ANNALS OF CARNEGIE MUSEUM

VOL. 69, NUMBER 1, PP. 23–67 18 FEBRUARY 2000

EOCENE DECAPOD CRUSTACEANS FROM PULALI POINT, WASHINGTON

CARRIE E. SCHWEITZER[1]

RODNEY M. FELDMANN[1]
Research Associate, Section of Invertebrate Paleontology

ANNETTE B. TUCKER[1]

ROSS E. BERGLUND[2]

ABSTRACT

A robust decapod fauna, including ten species in nine genera, has been recovered from the Eocene ?Aldwell Formation near Pulali Point, Washington. New taxa include *Portunites macrospinus* n. sp., *Carpilius occidentalis* n. sp., *Pulalius dunhamorum* n. gen. and sp. *Pulalius vulgaris* (Rathbun, 1926) new combination has been removed from *Zanthopsis* McCoy. *Palaeopinnixa rathbunae* new name is offered as a replacement name for *Pinnixa eocenica* Rathbun which is herein referred to *Palaeopinnixa* Via. *Palaeopinnixa* is placed within the Hexapodidae. This is the first notice of *Carpilius* Leach *in* Desmarest in the eastern Pacific region. The decapod fauna is typical of those previously reported from deep-water, continental slope settings of the Pacific Northwest with the exception of the occurrence of *Carpilius*, which has a mainly tropical distribution, and *Palaeopinnixa* which has previously been reported primarily from lower-latitude settings.

KEY WORDS: Decapoda, Brachyura, Eocene, Olympic Peninsula, Washington

INTRODUCTION

A previously undescribed decapod fauna from Eocene rocks at Pulali Point, Washington, has yielded ten species in nine genera, including one new genus and four new species. The decapod fauna was mentioned by Squires et al. (1992) and illustrated by Tucker et al. (1994); however, neither report provided a detailed systematic treatment of the fauna. The fauna is composed of several decapod taxa common in continental slope deposits of the Pacific Northwest including *Macroacaena* Tucker, *Laeviranina* Lörenthey and Beurlen, *Raninoides* H. Milne Edwards, *Portunites* Bell, *Branchioplax* Rathbun, *Pulalius* n. gen., and *Neopilumnoplax* Serène *in* Guinot. This report marks the first notice of the genus *Carpilius* Leach *in* Desmarest in the fossil record, based upon material other than a manus, and on the west coast of North America. This decapod fauna is significant biogeographically because it represents a mix of taxa typical of the west coast of North America (Rathbun, 1926; Tucker and Feldmann, 1990; Feldmann et al., 1991; Schweitzer and Feldmann, 1999) and taxa not previously reported from the eastern Pacific region.

Institutional abbreviations used throughout this paper are: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; GHUNLPam, Geology Col-

[1] Department of Geology, Kent State University, Kent, Ohio 44242.
[2] 11689 NE Sunset Loop, Bainbridge Island, Washington 98110.
Submitted 3 December 1998.

lection, National University of La Pampa, Santa Rosa, Argentina; In., The Natural History Museum, London, United Kingdom; SM, Sedgwick Museum, Cambridge University, Cambridge, United Kingdom; USNM, United States National Museum of Natural History, Washington, D.C.; and JSHC, private collection of J. S. H. Collins, Forest Hill, London, England.

Geologic Setting

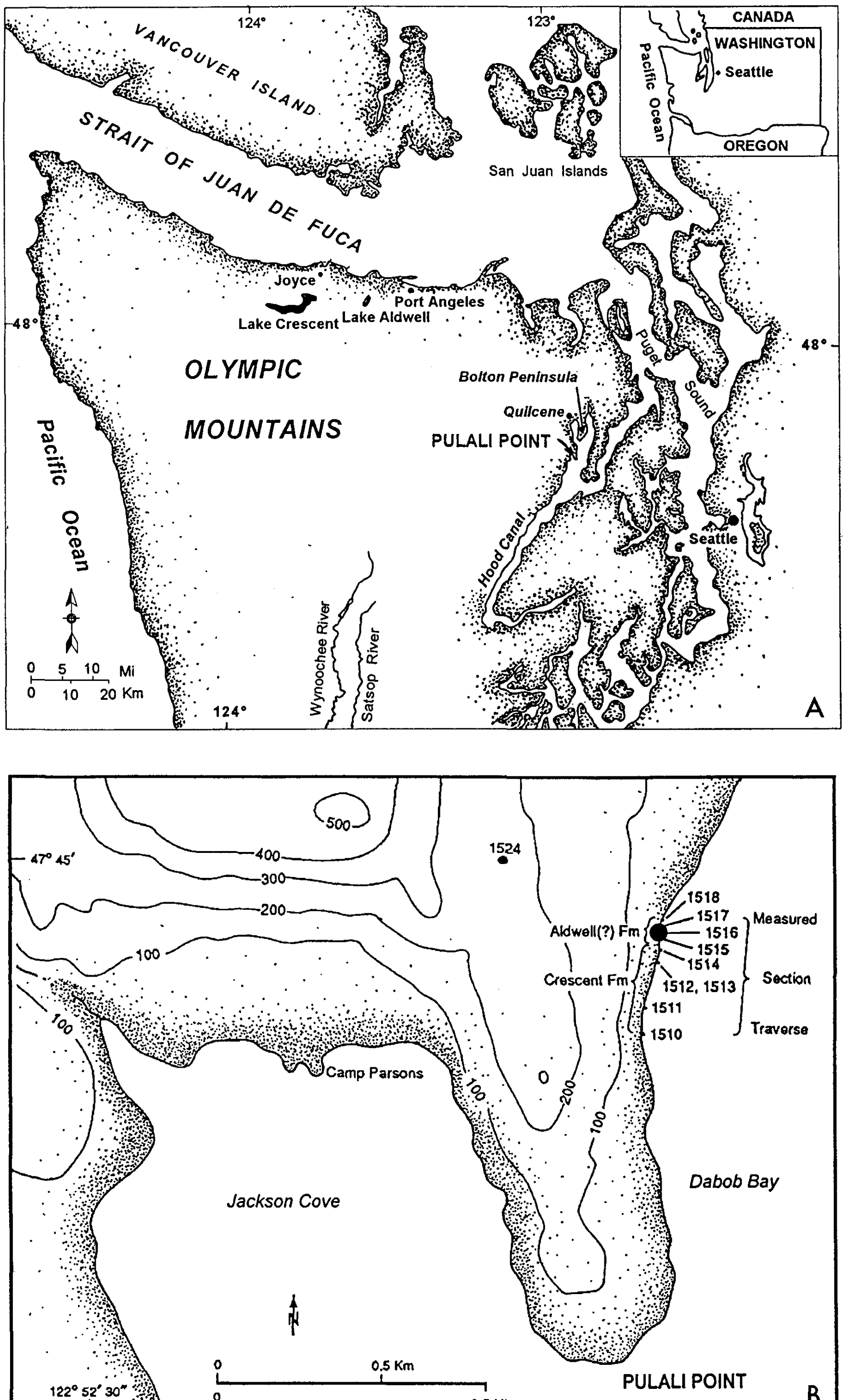
Decapod fossils were collected from the northeast coast of Pulali Point which extends into the Hood Canal of Puget Sound, south of Quilcene, Washington, in the N1/2, Sec. 18, T26N, R1W, of the Seabeck 7.5 minute quadrangle (Fig. 1). The section at Pulali Point (Fig. 2) includes two major units, the Crescent Formation and an overlying sedimentary sequence that has been questionably assigned to the Eocene Aldwell Formation based upon lithology, paleontology, age, and geographic location (Squires et al., 1992). Squires et al. (1992) determined that the unit should be referred either to the Aldwell or the Humptulips Formation, because the two units are similar in both age and lithology. They assigned the sedimentary rocks at Pulali Point to the ?Aldwell Formation because that unit crops out within 15 km to the north of the site. The Humptulips Formation crops out about 80 km to the southwest of Pulali Point (Squires et al., 1992). Because our study is concerned primarily with decapod systematics, we have no basis for offering new information concerning the identity of the rocks and concur with their decision to assign the rocks to the ?Aldwell Formation.

The Crescent Formation, which at Pulali Point occurs as basalts alternating with basaltic sandstone, basalt pebble conglomerate, and siltstone, lies unconformably beneath the sedimentary sequence referred to as the ?Aldwell Formation (Squires et al., 1992). They reported one decapod fossil, a specimen of *Glyphithyreus weaveri* (Rathbun) from the Crescent Formation, but no decapods in this report were recovered from that unit. The Crescent Formation was reported to be of Penutian to Ulatisian age based upon calcareous nannofossils, benthic foraminifera, and macrofossils (Squires et al., 1992). Babcock et al., (1994:145) reported that the Crescent Formation in the vicinity of Pulali Point had an age of 50.5–1.6 ma based upon ^{40}Ar-^{39}Ar geochronometry.

The sedimentary sequence at the Pulali Point locality, which is assigned to the ?Aldwell Formation, unconformably overlies the Crescent Formation. It consists of boulder conglomerate, sandy siltstone, and siltstone with gradational contacts between each (Squires et al., 1992). The boulder conglomerate, located at the base of the section, contains crab fossils in siltstone concretions occurring with a predominance of basalt boulders (Squires et al., 1992). The concretions were considered by Squires et al. (1992) to have been reworked. Decapods were also recovered from the silty sandstone facies and were contained within reworked, well-indurated siltstone concretions (Squires et al., 1992). Squires et al. (1992) reported a middle Eocene (early Narizian) age for the formation based upon benthic foraminifera and macrofossils. Babcock et al. (1994) reported that the ?Ald-

→

Fig. 1.—A. Locality map of the Olympic Peninsula, Washington, showing the Pulali Point collecting locality (modified from Squires et al., 1992). B. Map of the Pulali Point area, indicating California State University, Northridge (CSUN) collecting localities, and the location at which the stratigraphic section in Figure 2 was measured (modified from Squires et al., 1992).


124°
123°
VANCOUVER ISLAND
STRAIT OF JUAN DE FUCA
CANADA
WASHINGTON
Seattle
Pacific Ocean
OREGON
San Juan Islands
Joyce
Port Angeles
Lake Crescent
Lake Aldwell
48°
48°
OLYMPIC
MOUNTAINS
Bolton Peninsula
Quilcene
PULALI POINT
Puget Sound
Pacific Ocean
Hood Canal
Seattle
Wynoochee River
Satsop River
0 5 10 Mi
0 10 20 Km
124°
A
500
400
300
200
100
100
47° 45′
1524
1518
1517
1516
1515
1514
1512, 1513
1511
1510
Measured
Section
Traverse
Aldwell(?) Fm
Crescent Fm
Camp Parsons
100
0
200
100
Dabob Bay
Jackson Cove
0 0.5 Km
0 0.5 Mi
122° 52′ 30″
PULALI POINT
B

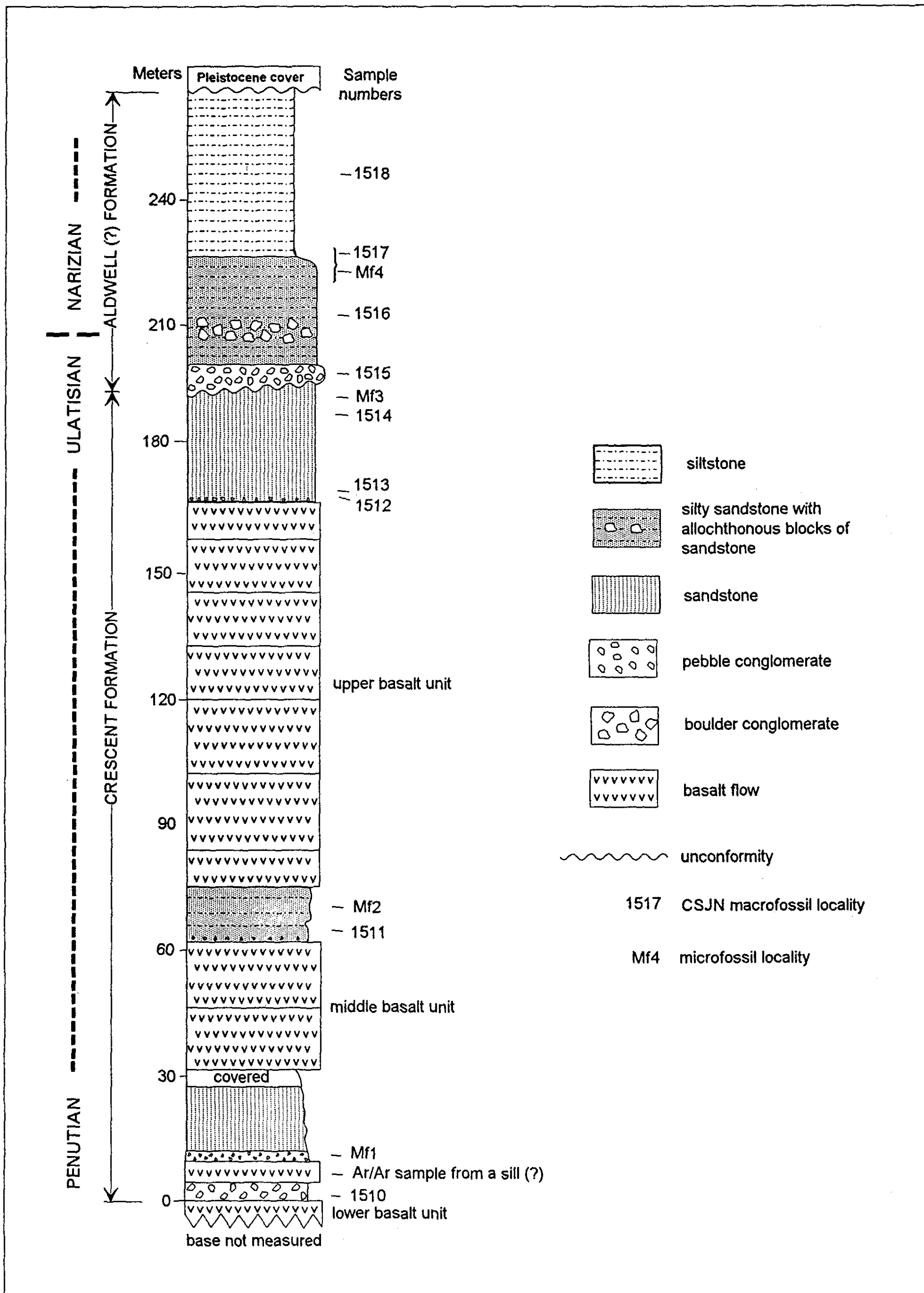


Fig. 2.—Stratigraphic section of the rocks exposed at Pulali Point. Decapods were reported by Squires et al. (1992) from CSUN macrofossil localities 1515 and 1516 (modified from Squires et al., 1992).

well rocks at Pulali Point interfinger with the Crescent basalts, suggesting that they were syndepositional and placing the age of the ?Aldwell Formation at Pulali Point as Penutian–Narizian age, the age of the Crescent Formation near Pulali Point. Squires et al. (1992) had not noted interfingering of these two units and instead described an angular unconformity between the two units. Decapod occurrences support an Eocene age for this unit.

Babcock et al. (1994) summarized the depositional environment of the Aldwell Formation sensu stricto as being cold, deep, and predominated by submarine landslides. The depositional environment of the ?Aldwell Formation at Pulali Point is reported to have been part of a deep-water, submarine fan complex (Squires et al., 1992). The basalt boulder conglomerates were considered to have been proximal turbidite deposits, and the silty sandstones were interpreted to have been derived from multiple provenances, based upon the occurrence of reworked concretions in that facies (Squires et al., 1992). Both the boulder conglomerate and the silty sandstone contain decapods, and these fossils were interpreted to have been derived from both deep- and shallow- water environments (Squires et al., 1992), also supporting the theory of multiple provenances for the sediments. Some of the decapods reported here have modern congeners that are typical of deep-water environments, including *Raninoides* (Tucker, 1995) and *Neopilumnoplax* (Feldmann et al., 1991). The fossil genus *Branchioplax* was reported from the Eocene Orca Group, suggested to have been deposited at bathyal depths (Feldmann et al., 1991). The two fossil genera *Portunites* and *Pulalius* have been reported from rocks on the west coast of North America that are interpreted to have been deep-water, continental-slope deposits. Conversely, the modern species of *Carpilius* have been reported from relatively shallow, sublittoral depths of approximately 5–35 m (Sakai, 1976). The mixed depth preferences of these decapods supports the interpretation that these rocks were deposited in a deep-water, continental-slope setting with some downslope mixing of the fauna, possibly explaining the reworked concretions.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1803
Infraorder Brachyura Latreille, 1803
Section Podotremata Guinot, 1977
Family Raninidae de Haan, 1841
Subfamily Lyreidinae Guinot, 1993
Genus *Macroacaena* Tucker, 1998

Type Species.— *Lyreidus succedanus* Collins and Rasmussen, 1992.

Remarks.—*Macroacaena* Tucker is characterized by possession of a tridentate front, two orbital fissures, an anterolateral margin with a hypertrophied spine at the anterolateral corner and usually a small protuberence just posterior to the midlength of the anterolateral margin, and a moderately distinct median ridge (Tucker, 1998). The fronto-orbital width of members of this genus is typically greater than the posterior margin (Tucker, 1998). Specimens from the Pulali Point locality are referred to the genus based upon possession of a moderately distinct ridge, an extremely reduced anterolateral spine, and a hypertrophied spine at the anterolateral corner. This combination of characters is unique to *Macroacaena* (Table 1). Characteristics of the rostrum or orbits are not available because the front is broken. The posterior width exceeds the fronto-orbital width, occupying

Table 1.—*Distinguishing characters of the dorsal carapace useful in differentiating among the genera* Lyreidus, Lysirude, *and* Macroaceana. *FOW = Fronto-orbital width, PW = posterior width.*

Character	*Lyreidus*	*Lysirude*	*Macracaena*
Carapace shape	Fusiform, much longer than wide	Carapace moderately wide	Carapace widest of the three genera
Orbital fissures	One	One	Two
Orbital teeth	One	One	Two
Dorsal ridge	Absent or indistinct	Absent or indistinct	Present
FOW vs. PW	FOW always narrower	FOW equal to or wider	FOW wider
Rostrum	Typically less produced	Typically more produced	Typically more produced
Front	Tridentate	Tridentate	Tridentate
Anterolateral spines	Short or absent	One hypertrophied; one much reduced	One hypertrophied; one much reduced
Anterolateral spines	One	Two or less often, one	Two

approximately 0.45 and 0.41 the maximum carapace width respectively. This falls outside the range typically ascribed to the genus by Tucker (1998), who described *Macroacaena* as having a fronto-orbital margin that is usually wider than the posterior margin (p. 325).

Distinguishing members of the genus *Macracoaena* from members of the two closely related genera *Lyreidus* de Haan and *Lysirude* Goeke can be difficult, as has been addressed by Tucker (1998) and Feldmann (1989, 1992). The three genera possess many overlapping characteristics that indicate that a morphological gradation exists with *Lyreidus* and *Macroacaena* as end members and *Lysirude* occupying an intermediate morphologic position (Table 1). However, the combination of characters of the dorsal carapace for each genus is unique, and distinguishing members of each genus is relatively straightforward if specimens are well preserved. The relative width of the front and the posterior margin should be used with care. For example, the two genera *Macroacaena* and *Lysirude* were characterized by Tucker (1998) as possessing a posterior width that is often less than the fronto-orbital width. *Lyreidus* was described as possessing a fronto-orbital width that is usually less than the posterior width and is always much less than one-half the maximum carapace width (p. 324). The specimen from Pulali Point, which has a combination of other characters that clearly place it in *Macroacaena*, has a posterior margin that is slightly wider than the fronto-orbital width, such as is often seen in *Lyreidus.* Additionally, Goeke (*in* Tucker, 1998) noted that the relative fronto-orbital width with respect to the total width in some species of *Lysirude* changes during growth, so that younger individuals typically possess relatively wider fronto-orbital margins. Therefore, it is possible that this character may not be useful in disinguishing among *Lyreidus*, *Lysirude*, and *Macroacaena.*

Macroacaena alseanus (Rathbun, 1932)
(Fig. 3B)

Lyreidus alseanus Rathbun, 1932:239, 240, 242, fig. 3, 4. Glaessner, 1960:17; Bennett, 1964:24; Feldmann, 1989:63–69, fig. 1.1, 1.2, 3.1–3.8, text fig. 4.1–4.3.
Lyreidus (*Lysirude*) *alseanus* Rathbun. Feldmann, 1992: 951, fig. 4.10, 4.11.

