

## ADDITIONS TO THE TERTIARY DECAPOD FAUNA OF THE PACIFIC NORTHWEST OF NORTH AMERICA

Carrie E. Schweitzer

Department of Geology, Kent State University, Kent, Ohio 44242 (e-mail: cschweitzer@stark.kent.edu)

### A B S T R A C T

Previously undescribed fossil material from the late Eocene Hoko River Formation and the Oligocene Makah Formation, Olympic Peninsula, Washington, provides new insight into the evolution and biogeography of five families of decapod crustaceans. New taxa include *Homola van-couverensis*, *Xeinostoma? antiqua*, and *Daldorfia himaleorhaphis*. New material makes it possible to provide a complete reconstruction of the dorsal carapace of *Macrocheira teglandi*, and a possible juvenile *Branchioplax washingtoniana* is described for the first time. The range of the genus *Homola*, known in modern oceans, has been extended into the late Early Cretaceous, and the occurrence of that genus in rocks of the Pacific coast of North America marks the first authentic report of the Homolidae from that region. The Cyclodorippidae is now known to have inhabited the Pacific coast of North America as early as the late Eocene. The geologic range of the genus *Daldorfia* now extends into the Oligocene, and its earliest known occurrence is from rocks of Washington, U.S.A.

The Tertiary decapod fauna of the Pacific Northwest of North America was originally studied in the early part of this century (Rathbun, 1926, among others), and numerous reevaluations and new occurrences have been reported recently by, among others: Berglund, Goedert, Feldmann, Schweitzer, Squires, and Tucker. The most abundant decapod taxa, in terms of numbers of individuals and species, belong to the Ctenochelidae Manning and Felder, Raninidae de Haan, Calappidae de Haan, Cancridae Latreille, Portunidae Rafinesque, Xanthoidea Macleay, and Goneplacidae Macleay (Rathbun, 1926; Tucker and Feldmann, 1990; Feldmann, Tucker, and Berglund, 1991; Berglund and Goedert, 1992, 1996; Tucker, 1998; Schweitzer and Feldmann, 1999, 2000a, b, c, in press; Schweitzer, 2000; Schweitzer *et al.*, 2000). Other families that have been described from that region, from less abundant material, include the Callianassidae Dana *sensu lato*, Albuneidae Stimpson, Majidae Samouelle, Atelecyclidae Ortmann, Cheiragonidae Ortmann, Hexapodidae Miers, and Pinnotheridae de Haan (Rathbun, 1926; Schweitzer and Feldmann, 1999; Schweitzer and Salva, 2000; Schweitzer and Boyko, 2000; Schweitzer and Feldmann, in press).

In the course of a major revision and

reevaluation of the decapod fauna of the Pacific coast of North America, three taxa, from the Homolidae de Haan, Cyclodorippidae Ortmann, and Daldorfiidae Rathbun, were discovered, each represented by single specimens. In addition, these three taxa, all of which are new species, represent the earliest authentic occurrences of these families in the Tertiary of the Pacific Northwest. The small number of individuals assignable to these three taxa suggests that they probably comprised a small percentage of the decapod fauna in their respective environments, because all three were recovered from localities that have been well collected by both amateurs and professionals over several decades. Other taxa are much more numerous at these localities, including the goneplacids, raninids, portunids, and ctenochelids, which apparently comprised much of the decapod fauna of these areas.

In addition to the new family records, a nearly complete reconstruction of the dorsal carapace of *Macrocheira teglandi* is now possible based upon new material. A possible juvenile *Branchioplax washingtoniana* is described and illustrated with the hope that recovery of more material makes it possible to provide a growth series for *B. washingtoniana* such as was provided for several species of *Carcinoplax* by Guinot (1989).

## SYSTEMATIC PALEONTOLOGY

## Superfamily Homoloidea de Haan, 1839

## Family Homolidae de Haan, 1839

*Discussion.*—Members of the Homolidae are characterized by possession of distinctive *lineae homolicae* paralleling the lateral margins of the carapace; deeply incised, distinctive, cervical and branchiocardiac grooves; an elongate, rectangular carapace; poorly defined orbits; spined margins; and well-ornamented dorsal carapaces. Both the biological and geological record of the family have received comprehensive treatment, resulting in evaluation of all known fossil and Recent species (Guinot and Richer de Forges, 1995; Collins, 1997).

Recognition of a new species of *Homola* from Washington, U.S.A., to be described below, constitutes the first verifiable occurrence of the family on the west coast of North America and also comprises the first confirmed occurrence of the genus *Homola* in the fossil record. Two taxa from the Pacific Northwest of North America have previously been assigned to the Homolidae, including the Oligocene *Palehomola gorrelli* Rathbun, 1926, from Oregon and *Homolopsis richardsoni* Woodward, 1896, from the Cretaceous of British Columbia (Rathbun, 1926). Examination of the holotype of *P. gorrelli* (USNM 352912) indicates that it is probably not a member of the family due to the lack of the *lineae homolicae* on the carapace, possession of which is diagnostic for the Homolidae. Illustrations of *H. richardsoni* (Collins, 1997, fig. 8) show no evidence of the *lineae homolicae*, but examination of type material of this species will be necessary to confirm this observation. Lack of *lineae homolicae* would preclude placement of either taxon within the Homolidae. Further, Collins (1997) placed *H. richardsoni* within *Palehomola*. Although neither *P. gorrelli* nor *H. richardsoni* appear to possess the *lineae homolicae*, the two do not appear to be congeneric. The front of *H. richardsoni* is much narrower than that of *P. gorrelli*, and the metabranchial regions of *P. gorrelli* are much more inflated and broader than those of *H. richardsoni*. The carapace of *H. richardsoni* is much more elongate than that of *P. gorrelli*. However, evaluation of the family placement of those two taxa is beyond the scope of this paper.

Genus *Homola* Leach, 1815

*Homola* Leach, 1815, p. 324. See Guinot and Richer de Forges (1995) for complete synonymy.

*Homolopsis* Bell, 1863, p. 28, pl. 5, figs. 1, 2 (part); Rathbun, 1917, p. 388, pl. 33, figs. 1–3; Mertin, 1941, p. 239, pl. 8, figs. 1, 2; Roberts, 1962, p. 179, 180, pl. 89, figs. 4, 5; Takeda and Fujiyama, 1983, p. 131, fig. 2, pl. 1, fig. 4, pl. 2, figs. 5–8; Bishop, 1992, p. 56, figs. 1–5.

*Hoplitocarcinus* Beurlen, 1928, p. 154; Collins, 1997, p. 61, fig. 5.

*Latheticocarcinus* Bishop, 1988, p. 378, fig. 1E–H, J, M. *Eohomola* Collins and Rasmussen, 1992, p. 16, fig. 8; Collins, Kanie, and Karasawa, 1993, p. 298; Jakobsen and Collins, 1997, p. 94, pl. 1, figs. 2–4, 6; Collins, 1997, p. 60, fig. 4.

*Metahomola* Collins and Rasmussen, 1992, p. 18. Collins, Kanie, and Karasawa, 1993, p. 297, fig. 2.2, 2.3.

*Type Species.*—*Homola spinifrons* Leach, 1815, by monotypy.

