neontologists.

The analysis herein tested trees that contain higher taxa, namely genera. Recognizing that species may be ancestral to other species or to higher taxa, but that higher

taxa may not be ancestral to other higher taxa, the characters of the genera analyzed in this study are those represented by the oldest known species for each genus. The reasoning behind this method was that the first occurrence of the species should come closest to representing the speciation event (cladogenesis) for the initiation of a new genus (see Wiley 1981:96). In the case of very poorly preserved fossil representatives, the next oldest taxon for which there was improved fossil material, was used. In the case of Recent taxa with no fossil record, characters of the type species were used.

This study used PAUP 3.1.1 (Phylogenetic Analysis Using Parsimony) for analysis of the data matrix (Swofford & Begle 1993). The PAUP program, run on a Macintosh computer, analyzed the data matrix (Appendix I) and inferred a hypothetical phylogeny using the principle of parsimony. Various choices were made to control the heuristic search. These selections were made based upon the least amount of constraint or a priori assumptions. All characters were treated equally and no characters were weighted, as weighting would have required a priori decision. Character states were unordered (Fitch parsimony); that is, each character with more than two states was permitted to transform directly from one state to any other state and transitions between any pair of character states were weighted equally for tree length (Quicke 1993:24). For any taxon with missing values, a character state was assigned by PAUP that would be most parsimonious given its location on the tree; however, only those characters that had non-missing values could actually affect the position of any taxon on the tree (Swofford & Begle 1993). The steepest descent option was set to on so that all trees from each round were examined; that is, no trees were discarded the moment a shorter tree was discovered. This allowed the maximum number of trees to be explored.

PAUP also provides several choices for optimizing character reconstructions. For characters of the unordered type, character tracings may turn out to be ambiguous as to the interpretation of homoplasies. The ambiguities can be resolved partially based upon acceleration or delay of transformations (Swofford & Maddison 1987). Of these, the ACCTRAN (=accelerated transformation optimization) tracing method, using the Ferris algorithm (Maddison & Maddison 1992:108), reveals those most-parsimonious assignments that accelerate character changes toward the root; thus, character state changes are placed as close to the root as possible so that homoplasies tend to be explained in terms of distal reversals to plesiomorphic states. Using this procedure forces reversals by maximizing early gains and tends to reduce the number of parallelisms allowed. If, in spite of a bias against them, a pattern of parallelisms continues to appear, one can then argue for adaptation for that trait (see Swofford & Begle 1993).

Multistate taxa, unusual in the present study, were treated as polymorphism. Using multiple states as polymorphism forces PAUP to assume that a terminal taxon is a heterogeneous group, which a supraspecific taxon is by its very nature. Although the oldest recognized species was used for characters traits in this study, there were a few occasions where the expression of two states by different species was deemed important for a true representation of the genus. For example, the oldest known species of *Lophoranina,* from the Cretaceous of Mexico, bears distinguishable cervical and branchial grooves not present in later species of the genus.

Finally, an outgroup was selected to polarize the character states. As previously discussed, the Raninidae do not have a reliable sister group. In fact, the immediate ancestor of the Raninidae remains enigmatic; therefore, the outgroup used for the original analysis was a "Hypothetical Ancestor." This outgroup method of attaching a "Hypothetical Ancestor" (Swofford & Be-