Material Examined.—CM 45822, 45823, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—Only one of the two specimens from Pulali Point is well preserved,

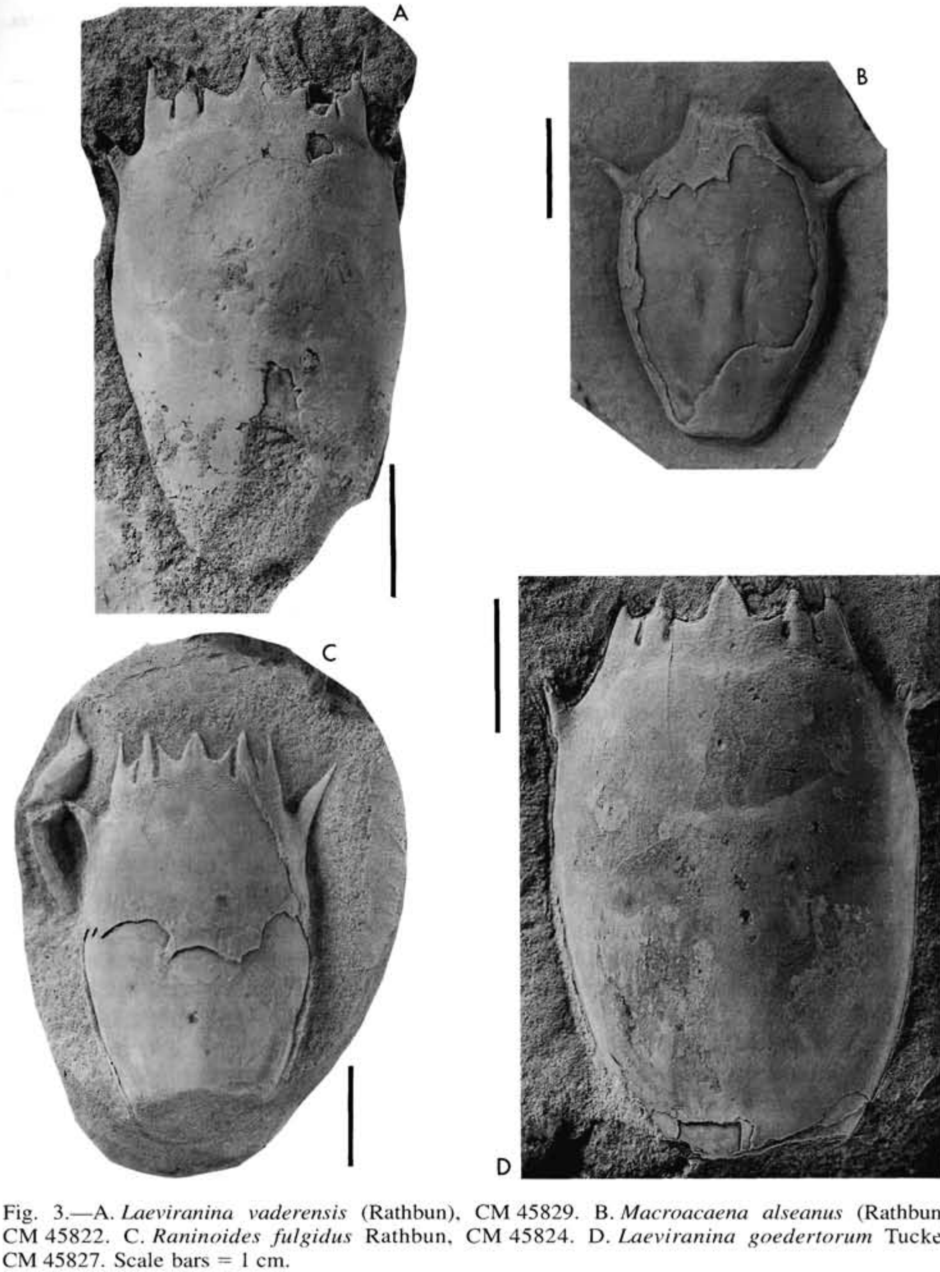


Fig. 3.—A. *Laeviranina vaderensis* (Rathbun), CM 45829. B. *Macroacaena alseanus* (Rathbun), CM 45822. C. *Raninoides fulgidus* Rathbun, CM 45824. D. *Laeviranina goedertorum* Tucker, CM 45827. Scale bars = 1 cm.

and unfortunately, the entire rostrum and orbital region are missing. Nevertheless, the specimens can be confidently referred to this species based on several characters. The length/width ratio is less than 0.65, the front is narrow and occupies about 0.41 the maximum carapace width, the anterolateral margin has an extremely reduced spine and a hypertrophied spine at the anterolateral angle, the lateral

Table 2.—*Number of species in the genera* Laeviranina *and* Raninoides *with wide orbital fissures, narrow orbital fissures, or grooves.*

Character of orbit	*Laeviranina*	*Raninoides*
Well-developed grooves	1	8
Narrow grooves	10	4
Fissures	1	1

margins are nearly straight, the posterolateral margins are slightly concave and converge posteriorly, and there is a moderately well-developed axial ridge on the dorsal carapace. All of these characteristics conform to the description of the species provided by Feldmann (1989).

Because the front is missing on this specimen, making it impossible to observe characteristics of the rostrum and orbits, it is possible to confuse it with members of another genus known from the Pacific Coast of North America, *Carinaranina* Tucker. Members of *Carinaranina* and *Macroacaena* look superficially similar if characters of the front are discounted. Species of *Carinaranina* typically possess a hypertrophied spine at the anterolateral corner but do not possess the reduced spine on the anterolateral margin (Tucker, 1998). This appears to be the best method of distinguishing *Macroacaena alseanus* (Rathbun) from members of *Carinaranina*, especially *C. naselensis* (Rathbun), which has a very narrow front as seen in species of *Macroacaena*. Other characteristics that distinguish members of *Carinaranina* from members of *Macroacaena* are the more well-developed axial ridge of *Carinaranina* that extends the entire length of the dorsal carapace onto the rostrum, the coarsely punctate ornamentation of *Carinaranina*, and the wider orbital grooves and better-developed orbital teeth of *Carinaranina*. Distinguishing members of the two genera is relatively straightforward if the orbits and rostrum are preserved since those areas are distinctly different in each genus.

Subfamily Raninoidinae de Haan, 1841

Remarks.—The problem of differentiating *Laeviranina* Lörenthey and Beurlen from *Raninoides* H. Milne Edwards has been addressed on numerous occasions. Tucker (1998) summarized previous work on this problem, noting that several criteria have been proposed to differentiate the two genera including the nature of the orbital fissures, the placement of the anterolateral spine with respect to the total length of the carapace, the presence or absence of a postfrontal ridge, and several characteristics of the sternum.

Laeviranina has been considered to possess orbital fissures, while *Raninoides* has been considered to possess orbital grooves; however, Tucker (1998) indicated that both character states occur in each genus. Data from 25 species analyzed in this study indicates that this character does indeed occur in both species (Table 2), but that there is a general tendency for members of the genus *Laeviranina* to possess narrow orbital grooves or fissures and for members of the genus *Raninoides* to possess relatively more open orbital grooves. Feldmann (1991) listed several features of the sternum that he believed could be used to differentiate the two genera, including the shape of sternal element four and the nature of the cleft in sternal element five. Tucker (1998) indicated that these sternal characteristics are mixed between the two genera as well. According to the key to the genera of the Raninoidinae provided by Tucker (1998), in species of *Raninoides*, the ster-

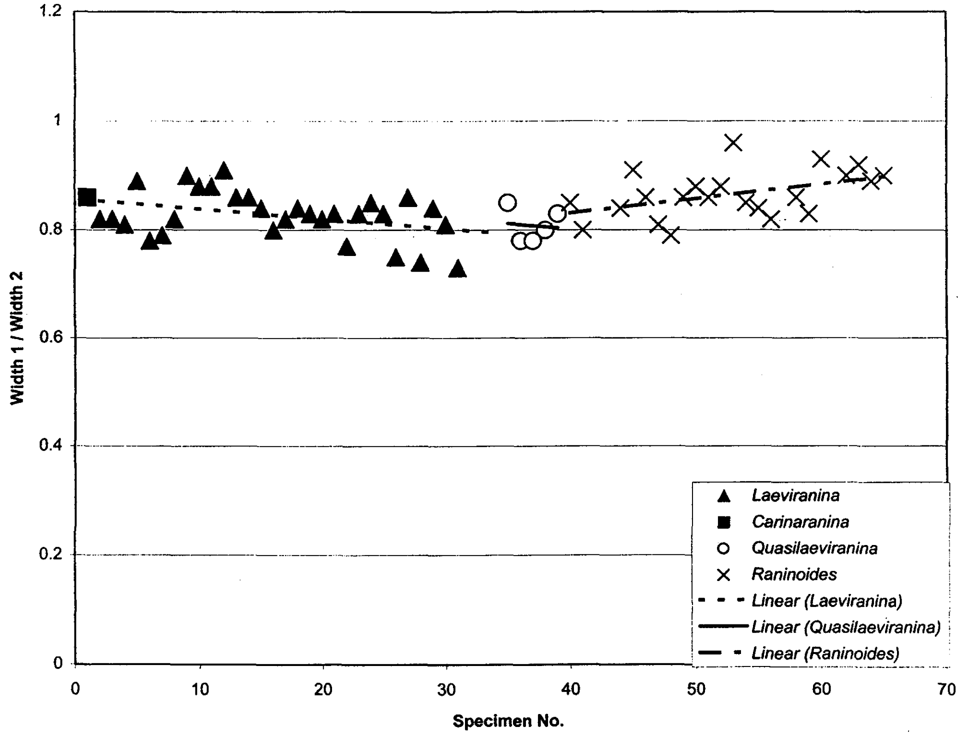


Fig. 4.—Specimens of *Laeviranina*, *Raninoides*, *Quasilaeviranina*, and *Carinaranina* plotted by the ratio of the width between the bases of the anterolateral spines (W2) to the maximum carapace width (W1). Linear regression lines show trends in ratios within taxa.

num between the third pereiopods is "usually quite wide" (p. 347), where it is known, and this same area, where known, is "moderately narrow" (p. 347) in species of *Laeviranina*. However, she did not list this as a useful character in differentiating the two genera (Tucker, 1998). It is necessary to bear in mind that the generic characteristics of the sternum of *Laeviranina* are not well known due to poor or lack of preservation (Tucker, 1998), so this character needs further investigation as more material becomes available. Tucker (1998) also noted that the ischium of the first pereiopod of species of *Raninoides* bears a spine; however, this element of the pereiopods of *Laeviranina* is unknown. This character could prove useful if more and better fossil material is discovered.

Members of the two genera have also been differentiated based on the relative width of the carapace with respect to the total length, the position of the anterolateral spines with respect to the total length, and the width of the fronto-orbital margin with respect to the maximum width. To test this, specimens and illustrations of specimens referred to nearly all species of both genera, as assigned by Tucker (1998), were measured, and relevant ratios were calculated. Scatter diagrams of the results of this work indicate that there is absolutely no difference between the two genera with respect to the ratios calculated (Fig. 4–6). Therefore, the relative width of the carapace, the position of the anterolateral spine, and the position of maximum width with respect to the total length of the carapace cannot

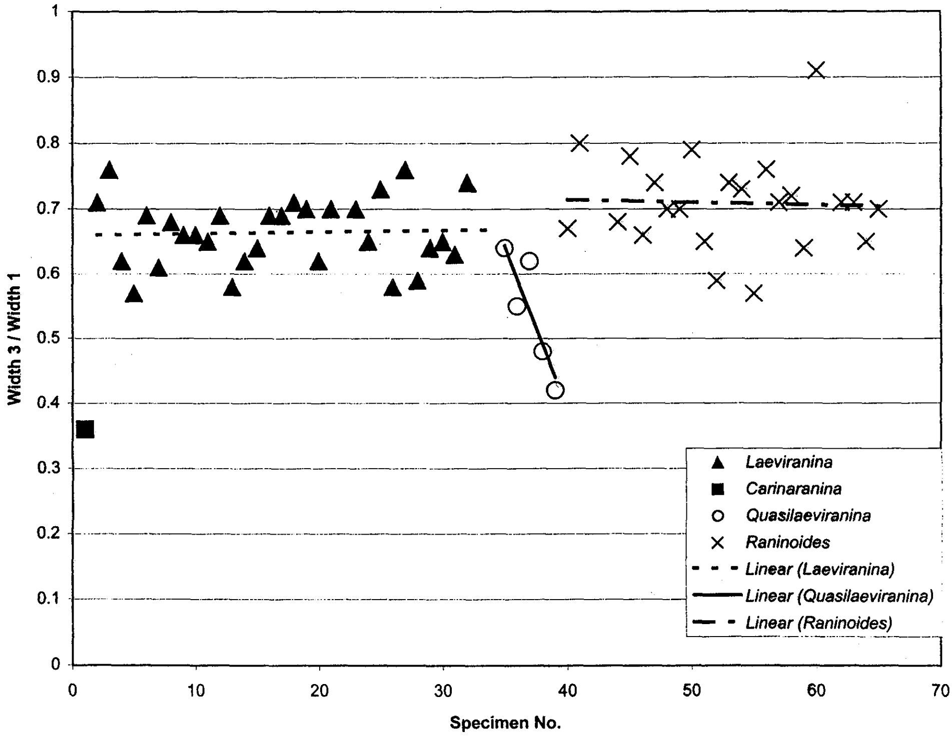


Fig. 5.—Specimens of *Laeviranina*, *Raninoides*, *Quasilaeviranina*, and *Carinaranina* plotted by the ratio of the fronto-orbital width (W3) to maximum carapace width (W1). Linear regression lines show trends in ratios within taxa.

be used reliably to differentiate between the two genera. Ratios for members of another closely related genus, *Quasilaeviranina* Tucker and the sole specimen of *Carinaranina* from Pulali Point, were included on the scatter diagrams for comparative purposes.

Tucker (1998) indicated that one characteristic that can reliably be used to differentiate between the two genera, especially in fossil taxa, is the presence or absence of a postfrontal ridge. Members of species currently assigned to *Laeviranina* possess such a ridge while members of most species of *Raninoides* do not. However, there are several problems that arise when using this single character to assign specimens to either *Laeviranina* or *Raninoides*. Use of the ridge to differentiate between the two genera may be hampered by differential preservation of the ridge, because in some specimens, the ridge is very poorly preserved. More importantly, members of several extant species of *Raninoides* possess weakly developed postfrontal ridges in some specimens. For example, specimens of *Raninoides louisianensis* Rathbun (USNM 12002; each of the USNM specimens contains a lot of several specimens, ranging from one to approximately 50 individuals) have a weakly developed postfrontal ridge marginally but the ridge is not developed axially. Members of *Raninoides bouvieri* Capart (USNM 121423) possess a very weak postfrontal ridge. Finally, members of the species *R. personatus* Henderson (USNM 216741) and *R. lamarcki* Milne Edwards and Bouvier

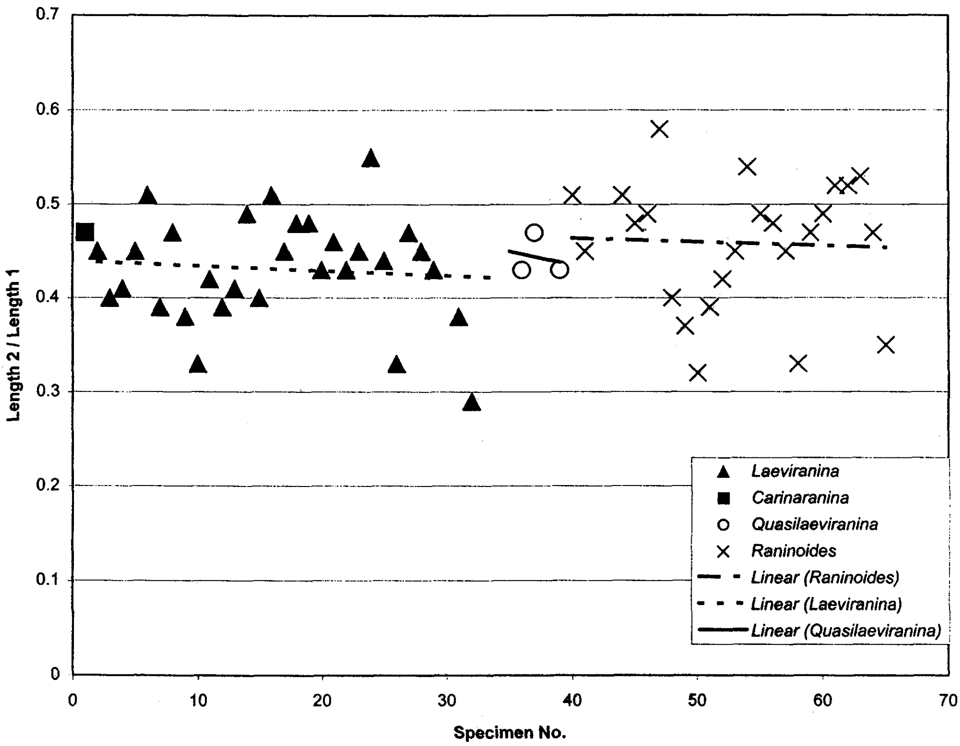


Fig. 6—Specimens of *Laeviranina*, *Raninoides*, *Quasilaeviranina*, and *Carinaranina* plotted by the ratio of the length to the position of maximum carapace width (L2) to the total length of the carapace (L1). Linear regression lines show trends in ratios within taxa.

(USNM 121660) possess weak postfrontal ridges which are best developed on larger specimens. Additionally, the degree of development of the ridges appears to vary within each species, sometimes, but apparently not always, associated with overall carapace size. Specimens of the extant species *R. benedicti* Rathbun (USNM 268507) and *R. loevis* (Latreille) (USNM 273193) exhibit the smooth, ridgeless, postfrontal regions that have traditionally been ascribed to members of that genus.

Generic assignment of taxa to *Raninoides* or *Laeviranina*, therefore, is difficult at best, especially since there are no unequivocal characters with which to accomplish this. While generic assignment of specimens with well- developed postfrontal ridges or smooth postfrontal regions is relatively straightforward, some taxa possess ridges that are poorly or variably developed. Development of a postfrontal ridge on several extant species of *Raninoides* casts further doubt upon the use of the postfrontal ridge as the only reliable means by which to distinguish between the two genera *Laeviranina* and *Raninoides*. It appears, therefore, that all of the characters that have been suggested as being useful for differentiating between the two genera are problematic, unreliable, and mixed between members of the two genera. While it is premature to assert that these two genera are synonymous, it is suggested that this possibility be further investigated, especially with regard to features of the sternum as first noted by Feldmann (1991).

Genus *Laeviranina* Lörenthey and Beurlen, 1929

Type Species.—*Ranina budapestinensis* [sic] Lörenthey, 1897:23.