*Included Species.*—*Homola adelphina* (Collins and Rasmussen, 1992), new combination, as *Eohomola*; *H. affinis* (Jakobsen and Collins, 1997), new combination, as *Eohomola*; *H. atlantica* (Roberts, 1962), new combination, as *Homolopsis*; *H. barbata* (Fabricius, 1793); *H. brevis* (Collins, Kanie, and Karasawa, 1993), new combination, as *Metahomola*; *H. centurialis* (Bishop, 1992), new combination, as *Homolopsis*; *H. coriolisi* Guinot and Richer de Forges, 1995; *H. dickinsoni* Eldredge, 1980; *H. dispar* (Roberts, 1962), new combination, as *Homolopsis*; *H. eldredgei* Guinot and Richer de Forges, 1995; *H. gibbosus* (Schlüter, 1879); *H. ikedai* Sakai, 1979; *H. mieensis* Sakai, 1979; *H. minima* Guinot and Richer de Forges, 1995; *H. orientalis* Henderson, 1888; *H. punctata* (Rathbun, 1917), new combination, as *Homolopsis*; *H. ranunculus* Guinot and Richer de Forges, 1995; *H. shapiro* (Bishop, 1988), new combination, as *Latheticocarcinus*; *H. spinifrons*; *H. vigil* A. Milne Edwards, 1880.

*Diagnosis.*—Carapace elongate, rectangular; pterygostomial region usually at right angles to the dorsal carapace but sometimes partially visible dorsally; *lineae homolicae* distinct; rostrum distinctly bifid or separated into two tiny spines at tip; cervical and branchiocardiac grooves distinct; anterolateral spine long, attenuated, directed forward; epibranchial and mesobranchial regions elongate, swollen; carapace ornamented with inflated swellings or spines.

*Discussion.*—Guinot and Richer de Forges (1995) evaluated all of the modern species

and genera assigned to the Homolidae. Diagnostic features of *Homola* that are commonly preserved in fossils include a flattened or slightly vaulted carapace that is elongate and rectangular in shape; extra-lineal portions of the carapace usually perpendicular to dorsal carapace; one, or rarely two, long anterolateral spines; a rostrum that is clearly bifid or separated into two tiny spinelets only at the tip; a cervical groove beginning just anterior to the anterolateral spine; and a prominent branchiocardiac groove. Members of *Homola* lack true orbits (Guinot and Richer de Forges, 1995: 319, 320). Further, Guinot and Richer de Forges (1995: 325) noted that species assigned to *Homola* are separable into two groups based upon the nature of the rostrum, which can be either distinctly bifid or divided into two tiny spines at the tip (p. 323). They did not refer any fossil taxa to *Homola* but mentioned a report of *Homola* sp. from the west coast of North America (Feldmann *et al.*, 1991; Guinot and Richer de Forges, 1995: 316). Collins (1997) placed this species from the west coast of North America within *Homola* with reservation.

In 1992, Collins and Rasmussen erected two new genera, *Eohomola* and *Metahomola*. Subsequently, Collins (1997) recognized that *Metahomola* was a junior synonym of *Hoplitocarcinus* Beurlen (1928) and referred several species to that genus, including *H. atlanticus* (Roberts, 1962); *H. brevis* (Collins, Kanie, and Karasawa, 1992); *H. centurialis* (Bishop, 1992); *H. gibbosus* (Schlüter, 1879); *H. punctatus* (Rathbun, 1917); and *H. shapiro* (Bishop, 1988). Collins (1997) placed *Latheticocarcinus shapiro*, the sole species of the genus, within *Hoplitocarcinus*, making *Latheticocarcinus* a junior synonym of *Hoplitocarcinus*. The synonymy herein of *Hoplitocarcinus* with *Homola* makes *Latheticocarcinus* a junior synonym of *Homola*. Collins (1997) also referred several taxa to *Eohomola*, including *E. adelphina* Collins and Rasmussen, 1992; *E. dispar* (Roberts, 1962); and *E. affinis* Jakobsen and Collins, 1996.

Examination of species of *Homola*, *Eohomola*, and *Hoplitocarcinus* indicates that the three genera are synonymous. Collins and Rasmussen (1992) recognized the close relationship of *Homola* to *Eohomola* and *Metahomola* (= *Hoplitocarcinus*) but argued that

the fossil taxa should remain separate from the then exclusively Recent *Homola* because of the lack of information on the internal and reproductive structures in the fossil taxa. Guinot and Richer de Forges (1995) recognized the strong morphologic similarity among species assigned to *Eohomola* and two Recent species of *Homola*, *H. barbata* and *H. minima*.

In fact, there are no distinct differences between the three genera. The two fossil genera possess all of the diagnostic characters for the genus as defined by Guinot and Richer de Forges (1995) including an elongate, rectangular carapace; poorly defined orbits; strongly developed cervical and branchiocardiac grooves; extra-lineal regions that are usually at right angles to the dorsal carapace; clearly defined *lineae homolicae*; long, attenuated anterolateral spines that project forward; and a well-ornamented dorsal carapace. Additionally, the shape of the epibranchial and mesobranchial regions is elongate and inflated in members of all three genera. Species of all three genera display transverse ridges extending onto the metabranchial region from the cardiac region. Finally, Recent members of *Homola* possess either a distinctly bifid rostrum or a rostrum that is bifid just at the tips. *Eohomola* was defined as possessing a bifid rostrum, and *Hoplitocarcinus* was defined as possessing a singular rostrum. Because this is the only character that separates these two genera, and because they possess all of the diagnostic characters of *Homola*, which can embrace both rostral types, the three genera are herein synonymized.

Several of the taxa now assigned to *Homola* were previously referred to other genera, including *Homolopsis*. However, several species remain within *Homolopsis*, and it is in fact a distinct genus. *Homola* is easily distinguished from the fossil genus *Homolopsis* based upon several criteria. The regions of *Homola* are inflated, whereas those of *Homolopsis* are flattened. In *Homolopsis*, the hepatic region is only partially differentiated from the protogastric region by a deeply incised groove, whereas in *Homola*, the hepatic region is a broadly inflated area. The epigastric and mesogastric regions of *Homola* are linear and inflated, whereas those of *Homolopsis* are spherical or ovate and less inflated. Species of *Homola* possess a narrow,

attenuated anterolateral spine that is directed forward, whereas species of *Homolopsis* possess a short, stout anterolateral spine that is directed laterally. The epibranchial region projects laterally in *Homolopsis* and is the point of maximum width of the carapace, whereas in *Homola* the epibranchial region does not project laterally and the maximum width occurs either at the epibranchial or metabranchial region. *Homolopsis* lacks the metabranchial ridges extending from the cardiac region that characterize *Homola*. The extra-lineal regions of *Homolopsis* are located dorsally, whereas in *Homola*, they are usually positioned vertically and at right angles to the dorsal carapace. *Homolopsis* is therefore a distinct form that is easily distinguished from *Homola*.

Included within *Homola* are all those Recent species assigned to the genus by Guinot and Richer de Forges (1995) and the taxa assigned to *Eohomola* and *Hoplitocarcinus* by Collins (1997). *Homola brevis* (Collins, Kanie, and Karasawa, 1993) is the earliest known member of *Homola*, reported from Turonian rocks of Japan. Tucker *et al.* (1987) referred several specimens recovered from the late Cretaceous of North Dakota to *Homolopsis punctata* Rathbun and synonymized *Homolopsis punctata* and *Homolopsis dispar* Roberts. Examination of the figures of the North Dakota material indicates that the specimens are not in fact referable to *Homolopsis punctata*. Further, *Homolopsis punctata* and *Homolopsis dispar* are not synonymous and are therefore each referred to *Homola* and retained as separate species.