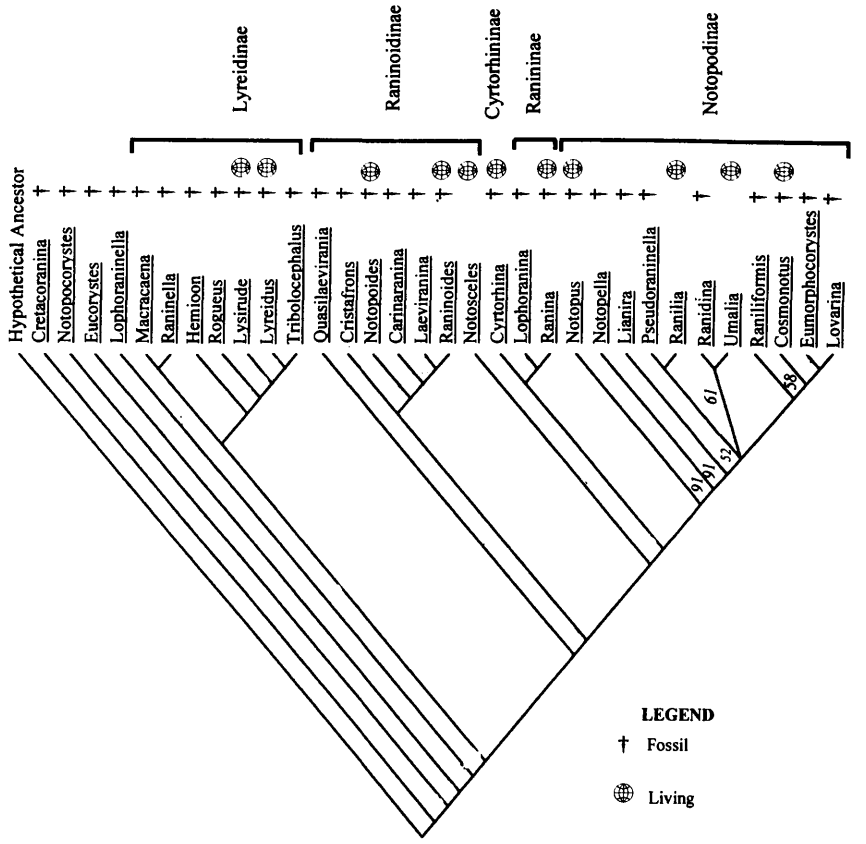

Fig. 20. Majority-rule consensus tree at 50%, where the consensus retains all groups found in over half of the rival trees. Tree illustrates consensus indices (100% where not otherwise indicated) indicating the percentage of the 33 shortest trees in which the figured arrangement of genera occurs.

gle 1993) was employed in order to polarize the characters, and only after first computing an unrooted tree for ingroup taxa.

Because of the large data matrix, the present study used the heuristic method to search for the most parsimonious tree, and when more than one tree resulted from an analysis, the resulting trees were computed for a Majority-rule consensus tree at 50%, where the consensus retained all groups found in over half of the rival trees (Swofford & Begle 1993). Trees generated as a consensus were constructed from a set of trees, rather than from the data directly. Although such trees thus are useful in systematic evaluation, they are not considered a true cladogram or a true phylogeny. The consensus tree was used here as a guide to the phylogeny of the Raninidae, rather than as a true cladogram.

The final "Majority-rule consensus" tree was compared to the taxonomic arrangement by Guinot (1993) to see if there was agreement at the higher taxonomic level of

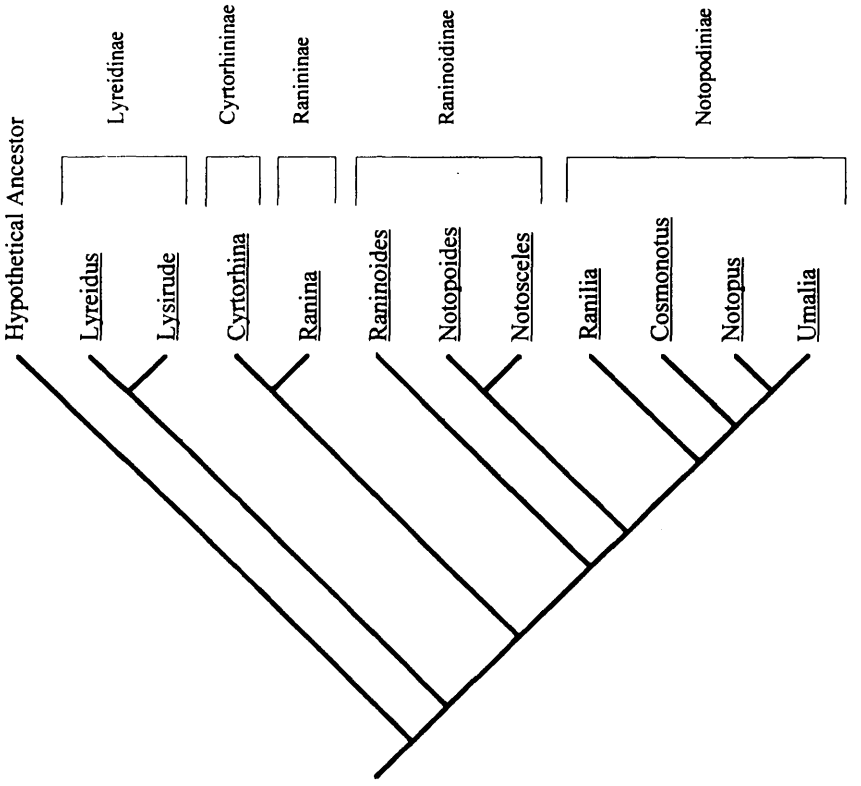

Fig. 21. One of three equally most-parsimonious alternative phylogenies for Recent genera of Raninidae.