Remarks.—Tucker (1998) provided a summary of all species that have been assigned to the genus *Laeviranina*, including several species from the Pacific Coast of North America that were originally assigned to the genus *Raninoides*. North American species originally assigned to *Raninoides* include *L. lewisanus* (Rathbun) and *L. vaderensis* (Rathbun); Tucker (1998) assigned them to *Laeviranina* based upon their possession of a postfrontal ridge. Upon examination of these two species, it is apparent that they are synonymous. Rathbun (1926) originally differentiated between the two species by observing that *L. lewisana* had a wider fronto-orbital width, a more anteriorly placed anterolateral spine, a less convex lateral margin, a straighter posterolateral margin, and a more convex dorsal surface. However, examination of illustrations of both *L. lewisana* and *L. vaderensis* in Rathbun's work (1926) shows that the fronto-orbital width to total width ratio is 0.70 and 0.68 respectively, not a significant difference. Further, examination of illustrations of specimens subsequently referred to each species by Tucker and Feldmann (1990) and Tucker (1998) shows that the two species do not differ substantially in the range of fronto-orbital width to total width ratios, averaging 0.70 in *L. lewisana* and 0.67 in *L. vaderensis*. Rathbun (1926) indicated that the anterolateral spine was placed more anteriorly in *L. lewisana*, and examination of her plates confirms this (plate 22, fig. 4, 5). However, examination of figures of specimens referred to each species by Tucker and Feldmann (1990) and Tucker (1998) indicates that the two species overlap in range in this ratio also. The length to the base of the anterolateral spine occupies an average of 0.20 of the total length in *L. lewisana* and 0.21 in *L. vaderensis*. Tucker (1995) reported that the orbital spines were slightly shorter than the rostrum in *L. lewisana* but she did not quantify the length of the orbital spines with respect to the rostrum for *L. vaderensis*. Rathbun's (1926) illustrations indicate that the orbital spines do not extend as far as the rostrum in *L. vaderensis*, but she did not comment on the length of the spines in her descriptions of either *L. vaderensis* or *L. lewisana*. Examination of figures of specimens referred to each species by Tucker and Feldmann (1990) and Tucker (1998) indicates that there is a range in orbital spine length with respect to the rostrum in both species, ultimately not providing a means of differentiating the two species. The orbital spines in specimens assigned to *L. lewisana* are typically longer than those of specimens of *L. vaderensis*, but there is a range in the length of the spines within each species.

Tucker (1998) provided several means by which the two species could be differentiated, including the greater width of the fronto-orbital margin in *L. lewisana* which has already been shown to be virtually the same in each species. She also suggested that the more egg-shaped, ovate carapace of *L. lewisana* might be used to distinguish the two genera. However, there appears to be a range of variation with regard to this character in both species, and in fact, Rathbun (1926) reported that the lateral margins of *L. lewisana* were "not so strongly outcurved behind the [anterolateral] spine" and that the posterolateral margin was straighter than that of *L. vaderensis* (p. 94), seemingly contradicting Tucker (1998). Tucker (1998) suggested that the posterior width of *L. lewisana* was slightly wider than that of *L. vaderensis*, but there is a large degree of overlap in the ratio of the posterior width to the maximum width in the two species in this character. Based upon measurements in Tucker (1995), the posterior width to maximum width ratio averages 0.46 in *L. vaderensis* with a range of 0.44–0.46 and that ratio averages 0.41 in *L. lewisana* with a range of 0.37–0.45. She also suggested that the anterolateral spines form a V-shaped angle with the anterolateral margin in *L. lewisana*, while in *L. vaderensis*, they form a U- shaped angle. Examination of plates of specimens referred to these two taxa by Rathbun (1926), Tucker and Feldmann (1990), and Tucker (1998) indicates that there is a range of variation in the shape of the angle in both species and that both U-shaped and V-shaped angles occur in each species. *Laeviranina vaderensis* was distinguished from *L. lewisana* by Tucker (1998) based on its less distinct postfrontal ridge that is steeply and tightly arched. However, it has been demonstrated above that use of the postfrontal ridge may not be useful in differentiating between *Raninoides* and *Laeviranina*, because the ridge can be variable in degree and nature of development within genera and even within species. Therefore, it seems unlikely that this particular character will be useful for differentiating taxa at the species level, especially when used as the sole distinguishing characteristic. Based upon this evidence, therefore, the two taxa are herein synonymized, with *L. lewisana* being the junior synonym.

Laeviranina vaderensis has previously been reported from the middle Eocene of Alaska and Oregon and the upper Eocene of Washington, and *L. lewisana* was previously reported from the Eocene of Washington. The range of *L. vaderensis* is therefore not extended either geographically or chronologically by the synonymy.

Laeviranina vaderensis (Rathbun, 1926)
(Fig. 3A)

Raninoides vaderensis Rathbun, 1926:93, pl. 22, fig. 5. Glaessner, 1929:372; Tucker and Feldmann, 1990:412, fig. 3.1, 3.2; Karasawa, 1992:1252.
Laeviranina vaderensis (Rathbun): Tucker, 1998:353, pl. 17, 18.
Raninoides lewisana Rathbun, 1926:94, pl. 22, fig. 4. Glaessner, 1929:372; Förster and Mundlos, 1982: 158.
Laeviranina lewisana (Rathbun): Glaessner and Withers, 1931:490, 491; Via, 1965:263; Via, 1969: 125; Tucker, 1998:351, fig. 15, 16.

Material Examined.—CM 45829–45832, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The specimens here referred to *L. vaderensis* possess several characters diagnostic of the species and are therefore confidently referred to this species. They possess an oblong carapace that ranges from being oblong-ovate to ovate. The fronto-orbital width occupies about 0.70 the maximum carapace width, and the orbital spines range from extending about half the length of the rostrum to extending to about the same length as the rostrum. The postfrontal ridge is subtle, arcuate, and slightly sinuous. The anterolateral spines extend more forward than laterally and form a U-shaped or V-shaped angle with the anterolateral margins. The posterolateral margins taper markedly to their intersection with the posterior margin. Some of the specimens here referred to *Laeviranina vaderensis* possess long orbital spines that extend to the same length as the rostrum, which is at the long end of the range of variation for the species. However, some specimens possess orbital spines that extend only about half the distance of the rostrum, clearly illustrating the range of variation in the species.

Laeviranina vaderensis has previously been reported from the middle Eocene Orca Group of Alaska, the middle Eocene of Oregon, and the upper Eocene Tejon Formation and Hoko River Formation of Washington (Tucker, 1998). This occurrence extends the geographic range of the species to the eastern Olympic Peninsula, Washington.

Laeviranina goedertorum Tucker, 1998
(Fig. 3D)

Laeviranina goedertorum Tucker, 1998:348, fig. 13, 14.

Material Examined.—CM 45827, 45828 deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The Pulali Point specimens referred to *Laeviranina goedertorum* Tucker possess a suite of characters that place them in this species as described by Tucker (1998). The specimens possess an elongate carapace that achieves its maximum width at about the midpoint and converges slightly posteriorly, as seen in *L. goedertorum.* The front on the Pulali specimens and *L. goedertorum* converges anteriorly, producing a relatively narrow fronto-orbital width of around 0.60 the maximum carapace width. The postfrontal ridge on *L. goedertorum* and the Pulali specimens is sinuous and moderately well developed. The orbital teeth are shorter than the rostrum in both the new specimens and *L. goedertorum.* The specimens are therefore confidently referred to this species.

The maximum carapace width of *Laeviranina goedertorum* has been described as being located about one-third the distance posteriorly on the carapace. Dimensions of the new specimens indicate that there is a range from about one-third the distance to just under half the distance posteriorly on the carapace. The posterolateral margins of the carapace do not converge as acutely in this species as they do in other species of the genus. *Laeviranina goedertorum* is therefore wider along its entire length than other species of the genus and possesses a relatively wide posterior margin that is markedly wider than that seen in *L. vaderensis.* The two species may also be distinguished based upon several other criteria as well. The front of *Laeviranina goedertorum* converges anteriorly, resulting in an overall narrower fronto-orbital width to maximum width ratio in *L. goedertorum* as compared to *L. vaderensis.* The postfrontal ridge of *L. goedertorum* is better developed and more sinuous than that of *L. vaderensis.*

Laeviranina goedertorum has previously been reported from the Eocene Hoko River Formation (Tucker, 1998). This occurrence in the Eocene Aldwell Formation extends the geographic range to the eastern Olympic Peninsula, Washington.

Genus *Raninoides* H. Milne Edwards, 1837

Type Species.—*Ranina laevis* Latreille, 1825.

Remarks.—The specimens here referred to *Raninoides* H. Milne Edwards lack a postfrontal ridge, the main characteristic that can be reliably used to differentiate between the two genera *Laeviranina* and *Raninoides.* These specimens can therefore be unequivocally assigned to *Raninoides* because they possess a completely smooth postfrontal region.

Raninoides fulgidus Rathbun, 1926
(Fig. 3C)

Raninoides fulgidus Rathbun, 1926:96–97.

Material Examined.—CM 45824–45826 deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—Two specimens from the Pulali Point locality exhibit a combination of characteristics that place them in the species *Raninoides fulgidus* Rathbun. The specimens possess relatively long orbital and anterolateral spines and wide orbital fissures, characteristic of the species *R. fulgidus*. The rostrum does not extend as far as the orbital spines as described for this species by Tucker (1998); however, she described the inner orbital fissure as being deeper than the outer. In the Pulali Point specimens, the fissures are the same length.

Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polybiinae Ortmann, 1893
Genus *Portunites* Bell, 1858

Type Species.—*Portunites incerta* Bell, 1858.

Remarks.—The diagnosis for the genus *Portunites* Bell given by Glaessner (1969) describes the genus as having a hexagonal carapace that is not much wider than long, a four-toothed front, an anterolateral margin with four or five teeth with the last being the longest, an arcuate ridge extending from the lateral tooth to the medial area, a straight or concave posterolateral margin, well-defined gastrocardiac regions, and fifth pereiopods with dactyli that are not flattened (p. R513). Tucker and Feldmann (1990) emended the generic diagnosis to include a paddlelike dactylus on the fifth pereiopod based on its presence in *Portunites alaskensis* Rathbun.

Glaessner (1969) did not mention the width of the orbits in this genus, each of which occupies a little over one-third the fronto-orbital width in most members of the genus and about one-fifth to one-quarter the maximum carapace width. The fronto-orbital width of most members of the genus occupies greater than two-thirds the maximum carapace width. Bell (1858:21) described the orbits in the type species, *P. incerta* Bell, as extending to the middle of the hepatic region, and measurements of individuals of this species indicate that the fronto-orbital width occupies approximately two-thirds the maximum width of the carapace. A cast of a previously unillustrated specimen of *P. incerta* (JSHC 1732d) (Fig. 7B) documents the great width of the orbits in the type species of the genus. The front is not clearly evident in previously published plates. The subsequently named British species including *P. stintoni* Quayle and *P. sylviae* Quayle and Collins have orbits that are similar in relative size to those of the type species. The orbits of *P. alaskensis* Rathbun are extremely large; the fronto-orbital width in this species occupies more than 0.70 the maximum width of the carapace. The fronto-orbital width of the new species to be described below, *Portunites macrospinus*, occupies 0.67 the maximum carapace width.

Two species of *Portunites* possess relatively narrow fronto-orbital width-to-width ratios but can be assigned to the genus based upon a combination of other important characters. The orbits of *Portunites insculpta* Rathbun occupy approximately 0.50 the maximum carapace width, but this taxon can be assigned to *Portunites* based upon its possession of a well-developed epibranchial ridge, carapace shape and regions typical of the genus, and four anterolateral spines excluding the outer orbital spines. *Portunites kattachiensis* Karasawa possesses a fronto-orbital width which occupies about 0.53 the maximum carapace width. However, *Portunites kattachiensis* has several other generic characters that clearly

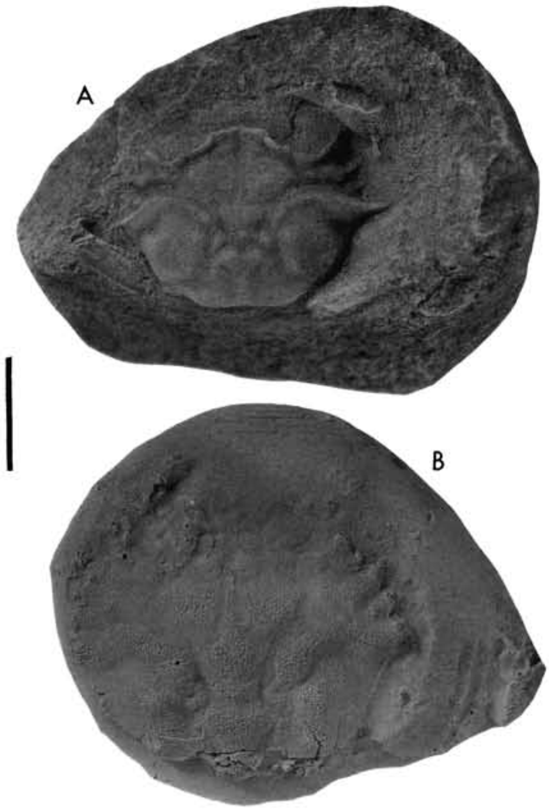


Fig. 7.—A. *Portunites macrospinus*, new species, holotype, CM 45833. B. Cast of *Portunites incerta* Bell, JSHC 1732d. Scale bar = 1 cm.

place it in *Portunites*, including a well-developed epibranchial spine, a relatively straight front with very small teeth, four anterolateral spines excluding the outer orbital spine, two orbital fissures, an ovate-hexagonal carapace, and carapace regions typical of species of *Portunites*. It is therefore suggested that the diagnosis of the genus be expanded to include a statement pertaining to the relatively great width of the orbits in members of this genus, occupying more than one-half and generally two-thirds or greater the maximum carapace width. The size of the orbits cannot be determined for *P. eocenica* Lörenthey and Beurlen, for which the type specimen has been lost (Quayle and Collins, 1981).

Portunites triangulum Rathbun differs from members of the genus *Portunites* in several important aspects. *Portunites triangulum* possesses rather small orbits; they occupy approximately 0.52 of the maximum width of the carapace, which does fall within the range for the genus. Schweitzer and Feldmann (1999) listed several differences between *Portunites triangulum* and other members of the genus, including overall carapace dimensions, the relative length of the anterolateral spines, definition of the carapace regions, and carapace shape. At that time those differences were considered to be specific; however, additional observations indicate that there are further differences between *Portunites triangulum* and other members of the genus. *Portunites triangulum* possesses four sharp spines on the front in addition to small inner-orbital spines; species of *Portunites* have only four spines or bosses including the inner-orbital spine. The epibranchial ridge on *Portunites triangulum* is not as well developed as on the other species of *Portunites* and it lacks the transverse ridges on the hepatic and protogastric regions typical of *Portunites*. Because of these important differences between this species and other species of *Portunites*, reevaluation of its generic assignment is necessary. Reassignment at this time is premature, but the problem currently is being addressed by two of the authors (Feldmann and Schweitzer) and other workers (Karasawa, personal communication, 1998). Because of the strong probability that *Portunites triangulum* will be removed from the genus, interpretations about the genus presented in this paper therefore will exclude this taxon.

It is also suggested herein that the diagnosis of the genus be emended to describe the frontal margin as ranging from relatively straight to possessing four blunt knobs or small spines. *Portunites incerta*, *P. stintoni*, *P. sylviae*, and *P. kattachiensis* all possess four very small, blunt knobs or spines on the frontal margin. The species *P. alaskensis* possesses four small but distinct and sharp spines, and *P. insculpta* Rathbun appears to possess four small spines. The new species *P. macrospinus* possesses two very small, blunt spines axially and blunt swellings on the inner-orbital margin which are not developed as spines. Because of this, it is necessary to state that the front in members of this genus may possess very small spines or blunt knobs, since the current diagnosis (Glaessner, 1969) indicates that the front must possess four spines. *Portunites triangulum* possesses rather large, well-developed spines on the frontal margin, again suggesting that it may be referrable to a different genus.

Portunites macrospinus, **new species**
(Fig. 7A, 8)

Diagnosis.—Carapace rounded-hexagonal in outline; postorbital spine extremely long, sharp, and attenuated; anterolateral spines sharp, last anterolateral spine extremely long, attenuated and sharp; orbits very broad and deeply excavated; carapace moderately vaulted; frontal spines very weakly developed.

Description.—Carapace rounded-hexagonal in outline; carapace length 64% maximum width; widest at position of last anterolateral spine; position of maximum width situated approximately one-third the total distance posteriorly; carapace moderately vaulted both transversely and longitudinally.

Front about 0.21 maximum carapace width; relatively straight; extending only slightly beyond orbits; with blunt bilobed projection axially; axially sulcate; very poorly developed blunt projections on inner orbital margin. Orbits large; fronto-orbital width about 0.67 maximum carapace width; each orbit about 0.35 fronto-orbital width; orbits sinuous, curving posteriorly, then slightly anteriorly, and finally posteriorly before intersecting anterolateral margin; directed anterolaterally; rimmed; two closed fissures; deeply excavated laterally and shallowly excavated axially.

Anterolateral margins short, bearing four or five spines including extra-orbital spine; extra-orbital spine extremely long, projecting anteriorly and well beyond the rostrum; acute and attenuated, sometimes with small triangular spine at base; next two anterolateral spines smaller, triangular, acute, projecting anterolaterally; last anterolateral spine longest, attenuated, acute, projecting laterally.

Posterolateral margins weakly concave, sinuous, with pronounced, rimmed reentrant at posterolateral corner. Posterior margin weakly concave; rimmed; about 0.31 maximum carapace width.

Carapace regions moderately well defined by grooves. Frontal region with two weakly inflated areas on either side of the axis; protogastric regions weakly ovate, moderately inflated, with very weak transverse ridge; hepatic regions with transverse ridge extending from second anterolateral spine across region; mesogastric region extremely narrow anteriorly and widening posteriorly, straight-sided anteriorly, convex posteriorly, posterior margin nearly straight; meso- and metagastric regions not differentiated; urogastric region weakly differentiated, narrow, depressed, with concave lateral margins; cardiac region rounded-triangular in shape, apex directed posteriorly, with two large swollen bosses

Table 3.—*Measurements (in mm) taken on the dorsal carapace of specimens of* Portunites macrospinus. *Orientation of measurements is illustrated in Figure 8. L1 = maximum length of carapace, W1 = maximum width of carapace, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width, W5 = orbital width.*

Specimen number	L1	W1	W2	W3	W5	W4
CM 45834	20.5	30.0	19.3	9.4	15.3	6.4
CM 45836	16.8	24.6	17.6	—	—	6.0
CM 45833	15.2	26.2	16.9	7.0	7.4	6.0
CM 45835	15.9	26.0	18.4	—	9.0	6.7

anteriorly placed on either side of the axis, very weakly developed boss at apex of triangle; intestinal region flattened.

Branchial regions not well differentiated; well-developed epibranchial ridge, extending from last anterolateral spine, curving first anteriorly, then posteriorly, terminating at lateral margin of mesogastric region; branchial region inflated axially, sloping to posterolateral margin, flattening along posterior margin.

Chelipeds poorly known, manus appearing to be rather short; venter unknown.

Measurements.—Measurements, in millimeters, taken on specimens of *Portunites macrospinus* are found in Table 3. The orientation of measurements taken is indicated in Figure 8.

Etymology.—The trivial name is a combination of "macro," meaning long, with the word "spine," to indicate the extremely long postorbital and anterolateral spines which are diagnostic for the species.

Types.—The holotype, CM 45833, and paratypes, CM 45834–45836, are deposted in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—Four specimens from the Pulali Point locality can be referred to this species. All four specimens exhibit most of the dorsal carapace, two of which are quite well preserved. Portions of the cheliped and fragments of pereiopods are present in all four specimens; however, none of these elements is well-enough preserved to permit description. No aspects of the venter were preserved.

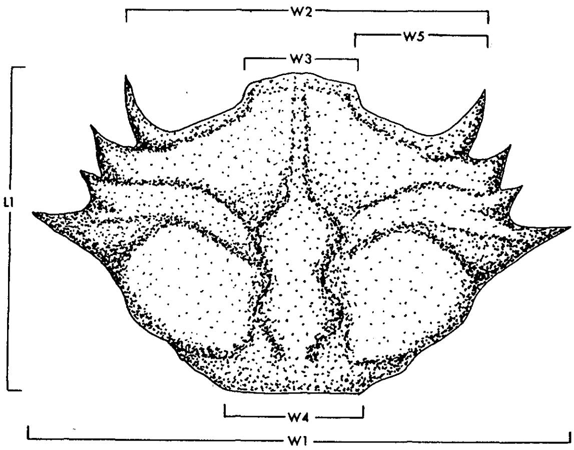


Fig. 8.—Line drawing of *Portunites macrospinus* showing position and orientation of measurements taken.