The synonymy of *Homola*, *Eohomola*, and *Hoplitocarcinus* extends the range of *Homola*, heretofore only questionably known in the fossil record from the Eocene, to the Turonian. Early Campanian species have been reported from the Western Interior of the United States (*H. centurialis*) (Bishop, 1992) and the Atlantic Coast of the United States (*H. atlanticus* and *H. dispar*) (Roberts, 1962). *Homola adelphina* and *H. punctata* have been reported from late Campanian to Maastrichtian rocks of Greenland and the Western Interior of the United States respectively. Tertiary species of *Homola* include *H. affinis* from Danian rocks of Greenland (Jakobsen and Collins, 1997) and the new species herein reported from Eocene rocks of Washington, U.S.A. The genus has a cosmopolitan distri-

bution in modern oceans (Guinot and Richer de Forges, 1995).

*Homola* appears to have evolved in the northwestern Pacific during the early Cretaceous and subsequently dispersed either eastward to North America via ocean currents or westward to Europe via the Tethys. The genus appears to have flourished in the Western Interior of the United States and the northern Atlantic region during the Cretaceous, and could easily have reached Denmark by Danian time via ocean currents in the North Atlantic Ocean. The occurrence of the genus in Eocene rocks of Washington is somewhat more difficult to explain. There are few Cretaceous exposures along the northeastern rim of the Pacific Ocean and, therefore, there are few Cretaceous decapods known from that region. It is possible that the genus was in fact present along the Pacific Rim; however, no fossil evidence has yet been found to support this assertion. Because of the widespread occurrence of the genus in the Northern Hemisphere by the late Cretaceous, it seems probable that the genus had a broad geographic range early in its history and has retained that broad distribution into the Recent where it is cosmopolitan. Clearly, this taxon was unaffected by the late Cretaceous extinction event(s). Another brachyuran taxon, *Necrocarcinus* Bell, 1863, has a similar distribution pattern as *Homola*. *Necrocarcinus* apparently evolved in Japan during the Aptian and subsequently dispersed to Europe, the Western Interior of North America, and Antarctica during the Cretaceous and to Eocene localities in Europe and the Pacific Northwest of North America (Schweitzer and Feldmann, 2000a). This suggests that Japan may have been an area of origin for brachyuran taxa during the Cretaceous and that those taxa subsequently dispersed to other localities via several dispersal routes. Unfortunately, the lack of Cretaceous exposures in relevant areas makes it difficult to test this hypothesis.

One other homolid genus has previously been reported from the North Pacific rim, *Prohomola* Karasawa, 1992, erected to accommodate *Homolopsis japonicus* (Yokoyama, 1911). Species of *Prohomola* share many features with species of *Homola*, including a similar shape and arrangement of the axial and branchial regions, but differ from species of *Homola* in several regards. The most striking difference is the narrow

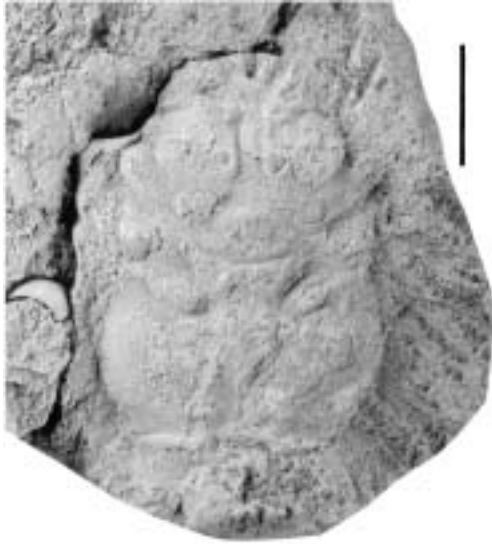


Fig. 1. *Homola vancouverensis*, new species, dorsal carapace of holotype, USNM 508588. Scale bar equal to 1 cm.

frontal margin and the two prominent spines on either side of the rostrum which are directed anterolaterally in *Prohomola*. No other homolid genus has such ornamentation on the frontal margin of the carapace, which easily distinguishes *Prohomola* from all other homolid genera.

***Homola vancouverensis*, new species**

Figs. 1, 2

*Homola* sp. Feldmann, Tucker, and Berglund, 1991, p. 360; Guinot and Richer de Forges, 1995, p. 316.

*Homola?* sp. Collins, 1997, p. 53.

*Types*.—The holotype and sole specimen, USNM 508588, is deposited in the United States National Museum of Natural History, Washington, D.C.

*Diagnosis*.—Carapace much longer than wide; regions well defined by deep grooves; pterygostomial regions vertical, at right angles to dorsal carapace; rostrum bifid, rostral spines long, separated to bases; metabranchial regions inflated, lateral margins convex.

*Etymology*.—The trivial name, suggested by Annette B. Tucker, Aurora, Ohio, is taken from Vancouver Island, the location from which the sediments comprising the Hoko River Formation are thought to have been derived.

*Description*.—Carapace much longer than wide,  $L/W = 1.40$ , rectangular in outline, widest at about the midlength of metabranchial

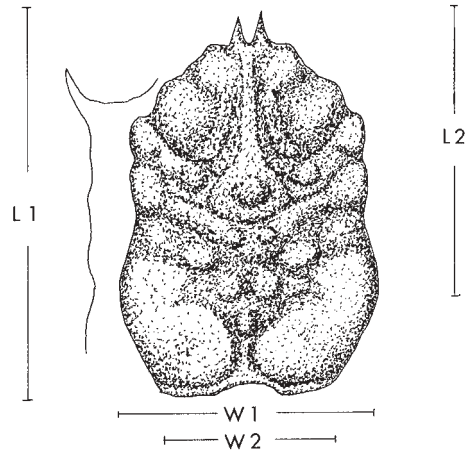


Fig. 2. Line drawing of *Homola vancouverensis*, illustrating position and orientation of measurements taken. Outline of position of detached pterygostomial region shown on left side of carapace.

region; regions well defined by broad, deep grooves; regions ornamented with fine tubercles and large inflated nodes; carapace weakly vaulted transversely, strongly vaulted longitudinally near anterior margin; *lineae homolicae* distinct.

Rostrum bifid, composed of two sharp spines separated to bases. Orbits not well defined, with blunt, central protuberance. Remainder of anterolateral margin short, sinuous. Lateral and posterolateral margins continuous, sinuous, defined by *lineae homolicae*. Posterior margin nearly straight laterally and concave centrally, rimmed, posterior width about 75 percent maximum carapace width. Cervical and branchiocardiac grooves deeply incised.

Protogastric region large, inflated; with several large swellings, ridge-like swelling parallel to inner margin of region, large central swelling, broad swelling near base of orbits. Mesogastric region with long, slender anterior process, process terminating just posterior to rostrum; posterior portion of region triangular, with large central swelling, posterior margin of region convex. Urogastric region widest anteriorly, narrowed posteriorly, bounded on anterior margin by cervical groove and posteriorly by branchiocardiac groove, with two central tubercles. Cardiac region triangular, apex directed posteriorly, with two swollen tubercles anteriorly and one posteriorly; bounded by deep grooves. Intestinal region depressed, narrow.