subfamily; that is, to explore the possibility that the same genera were grouped together on the consensus tree as were grouped by Guinot (1993) using traditional means and a different data set. The "Majority-rule consensus" of these 33 trees is illustrated in Fig. 20. The subfamilies designated by Guinot (1993) are indicated on this tree. *Lophoraninella* and *Notosceles* appear out of place on the tree (Fig. 20) based upon accepted systematics of those taxa. *Lophoraninella* tended to shift to different positions on the tree with the any change in characters or taxa in the data matrix. This is likely the result of insufficient data for that taxon. *Notosceles* was placed at the base of the Raninae (Fig. 20); however, upon analysis of only living genera, *Raninoides, Notopoides* and *Notosceles* formed a clade (Fig. 21).

Excluding the taxa discussed above, there is reasonable congruence between the present cladistic analysis and Guinot's arrangement of subfamilies within the Raninidae. After making some adjustments to the tree (Fig. 20) to reflect presently accepted systematics, the new tree was tested to see how many steps the changes added to the most parsimonious tree. These changes added only 5 steps, which is insig-

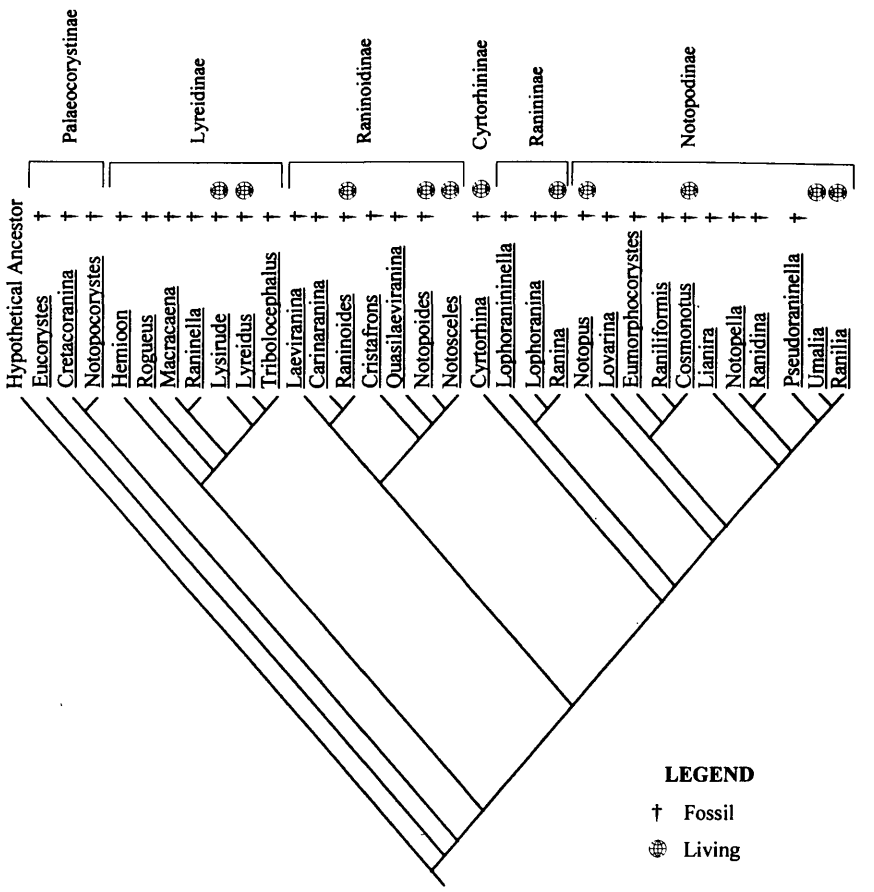

Fig. 22. "Constraint" tree built by testing each clade separately using the outgroup method and physically moving some genera. Testing the "constraint" tree resulted in adding 12 steps to the total length.

nificant. Therefore, a final tree was constructed (Fig. 22) placing these taxa in their currently accepted systematic positions.