The new species can be distinguished immediately from all other members of the genus because of its extremely long, attenuated postorbital spine; sinuous, deeply excavated orbits; and sharp, attenuated anterolateral spines. The new species is most like the three species *Portunites alaskensis*, *P. kattachiensis*, and *P. hexagonalis* Nagao, but differs from those species in several ways. *Portunites alaskensis* has a well-developed ridge on the hepatic region that extends onto the protogastric region; this ridge is weakly developed in *P. macrospinus*. The carapace of *Portunites macrospinus* is more ovate and less hexagonal than that of *P. alaskensis*, and the frontal teeth, especially the axial pair, of *P. alaskensis* are much better developed than in *P. macrospinus*. *Portunites alaskensis* possesses three well-developed bosses on the cardiac region, while only two well-developed bosses are present on that region in *P. macrospinus*. Furthermore, the carapace in *P. alaskensis* is more flattened than that of *P. macrospinus*, which has a moderately vaulted carapace. The spines on *P. hexagonalis* are shorter and more triangular than those of *P. macrospinus*. The last anterolateral spine is directed slightly posterolaterally in *P. hexagonalis*, while that of *P. macrospinus* is directed laterally. The frontal spines of *P. hexagonalis* are much better developed than in *P. macrospinus*.

Portunites macrospinus can be differentiated from *P. kattachiensis* because *P. macrospinus* has wider, more widely spaced orbits, longer and more attenuated anterolateral spines, and a less tightly arched epibranchial ridge than *P. kattachiensis*. Furthermore, the epibranchial ridge in *P. kattachiensis* terminates in a tubercle, and there is a tubercle on the protogastric region and two tubercles on the branchial region in *P. kattachiensis*; all of these are missing in *P. macrospinus*. Additionally, *P. kattachiensis* has a much better developed urogastric region than does *P. macrospinus*.

The description of this new species brings the number of species to nine that are referrable to the genus *Portunites*. This occurrence brings the number of species of *Portunites* in North America to three and the number of North Pacific species to five. The five species from the North Pacific region (*P. alaskensis*, *P. hexagonalis*, *P. insculpta*, *P. kattachiensis*, and *P. macrospinus*) are more similar morphologically and therefore are probably more closely related to each other than to the other species of the genus, which are known from the Eocene of Europe. Species from the North Pacific range in age from Eocene to Oligocene. *Portunites macrospinus* is currently known only from the Eocene Aldwell Formation and the Pulali Point localities, not extending the geologic range of the genus.

Superfamily Xanthoidea Dana, 1851
Family Xanthidae Dana, 1851
Genus *Pulalius*, **new genus**

Type Species.—*Zanthopsis vulgaris* Rathbun, 1926.

Diagnosis.—Carapace ovate or hexagonal, highly vaulted longitudinally; carapace regions inflated; front four-lobed; orbits oval, with one orbital fissure; epibranchial region forming linear transverse ridge across dorsal carapace; anterolateral margin with three small, blunt spines, last spine longest, last spine at end of transverse epibranchial ridge; branchial region large and inflated; posterolateral margins convex; abdominal somites free.

Etymology.—The genus takes its name from Pulali Point, a prominent geographic feature near the collecting locality for the new species, *Pulalius dunhamorum*, to be described below.

Remarks.—The collection of previously undescribed fossils from the Aldwell Formation contains a group of specimens that are clearly congeneric with specimens assigned to *Zanthopsis vulgaris* Rathbun and which have been assigned to the new species described below. The new species and *Z. vulgaris* share many significant features. The two species possess a four-lobed front which occupies about 0.25 the maximum carapace width; oval orbits with one orbital fissure; an anterolateral margin with three blunt spines with the last being the longest; broad, inflated protogastric regions with well-defined lateral margins and poorly defined axial margins; inflated carapace regions; a carapace that is highly vaulted longitudinally; an inflated epigastric region that forms a transverse ridge; large, inflated metabranchial regions; flattened intestinal regions; convex anterolateral and posterolateral margins; a similar arrangement and shape of the mesogastric, urogastric, and cardiac regions; an abdomen with somites 3–5 free; sternites of similar size and shape; and major chelae with similar shape and ornamentation. Based on these numerous similarities, it is apparent that the two species must be congeneric.

Inspection of all known species of the genus *Zanthopsis* McCoy indicates that *Z. vulgaris* and the new species differ significantly from the type species, *Z. leachi* Desmarest, and cannot be retained in that genus. According to Glaessner's (1969) diagnosis for the genus, *Zanthopsis* sensu stricto and *Zanthopsis vulgaris* share some characters, including a four-lobed front and a vaulted carapace; however, species of *Zanthopsis* sensu stricto possess large, nodular bosses or tubercles on the branchial regions of the carapace and exhibit fusion of abdominal somites 3–5. *Zanthopsis vulgaris* does not possess either characteristic.

McCoy (1849) erected the genus *Zanthopsis* and designated *Z. leachi* as the type species. He also described several other species of *Zanthopsis*, all of which possess nodular bosses on the dorsal carapace. Bell (1858) illustrated the type species and two of McCoy's species, *Z. bispinosa* McCoy and *Z. unispinosa* McCoy. Inspection of McCoy's (1849) descriptions and Bell's (1858) plates indicates that *Zanthopsis* sensu stricto and *Zanthopsis vulgaris* are not at all closely related. The carapace shape in *Zanthopsis* sensu stricto is rounded or oval; in *Zanthopsis vulgaris* the carapace is rounded-hexagonal. The carapace regions of *Zanthopsis* sensu stricto are indistinct and faintly marked by wide, shallow grooves. *Zanthopsis vulgaris* has well-defined carapace regions that are marked by narrow grooves. The carapace regions of the two taxa are completely different in terms of shape, ornamentation, and degree of inflation. The protogastric region of *Zanthopsis* sensu stricto is narrow and poorly delimited. In *Z. vulgaris*, those regions are broad, inflated, and well delimited by grooves on the lateral margins. The hepatic region is better developed, more inflated, and of an overall broader shape than in *Zanthopsis* sensu stricto. *Zanthopsis vulgaris* has one orbital fissure; members of *Zanthopsis* sensu stricto have none. The epibranchial region of *Z. vulgaris* is swollen and forms a transverse ridge; in *Zanthopsis* sensu stricto, this region does not appear to be differentiated at all. The branchial region of *Zanthopsis* sensu stricto is ornamented by large tubercles or bosses; there are no bosses on the branchial region of *Z. vulgaris*, which also has an overall larger and more inflated branchial region. The shape of the urogastric and cardiac regions are completely different. The urogastric region in *Z. vulgaris* is extremely constricted and flattened and the cardiac region is broadly triangular; both regions are very well defined. In *Zanthopsis* sensu stricto, these regions are not well defined and possess tubercles or bosses. The male abdomen of *Zanthopsis* sensu stricto exhibits fusion of the third through fifth somites, while in *Z. vulgaris*, these somites are free. For all of these reasons, *Zanthopsis vulgaris* is herein referred to the new genus *Pulalius* and is designated as the type species for that genus.

Three other species from the Tertiary of the west coast of North America have been referred to the genus *Zanthopsis*. *Zanthopsis sternbergi* Rathbun, from the Cretaceous of California (Rathbun, 1926), is known only from a claw, making confirmation of its placement in the genus difficult. *Zanthopsis hendersonianus* Rathbun from the Oligocene of Oregon and the Eocene of California (Rathbun, 1926) displays characteristics that place it within *Zanthopsis* sensu stricto. *Zanthopsis rathbunae* Kooser and Orr (*not* sensu Maury) resembles members of the Hepatinae Stimpson of the Calappidae de Haan and is currently being reevaluated by two of us (Schweitzer and Feldmann) to determine its generic and familial placement.

Some other species referred to *Zanthopsis* sensu stricto have been removed to other genera or families or should be reevaluated. *Zanthopsis peytoni* Stenzel and *Z. carolinensis* Rathbun may be compared with members of the genus *Harpactocarcinus* A. Milne Edwards. *Zanthopsis terryi* Rathbun and *Zanthopsis rathbunae* Maury were removed to the genus *Eriosachila* Blow and Manning by Blow and Manning (1996; Blow, personal communication, 1998). Both *Z. cretacea* Rathbun and *Z. kressenbergensis* Meyer possess a long lateral spine, which is not characteristic of members of either *Zanthopsis* sensu stricto or *Pulalius*, suggesting that their generic placement should be reconsidered.

Possession of a vaulted carapace with inflated regions; very small, blunt anterolateral teeth; a relatively simple arrangement of regions; and a distinctive transverse epibranchial ridge set *Pulalius* apart from all other members of the Xanthidae. Some other xanthid genera possess a more or less well-developed transverse ridge, and these were assigned to the subfamily Menippinae Ortmann by Sakai (1976). These genera include *Ozius* H. Milne Edwards, *Pseudozius* Dana, *Sphaerozius* Stimpson, and *Lydia* Gistel. However, members of this subfamily possess several characteristics that cannot accommodate *Pulalius*, including a carapace that is significantly wider than long or nearly circular instead of ovate-hexagonal as seen in *Pulalius*, carapace regions that are much less inflated than *Pulalius*, carapaces that are much less vaulted than *Pulalius*, more and larger anterolateral teeth than *Pulalius*, a branchial ridge that ends in the penultimate tooth instead of the last anterolateral tooth as in *Pulalius*, and better developed anterolateral and frontal teeth than in *Pulalius*.

Other families contain genera with transverse ridges on the dorsal carapace, but none can accommodate *Pulalius*. Members of the Portunidae typically possess a transverse ridge on the dorsal carapace, but portunids usually have a flattened dorsal carapace, a dentate front, and a dentate anterolateral margin with at least three well-developed spines; these characteristics are not seen in *Pulalius*. Further, in all but one subfamily of the Portunidae, the dactylus of the fifth pereiopod is paddlelike. In the new species to be described below, the dactylus of the fifth pereiopod is long and lanceolate.

The Retroplumidae Gill have transverse carapace ridges, but they are of an altogether different placement and conformation. Retroplumids have extremely wide orbits, a narrow front, and a flattened carapace, none of which are characteristic of *Pulalius*. Additionally, the carapace regions of *Pulalius* have an overall different conformation than members of the Retroplumidae.

Pulalius vulgaris appears to be superficially similar to some members of the Goneplacidae Dana. Goneplacids typically possess a quadrate carapace, a straight front, and a flattened dorsal carapace (Williams, 1984; Tucker and Feldmann, 1990), which are not characteristic of *Pulalius*. However, distinguishing between the Xanthidae and the Goneplacidae can be extremely difficult. Tucker et al. (1994) described sternal characteristics that can sometimes be used to distinguish between xanthids and goneplacids. In typical xanthids and some goneplacids, the sternum is narrow and the eighth thoracic sternite is not visible because the abdomen obscures it. In other goneplacids, the sternum is wider and a small part of the eighth sternite is therefore visible in ventral view (Tucker et al., 1994). The goneplacid species *Branchioplax washingtoniana* Rathbun, also known from Tertiary deposits of Washington, displays a conformation of the carapace regions that is very similar to that seen in *Pulalius vulgaris*. The sternum of *Branchioplax washingtoniana* is also xanthidlike because the eighth sternite is not visible in ventral view, and therefore cannot be used to distinguish between the two taxa. However, *Pulalius vulgaris* possesses a distinctly four-lobed front, inflated carapace regions, a rounded carapace, and a highly vaulted carapace, distinguishing it from *Branchioplax washingtoniana*, which has a straight front, flattened carapace regions, and a carapace that is rounded-hexagonal in shape. *Pulalius* can be differentiated from members of the goneplacid genus *Speocarcinus* Stimpson because the latter has a much less vaulted carapace, less inflated carapace regions, and a more square carapace. Additionally, *Speocarcinus* exhibits a distinctly goneplacidlike sternum in which the eighth sternite is clearly visible on either side of the abdomen, while *Pulalius* exhibits a typically xanthidlike abdomen and sternum. In summary, use of the sternum to differentiate between members of the Xanthidae and Goneplacidae must be used with extreme caution because the method does not work in all cases.

The new genus ranges from late Eocene to Oligocene rocks in British Columbia, Washington, and Oregon (Rathbun, 1926; Berglund, personal records). According to Berglund, members of the genus have been found in several rock units including the late Eocene Keasey Formation (Armentrout, 1987; Snavely, 1987), the late Eocene to early Miocene Lincoln Formation (Rau, 1964; Prothero and Armentrout, 1985; Armentrout, 1987; Babcock et al., 1994), the Oligocene Blakely and Marrowstone formations (Armentrout and Berta, 1977), the Eocene to Oligocene Makah Formation (Snavely et al., 1980), the Eocene ?Aldwell Formation at Pulali Point, Washington (Squires et al., 1992), and the Oligocene of Nootka Island, British Columbia (Jeletzky, 1973).

Pulalius dunhamorum, **new species**
(Fig. 9–11)

Diagnosis.—Carapace ovate; anterolateral and posterolateral margins convex, posterolateral margins especially so; regions inflated, especially the branchial regions; epibranchial region with prominent inflated ridge extending from last anterolateral spine to axial area; anterolateral teeth small, blunt, rounded.

Description.—Carapace ovate in outline, wider than long, maximum width about 1.2 times length, widest between last anterolateral spine, position of maximum width approximately 50% total length. Carapace strongly vaulted longitudinally, moderately vaulted transversely, vaulting most extreme at posterior part of mesogastric region.

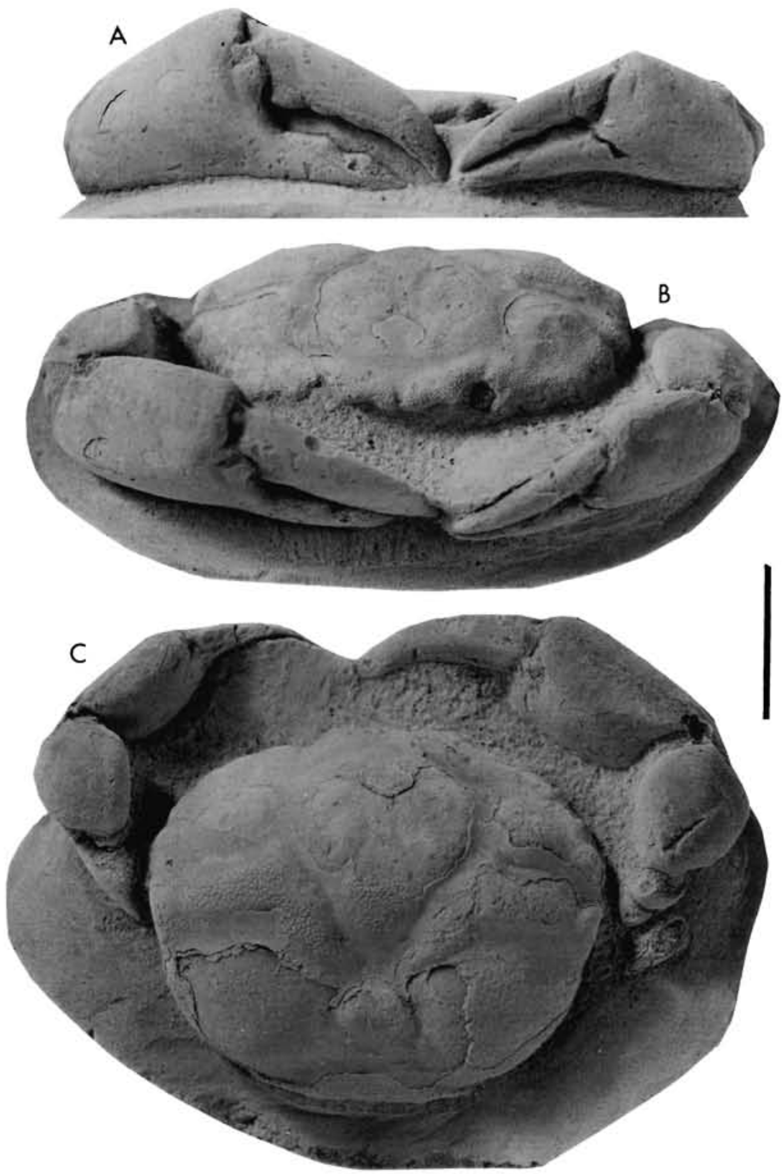


Fig. 9.—*Pulalius dunhamorum* new species, holotype, CM 45837. A. Anterior view showing chelipeds. B. Oblique anterior view showing orbits. C. Dorsal carapace. Scale bar = 1 cm.

Front approximately 0.25 maximum carapace width, produced beyond orbital teeth, sinuous in antero-oblique view, margin downturned; bearing four small, blunt teeth, outer teeth rounded, inner teeth small, rounded, closely spaced, separated by narrow, V-shaped medial notch, base of notch extending posteriorly into narrow sulcus. Orbits small, deep, slightly ovate in anterior view, directed forward and slightly upward; eyestalks appear to fill orbits; supraorbital margins raised with one closed fissure near midpoint.

Anterolateral margins with flanks turned under, very thick, sides nearly vertical at maximum width of carapace, becoming less so toward anterior; convergent anteriorly. Anterolateral margin bearing

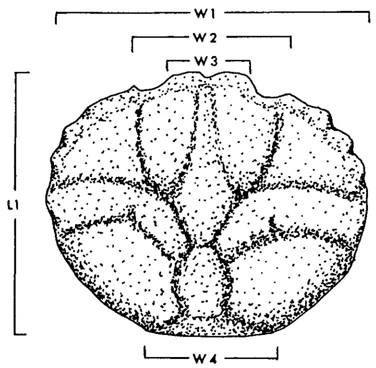


Fig. 11.—Line drawing of *Pulalius dunhamorum* showing position and orientation of measurements taken.

three blunt nodes; largest node at anterolateral angle located at termination of broad epibranchial ridge; nodes 1 and 2 smaller than third; nodes 1 and 2 separated by small triangular notch; nodes 2 and 3 separated by broad, shallow notch; nodes separated from extra-orbital angle by sinuous area, sometimes bearing one small, very blunt node. Posterolateral margins convex; posterior margin nearly straight, approximately 0.50 maximum carapace width.

Regions well defined by grooves; carapace surface finely granular except in grooves. Epigastric region small, weakly inflated; protogastric region longer than wide, separated from front by shallow postorbital furrow, narrowing distally into triangular point; hepatic region inflated, possessing bulbous swelling medially and flattening towards anterolateral margin; mesogastric region narrow anteriorly, widening posteriorly into a triangular area, lateral margins concave, posterior margin convex; urogastric region deeply depressed, narrowing distally, lateral margins very concave, highly restricted centrally; cardiac region moderately inflated, defined laterally by deep branchiocardiac grooves, narrowing distally, anterior portion of region most inflated and bearing two transverse pits; intestinal region poorly defined, flattened, broad, extending to posterolateral corner.

Cervical groove deep, well defined, interrupted axially by urogastric region; broad and shallow along anterior margin of epibranchial ridge, ending at base of second anterolateral node; branching at distal end into two short grooves anteriorly and posteriorly around second anterolateral node; posterior branch terminating at carapace margin between second and third anterolateral nodes; anterior branch extending through notch separating first and second anterolateral node onto subhepatic region.

Epibranchial region marked by prominent, inflated, arcuate, transverse ridge; extending from third anterolateral node anteriorly and then sharply posteriorly, terminating at lateral margin of urogastric region in sharp triangle. Branchial region strongly inflated, pentagonal, accentuating broadly rounded posterolateral margin of carapace.

Abdominal somites 1 and 2 approximately equal in width, somite 2 about twice as long as somite 1, lower margin of somite 2 convex, lower margin slightly sinuous; somite 3 widest of all somites, about 0.3 maximum carapace width, lateral corners rounded, upper margin slightly sinuous, posterior margin weakly concave; somites 4 and 5 about twice as wide as long; somite 4 slightly wider than somite 5, somite 4 widening posteriorly, lateral margins of somites 4 and 5 weakly concave, upper and lower margins of somite 4 and 5 nearly straight; somite 6 1.5 times as wide as long, margins nearly straight; telson equilaterally triangular, apices rounded; weak axial ridge extending from somites 1–6.