Hepatic region narrow, rectangular, directed anterolaterally, with two broad swellings, one axial and one on lateral margin. Epibranchial region small, triangular, swollen, with large central tubercle. Mesobranchial region small, ovate, with central oblong swollen ridge. Metabranial region large, lateral margins convex, inflated anteriorly, with spherical swelling posteriorly.

Pterygostomial region not well known, with long, attenuated spine anteriorly, appearing to have been vertical and at right angles to dorsal carapace.

*Measurements.*—Measurements (in mm) taken on the holotype: maximum width (W1) = 18.7, maximum length (L1) = 26.2, posterior width (W2) = 13.9, length to point of maximum width (L2) = 20.0. Position and orientation of measurements taken are illustrated in Fig. 2.

*Occurrence.*—The specimen was recovered from the late Eocene Hoko River Formation, several hundred meters inland from the south shore of the Strait of Juan de Fuca near Neah Bay, in the SW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Sec. 4, T33N, R15W, Cape Flattery Quadrangle, Clallam County, Washington, 7.5' series. This is locality RB32 of Ross E. Berglund, Bainbridge Island, Washington.

*Discussion.*—The sole specimen is preserved in a concretion and retains the dorsal carapace and the left extra-lineal region; the outline and position of the extra-lineal region is illustrated in Fig. 2. The extra-lineal region is separated from the carapace, which probably occurred during burial and diagenesis. It appears to have been positioned vertically, at right angles to the dorsal carapace, before the separation. The venter and appendages are unknown.

*Homola vancouverensis* differs from all other species of *Homola* in possessing a strongly bifid rostrum composed of two sharp, distinct spines separated to their bases and a convex, inflated metabranial region. Other species referred to *Homola* either have rostra that are bifid only at the tips or bifid rostra that are composed of spines that are neither as long nor as well separated as those of *H. vancouverensis*. Further, other species of *Homola* have metabranial regions with lateral margins that are nearly straight, whereas those of *H. vancouverensis* are markedly convex.

The occurrence of *Homola vancouverensis* in Eocene rocks of Washington constitutes the first notice of the genus and the family on the Pacific rim of North America but does not extend the geologic range of either.

#### Superfamily Cyclodorippoidea Ortmann, 1892

Family Cyclodorippidae Ortmann, 1892  
Subfamily Xeinostominae Tavares, 1992b

*Diagnosis.*—Carapace obovate or rectangular; moderately vaulted longitudinally and transversely. Rostrum medially sulcate; bifid, trifid, or triangular. Orbits well developed, with broad, well-developed rim; often with orbital spines and fissures. Frontal region flattened; protogastric region broad; mesogastric region not extending to rostrum; epibranchial region widened and inflated laterally; mesobranchial region widened and inflated axially; cardiac region obovate; intestinal region poorly developed or absent; posterior margin concave.

*Discussion.*—Tavares (1991) recognized that the Cyclodorippidae Alcock, 1896, was a senior synonym for the Tymolidae and provided a detailed study of the group (Tavares, 1993). The diagnosis for the Cyclodorippidae provided here is based upon those characters that are commonly preserved in fossil specimens. The specimen here referred to *Xeinostoma? antiqua* n. sp. displays all of the diagnostic characters for the family and is referred to that family with confidence. However, the generic designation is provisional, because the rostrum and orbits are broken or missing on the fossil specimen. The specimen was assigned to the genus within the family embracing the most similar species to the new material in lieu of creating a new genus based upon incomplete material; therefore, more and better preserved material will be necessary to confirm this generic assignment.

Glaessner (1969) assigned several fossil taxa, including *Binkhorstia* Noetling, 1881; *Doratiopus* Woods, 1953; *Falconoplax* Van Straelen, 1933; *Torynomma* Woods, 1953; and *Tymolus* Stimpson, 1858, to the Tymolinae (= Cyclodorippidae) of the Dorippidae Macleay, 1838. The Cretaceous *Torynomma* was subsequently placed within the Torynommatidae Glaessner, 1980, along with *Eodorippe* Glaessner, 1980. Glaessner (1980) placed the Torynommatidae within the Cyclodorip-



Fig. 3. *Xeinostoma? antiqua*, new species, dorsal carapace of holotype, USNM 508589. Scale bar equal to 1 cm.

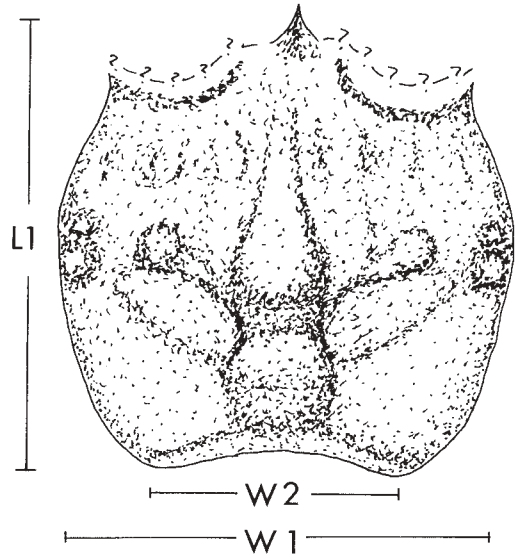


Fig. 4. Line drawing of *Xeinostoma? antiqua*, illustrating position and orientation of measurements taken.

poidea and suggested that the Tornyommatidae may be an ancestral family within the group. *Falconoplax* was removed to the Goneplacidae (Tavares, 1992a). The remaining two genera that Glaessner placed within the Tymolinae, *Binkhorstia* and *Doratiopus*, have not been evaluated here. *Binkhorstia* was placed within the Carcineretidae (Collins *et al.*, 1995); however, that genus is probably not a member of that family because it lacks diagnostic transverse carapace ridges, has a more equilateral carapace shape, and has a narrower rostrum than typical carcineretids (Feldmann, personal communication). The Cyclodorippidae, therefore, has a limited fossil record, consisting until now only of *Tymolus*, reported from the Miocene of Japan (Karasawa, 1993) and the Pacific Northwest of the United States (R. E. Berglund, personal communication). This report of a new species of the Cyclodorippidae extends the known geologic range of the family to the Eocene, suggesting that the family evolved in the North Pacific Ocean.

Genus *Xeinostoma* Stebbing, 1920  
*Xeinostoma? antiqua*, new species  
 Figs. 3, 4

*Types*.—The holotype and sole specimen, USNM 508589, is deposited in the United

States National Museum of Natural History, Washington, D.C.

*Diagnosis*.—Carapace about as long as wide, widest at position of lateral nodes, about one-third the distance posteriorly on carapace; rostrum deeply sulcate medially, appearing to be triangular; orbits with broad rims; lateral margins with two nodes located about one-third the distance posteriorly on carapace; protogastric region with longitudinally inflated areas; epigastric region with large swelling laterally; mesogastric region narrowed laterally.

*Etymology*.—The trivial name is derived from the Latin root “antiquus,” meaning old, recognizing this occurrence as the oldest for the genus.

*Description*.—Carapace ovate, about as long as wide,  $L/W = 1.04$ , widest at position of lateral nodes; regions weakly inflated, defined by narrow grooves; carapace surface finely and densely granular; vaulted transversely and longitudinally.