Ranina and *Cyrtorhina* formed a clade on the Recent consensus tree. Interestingly, as discussed previously, Monod (1956:49) considered *Cyrtorhina* to be very close to *Ranina,* but indicated that the two genera were differentiated by the shape of the dactyli of pereiopods 3 to 4, the supraorbital and anterolateral teeth, and by the palm and fingers of the chelipeds. Serène & Umali (1972:49) considered *Cyrtorhina* closer to *Symethis,* but stated that the male pleopods resembled those of *Raninoides.* Observations in this study indicated that the sternal configurations of *Cyrtorhina* and *Raninoides* were very different. Furthermore, sternites 2 and 3 on *Cyrtorhina* are broad in front and taper posteriorly, while the same

elements on the sterna of *Ranina* widen posteriorly. Although analysis of the Recent genera did not support *Cyrtorhina* and *Ranina* each forming a monotypic subfamily, for reasons just stated they have been retained as subfamilial groups.

Conclusions

The systematic review of the Raninidae places 32 genera, embracing 190 species, into six subfamilies: the Ranininae, Cyrtorhininae, Lyreidinae, Raninoidinae, Notopodinae, and the re-established Paleocorystinae. The monogeneric subfamily Symethinae was elevated to the rank of family, under the Raninoidea, based upon its unusual morphology, especially the characteristic of seven gills, compared to eight for the rest of the family. *Lyreidus* and *Notopocorystes,* both containing subgenera, were re-evaluated and the subgeneric groups were elevated to the level of genus. Three new genera were erected, *Carinaranina, Quasilaeviranina,* and *Macracaena,* as well as the two new species mentioned, *Laeviranina goedertorum,* and *Carinaranina marionae.*

Cladistic analysis of the recognized genera embraced within the Raninidae indicated that the subfamilial divisions of Guinot (1993) are useful for fossils as well as living taxa. Cladistic analysis also indicated the need for a reestablished subfamily, the Palaeocorystinae, to embrace the oldest genera within the Raninidae, *Notopocorystes, Eucorystes,* and *Cretacoranina.*

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Appendix 1.—Data matrix used for phylogenetic analysis of Raninidae. ? = missing data.