Sternum slightly longer than wide, widest at sternite 6, ovate; sternites 1 and 2 form equilateral triangle, surface weakly inflated, lateral margins slightly concave, apex sharp; sternite 3 with sinuous upper margin, lateral margins rounded, posterior margin converging distally, broad sulcus axially; sternite 4 with very concave anterior and posterior margins, with central and lateral depressions, blunt episternal projections; sternite 5 wider than sternite 4 and widest of all sternites, directed anterolaterally, upper and lower margins nearly straight, possessing sharp episternal projections; sternite 6 widening distally, directed slightly anterolaterally, upper and lower margins straight, with sharp episternal projections; sternite 7 directed slightly posterolaterally, upper and lower margins nearly straight, widening distally, with sharp episternal projections; sternite 8 about as wide as long, appearing to possess weak episternal projections, not well known; surface of all sternites granular.

Table 4.—*Measurements (in mm) taken on the dorsal carapace of specimens of* Pulalius dunhamorum. *Orientation of measurements is illustrated in Figure 11. L1 = maximum length, W1 = maximum width, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width.*

Specimen number	W1	W2	W3	W4	L1
CM 45837	36.5	16.0	9.2	17.0	29.7
CM 45845	36.0	17.6	—	15.6	30.3
CM 45839	32.6	14.8	8.2	14.1	27.1
CM 45844	26.0	12.5	7.6	12.6	21.6
CM 45843	36.1	17.0	9.4	8.6	30.0
CD 45838	46.8	—	—	17.3	38.8
CM 45842	31.7	14.8	8.6	14.0	28.3
CM 45840	27.9	13.0	7.0	12.8	23.2
CM 45841	36.7	17.7	9.3	13.2	31.1

Pterygostomial region triangular, incised by broad shallow groove extending from notch separating first and second anterolateral nodes; exopod of third maxilliped much longer than wide, outer margins nearly straight, widening slightly posteriorly, then converging to triangular point at posteriormost end; ischium of endopod somewhat longer than wide, upper margin nearly straight, outer margin slightly concave, inner margin weakly convex, lower margin weakly concave, narrow sulcus located about one-third the distance distally from inner margin; basis triangular, widening anteriorly.

Chelipeds unequal, both robust. Carpus of major cheliped longer than high, widening distally, distal margin nearly straight, upper margin very convex, lower margin concave, tapering to very narrow proximal margin, bulbous. Merus of major cheliped longer than high, lower margin weakly convex, appearing to be rather bulbous. Manus of major cheliped widening distally; lower margin extending nearly straight, then extending obliquely at propodus; outer surface highly vaulted transversely and longitudinally; upper margin weakly rounded, small blunt tooth at proximal corner; proximal margin sinuous, with broad inflated area centrally and blunt tooth at intersection with lower margin; distal margin sinuous, with trapezoidal projection centrally, distal margin extending obliquely between upper and lower margins.

Fixed finger of major cheliped slightly deflected; occlusal surface with four large, blunt teeth, first and third approximately equal in size, second largest and broadly triangular, fourth smallest, remainder of occlusal surface with small denticles; widest proximally and narrowing distally, tip upturned slightly, outer surface with setal pits arranged linearly below denticles, denticles also with setal pits.

Movable finger of major cheliped highly arched; narrowing distally; occlusal surface bearing at least three teeth, first tooth wide, blunt; second and third bluntly triangular, second larger than third, remainder of occlusal surface smooth or with small denticles. Each finger more darkly pigmented than remainder of carapace.

Minor chela similar in shape to major chela except not as bulbous and with more slender fingers; finger more weakly arched.

Basis of pereiopod 2 tubular; higher than long; merus much longer than high; carpus appearing to be longer than high. Basis of pereiopod 3 tubular, higher than long, distal margin concave; merus much longer than high, surface granular; ischium slightly longer than high; carpus longer than high, widening distally; manus longer than high. Basis of pereiopod 4 tubular, higher than long, distal margin concave; ischium not well known; merus much longer than high; carpus longer than high, widening distally. Basis and ischium of pereiopod 5 not known; merus much longer than high; carpus somewhat longer than high; propodus longer than high; dactylus much longer than high, lanceolate, tapering to sharp point distally.

Measurements.—Measurements of the dorsal carapace are given in Table 4, and orientation of measurements is illustrated on Figure 11. Measurements of the venter are given in Table 5, and measurements of the major and minor chelae are given in Table 6.

Types.—The holotype, CM 45837, and paratypes, CM 45838–45846, are deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Etymology.—The specific name honors Mr. and Mrs. George Dunham of Brinnon, Washington, who

Table 5.—*Measurements (in mm) taken on the sternum of specimens of* Pulalius dunhamorum. *L = length, W = width.*

Specimen number	Max. L of sternum	Max. W of sternum	Max. W of abdomen	Max. L of abdomen	W-telson
CM 45844	15.2	13.7	—	—	—
CM 45840	>14.2	14.5	8.7	9.1	5.0
CM 45838	27.8	22.8	14.2	13.1	8.1

kindly allowed collecting on their property and access to the cobble beaches of Pulali Point, Washington.

Remarks.—Ten specimens are herein referred to this species. The specimens are extremely well preserved, with some retaining cuticular material. At least three of the specimens appear to be corpses, based upon their possession of the venter, but others may also be corpses based upon retention of the chelae. All of the specimens were preserved in concretions. The nine specimens of *Pulalius dunhamorum* exhibit a range of variation in some characteristics. For example, some specimens, CM 45838 and CM 45842, possess a somewhat more hexagonal carapace than the other specimens. Additionally, the development of the anterolateral teeth ranges from weak to extremely reduced or almost nonexistent.

Pulalius dunhamorum can be differentiated from the only other species in the genus, *P. vulgaris*, in several ways. *Pulalius dunhamorum* possesses a more linear, well-developed epibranchial ridge while that of *P. vulgaris* is arcuate and discontinuous. The posterolateral margins of *P. dunhamorum* are shorter and much more convex and the anterolateral margins are also more convex than those of *P. vulgaris*. The carapace of *P. dunhamorum* is not as highly vaulted longitudinally and the anterolateral spines are not as well developed as in *P. vulgaris*. The urogastric region is more depressed in *P. dunhamorum* than in *P. vulgaris*. The overall shape of *P. dunhamorum* is rounder and more ovate than that of *P. vulgaris*, which has a more hexagonal carapace.

The new species has been reported only from the Pulali Point locality.

Family Carpiliidae Ortmann, 1893

Remarks.—Traditionally, *Carpilius* Leach, 1823, has been referred to the Xanthidae (Rathbun, 1930; Glaessner, 1969; Sakai, 1976; Manning and Holthuis, 1981; Dai and Yang, 1991). However, Guinot (1978) presented compelling arguments for separation of *Carpilius* and the related genera, *Palaeocarpilius* A. Milne Edwards, 1862, and *Ocalina* Rathbun, 1929, into a separate family, the Carpiliidae. We concur. In that same year, Collins and Morris (1978) also referred to the Carpiliidae and assigned two new species from Pakistan to their new genus

Table 6.—*Measurements (in mm) taken on the major and minor chelae of* Pulalius dunhamorum. *L = length.*

Specimen	Height	Length	L-Movable finger	L-Palm
CM 45838	19.0	40.4	26.2	29.2
CM 45837	>11.0	>30.0	19.7	23.1
CM 45845	12.3	27.7	16.8	20.8
CM 45838 (minor)	13.0	32.4	19.0	22.6
CM 45837 (minor)	10.4	25.7	15.4	17.7

Proxicarpilius Collins and Morris, 1978. To these four genera must be added *Eocarpilius* Blow and Manning, 1996 and *Harpactoxanthopsis* Via, 1959.

The characters of the dorsal carapace which unite these genera include a generally oval outline which is wider than long. The front is downturned and is either simple and triangular or undulatory, with a pair of inner orbital projections and a pair of generally smaller projections on either side of a shallow axial depression. The orbits are small, entire, and circular. The anterolateral margin may be smooth or may bear one or more blunt projections. The anterolateral corner is unmodified in some and bears a blunt projection extending onto the carapace as a subtle ridge on others. The carapace surface is generally smooth, the carapace regions are weakly defined or not discernable, and the carapace is strongly vaulted longitudinally. The characters of the appendages, sternum, and other features that define the family are given by Guinot (1978).

Genus *Carpilius* Leach *in* Desmarest, 1823

Type Species.—*Cancer maculatus* Linnaeus, 1758.

Remarks.—The Carpiliidae includes four genera known only from the fossil record and a single genus, *Carpilius*, that ranges into the Recent. The genera are distinguished from one another on the basis of the configuration of the front and on the nature of the anterolateral margin. In these regards, the specimens from Pulali Point must be assigned to *Carpilius*. The front bears four projections that extend forward and downward, very much like those of the type species, *C. maculatus*. The anterolateral margin is generally unmodified, although there is a very subtle angulation just in advance of the projection defining the anterolateral corner. The form of the anterolateral corner and the ridge projecting onto the carapace surface is nearly identical to those developed on extant species.

Recognition of the Pulali Point specimens as representatives of *Carpilius* provides the first authentic documentation of that genus in the fossil record. Although specimens from the Miocene of central Europe have previously been assigned to *Carpilius* (Müller, 1984), that species, *C. antiquus* Glaessner, 1928, has subsequently been assigned to *Eocarpilius* (Feldmann et al., 1998). Karasawa (1993) reported *Carpilius* from Miocene rocks of southwestern Japan, but that occurrence was based only upon a portion of a manus. Thus, the geologic range of *Carpilius* has been extended from Eocene to Recent.

Carpilius occidentalis, **new species**
(Fig. 12, 13)

Diagnosis.— Typical-sized *Carpilius* with subtle swelling on anterolateral margin just in advance of well-defined prominence on anterolateral corner; straight posterolateral margin as long as anterolateral margin. Gastric region weakly defined, branchiocardiac groove well defined for genus.

Description.—Moderate-sized carpiliid; carapace width approximately 1.4 times length, ovoid outline, flattened transversely, strongly arched longitudinally, regions weakly defined.

Front about 0.24 maximum width, downturned, bilobed axially, bounded by rounded inner orbital projections. Orbits smoothly rounded, complete, with subtle orbital rim. Fronto-orbital margin about equal in width to posterior margin, approximately 0.43 maximum width. Anterolateral margin smooth, with subtle rim, curvature increasing toward anterolateral corner which is marked by a swollen prominence extending onto carapace as a faint ridge. Less distinct swelling developed on anterolateral margin in advance of anterolateral corner. Maximum width developed at anterolateral corner situated

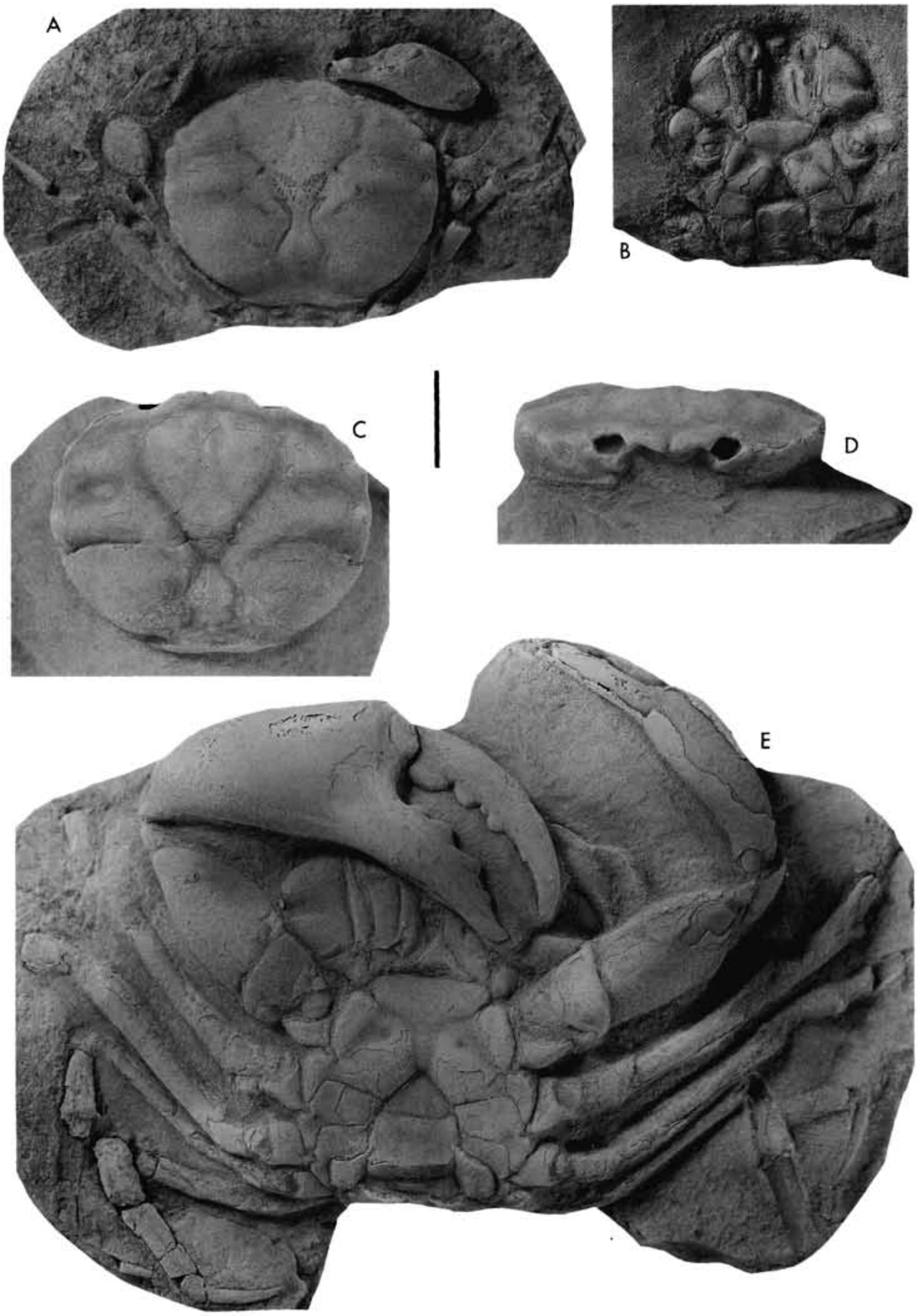


Fig. 10.—*Pulalius dunhamorum* new species. A. Dorsal carapace, CM 45840. B. Ventral surface of carapace, CM 45844. C. Dorsal carapace, CM 45839. D. Anterior view showing orbits, CM 45839. E. Venter and appendages, CM 45838. Scale bar = 1 cm.

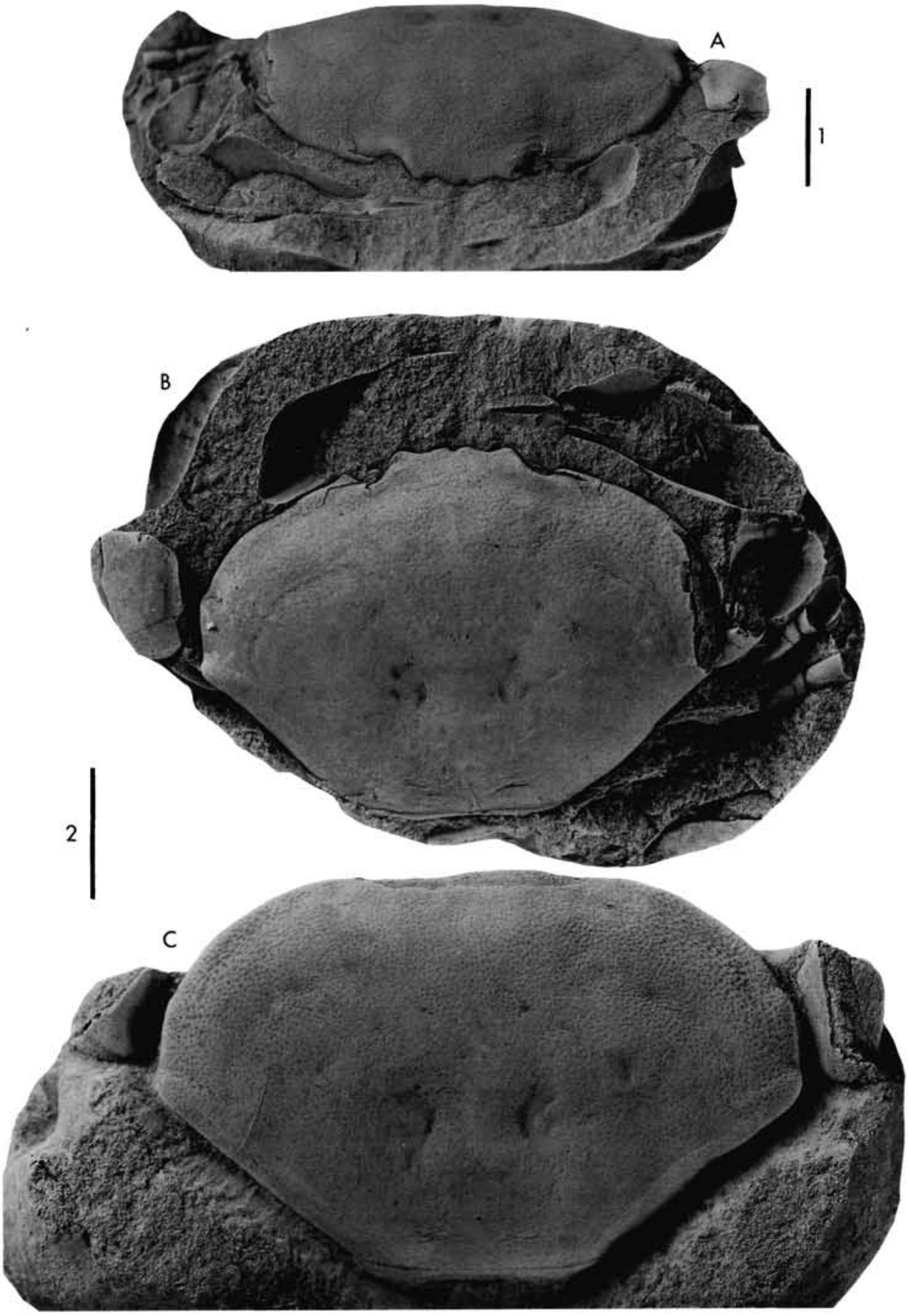


Fig. 12.—*Carpilius occidentalis* new species. A. Anterior view, holotype, CM 45847. B. Dorsal carapace, holotype, CM 45847. C. Dorsal carapace, CM 45848. Scale bar 1 for A and B and scale bar 2 for C. Scale bars = 1 cm.

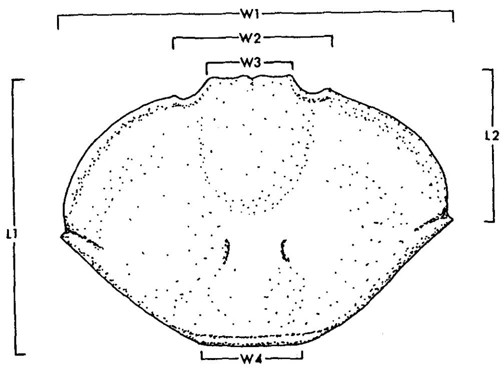


Fig. 13.—Line drawing of *Carpilius occidentalis* showing position and orientation of measurements taken.

at point about 0.66 maximum length. Posterolateral margin straight, intercepting straight posterior margin at about 140° angle. Posterior margin with narrow, distinct rim.

Carapace regions poorly defined as broadly domed surfaces and shallow grooves. Gastric region longer than wide, bounded by very shallow parabolic groove. Urogastric region about 0.13 maximum width, well defined by narrow, arcuate grooves laterally. Cardiac region about 0.24 maximum width, widest near anterior, tapering to indistinct intestinal region. Hepatic region separated from smooth branchial region by depression paralleling anterolateral margin.