Rostrum downturned, medially sulcate, appearing to be triangular. Orbits not completely known, broadly rimmed. Anterolateral and posterolateral margins continuous, two large nodes positioned about one-third the distance posteriorly on carapace; lateral margins convex anteriorly and nearly straight posteriorly.

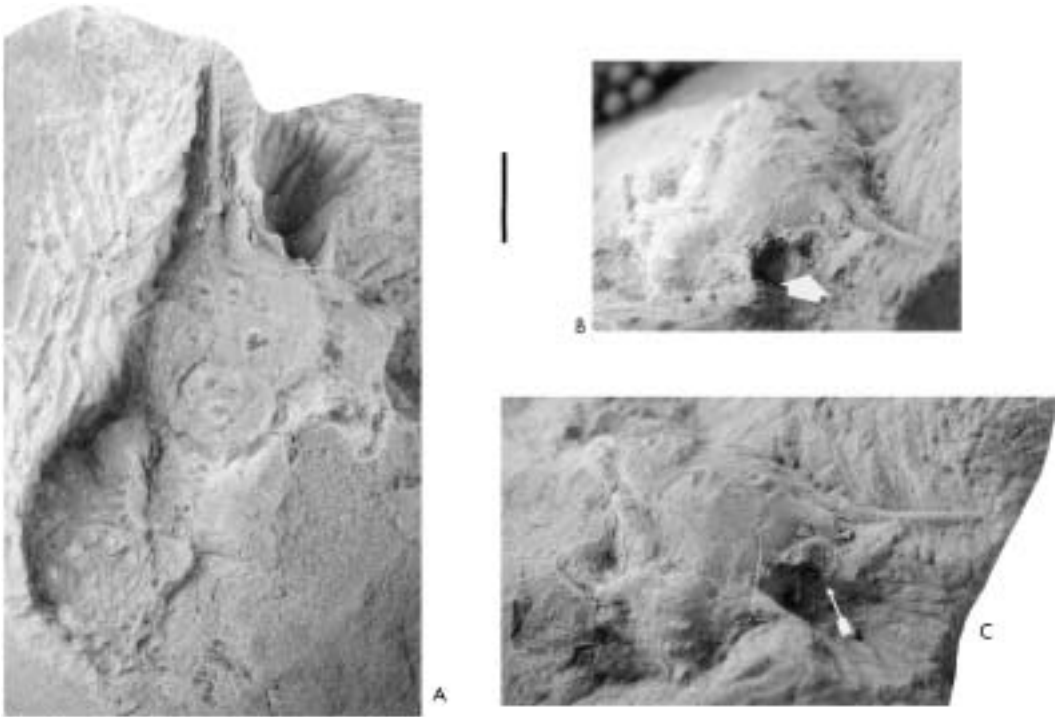


Fig. 5. *Macrocheira teglandi* (Rathbun, 1926), USNM 508590. A, dorsal carapace; B, oblique frontal view of front and rostrum showing orbit, indicated by arrow; C, lateral view showing orbit, indicated by arrow. Scale bar equal to 1 cm.

Posterior margin concave, rimmed, posterior width about 68 percent maximum carapace width. Frontal region just posterior to rostrum and orbits flattened. Protogastric and hepatic regions continuous, with three longitudinal swellings. Mesogastric region with narrow anterior process, anterior process narrowing anteriorly, terminating before reaching rostrum; posterior portion of region inflated, with convex posterior margin. Urogastric region depressed, laterally constricted. Cardiac region obovate, narrowing distally, inflated anteriorly.

Epibranchial region oriented about 60 degrees to axis, widened with spherical swelling laterally and narrowed and flattened axially. Mesogastric region widened axially and narrowed distally, weakly inflated. Metabranchial region weakly inflated axially, inflation continuous with inflation of anterior portion of cardiac region.

Lateral sides steep. Venter and appendages unknown.

*Measurements.*—Measurements (in mm) taken on the sole specimen of *Xeinostoma?*

*antiqua*: maximum width (W1) = 4.4, maximum length (L1) = 4.6, posterior width (W2) = 3.0. The position and orientation of measurements taken are illustrated in Fig. 4.

*Occurrence.*—The specimen was collected from the RB32 locality of Berglund, described above.

*Discussion.*—The specimen is herein referred to *Xeinostoma* based upon the obovate carapace shape, which achieves its maximum width about one-third the distance posteriorly on the carapace; the moderately concave, rimmed posterior margin; the shape and ornamentation of the carapace regions; and the deeply sulcate triangular shape of the rostrum. All of these characters are shared among Recent members of *Xeinostoma* and *X.?* *antiqua*. *Xeinostoma?* *antiqua* differs from other members of the genus in possessing large, lateral nodes and an inflated spherical swelling on the epibranchial region. However, these differences are not considered to be sufficient to create a new genus.

The specimen was preserved in a concretion along with a second decapod specimen



and a gastropod. The small size of *Xeinostoma? antiqua*, which is slightly smaller than the average size for the genus, may account for the lack of specimens that have been recovered. The locality from which the specimen was collected has yielded hundreds of specimens of a wide variety of decapod taxa. *Xeinostoma? antiqua* is much smaller than these other taxa, often by several orders of magnitude, which could easily explain its being overlooked by collectors.

Superfamily Majoidea Samouelle, 1819  
 Family Majidae Samouelle, 1819  
 Subfamily Inachinae Alcock, 1895  
 Genus *Macrocheira* de Haan, 1839  
*Macrocheira teglandi* Rathbun, 1926  
 Figs. 5, 6

*Macrocheira teglandi* Rathbun, 1926, p. 148, fig. 6;  
 Schweitzer and Feldmann, 1999, p. 249, figs. 10, 11.

**Material Examined.**—The specimen, USNM 508590, is deposited in the United States National Museum of Natural History, Washington, D.C.

**Emendation to Diagnosis.**—Rostrum bifid, elongate, rostral elements tubular; orbits large, with ocular eave and preorbital, intercalated, and postorbital spines; anterolateral spine blunt, triangular.

**Emendation to Description.**—Rostrum bifid, elongate, rostral elements tubular, parallel basally and diverging distally, tips of elements unknown. Orbits large, directed slightly anterolaterally; ocular eave narrow, rimmed, situated at base of rostrum, terminating distally in short, triangular spine, spine directed anterolaterally; intercalated spine small, triangular, directed anterolaterally; postorbital spine long, sharp, directed anterolaterally at steeper angle than preorbital spine and intercalated spine.

Protogastric region inflated, ornamented with about three large tubercles; mesogastric region circular posteriorly and elongate anteriorly, anterior projection very weakly defined. Anterolateral spine blunt, triangular, directed anterolaterally at about 45 degree angle.

**Measurements.**—Measurements (in mm) taken on the dorsal carapace: frontal width (measured just anterior to preorbital spine) = 10.0, fronto-orbital width = 27.2.