Taxa of Raninidae	Characters																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Hypothetical Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carinaranina +	1	1	1	1	2	0	2	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	?	0	?	1	1	1	1	0	0	0	2	3
Cosmonotus 0 +	1	1	1	2	3	2	3	3	3	2	0	2	1	0	1	2	?	2	1	1	1	1	0	0	0	1	1	0	1	1	1	1	0	1	1
Cretacoranina +	0	0	0	0	0	0	0	2	0	1	0	1	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Cristafrons +	0	0	0	1	0	0	1	2	0	0	1	0	0	2	1	1	1	1	0	0	1	0	0	?	0	?	?	?	?	?	?	?	?	2	3
Cyrtorhina 0 +	1	1	0&2	1	0	0	1	2	0	2	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	1	1	1	0	0	0
Eucorystes +	0	0	0	0	0	3	1	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	0	1
Eumorphocorystes +	0	0	1	1	2	1	2	1	0	1	0	1	1	0	1	2	1	1	1	1	1	1	1	?	0	?	?	?	?	?	?	?	?	2	2
Hemioon +	1	1	1	0	0	0	1	1	0	0	1	0	0	0	2	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1
Laeviranina +	1	1	0	1	1	0	2	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0&1	?	0	?	1	0	1	0	0	0	0	2	1
Lianira +	1	1	1	1	2	0	2	2	0	1	1	0	0	2	0	1	0	2	0	2	1	1	1	0	0	1	1	0	1	0	1	?	0	1	3
Lophoranina +	0&1	0&1	0	0	0	1	0	2	0	1	1	1	0	2	0	1	1	0	0	0	0	0	0	?	0	?	1	0	1	0	1	1	0	0	3
Lophoraninella +	0	1	2	0	2	1	1	2	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	0	0
Lovarina +	1	1	1	1	1	1	2	2	0	1	1	0	1	0	0	2	0	2	0	1	1	1	1	?	0	?	?	?	?	?	?	?	?	2	1
Lyreidus 0 +	1	1	1	1	1	0	3	0	0	2	1	0	0	0	1	0	1	2	1	2	1	0	0	0	1	0	1	0	1	0	0	0	1	2	0
Lysirude 0 +	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	2	1	2	1	0	0	0	1	0	1	0	1	0	0	0	1	2	0
Macracaena +	1	1	1	1	1	0	1	1	0	0	0	0	0	2	0	0	1	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	2	2
Notopella +	1	1	1	1	2	0	2	2	0	0	1	0	0	0	1	0	0	2	0	2	1	0	1	?	0	?	?	?	?	?	?	?	?	0	3
Notopocorystes +	0	0	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	1	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Notopoides 0 +	1	1	0	1	2	0	3	3	3	2	1	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	1	0
Notopus 0 +	1	1	0	1	2	0	2	2	0	1	0	0	0	1	1	0	0	2	0	2	0	1	0	0	0	1	1	0	1	1	1	1	0	0	1
Notosceles 0	1	1	2	1	2	0	2	2	0	1	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0	0	2	1
Pseudoraninella +	1	1	2	1	2	0	2	2	0	?	1	?	0	2	2	0	0	0	1	2	2	1	1	?	0	?	?	?	?	?	?	?	?	1	3
Quasilaeviranina +	1	1	0	1	1	0	2	2	0&3	1&2	1	0	0	0	1	0&1	1	1	1	1	1	0	0	?	0	?	1	0	1	0	0	0	0	2	3
Ranidina +	1	1	1	1	2	0	2	2	0	1	0	0	0	0	1	0	?	2	1	2	2	0	1	?	0	?	?	?	?	?	?	?	?	1	3
Ranilia 0 +	1	1	2	1	1	0	2	2	0	1	1	1	0	0	1	0	0	0	1	1	2	1	1	0	0	1	1	0	1	1	1	1	0	0	3
Raniliformis +	1	1	1	1	0	2	2	2	0	0	1	?	1	0	1	2	0	2	1	1	1	0	1	?	0	?	?	?	?	?	?	?	?	1	1
Ranina 0 +	1	1	1	0	0	0	1	2	1	0	1	1	0	2	0	0	1	0	0	0	1	0	?	?	0	?	1	0	1	0	1	1	0	0	3
Raninella +	1	1	0	1	0	0	1	1	0	1	0	0	0	2	1	0	1	0	1	1	0	0	0	?	0	1	?	?	?	?	?	?	?	1	2
Raninoides 0 +	1	1	1	1	1	0	2	2	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0&1	0	0	1	1	0	1	0	0	0	0	2	1
Rogueus +	1	1	1	0	0	0	2	2	1	0	1	0	0	0	0	0	1	0	1	2	1	0	0	?	0	?	1	0	1	0	1	?	1	2	1
Tribolocephalus +	1	1	1	1	1	0	3	3	3	2	0	0	0	0	0	0	1	?	1	2	1	0	0	?	1	?	?	?	?	?	?	?	?	2	3
Umalia 0	0	0	2	1	2	3	2	2	0	1	0	0	0	0	1	0	0	2	1	2	1	0	0	1	0	1	1	0	1	1	1	1	0	1	3

Appendix II

Character 1—Obvious cervical groove
1–0: Present
1–1: Absent

Character 2—Obvious branchiocardiac groove
2–0: Present
2–1: Absent

Character 3—Postfrontal region
3–0: Ridged—a postfrontal terrace or raised area
3–1: Undifferentiated or flat
3–2: Rough or granulated

Character 4—Rostrum
4–0: Bifid or trilobate rostrum
4–1: Single, triangular rostrum
4–2: No rostrum

Character 5—Axis of rostrum
5–0: Sulcate
5–1: Flat
5–2: Ridged
5–3: No rostrum

Character 6—Carapace surface type
6–0: Smooth or finely punctate
6–1: Terraced
6–2: Scabrous
6–3: Granulate

Character 7—The number of anterolateral spines
7–0: Three or more
7–1: Two
7–2: One
7–3: None or extremely reduced

Character 8—Position of the anterolateral spine, or the longest spine in the case where there is more than a single spine. Position measured as distance of spine from the orbital margin relative to distance between orbital and posterior margins.
8–0: Between ½ and ⅓ the total length of the carapace as measured from the orbital ridge to the posterior margin
8–1: Between ⅓ and ¼
8–2: Between ¼ and the front
8–3: No anterolateral spine