Carapace surface with fine setal pits, more numerous and larger along anterior and anterolateral margins.

Measurements.—Measurements taken on specimens of *Carpilius occidentalis* are given in Table 7, and the orientation of those measurements is shown in Figure 13.

Types.—The holotype, CM 45847, and paratype, CM 45848, are deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Etymology.—The species takes its trivial name from its occurrence on the eastern Pacific rim.

Remarks.—Two specimens from the Pulali Point region can be referred to this species. Both are extremely well preserved; however, the front is broken away on the paratype. Fragments of the proximal elements of the pereiopods are preserved as is a portion of the right cheliped on the holotype. Unfortunately, preservation of this element is not sufficient to permit a good description. The ventral surface of this crab remains unknown.

Comparison with extant species within the genus permits distinguishing the Eocene form as a new species. The anterolateral corner of *C. occidentalis* is

Table 7.—*Measurements (in mm) taken on the dorsal carapace of specimens of* Carpilius occidentalis. *Position and orientation of measurements is illustrated in Figure 13. L1 = maximum length, L2 = length to maximum width, W1 = maximum width, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width.*

Specimen number	L1	L2	W1	W2	W3	W4
CM 45847	31.5	20.5	44.2	18.0	10.7	19.0
CM 45848	36.0	21.0	55.7	—	—	22.0

situated at about the midlength, and the posterolateral margins converge posteriorly to form an angle of about 98°. In all of the living species, the anterolateral corner is positioned in the posterior half of the carapace, and the posterolateral margins converge at angles between 110–118°. The curvature of the anterolateral margin of *C. occidentalis* is very much like that of *C. convexus* (Forskål); however, the point of inflection on the former species is a moderately well-defined prominence whereas none is present on *C. convexus*. The front on *C. occidentalis* bears four lobes, the axial pair being only slightly smaller than the inner orbital lobes. The axial region of *C. corallinus* (Herbst) is not bilobed; that region on the other two species is bilobed but the axial lobes are markedly smaller than the inner orbital lobes. The overall carapace surface is very smooth on all living species except *C. convexus*. On that species, the branchiocardiac groove is evident as a subtle demarkation that can be discerned between the gastric regions and the branchial regions. That same level of development is present on *C. occidentalis*.

In summary, the carapace morphology within the Carpiliidae has remained relatively conservative since the appearance of the family in the Eocene. The number of genera assigned to the family was greatest in the Eocene and has been reduced, possibly to a single genus, *Carpilius*, in modern environments. Sakai (1976) placed *Liagore* de Haan, 1833, with *Carpilius* in the Alliance Carpilioida. Guinot (1978), however, rejected that association and *Liagore* will be retained in the Xanthidae sensu lato until specimens can be examined in the light of the familial characters designated by Guinot.

Family Goneplacidae Macleay, 1838
Genus *Branchioplax* Rathbun, 1916
Branchioplax washingtoniana Rathbun, 1916
(Fig. 14A)

Branchioplax washingtoniana Rathbun, 1916:344. Rathbun, 1926:42, plate 9, fig. 6; Tucker and Feldmann, 1990:415, fig. 6, 7.1, 7.3.

Material Examined.—CM 45849–45851, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The Pulali Point specimens are referred to this taxon based on their possession of a relatively square, equidimensional carapace; anterolateral teeth; well-defined regions, inflated branchial regions; and a straight front. The specimens conform well to the descriptions of the species provided by Rathbun (1916, 1926) and Tucker and Feldmann (1990).

Genus *Neopilumnoplax* Serène *in* Guinot, 1969
Neopilumnoplax hannibalanus (Rathbun, 1926)
(Fig. 14C)

Pilumnoplax hannibalanus Rathbun, 1926:37, 39, plate 10, fig. 1–4.
Neopilumnoplax hannibalanus (Rathbun): Tucker and Feldmann, 1990:418, fig. 7.2, 7.4, 8.

Material Examined.—CM 45855–45869, CM 45901, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The Pulali Point specimens are referred to *Neopilumnoplax hannibalanus* based upon their possession of a straight front, flattened carapace, well-developed anterolateral teeth, prominent midorbital suture, arcuate posterolateral margins, and coalesced first and second anterolateral teeth. The specimens con-

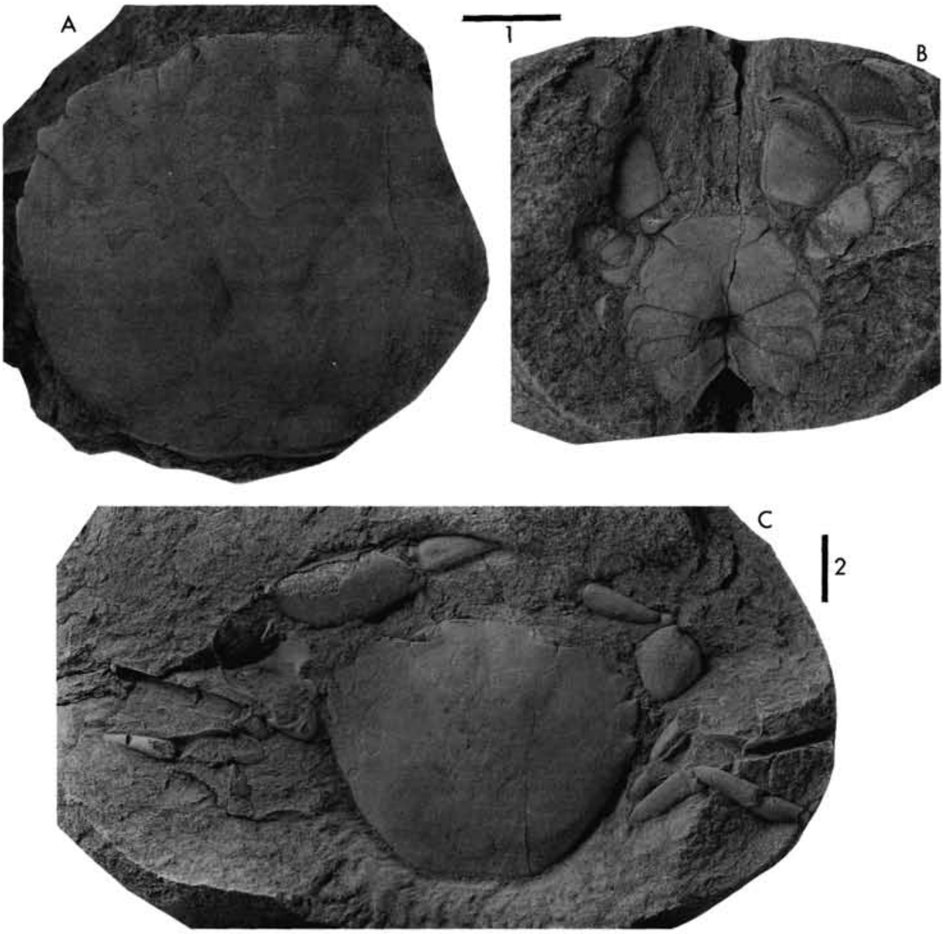


Fig. 14.—A. *Branchioplax washingtoniana* Rathbun, CM 45850. B. Venter of unknown goneplacid, CM 45852. C. *Neopilumnoplax hannibalanus* (Rathbun), CM 45855. Scale bar 1 for A and B and Scale bar 2 for C. Scale bars = 1 cm.

form very well to both Rathbun's (1926) description and the emended description of the species provided by Tucker and Feldmann (1990).

Differentiating between *Branchioplax washingtoniana* and *Neopilumnoplax hannibalanus* can be extremely difficult, as has been addressed by Tucker and Feldmann (1990). They suggested that *N. hannibalanus* has more posteriorly convergent posterolateral margins and more poorly marked regions than *B. washingtoniana*. Additionally, *B. washingtoniana* possesses much more inflated branchial regions than does *N. hannibalanus*, which provides the best means of differentiating the two taxa. *Neopilumnoplax hannibalanus* appears to have sharper, better developed anterolateral teeth than does *B. washingtoniana*, but this characteristic does not always hold and should be used with caution.

As has been discussed above, Tucker et al. (1994) provided a means by which some goneplacids could be distinguished from xanthids. Three of the goneplacid specimens in this study, CM 45852–45854, possess well-preserved sterna, and on these specimens, the eighth sternite is clearly obscured by the abdomen (Fig. 14B). Unfortunately, none of the three specimens exhibits dorsal carapace material, making them impossible to assign to a genus or species. However, the sterna correspond very closely to those illustrated by Tucker and Feldmann (1990) as belonging to the two species *Branchioplax washingtoniana* and *Neopilumnoplax hannibalanus*. Tucker and Feldmann (1990) suggested that the two taxa differ in the conformation of the sixth abdominal somite which has convex sides in *Branchioplax washingtoniana* and straight or concave sides in *Neopilumnoplax hannibalanus*. This character was not useful in assigning the three venters to a taxon, because the lateral margins are intermediate between the two conditions.

Section Thoracotremata Guinot, 1977
Superfamily Hexapodoidea Miers, 1886
Family Hexapodidae Miers, 1886

Remarks.—The Hexapodidae was raised to family level by Manning and Holthuis (1981) based upon the possession of three pairs of walking legs in this group instead of four as in other decapod families. They considered the Hexapodidae to be closely related to the Goneplacidae (Manning and Holthuis, 1981). In addition to loss of the fifth pereiopod, the eighth sternite is much reduced and is hidden by the seventh sternite and the posterior margin of the dorsal carapace (Gordon, 1971). Genera within the Hexapodidae are distinguished by the shape and degree of fusion of the abdomen, form of the third maxillipeds, shape of the eye, development of the sternal grooves of the abdomen, and the structure of the male pleopod (Manning and Holthuis, 1981). The specimens from Pulali Point are referred to the Hexapodidae because they possess four pairs of pereiopods and have no evidence of an eighth sternite.

Extant genera of the Hexapodidae include *Hexapinus* Manning and Holthuis, *Hexaplax* Doflein, *Hexapus* de Haan, *Lambdophallus* Alcock, *Paeduma* Rathbun, *Parahexapus* Balss, *Pseudohexapus* Monod, *Spiroplax* Manning and Holthuis, *Stevea* Manning and Holthuis, *Thaumastoplax* Miers, and *Tritoplax* Manning and Holthuis. Genera described from the fossil record include *Goniocypoda* Woodward, *Thaumastoplax*, *Hexapus*, *Stevea*, and *Prepaeduma* Morris and Collins. *Prepaeduma* possesses five pereiopods; Morris and Collins (1991) considered it to be an ancestor to *Paeduma* in which the fifth pereiopod was not yet fully suppressed. Beschin et al. (1994) doubted its placement in the Hexapodidae based upon its possession of five pairs of pereiopods; reevaluation of that genus by two of the authors (Schweitzer and Feldmann) is in progress.

Fossil hexapods have not previously been reported from North America. Fossil species of *Palaeopinnixa*, with the referral of several species to that genus to be discussed below, have been reported from Spain, Panama, Peru, Trinidad, and Argentina, (Rathbun, 1918; Woods, 1922; Via, 1966; Collins and Morris, 1976; Feldmann et al., 1995). *Hexapus nakajimai* Imaizumi has been described from the Miocene of Japan (Imaizumi, 1959), and *Hexapus pinfoldi* Collins and Morris has been reported from Pakistan (Collins and Morris, 1978). At least eight species of the hexapod genus *Goniocypoda* have been reported from England, Europe, Africa, and India (Woodward, 1867; Bittner, 1893; Carter, 1898; Glaessner, 1933; Remy and Tessier, 1954; Secretan, 1971; Crane, 1981; Crane and Quayle, 1986). The genus *Stevea* has been reported from the Eocene of Italy (Beschin et al., 1994).

Genus *Palaeopinnixa* Via, 1966

Type Species.—*Palaeopinnixa rathbunae* new name for *Pinnixa eocenica* Rathbun, 1926, by original designation. Via (1966) designated *Pinnixa eocenica* Rathbun, 1926 as the type species of his new subgenus *Pinnixa* (*Palaeopinnixa*). However, the referral herein of both *Thaumastoplax eocenica* Woods, 1922 and *Pinnixa eocenica* Rathbun, 1926 to *Palaeopinnixa* makes *Pinnixa eocenica* Rathbun a junior homonym. Therefore, the substitute name, *Palaeopinnixa rathbunae* is provided for Rathbun's (1926) species, which remains the type species for the genus as designated by Via (1966).

Included Species.—*Palaeopinnixa rathbunae* Rathbun, 1926 (formerly *Pinnixa eocenica*); *P. eocenica* Woods, 1922 as *Thaumastoplax*; *P. intermedia* (Collins and Morris, 1976), as *Thaumastoplax*; *P. mytilicola* Via, 1966; *P. perornata* Collins and Morris, 1976 (In the title for the original species description, the trivial name was erroneously spelled *porornata*. Derivation of the name as well as consistent spelling as *perornata* throughout the text indicate that *perornata* was the intended trivial name.); *P. prima* (Rathbun, 1918), as *Thaumastoplax*; *P. rocaensis* (Feldmann et al., 1995), as *Thaumastoplax*.

Diagnosis.—Carapace wider than long, length to width radio about 0.67, carapace widest just anterior to posterolateral reentrants; carapace rounded rectangular to ovoid, narrowing weakly anteriorly; carapace regions distinct; front widened distally, extending well beyond orbits, axially sulcate, frontal width to fronto-orbital width ratio about 0.42; orbits wider than high, with sinuous upper margins, moderately deeply excavated, fronto-orbital width to width ratio about 0.55; lateral rim absent or weakly developed; posterolateral reentrant well-developed; posterolateral width to maximum width ratio about 0.80; fronto-orbital width to posterior width ratio about 0.55; abdominal somites 3–5 fused in males; fourth sternite with anterior projections; third pereiopod longest.

Material Examined.—*Thaumastoplax intermedia*, In.60008 (holotype); *T. prima*, USNM 324227 (holotype); USNM 324228 (paratype); *T. eocenica* Woods, SM C 1394 (holotype); *Pinnixa (Palaeopinnixa) perornata*, In.61361 (holotype); *T. rocaensis*, GHUNLPam 7006 (holotype); GHUNLPam 7007–7009, 7026, 7027.

Discussion.—Via (1966) erected the subgenus *Palaeopinnixa* to embrace the new species *Pinnixa* (*Palaeopinnixa*) *mytilicola* as well as *Pinnixa eocenica* Rathbun which was designated as the type species for the subgenus. Newly collected specimens referrable to *Pinnixa eocenica* sensu Rathbun, described herein, possess four pairs of pereiopods and seven sternites; therefore, the subgenus *Palaeopinnixa* is removed from *Pinnixa* and the Pinnotheridae and is elevated to generic status. Because of the homonymy discussed above, the type species for the genus is *Palaeopinnixa rathbunae* new name.

Four fossil species previously assigned to *Thaumastoplax*, *T. intermedia*, *T. prima*, *T. eocenica* Woods, and *T. rocaensis*, are clearly congeneric with *Palaeopinnixa rathbunae* and *Pinnixa* (*Palaeopinnixa*) *mytilicola* and are therefore assigned to *Palaeopinnixa*. These fossil species possess all of the diagnostic characters of *Palaeopinnixa* including a rounded to ovoid carapace, distinct carapace regions, a front that is flared and axially sulcate, a well-developed posterolateral reentrant, and a posterior width-to-width ratio of about 0.80.

The new specimens cannot be referred to any of the genera previously known from the fossil record. Members of the genus *Goniocypoda* possess an extremely wide fronto-orbital margin which occupies more than 0.60 the maximum carapace width. Members of that genus also possess an extra-orbital tooth that can range from small to large; the fossils described here do not possess an extra-orbital tooth and have a fronto-orbital width to maximum width ratio of approximately 0.44. In the genus *Hexapus*, individuals possess deep sternal grooves, which the fossils here referred to *Palaeopinnixa* do not possess. Members of the genus *Stevea* have stridulating ridges on the pterygostomial region and exhibit fusion of somites 2–6; neither condition is exhibited on the new specimens.

The new specimens can be easily differentiated from most extant genera of the Hexapodidae. The sole extant species of *Thaumastoplax* has much smaller orbits and rostrum, a rectangular carapace, a convex posterolateral margin, and poorly defined carapace regions which clearly distinguish it from species of *Palaeopinnixa*. Members of *Lambdophallus* possess a well-developed sternal groove, which species of *Palaeopinnixa* do not possess. In the genus *Paeduma*, individuals exhibit fusion of somites 3 and 4 and somites 5 and 6, a pattern not seen in the Pulali Point specimens. Members of the two genera *Parahexapus* and *Pseudohexapus* possess a ridge that parallels the lateral margin of the carapace, a characteristic not seen in the specimens here referred to *Palaeopinnixa*. In the genus *Tritoplax*, the telson is distinctly trilobed; the telson in the specimens here referred to *Palaeopinnixa* forms an equilateral triangle. The male abdomen in members of the genus *Spiroplax* is very broad and exhibits somewhat convex lateral margins (Manning and Holthuis, 1981:177), while the male abdomen in the specimens described herein is narrow and has concave lateral margins. The sole species of *Spiroplax* has a much more rounded carapace than the new specimens. Additionally, the carapace is equidimensional in *Spiroplax*, while in the new specimens it is about 1.5 times as wide as long. Members of the two genera *Hexapinus* and *Hexaplax* are distinguishable from members of *Palaeopinnixa* because *Palaeopinnixa* has better developed carapace regions and a more rounded carapace.

Palaeopinnixa rathbunae new name
(Fig. 15–17)

Pinnixa eocenica Rathbun, 1926:34, plate 1, fig. 3, 4.
Pinnixa (*Palaeopinnixa*) *eocenica* Rathbun, 1926. Via, 1966:2, fig. 1.

Diagnosis.—Carapace subrectangular, with rounded anterolateral corners; branchial regions moderately well defined; orbits well developed, with sinuous upper margin; rostrum widening anteriorly.

Emendation to Description.—Carapace wider than long (L/W = 68.4%); surface finely granular, granules better developed on posterior of carapace; lateral sides steep; carapace convex longitudinally and weakly vaulted transversely; carapace regions weakly inflated; carapace grooves moderately to weakly developed.

Frontal margin about 0.18 maximum carapace width. Orbits well developed, directed forward, subrectangular in shape; upper margin sinuous, subtly rimmed. Rostrum about as wide as an orbit, subrectangular, widening anteriorly, sulcate medially, anteriormost edge flattened, lateral margins forming inner margins of orbits. Fronto-orbital width about 0.44 maximum carapace width.

Anterolateral margin rounded, continuous with lateral margin, weak ridge sometimes developed along edge of anterolateral and lateral margins, lateral sides steeply rounded, well developed. Posterolateral corners forming concave reentrants into carapace margin. Posterior margin about 0.84 maximum carapace width, very slightly sinuous.

Carapace grooves ranging from moderately defined to poorly defined. Cervical groove extending in broad sinuous U-shape from anterolateral margin posteriorly to axial region, moderately well developed posteriorly and weakly developed anteriorly.