**Occurrence.**—The sole specimen was recovered from the Jansen Creek Member of the

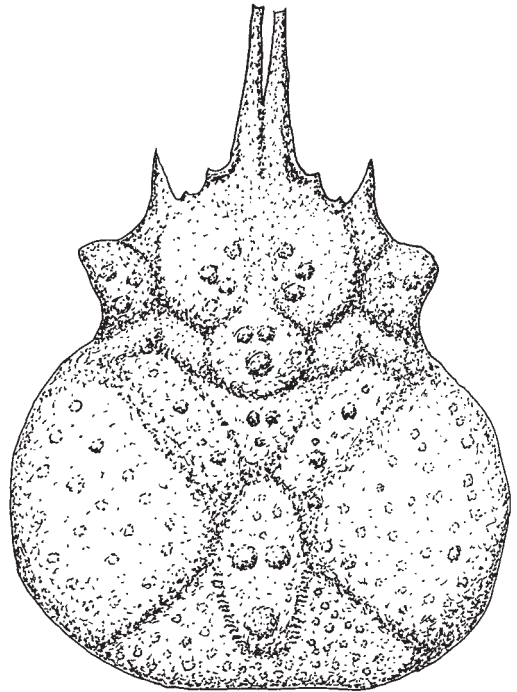


Fig. 6. Line drawing of *Macrocheira teglandi* illustrating position and orientation of measurements taken. Posterior portion of carapace modified from Schweitzer and Feldmann (1999).

Oligocene Makah Formation, exposed on the Olympic Peninsula, Washington, at the mouth of Jansen Creek in the SE  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Sec. 26, T33N, R14W, Clallam Bay Quadrangle, Clallam County, Washington, 7.5' series. This is locality RB19 of Ross Berglund.

**Discussion.**—The new specimen permits a detailed description of the rostrum and orbits of *Macrocheira teglandi* that has not been possible before. Previous illustrations have been of incomplete material, none of which has a well-preserved front (Rathbun, 1926; Schweitzer and Feldmann, 1999). Schweitzer and Feldmann (1999) provided an emendation to the description of the posterior portion of the dorsal carapace of *M. teglandi* based upon material collected from the late Oligocene to early Miocene Pysht Formation. The reconstruction of the entire dorsal carapace provided here (Fig. 6) is based upon the drawing from Schweitzer and Feldmann (1999) and the new material.

One other species of *Macrocheira* is known from the Tertiary of western North America, *M. longirostra* Schweitzer and Feldmann,

1999, from the Eocene Quimper Sandstone. Schweitzer and Feldmann (1999) differentiated *M. longirostra* from *M. teglandi* based upon the long rostrum, dense ornamentation, and larger tubercles of *M. longirostra*. In addition, *M. teglandi* has much smaller orbital spines than does *M. longirostra*, and the orbital and anterolateral spines of *M. longirostra* are much sharper and more attenuated than those of *M. teglandi*. The occurrence of *M. teglandi* in Oligocene rocks of the Makah Formation extends the range of the species into the middle Oligocene but does not substantially enlarge the geographic distribution.

Superfamily Parthenopoidea Macleay, 1838  
 Family Daldorfiidae Rathbun, 1904  
 Genus *Daldorfia* Rathbun, 1904

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

*Discussion*.—The Daldorfiidae are typified by possession of a pyriform dorsal carapace, well-defined carapace regions, a simple rostrum, a heavily ornamented carapace, branchial regions that project markedly laterally, and long or stout chelipeds. The family is not well represented in the fossil record, and many of the reports are based upon portions of the appendages. Karasawa and Kato (1996) summarized the occurrences of the Parthenopidae *sensu lato* in the fossil record. Several parthenopoids have been previously reported from the fossil record of the Pacific coast of North America, but none can accommodate the new taxon. Rathbun (1926) reported *Mesorhoea idae* Rathbun, 1926, and *Heterocrypta occidentalis* Dana, 1854, from portions of the pereopods only, but neither taxon can accommodate the stout, heavily ornamented pereopods of the new species of *Daldorfia* described herein. Other fossil occurrences of *Mesorhoea* are only from pereopod fragments (Glaessner, 1969).

Karasawa and Kato (1996) described *Daldorfia nagashimai* from upper Miocene to lower Pliocene rocks of Japan. The new taxon from Washington is clearly congeneric with *D. nagashimai*. The two taxa have a similar shape and arrangement of axial and branchial regions; coarse, dense ornamentation; laterally projecting branchial regions, and heavily ornamented first pereopods. Karasawa and Kato (1996) reported that the rostrum was triangular, but examination of illustrations of

*D. nagashimai* (fig. 2, p. 46) suggests that the front is broken and that it in fact may be blunt and nearly straight such as in the new species from Washington. The two taxa are best placed within *Daldorfia*, although there are some differences between the fossil taxa and the Recent species. Recent species of *Daldorfia* have a broadly triangular front that is deeply sulcate axially, which both the fossil taxa lack. The margins of Recent *Daldorfia* are not as heavily ornamented as those of the fossil species. The mesobranchial region of Recent *Daldorfia* has a triangular marginal projection, whereas the two fossil species have nearly straight fronts that are not deeply sulcate. The area surrounding the urogastric region of *Daldorfia* is deeply sulcate, whereas that of the fossil species is not markedly sulcate. The epibranchial region of Recent *Daldorfia* is spherical and does not extend to the axial regions, whereas that of the two fossil species is elongate and borders the urogastric region. In all other respects, the two fossil species resemble Recent species of *Daldorfia*. Furthermore, genera within the Parthenopoidea are quite variable in ornamentation, the shape and arrangement of the branchial regions, and the shape of the front, so that the range of variation exhibited by the fossil species is consistent with that of taxa within the superfamily.

Rathbun (1926) described several crabs of the Majidae, which superficially resemble the parthenopoids in shape and ornamentation. The new fossil material is easily excluded from those taxa. *Macrocheira teglandi*, discussed above, has much finer ornamentation and does not have the laterally elongated branchial regions typical of parthenopoids. *Loxorynchus grandis* Stimpson, 1859, from Pliocene-Pleistocene rocks of California (Rathbun, 1926), has a heavily ornamented carapace but lacks the well-differentiated carapace regions and laterally elongate branchial regions of parthenopoids.

*Daldorfia himaleorhaphis*, new species  
 Figs. 7, 8

*Types*.—The holotype and sole specimen, USNM 508591, is deposited in the United States National Museum of Natural History, Washington, D.C.

*Diagnosis*.—Carapace wider than long, L/W about 0.65, widest at midlength of meso-