Character 9—Character of major anterolateral spine
9–0: Simple, single spine
9–1: Complex spine with one or more subspines
9–2: No spine

Character 10—Anterolateral spine length—length judged relative to rostrum and extraorbital spine length; longer than either was considered long and shorter was considered short
10–0: Long
10–1: Short
10–2: Very reduced or none

Character 11—Longitudinal carina
11–0: Present, at least in part
11–1: Absent

Character 12—Sides of the rostrum almost parallel. This character is used to define both very narrow, single rostral projections and wider, often bifid rostral projections
12–0: Not parallel
12–1: Parallel
12–2: No rostrum

Character 13—Relative length of the extraorbital spines
13–0: Shorter than or equal to the length of the rostrum
13–1: Longer than rostrum
13–2: Not produced beyond orbital margin

Character 14—Shape of the outer margin of the extraorbital spines
14–0: Straight
14–1: Concave
14–2: Convex

Character 15—Orientation of the outer margin of the extraorbital spine
15–0: Directed forward
15–1: Converging toward long axis of carapace
15–2: Diverging from long axis of carapace

Character 16—Character of the extraorbital spines
16–0: Single spine
16–1: Bifid or multiple spines
16–2: No spines protruding beyond orbital margin

Character 17—Characteristics of the inner orbital tooth
17–0: Produced beyond supraorbital ridge
17–1: Even with supraorbital ridge

Character 18—Median orbital tooth—a tooth or spine between the extraorbital tooth and the inner orbital tooth
18–0: Produced beyond orbital ridge
18–1: Not produced beyond orbital ridge
18–2: No tooth

Character 19—Inner orbital fissure—the fissure separating the inner orbital tooth from the next tooth, whether the median tooth or the extraorbital tooth
19–0: Open
19–1: Closed

Character 20—Outer orbital fissures
20–0: Open
20–1: Closed or
20–2: No obvious fissure, sometimes as the result of the spines or teeth protruding from the edge of the supraorbital margin and sometimes because there is no intervening midorbital tooth

Character 21—Character of the supraorbital fissures
21–0: Deep, obvious fissures
21–1: Shallow fissures—almost obscure
21–2: No obvious fissures

Character 22—The orientation of the orbits—expressed as anteriorly directed, horizontal orbits or orbits that are directed obliquely downward
22–0: Horizontal
22–1: Obliquely downward

Character 23—Cardiac furrows—arcuate grooves along lateral edges of cardiac region
23–0: Present
23–1: Absent

Character 24—The width of the posterior margin relative to the width of the first abdominal somite
24–0: Posterior margin greater than width of abdomen
24–1: Width of posterior margin equal to or less than width of abdomen

Character 25—Relative width of posterior margin—as compared to the fronto-orbital margin
25–0: Width of posterior margin less than fronto-orbital margin
25–1: Width of posterior margin greater than fronto-orbital region

Character 26—Spine present on abdominal somite three or four
26–0: Present
26–1: Absent

Character 27—Relative size of fused thoracic sternites one to three
27–0: Sternites 1 to 3 reduced in size, quite small
27–1: Sternites 1 to 3 not reduced in size

Character 28—The juncture of fused sternites 1 to 3 with sternite 4
28–0: Direct fusion with no elongation between elements 3 and 4
28–1: An elongated, parallel-sided "neck" between elements 3 and 4

Character 29—The width of the anterior of sternite 4 relative to the width of the posterior of sternite 4
29–0: Posterior greater than anterior
29–1: Anterior greater than, or equal to, the posterior
29–2: Extremely narrow and linear

Character 30—Anterior shape of sternite 4
30–0: Not alate
30–1: Alate or narrowed

Character 31—Width of the posterior of sternite 5
31–0: Somewhat reduced
31–1: Very reduced

Character 32—Visibility of sternite 6
32–0: Visible
32–1: Not visible

Character 33—Abdominal hooking mechanism ("pterygoid processes" sensu Bourne, 1922:69)
33–0: Absent
33–1: Present

Character 34—Ratio of width to length
34–0: Ratio greater than 80%
34–1: Ratio 70 to 79%
34–3: Ratio less than 70%

Character 35—Position of greatest width
35–0: Anterior half
35–1: Between half and one-third
35–2: Between anterior one-third and one-fourth
35–3: Anterior one-fourth to front