Protogastric region moderately inflated, two small swellings located at base of rostrum; hepatic

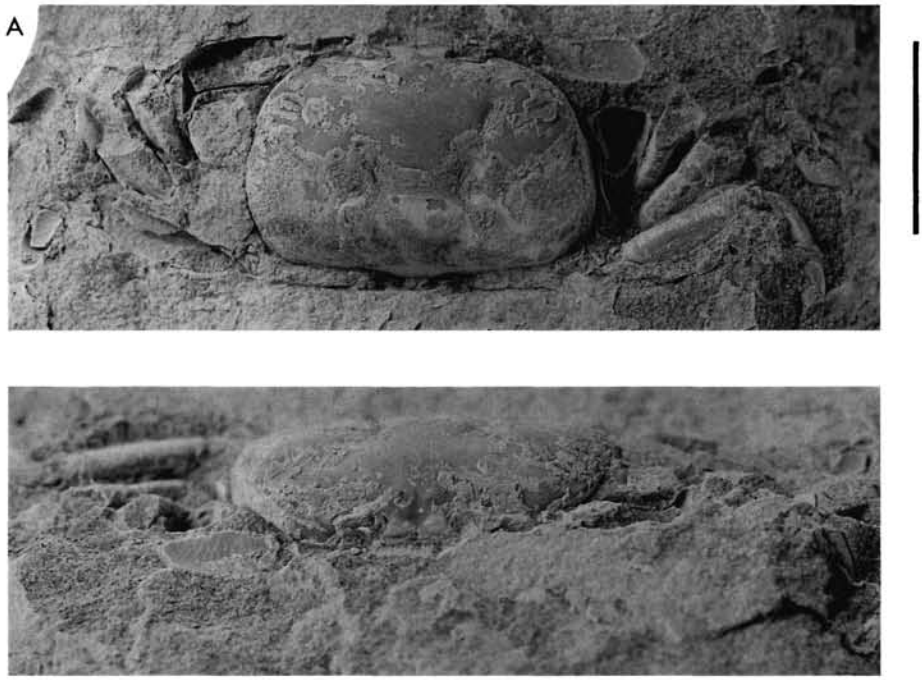


Fig. 15.—*Palaeopinnixa rathbunae* new name, CM 45870. A. Dorsal carapace and appendages. B. Anterior view showing orbits. Scale bar = 1 cm.

region bounded by weakly developed grooves, somewhat flattened; branchial region moderately inflated, surface uneven with localized bulbous swellings, two swellings located on either side of the urogastric and cardiac regions, ornamented with granules, granules especially well developed posteriorly; metabranchial region flattened, not well ornamented, separated from branchial region by groove, groove well defined laterally and disappearing axially, groove extending from lateral margin axially and posteriorly.

Mesogastric region triangular, very narrow anteriorly, widening posteriorly, lateral margins concave, posterior margin convex, bounded by poorly developed grooves, grooves best developed posteriorly, two axial pits located on groove defining posterior margin. Urogastric region wider than long, constricted axially, upper margin concave, lower margin weakly concave, lateral edges bounded by rather deep, broad pits. Cardiac region subtriangular in shape, apex directed posteriorly; possessing three broad, weakly developed granules arranged in a triangular pattern, apex directed posteriorly; region weakly inflated.

Buccal frame rectangular; ischium of endopod of third maxilliped slightly longer than wide, narrowing anteriorly, lateral margins straight, anterior margin slightly convex, posterior margin sinuous; remainder of third maxilliped unknown. Subhepatic and sub-branchial regions finely granular; pterygostomial region finely granular, arcuate ridge paralleling entire length of lower margin, short ridge paralleling adaxial half of upper margin.

Sternum of male wider than long (L/W = 46.7%), semicircular in shape, lateral margins convex, widest at about midlength, narrowing anteriorly and posteriorly. Sternites 1–4 fused; broadly triangular; faint evidence of suture lines, suture between sternites 1 and 2 most distinct; surface finely granular; projection on anterior portion directed anteriorly, appearing to be associated with sternite 2, rounded and approximately equidimensional in shape; lower margin of sternite 4 with episternal projection, first pereiopod associated with sternite 4.

Sternite 5 wider than long, widest of sternites, finely granular, with episternal projections, lengthening laterally, associated with base of pereiopod 2. Sternite 6 wider than long but not as wide as sternite 5, lengthening laterally, with episternal projections, finely granular, associated with base of

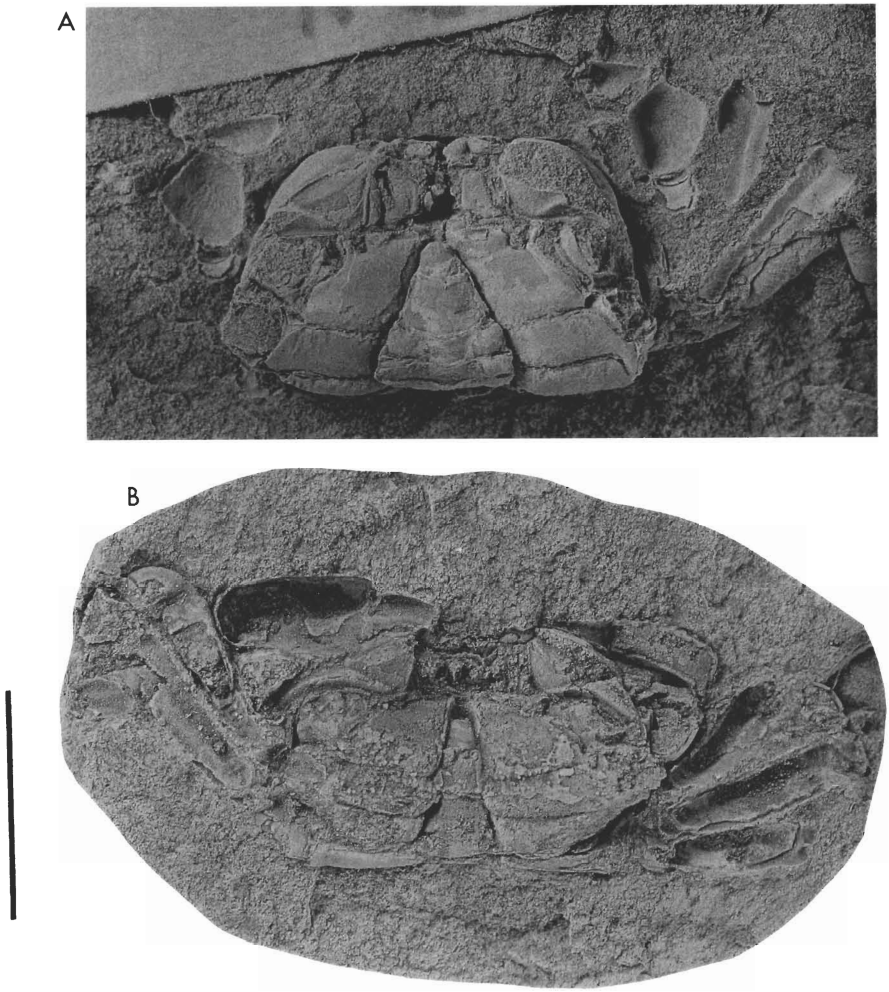


Fig. 16.—*Palaeopinnixa rathbunae*, new name. A. Venter of female, CM 45881. B. Venter of male, CM 45876. Scale bar = 1 cm.

pereiopod 3. Sternite 7 wider than long but not as wide as sternite 6, surface granular, lengthening laterally, associated with base of pereiopod 4. Sternite 8 and pereiopod 5 unknown.

Sternum of female wider than long (L/W = 45.3%); semicircular in shape, lateral margins convex; widening posteriorly, widest at posterior margin of carapace. Sternites 1–4 fused; broadly triangular; faint evidence of suture lines, suture between sternites 1 and 2 most distinct; surface finely granular; two anterior projections, directed anterolaterally, associated with sternites 2 and 3, projection on sternite 2 rounded and equidimensional, projection on sternite 3 longer and narrower; lower margin of sternite 4 with episternal projection, pereiopod 1 associated with sternite 4.

Sternite 5 of female wider than long, finely granular, with episternal projections, lengthening laterally, widest of all sternites, associated with base of pereiopod 2. Sternite 6 wider than long, almost as wide as sternite 5, with episternal projections, surface finely granular, associated with base of pereiopod 3. Sternite 7 wider than long but not as wide as sternite 6, surface finely granular, lengthening laterally, associated with base of pereiopod 4. Sternite 8 and pereiopod 5 unknown.

Abdomen an isosceles triangle in females, 1.2 times as long as wide, about 0.36 maximum width of sternum, straight-sided; telson isosceles triangular, apex appearing to be rounded, telson extending

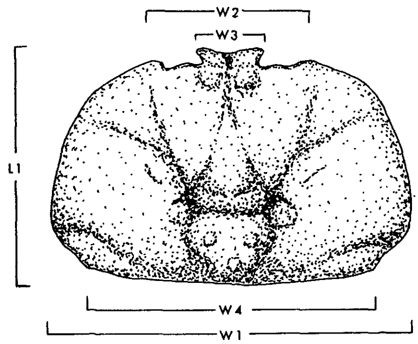


Fig. 17.—Line drawing of *Palaeopinnixa rathbunae*, new name, showing position and orientation of measurements taken.

slightly beyond suture of sternites 1 and 2; somites 5 and 6 fused, widening posteriorly, lateral margins slightly convex, lower margin convex, upper margin concave, about equidimensional when measured at maximum dimensions, possessing broadly rounded medial ridge; somite 4 wider than long, upper margin concave, lower margin convex, lateral margins slightly convex, widening posteriorly; somites 2 and 3 widest of somites; somite 3 much wider than long, upper margin slightly concave, lateral margins nearly straight, lower margin sinuous, widening posteriorly; somite 2 much wider than long, upper and lower margins sinuous, lateral margins weakly convex; somite 1 wider than long, narrowing posteriorly, upper margin sinuous, lower margin sinuous, lateral margins convex, medial swelling and weak lateral swellings; all somites except telson with rounded medial projection on lower margins, also with broad medial swellings and marginal swellings.

Abdomen of male narrowly triangular, approximately 1.65 times as long as wide, about 0.27 maximum sternal width, surface of somites granular, abdomen with weakly concave sides, widening posteriorly. Telson longer than wide, isosceles triangular in shape, apex rounded, extending beyond suture of sternites 1 and 2; somite 6 trapezoidal in shape, longer than wide, upper and lower margins nearly straight, lateral margins slightly concave; somites 3, 4, and 5 fused, fusion lines weakly developed, trapezoidal in shape, upper margin straight, lateral margins sinuous, weak medial swelling posteriorly and somewhat more well- developed lateral swellings posteriorly, lower margin weakly convex; somite 2 wider than long, upper margin weakly concave, lower margin weakly convex, lateral margins rounded, broad, gently swollen area medially; somite 1 poorly known.

Pereiopods ornamented with fine granules. Coxae of pereiopods 2–4 longer than wide, cylindrical. Merus of pereiopod 4 much longer than high, triangular in crosssection, lateral margins slightly sinuous; carpus about as long as high, widening distally, convex upper margin, concave lower margin, distal margin concave; propodus slightly longer than high. Merus of pereiopod 3 much longer than high, triangular in cross section, lateral margins slightly sinuous; carpus about as long as high, widening distally, convex upper margin, concave lower margin, concave distal margin, very short proximal margin. Merus of pereiopod 2 much longer than high, triangular in cross section, lateral margins slightly sinuous; carpus about as long as high, widening distally, convex upper margin, concave lower margin, distal margin concave. Chelipeds appearing to be unequal. Manus of major cheliped stout, longer than high, widening distally, surface finely granular, with sharp spine on lower proximal corner, spine extending posteriorly; carpus of cheliped about equidimensional, stout, bulbous; fingers arched, widest proximally and becoming narrow distally, appearing to possess moderately large denticles on occlusal surface. Manus of minor cheliped about equidimensional; fingers longer than manus, appearing to be finely granular, possessing moderately large denticles on occlusal surfaces; carpus equidimensional, stout, bulbous.

Measurements.—See Table 8 for measurements (in millimeters) taken on the dorsal carapace and Table 9 for measurements taken on the venter of specimens of *Palaeopinnixa rathbunae*. Position and orientation of measurements taken on the dorsal carapace are shown in Figure 17.

Material Examined.—CM 45870–45900, 45903, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, are referrable to this species.

Table 8.—*Measurements taken (in mm) on the dorsal carapace of* Palaeopinnixa rathbunae. *Position and orientation of measurements taken are illustrated in Figure 17. L1 = maximum length, W1 = maximum width, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width.*

Specimen number	L1	W1	W2	W3	W4	L2
CM 45897	11.1	16	9.3	3.6	13.3	10
CM 45899	>7.5	>12.2	—	—	10.2	>7.5
CM 45900	9.8	13.8	6	2.2	—	9
CM 45896	>10.3	15.9	—	—	—	>10.3
CM 45886	>9.0	14.3	—	—	—	>9.0
CM 45874	>11.0	16	—	—	13.9	>11.0
CM 45898	>11.0	15.7	—	—	—	11
CM 45872	8.5	12.7	5.7	—	9.9	8
CM 45888	—	16.4	7	3.2	—	—
CM 45891	>9.0	13.6	—	—	—	>9.0
CM 45870	12.2	16.9	7	3.3	13.8	>10.5
CM 45873	>9.8	>13.5	—	—	10.8	<9.8
CM 45885	8.6	12.9	6.2	1.8	10.4	8.3
CM 45895	>8.3	13.1	5.5	—	—	>8.3
CM 45887	>7.9	11.3	5.8	—	9.5	>7.7
CM 45883	10.3	16	6.7	1.9	12.3	9.7
CM 45884	>9.0	16	7.7	2.6	—	>7.7
CM 45889	10.6	15.9	7	2.5	—	9.7
CM 45871	11.1	16.5	7.5	3	13.6	10
CM 45892	>9.2	14.2	5.3	2.6	—	8.5
CM 45875	9.9	16	6.7	—	12.5	—
CM 45880	>10.0	16	7	—	13.6	>10.0
CM 45881	—	16.8	6.9	3.1	—	—
CM 45894	6.5	10	4.5	—	7.6	—
CM 45903	7.1	10.4	5	2.8	8	—
CSH 37	6.7	9.4	4.7	—	—	—
CSH 38	6.3	8.9	—	—	—	—
CSH 39	4	5.4	—	—	—	—

Two specimens, CM 45872 and CM 45873 were collected at the Pulali Point locality. Several of the specimens, CM 45871, 45876, 45877, 45879–81, 45883, 45887–89, 45891–93, 45896–99, and 45900 were collected from the Eocene Hoko River Formation at the RB32 locality of Berglund, located in the SW1/4, NW1/4, Sec. 4, T33N, R15W, Cape Flattery Quadrangle, Clallam County, Washington, 7.5 minute series, near Neah Bay. CM 45870, 45874, 45875, and 45878 were collected from the RB33 locality of Berglund, located in the W1/2, N1/4, Sec. 4, T33N, R15W, Cape Flattery Quadrangle, 15 minute series, near west Kydikabbit. CM 45884 and 45885 were collected from the RB31 locality of Berglund located in the E1/2, Sec. 4, T33N, R15W, Cape Flattery Quadrangle, Clallam County, Washington, in the intertidal zone west of Kydikabbit, Washington. CM 45882, 45894, and 45895 were collected from an unknown locality. CM 45890 and 45886 were reported as having been collected from the RB29 locality of Berglund; however, details are not available.

Table 9.—*Measurements (in mm) taken on the venters of* Palaeopinnixa rathbunae. *W1 = maximum width of sternum, L1 = maximum length of sternum, W2 = maximum width of abdomen, L2 = maximum length of abdomen.*

Specimen number	W1	L1	W2	L2	Sex
CSH 27	14.9	6.7	—	—	Female?
CSH 29	13.5	5.8	3.6	5.4	Male
CSH 30	14.7	7.4	3.9	7.0	Male
CSH 31	18.1	8.0	6.4	7.5	Female
CSH 28	16.1	7.5	5.9	7.3	Female

Remarks.—*Palaeopinnixa rathbunae* may be distinguished from other members of the genus in several ways. *Palaeopinnixa eocenica* possesses small orbits that are directly slightly axially; the orbits of *P. rathbunae* are larger and are directed forward. The front in *P. eocenica* is more narrow and less flared than that of *P. rathbunae*. The carapace regions of *P. eocenica* are poorly marked; in *P. rathbunae* the carapace regions are weakly but noticeably defined. *Palaeopinnixa eocenica* has a much more rounded carapace and more rounded lateral margins than does *P. rathbunae*, which has a more rectangular carapace. *Palaeopinnixa intermedia* Collins and Morris from the Miocene of Trinidad possesses a more rectangular carapace, straighter lateral margins, and narrower mesogastric, urogastric, and cardiac regions than does *P. rathbunae*. *Palaeopinnixa prima* Rathbun from the Oligocene of Panama possesses less clearly defined carapace regions than does *P. rathbunae*. *Palaeopinnixa prima* has a very sharp anterolateral margin and steep to slightly concave lateral sides, while *P. rathbunae* lacks a sharp anterolateral margin and has more rounded, slightly convex lateral sides. The metabranchial region in *P. rathbunae* is much more depressed and more clearly defined than that of *P. prima*. The lateral margins of the carapace of *Palaeopinnixa rocaensis* Feldmann et al., from the earliest Paleocene of Argentina, are much less rounded than those of *P. rathbunae*, which are markedly convex. Additionally, *P. rocaensis* achieves its maximum width at approximately the midlength; *P. rathbunae* reaches its maximum width about three-quarters the distance posteriorly on the carapace.

Although all of the specimens may be assigned to *Palaeopinnixa rathbunae*, there is a range of morphological variation in several aspects of the dorsal carapace. Development of the carapace grooves varies among specimens. Those specimens that appear to have well-developed grooves also are molds of the interior, suggesting that this apparent difference in development may be related to manner of preservation. The ridge paralleling the anterolateral and lateral margins is well developed in some specimens such as CM 45875 and absent in others such as CM 45870. This may be due to abrasion before or during burial, weathering of the specimen at surface conditions, or variation within the population. In the case of CM 45870, the carapace is badly weathered, perhaps accounting for the absence of the ridge. Ornamentation of the dorsal carapace is also variable, again probably due to both variation in the population and to weathering and abrasion of the specimens. Most of the specimens appear to be highly weathered and retain no ornamentation. Those that retain cuticle range from being finely granular to punctate. CM 45872 is finely granular on the posterior portion of the carapace, and CM 45870 possesses fine granules on the branchial region. While these ranges in variation exist, there seems to be no pattern in the variation and the magnitude of the variations is not sufficient to warrant removal of any of the specimens from this taxon.

Many of the specimens possess asymmetrical bulbous swellings on the dorsal carapace. In some specimens, the bulbous areas of the epibranchial regions are more well developed than in others. These swellings could be attributed to several factors. One is infestation by bopyrid isopods (Glaessner, 1969; Hessler, 1969; Overstreet, 1983), which could explain some of the asymmetries. Other cases can probably be explained by deformation or weak crushing of the carapace so as to slightly deform it.

The overwhelming majority of specimens possess some portions of the appendages suggesting that most of the specimens are corpses and that the animals were living near the site of deposition or were buried rapidly. The excellent preservation of some of the carapace material and appendages also supports this interpretation. However, the deformation of some of the carapaces suggests at the very least the material was crushed by compaction of the sediment.

Interestingly, there is a difference in the shape of the sterna of males and females as well as the typical differences in the shape of the abdomina. The sternum of the male is semicircular in shape and widest at the midlength while that of the female is widest at the posterior margin of the carapace. The sternites also appear to be wider in the females than in the males because more of the sternites are visible in ventral view in females than in males. In both males and females sternite 5 is widest and the sternum extends to the base of the buccal frame.

DISCUSSION

While an in-depth analysis of the biogeography of these decapods is premature, some overall patterns are clear. Most of the genera herein reported from the Pulali Point locality are well known and commonly reported from Tertiary rocks of the west coast of North America, including *Macroacaena*, *Laeviranina*, *Raninoides*, *Portunites*, *Pulalius*, *Branchioplax*, and *Neopilumnoplax*. *Carpilius* and *Palaeopinnixa* are the only genera that have not previously been reported from the west coast of North America.

Several members of the decapod fauna recovered from Pulali Point are known only from the Northern Hemisphere. Members of the genus *Macroacaena* have been reported from the Cretaceous and the Paleocene of Greenland and Japan, and the Eocene and Oligocene of Oregon and Washington (Tucker, 1995). *Portunites* has been reported from England, Europe, Japan, and the west coast of North America (Schweitzer and Feldmann, 1999), and *Pulalius* is known only from the west coast of North America. *Branchioplax* has been reported from western North America, Japan, and Europe (Karasawa, 1992) with a (very) questionable occurrence from Senegal (Remy and Tessier, 1954). These genera may have either a Tethyan or a north Polar distribution; Karasawa (1992) suggested that both *Portunites* and *Branchioplax* have a Tethyan distribution.