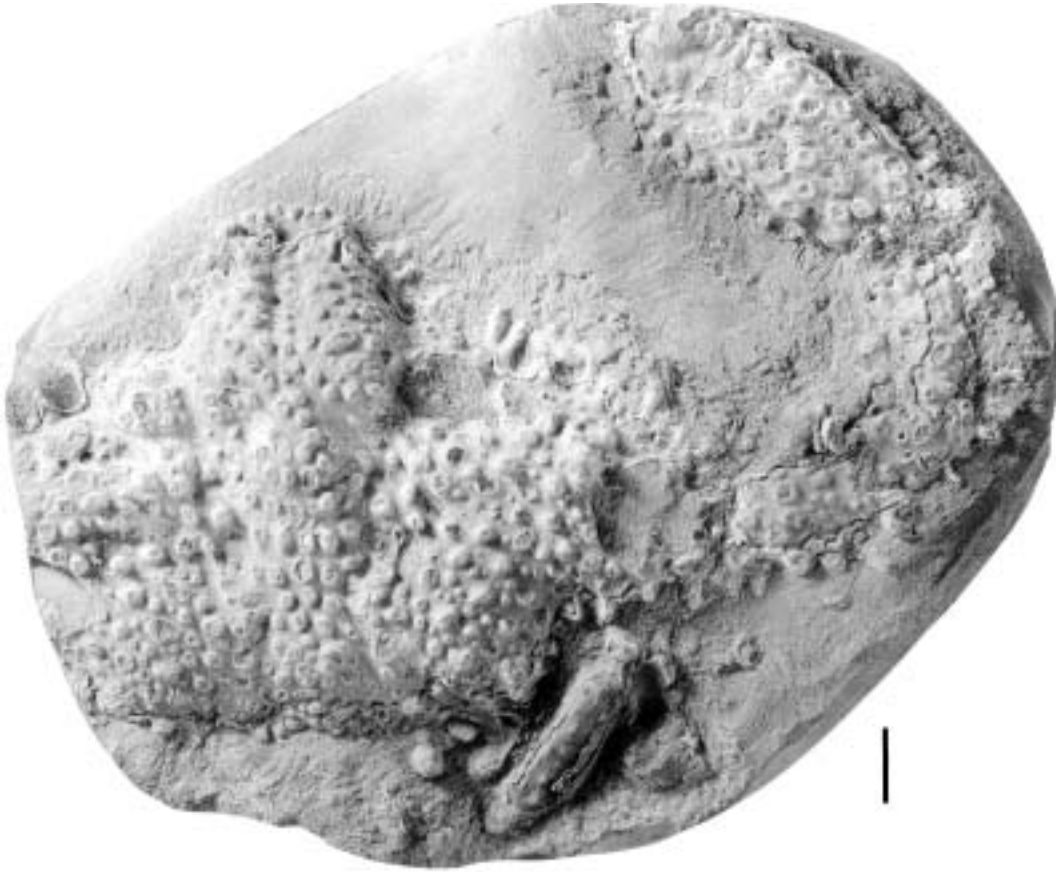


Fig. 7. *Daldorfia himaleorhaphis*, new species, dorsal carapace of holotype, USNM 508591. Scale bar equal to 1 cm.

branchial region; carapace densely ornamented with tubercles of varying sizes; front broad, nearly straight, ornamented with several large tubercles; anterolateral and lateral margins ornamented with sharp, needle-like spines; branchial regions projecting laterally, well differentiated; first pereiopods ornamented with numerous sharp spines and granules.

*Etymology.*—The trivial name is derived from the Greek roots “himaleos,” meaning abundant, and “rhapsis,” meaning needle, in reference to the numerous needle-like spines on the anterolateral and lateral margins of the carapace.

*Description.*—Carapace wider than long, L/W about 0.65, widest about two-thirds the distance posteriorly on carapace at the mid-length of the mesobranchial region; moderately vaulted longitudinally and transversely; carapace regions well defined by broad

grooves; carapace surface heavily ornamented with tubercles of varying sizes.

Front broad, nearly straight, with about four large marginal tubercles, slightly downturned, axially sulcate, about 16 percent max-

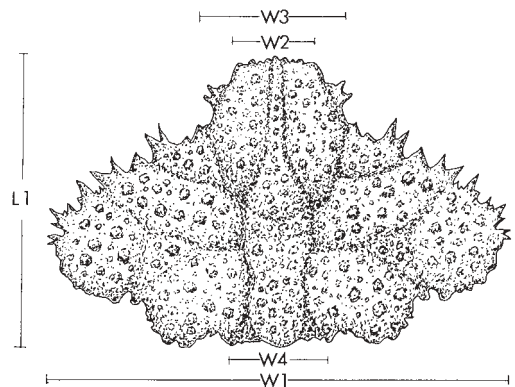


Fig. 8. Line drawing of *Daldorfia himaleorhaphis* illustrating position and orientation of measurements taken.

imum carapace. Orbits small, circular, directed anterolaterally, weakly rimmed, inner orbital angle with blunt tubercle, outer orbital angle with triangular spine, fronto-orbital width about 24 percent maximum carapace width. Anterolateral margin short, with several sharp, triangular spines. Lateral margin convex, with several large, sharp spines, axes of spines usually perpendicular to margin. Posterolateral margin short, convex, ornamented with small spines. Posterior margin about 24 percent maximum carapace width; with large, blunt spine at corner; concave laterally and convex axially; entire margin ornamented with blunt tubercles.

Protogastric region ovate, inflated, ornamented with tubercles of varying sizes. Mesogastric region with long, slender anterior process, process ornamented with linear array of tubercles, lateral margins nearly straight; posterior portion of region triangular, posterior margin convex. Urogastric region weakly differentiated, lateral margins concave. Cardiac region trapezoidal, narrowest posteriorly, weakly differentiated. Intestinal region ovate, depressed posteriorly, widest at about midlength.

Hepatic region small, positioned considerably below elevation of protogastric region, inflated, ornamented with several tubercles. Epibranchial region transversely oblong, positioned above elevation of hepatic region, inflated, heavily ornamented. Mesobranchial region triangular overall, separated into two subregions; outer subregion largest, inflated, circular in shape, heavily ornamented; inner subregion small, triangular, not well differentiated from rest of region, not as heavily ornamented as rest of region. Metabranchial region ovate, inflated, heavily ornamented.

Merus, carpus and manus of first pereopod not well known; heavily ornamented with tubercles of varying sizes, tubercles largest on manus; lower margin of merus and carpus ornamented with long, sharp spines.

*Measurements.*—Measurements (in mm) taken on the dorsal carapace of the holotype of *Daldorfia himaleoraphis*: maximum width (W1) = 74.4, maximum length (L1) = 48.1, frontal width (W2) = 12.0, fronto-orbital width (W3) = 17.6, posterior width (W4) = 18.2. Position and orientation of measurements taken are illustrated in Fig. 8.

*Occurrence.*—The sole specimen was recovered from RB19 in the Jansen Creek Mem-

ber of the Oligocene Makah Formation at the locality described above.

*Discussion.*—The single specimen of *Daldorfia himaleoraphis* n. sp. was collected in a concretion with part of the right first pereopod preserved in place, suggesting that the specimen could be a corpse. The marginal spines and dense ornamentation are well preserved on much of the carapace so that a reasonably complete description of the dorsal carapace has been framed. *Daldorfia himaleoraphis* is most like *D. nagashimai*, but *D. himaleoraphis* has finer, more dense carapace ornamentation and appears to have more numerous and more slender marginal spines than *D. nagashimai*. The branchial regions of *D. himaleoraphis* are better differentiated than those of *D. nagashimai*. *Daldorfia himaleoraphis* differs from Recent species of *Daldorfia* because it has a blunt, straight front and branchial regions that extend much further laterally than those of the Recent species. The front of Recent species of *Daldorfia* is deeply sulcate, whereas that of *D. himaleoraphis* is weakly sulcate. The Recent species are widest about three-quarters or more the distance posteriorly, whereas *D. himaleoraphis* is widest about two-thirds the distance posteriorly.

The occurrence of *Daldorfia* in Oligocene rocks of Washington marks the earliest known occurrence of the genus and extends the range of the genus to the west coast of North America. The other fossil species, *D. nagashimai*, has been reported from late Miocene to early Pliocene rocks of Japan, and Recent species inhabit the Indo-Pacific and eastern Atlantic Oceans (Karasawa and Kato, 1996). The genus may have evolved in the eastern Pacific Ocean and subsequently dispersed to the western Pacific via ocean currents and to the Atlantic Ocean via the Straits of Panama.