The closely related genera *Laeviranina* and *Raninoides* each have widespread distributions. *Laeviranina* is known only from fossil occurrences and has been reported from Europe, South America, North America, New Zealand, and Pakistan (Tucker, 1995). *Raninoides*, which ranges from the Eocene to the Recent, has a cosmopolitan range having been reported from the Atlantic, Pacific, and Indian oceans and the Caribbean and Central America. The oldest occurrence of *Laeviranina* is from the Paleocene of Alabama and Greenland, and the earliest report of *Raninoides* is from Eocene rocks of Japan (Tucker, 1995).

Carpilius has been reported from the fossil record in Japan and from the Pulali Point locality. However, the occurrence in Japan is based only upon a portion of a manus (Karasawa, 1993), so its use in biogeographic analysis awaits more complete material. The genus is currently known from the Indo-Pacific region and from the western Atlantic and Caribbean. *Neopilumnoplax* is known from the fossil record only on the west coast of North America and is currently found in the Indo- Pacific region, a similar biogeographic pattern to that of *Carpilius*.

The genus *Palaeopinnixa* has previously been reported from Eocene rocks of Panama, Peru, Trinidad, and the Paleocene of Argentina, and from Miocene rocks of Spain (Rathbun, 1918; Woods, 1922; Rathbun, 1926; Via, 1966; Collins and Morris, 1976; Feldmann et al., 1995). The first occurrence of the genus is in Paleocene rocks of Argentina, and the genus appears to have subsequently dispersed northward into the western Pacific Ocean during the Eocene and into the northeastern Atlantic Ocean by the Miocene.

ACKNOWLEDGMENTS

The specimens that formed the basis of this study were collected by R. and M. Berglund, J. and G. Goedert, G. Dunham, B. Buchanan, and A. Tucker. H. Schasse, of the Washington Division of Geology and Earth Sciences, originally discovered the crab concretions at the Pulali Point, Washington, locality and notified K. Kaler, who referred the material to R. Berglund. Mr. and Mrs. G. Dunham of Brinnon, Washington, kindly allowed access to the Pulali Point locality via their private property. W. Rau provided micropaleontological data. Type material was examined at The Natural History Museum, London, with the assistance of A. Ross and at the Sedgwick Museum in Cambridge with the assistance of M. Dorling and R. Long. M. Dorling of the Sedgwick Museum, Cambridge University; W. Blow, United States National Museum, Washington, D.C.; W. Orr, Condon Museum of Geology, University of Oregon; and J. Carter, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, all kindly loaned comparative material for this study. R. B. Manning provided access to specimens at the United States National Museum and offered numerous useful comments on the systematics of the taxa discussed in this paper. H. Karasawa, Mizunami Fossil Museum, Mizunami, Japan, and H. Kato, Natural History Museum and Institute, Chiba, Japan, provided access to material at their respective institutions. Travel for examination of Japanese fossil material and specimens deposited in museums in the United Kingdom was funded by National Geographic Society Grant 6265-98 to Feldmann and Schweitzer.

LITERATURE CITED

ARMENTROUT, J. M. 1987. Cenozoic stratigraphy, unconformity-bounded sequences, and tectonic history of southwestern Washington. Pp. 291–320, *in* Selected Papers on the Geology of Washington (J. E. Schuster, ed.). Washington Division of Geology and Earth Resources Bulletin 77.

ARMENTROUT, J. M., AND A. BERTA. 1977. Eocene–Oligocene foraminiferal sequence from the northeast Olympic Peninsula, Washington. Journal of Foraminiferal Research, 7:216–233.

BABCOCK, R. S., C. A. SUCZEK, AND D. C. ENGEBRETSON. 1994. The Crescent "terrane," Olympic Peninsula and southern Vancouver Island. Washington Division of Geology and Earth Resources, 80:141–157.

BELL, T. 1858. A Monograph of the Fossil Malacostracous Crustacea of Great Britain, Part 1, Crustacea of the London Clay. Palaeontological Society, London, United Kingdom.

BENNETT, E. W. 1964. The marine fauna of New Zealand: Crustacea Brachyura. (New Zealand Oceanographic Institute, Memoir 22.) New Zealand Department of Scientific and Industrial Research Bulletin, 153:1–119.

BESCHIN, C., A. BUSULINI, A. DE ANGELI, AND G. TESSIER. 1994. I crostacei Eocenici della cava "Boschetto" di nogarole Vicentino. Lavori, Società Venziana de Scienze Naturali, 19:159–215.

BITTNER, A. 1893. Decapoden des pannonischen Tertiärs. Sitzungberichte der Kaiserlichen Akademie der Wissenschaften Wien, Abteilung I, 102:10–37.

BLOW, W. C., AND R. B. MANNING. 1996. Preliminary descriptions of 25 new decapod crustaceans from the middle Eocene of the Carolinas, U.S.A. Tulane Studies in Geology and Paleontology, 29:1–25.

CARTER, J. 1898. A contribution to the palaeontology of the decapod Crustacea of England. Quarterly Journal of the Geological Society of London, 54:15–44.

COLLINS, J. S. H., AND S. F. MORRIS. 1976. Tertiary and Pleistocene crabs from Barbados and Trinidad. Palaeontology, 19:107–131.

———. 1978. New lower Tertiary crabs from Pakistan. Palaeontology, 21:957–982.

COLLINS, J. S. H., AND H. W. RASMUSSEN. 1992. Upper Cretaceous–Lower Tertiary decapod crustaceans from west Greenland. Grønlands Geologiske Unders gelse Bulletin, 162:1–46.

CRANE, M. D. 1981. Hexapod crabs of the genus *Goniocypoda* H. Woodward from the upper Eocene of Hampshire. Zoological Journal of the Linnean Society, 72:1–19.

CRANE, M. D., AND J. QUAYLE. 1986. Two new hexapod crabs of the genus *Goniocypoda* Woodward (Crustacea, Decapoda) from the Hampshire Basin. Tertiary Research, 7:101–105.

DAI, A., AND S. YANG. 1991. Crabs of the China Seas. China Ocean Press, Beijing, Peoples' Republic of China.

DANA, J. D. 1851. Conspectus Crustaceorum quae in Orbis Terrarum Circumnavigatione, Carolo Eilkes e Classe Riepublicae faederate Duce, Lexit et Descripsit. Proceedings of the Academy of Natural Sciences of Philadelphia, 5:247–254.

DE HAAN, W. 1833–1849. *Crustacea.* Pp. 109–164, *in* Fauna Japonica 4, XVII, XXXI (P. F. de Siebold). J. Muller, Amsterdam, The Netherlands.

DESMAREST, A. G. 1823. Malacostracés. Dictionnaire des sciences naturelles, 28:138–425.

FELDMANN, R. M. 1989. *Lyreidus alseanus* Rathbun from the Paleogene of Washington and Oregon, USA. Annals of Carnegie Museum, 58:61–70.

———. 1991. Decapod Crustacea from the Tapui Glauconitic Sandstone (Bartonian: middle Eocene) in the Waitaki Valley, South Island, New Zealand. New Zealand Journal of Geology and Geophysics, 34:17–22.

———. 1992. The genus *Lyreidus* de Haan, 1839 (Crustacea, Decapoda, Raninidae): Systematics and biogeography. Journal of Paleontology, 66:943–957.

FELDMANN, R. M., A. B. TUCKER, AND R. E. BERGLUND. 1991. Paleobathymetry of decapod crustaceans, Washington. National Geographic Research and Exploration, 7:352–363.

FELDMANN, R. M., S. CASADÍO, L. CHIRINO-GALVEZ, AND M. AGUIRRE-URRETA. 1995. Fossil decapod crustaceans from the Jaguel and Roca formations (Maastrichtian–Danian) of the Neuquén Basin, Argentina. Paleontological Society Memoir 43.

FELDMANN, R. M., K. L. BICE, C. S. HOPKINS, E. W. SALVA, AND K. PICKFORD. 1998. Decapod crustaceans from the Eocene Castle Hayne Limestone, North Carolina: Paleoceanographic implications. The Paleontological Society Memoir, 48:1–28.

FÖRSTER, R., AND R. MUNDLOS. 1982. Krebse aus dem Alttertiär von Helmstedt und Handorf (Niedersachsen). Palaeontographica, Abteilung A, 179:148–184.

GLAESSNER, M. F. 1928. Die dekapodenfauna des Österreichischen Jungtertiärs. Jahrbuch Geologischen Bundesanstalt Wien, 78:161–219.

———. 1929. Crustacea Decapoda. Pp. 1–464, *in* Fossilium Catalogus I: Animalia, Part 41 (J. F. Pompeckj, ed.). W. Junk, Berlin, Germany.

———. 1933. New Tertiary crabs in the collection of the British Museum. Annals and Magazine of Natural History, Series 10, 12:1–28.

———. 1960. The fossil decapod Crustacea of New Zealand and the evolution of the Order Decapoda. New Zealand Departent of Scientific and Industrial Research, New Zealand Geological Survey, Palaeontological Bulletin, 31:5–79.

———. 1969. Decapoda. Pp. R400–R566, *in* Treatise on Invertebrate Paleontology, Part R, Arthropoda 4 (R. C. Moore, ed.). Geological Society of America and University of Kansas Press, Lawrence, Kansas.

GLAESSNER, M. F., AND T. H. WITHERS. 1931. On London Clay crabs of the family Raninidae. Annals and Magazine of Natural History, London, 8:484–493.

GORDON, I. 1971. On the thoracic sternum in the subfamily Hexapodinae (Brachyura, Goneplacidae). Crustaceana, 21:106–110.

GUINOT, D. 1969. Recherches préliminaires sur les groupements naturels chez les crustacés décapodes brachyoures. VII. Les Goneplacidae. Bulletin du Muséum National d'Histoire Naturelle, 2 Série, 41:507–528.

———. 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. Compte Rendu Académie des Science de Paris, Série D, 285:1049–1052.

———. 1978. Principes d'une classification évolutive des crustacé décapodes brachyoures. Bulletin Biologique de la France et de la Belgique, 112:209–292.

———. 1993. Données nouvelles sur les Raninoidea de Haan, 1841 (Crustacea Decapoda Brachyura Podotremata). Compte Rendu, Academie Science Paris, Sciences de la vie/Life Sciences, 316: 1324–1331.

HESSLER, R. R. 1969. Peracarida. Pp. R360–R393, *in* Treatise on Invertebrate Paleontology, Part R, Arthropoda 4 (R. C. Moore, ed.). Geological Society of America and University of Kansas Press, Lawrence, Kansas.

IMAIZUMI, R. 1959. A fossil crab, *Hexapus nakajimai* n. sp. from Joban coal field. Recent Progress of Natural Science (Japan), 30:25–30.

JELETZKY, J. A. 1973. Age and depositional environment of the lower part of the Escalante Formation, western Vancouver Island, British Columbia (92-E): Mollusks, versus foraminifers. Canadian Journal of Earth Sciences, 10:331–365.

KARASAWA, H. 1992. Fossil decapod crustaceans from the Manda Group (middle Eocene), Kyushu, Japan. Transactions and Proceedings of the Palaeontological Society of Japan, New Series, 167: 1247–1258.

———. 1993. Cenozoic decapod Crustacea from southwest Japan. Bulletin of the Mizunami Fossil Museum, 20:1–92.

LATREILLE, P. A. 1802–1803. Histoire naturelle, générale et particulière, des crustacés et des insectes, Volume 3. F. Dufart, Paris, France.

———. 1825. Histoire naturelle, générale et particulière, des Crustacés et des Insectes. Ouvrage faisant suite aux ouvres de Leclerc de Buffon, et partie du cours complet d'Histoire naturelle rédigé par C. S. Sonnini, membre de plusiers sociétés savants, Volume VI. F. Dufart, Paris, France.

LEACH, W. E. 1823. Pp. 139–425, *in Malacostracés*: Dictionnaire des Sciences Naturelles, Volume 28 (A. G. Desmarest, ed.). F. G. Levreault, Paris, France.

LINNAEUS, C. VON. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis: edition 10, volume 1, Laurentii Salvii (Homiae).

LÖRENTHEY, E. 1897. Beiträge zur Decapodenfauna des ungarischen Tertiär. Természetrajzi-Füzetek, 21:1–133.

LÖRENTHEY, E., AND K. BEURLEN. 1929. Die fossilen decapoden der länder der Ungarischen Krone. Geologica Hungarica, Series Palaeontologica, Fasciculus 3.

MACLEAY, W. S. 1838. Illustrations of the Annulosa of South Africa. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith, Pp. 53–71, *in* Illustrations of the Zoology of South Africa, Invertebrates (A. Smith, ed.). Smith, Elder, and Company, London, United Kingdom.

MANNING, R. B., AND L. B. HOLTHUIS. 1981. West African brachyuran crabs (Crustacea: Decapoda). Smithsonian Contributions to Zoology, 306:1–379.

MCCOY, F. 1849. On the classification of some British fossil Crustacea, with notices of the new forms in the University Collection at Cambridge. Annals and Magazine of Natural History, Second Series, 4:161–179.

MIERS, E. J. 1886. Report of the Brachyura collected by H. M. S. Challenger during the years 1873–76. Pp. 1–362, *in* Report of the Scientific Results of the Voyage of H. M. S. Challenger during the Years 1873–76 (C. W. Thomson and J. Murray, eds.). Zoology, Johnson Reprints, New York, New York.

MILNE EDWARDS, A. 1862–1865. Monographie des crustacés de la famille cancériens. Annals des Sciences Naturelles, Zoologie, Series 4, 18(1862):31–85; 20(1863):273–324; Series 5, 1(1864): 31–88; 3(1865):297–351.

MILNE EDWARDS, H. 1837. Histoire naturelle des crustacés comprenant l'anatomie, la physiologie, et la classification des animaux, 2:1–532. Paris, France.

MORRIS, S. F., AND J. S. H. COLLINS. 1991. Neogene crabs from Brunei, Sabah, and Sarawak. Bulletin of the British Museum of Natural History (Geology), 47:1–33.

MÜLLER, P. 1984. Decapod crustacea of the Badenian. Institutum Geologicicum Hungaricum, Geologica Hungarica, Series Palaeontologica, Fasciculus 42.

ORTMANN, A. E. 1893. Die decapoden–krebse des Strassburger Museums. 7. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) 2. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Zoologischen Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, 7:411–495.

OVERSTREET, R. M. 1983. Metazoan symbionts of crustaceans. Pp. 156–250, *in* The Biology of Crustacea, Volume 6, Pathobiology (A. J. Provenzano, Jr., ed.). Academic Press, New York, New York.

PROTHERO, D. R., AND J. M. ARMENTROUT. 1985. Magnetostratigraphic correlation of the Lincoln Creek Formation, Washington: Implications for the age of the Eocene/Oligocene Boundary. Geology, 13:208–211.

QUAYLE, W. J., AND J. S. H. COLLINS. 1981. New Eocene crabs from the Hampshire Basin. Palaeontology, 24:733–758.

RAFINESQUE, C. S. 1815. Analyse de la nature, ou tableau de l'Universe et des corps organisée. Palermo, Italy.

RATHBUN, M. J. 1916. Description of a new genus and species of fossil crab from Port Townsend, Washington. American Journal of Science, 41:344–346.

———. 1918. Contributions to the geology and paleontology of the Canal Zone, Panama, and geologically related areas in Central America and the West Indies. Decapod crustaceans from the Panama region. United States National Museum Bulletin 103:123–184.

———. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America. United States National Museum Bulletin 138.

———. 1929. A new crab from the Eocene of Florida. Proceedings of the United States National Museum, 73:1–6.

———. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. United State National Museum Bulletin 152.

———. 1932. New species of fossil Raninidae from Oregon. Journal of the Washington Academy of Science, 22:239–242.

RAU, W. W. 1964. Foraminifera from the Olympic Peninsula, Washington. Geological Survey Professional Paper 374-G.

REMY, J. M., AND F. TESSIER. 1954. Décapodes nouveaux de la partie ouest du Sénégal. Bulletin de la Societé Geologique de France, Series 6, 4:185–191.

SAKAI, T. 1976. Crabs of Japan and the Adjacent Seas. Kodansha Ltd., Tokyo, Japan.

SCHWEITZER, C. E., AND R. M. FELDMANN. 1999. Fossil decapod crustaceans of the late Oligocene to early Miocene Pysht Formation and the late Eocene Quimper Sandstone, Olympic Peninsula, Washington. Annals of Carnegie Museum, 68:215–273.

SECRÉTAN, S. 1971. La fauna de Crustacés décapodes des calcaires à Alvéolines Yprésiens des Corbieres septentrionales (Aude). Geobios, 4:117–141.

SNAVELY, P. D., JR. 1987. Tertiary geologic framework, neotectonics, and petroleum potential of the Oregon–Washington margin. Pp. 305–335, *in* Geology and Resources Potential of the Continental Margin of Western North America and Adjacent Ocean Basins—Beaufort Sea to Baja California (D. W. Scholl, A. Grantz, and J. G. Vedder, eds.). Circum-Pacific Council for Energy and Mineral Resources, Earth Science Series Volume 6.

SNAVELY, P. D., JR., A. R. NIEM, N. S. MACLEOD, J. E. PEARL, AND W. W. RAU. 1980. Makah Formation—A deep marginal basin sequence of late Eocene and Oligocene age in the northwestern Olympic Peninsula, Washington. Geological Survey Professional Paper 1162-B.

SQUIRES, R. L., J. L. GOEDERT, AND K. L. KALER. 1992. Paleontology and stratigraphy of Eocene rocks at Pulali Point, Jefferson County, eastern Olympic Peninsula, Washington. Washington Division of Geology and Earth Resources Report of Investigations 31.

TUCKER, A. B. 1995. A systematic evaluation of fossil Raninidae from the Twin River Group, Olympic Peninsula, Washington, and a re-examination of the Raninidae. Unpublished Ph.D. Dissert., Kent State University, Kent, Ohio.

———. 1998. Systematics of the Raninidae (Crustacea: Decapoda: Brachyura), with accounts of three new genera and two new species. Proceedings of the Biological Society of Washington, 111:320–371.

TUCKER, A. B., AND R. M. FELDMANN. 1990. Fossil decapod crustaceans from the lower Tertiary of the Prince William Sound region, Gulf of Alaska. Journal of Paleontology, 64:409–427.

TUCKER, A. B., R. E. BERGLUND, AND R. M. FELDMANN. 1994. Deep-water decapod crustaceans from the Aldwell Formation (middle Eocene) at Pulali Point, Jefferson County, Washington. Abstracts with Program of the Geological Society of America Annual Meeting, 7A-56.

TUCKER, A. B., R. M. FELDMANN, AND C. L. POWELL II. 1994. *Speocarcinus berglundi* n. sp. (Decapoda: Brachyura), a new crab from the Imperial Formation (late Miocene–late Pliocene) of southern California. Journal of Paleontology, 68:800–807.

VIA, L. 1959. Decápodos fósiles del Eoceno español. Boletin Instituto Geologico y Minero de España, 70:333–395.

———. 1965. Raninidos fósiles del Eoceno. Contributión al estudio paleontológico de la familia "Raninidae" (Crustaceós decápodos). Boletin Instituto Geologico y Minero de España, 76:233–275.

———. 1966. *Pinnixa (Palaeopinnixa) mytilicola*, nuevo braquiuro fósil, en el mioceno marino del Vallés (Barcelona). Acta Geologica Hispanica, 1:1–4.

———. 1969. Crustáceos decápodos del Eoceno Español. Pirineos, 91–94:1–479.

WILLIAMS, A. B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast. Smithsonian Institution Press, Washington, D.C.

WOODS, H. 1922. Crustacea from the Eocene deposits of Peru. Pp. 114–118, *in* Geology of the Tertiary and Quaternary Periods in the North-west Part of Peru (T. O. Bosworth, ed.). Macmillan and Co., London, United Kingdom.

WOODWARD, H. 1867. On a new genus of shore-crab, *Goniocypoda edwardsi* from the lower Eocene of Hampshire. Geological Magazine, 4:529–531.