Family Goneplacidae Macleay, 1838

Genus *Branchioplax* Rathbun, 1916

*Type Species.*—*Branchioplax washingtoniana* Rathbun, 1916, by monotypy.

?*Branchioplax washingtoniana* Rathbun,  
1916

Figs. 9, 10

*Material Studied.*—The specimen, USNM 508592, is deposited in the United States Na-



Fig. 9. Juvenile *Branchioplax washingtoniana* Rathbun, 1916, dorsal carapace, USNM 508592.

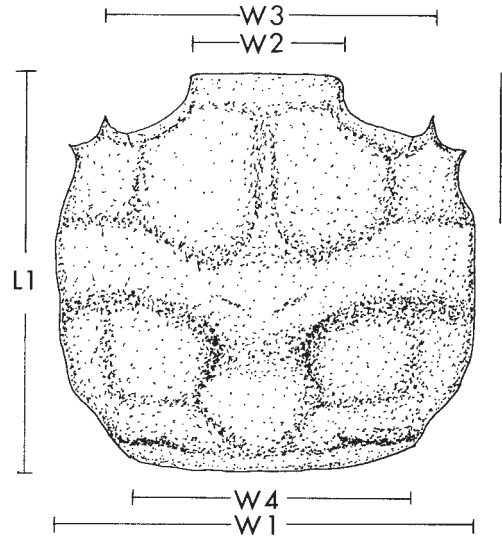


Fig. 10. Line drawing of juvenile *Branchioplax washingtoniana* illustrating position and orientation of measurements taken.

tional Museum of Natural History, Washington, D.C.

*Description of Specimen.*—Carapace nearly square,  $L/W = 0.95$ , carapace widest about half the distance posteriorly on the carapace; carapace highly vaulted longitudinally and moderately vaulted transversely; regions inflated, defined by broad, shallow grooves; carapace ornamented with fine, closely spaced granules.

Front broad, nearly straight, about 37 percent maximum carapace width. Orbits circular, directed anterolaterally, rimmed, with one orbital fissure, fronto-orbital width about 75 percent maximum carapace width; outer orbital corner with triangular spine, spine directed forward. Anterolateral and posterolateral margins continuous; one small triangular spine just posterior to outer orbital spine, lateral margin concave just posterior to spine, concavity followed by two blunt protuberances, remainder of lateral margin convex. Posterolateral corner with small reentrant. Posterior margin rimmed, nearly straight, posterior width about 80 percent maximum carapace width.

Epi-gastric region weakly inflated. Proto-gastric region about as wide as long, weakly inflated. Mesogastric region with long, narrow anterior process, process with nearly straight lateral margins; posterior portion of region triangular, with blunt ridge extending transversely across and continuous with epi-branchial ridge so that a ridge extends across entire carapace width. Urogastric region de-

pressed, laterally constricted. Cardiac region triangular, two tubercles positioned anteriorly on either side of axis, cardiac region with central transverse ridge continuous with inflated area of branchial region.

Hepatic region very weakly inflated, not well differentiated. Branchial region with arcuate ridge, continuous with mesogastric ridge. Remainder of branchial region inflated, with inflated swellings axially, swellings continuous with cardiac ridge so that a continuous ridge extends across the posterior portion of the carapace.

Venter and appendages unknown.

*Measurements.*—Measurements (in mm) taken on USNM 508592: maximum carapace width ( $W1$ ) = 14.3, maximum carapace length ( $L1$ ) = 13.6, length to point of maximum width = 6.9, frontal width ( $W2$ ) = 5.3, fronto-orbital width ( $W3$ ) = 10.8, posterior width ( $W4$ ) = 11.4. Position and orientation of measurements taken are illustrated in Fig. 10.

*Occurrence.*—The specimen was collected from the late Eocene Hoko River Formation at RB32 of Ross Berglund as described above.

*Discussion.*—Specimens of *Branchioplax washingtoniana* are common within rocks of the Hoko River Formation exposed at the northwest tip of the Olympic Peninsula,

Washington. Literally hundreds of specimens have been recovered from that area. All of the specimens examined by the author have been adults, based upon their relatively large size and their ventral morphology, when observable. Juveniles have yet to be reported from any locality along the Pacific Northwest of North America.

The specimen here described and tentatively referred to *Branchioplax washingtoniana* is clearly referable to the Goneplacidae, based upon its broad, straight front; circular orbits; flattened carapace; short anterolateral margins with few spines; and poorly developed carapace regions. The specimen is very small in size and is at least an order of magnitude smaller than typical adult *Branchioplax* individuals. Because the specimen is clearly assignable to the Goneplacidae, and because numerous specimens of *B. washingtoniana* have been recovered from the Hoko River Formation, I have considered the specimen to be a juvenile member of *B. washingtoniana*.

The specimen differs from adult *Branchioplax washingtoniana* in several aspects. The anterolateral margins are much shorter and the spines are much more discrete and attenuated in the juvenile than those of adult *B. washingtoniana*. The grooves are much more deeply incised in adults of *B. washingtoniana* than in the juvenile specimen, in which the regions are developed as broadly inflated regions. Superficially, the specimen resembles some species of *Carcinoplax* H. Milne Edwards, 1852. The shape of the carapace, the arrangement of carapace regions, the length of the anterolateral margin, and the number of anterolateral spines are very similar to that of *Carcinoplax purpurea* Rathbun, 1914, and *C. monodi* Guinot, 1989.

Nevertheless, the juvenile has many characteristics that are very similar to those of adult *B. washingtoniana*, including the shape and arrangement of carapace regions, the shape of the front and orbits, and the number of anterolateral spines. Additionally, Guinot (1989) demonstrated that the shape of the anterolateral margins and spines changes with growth in numerous species of *Carcinoplax*. Because the specimen resembles *B. washingtoniana* in so many respects, it seems premature to assign the specimen to a new species of *Carcinoplax* or any other genus, especially considering that *B. wash-*

*ingtoniana* is extremely common at the locality from which the specimen was collected and that *Carcinoplax* has never been reported from the eastern Pacific Ocean. Therefore, the specimen is here tentatively referred to *B. washingtoniana* as a juvenile member until more specimens are discovered that may make an alternative interpretation possible.

The specimen was preserved in a concretion and is probably a molt because the venter and appendages were not preserved. Hopefully, this report will stimulate collection of small concretions, which are likely to be overlooked in favor of the larger concretions containing adult specimens, so that determination of the true affinities of this individual are possible. Also, collection of more material may make it possible to reconstruct a growth series for *Branchioplax washingtoniana* as was done by Guinot (1989) for species of *Carcinoplax*.

#### ACKNOWLEDGEMENTS

Ross E. Berglund, Bainbridge Island, Washington, donated the material described in this paper, and his generosity is, as always, appreciated. The manuscript was greatly improved by the comments of R. M. Feldmann, Kent State University, Kent, Ohio. A. B. Tucker, Aurora, Ohio, provided helpful information on *Homola vancouverensis* n. sp. and suggested the trivial name. H. Karasawa, Mizunami Fossil Museum, Mizunami, Japan, and an anonymous reviewer provided careful reviews of the manuscript, which are much appreciated. Karasawa and H. Kato, Natural History Museum and Institute, Chiba, Japan, provided access to comparative material at their respective institutions. R. B. Manning, late of the United States National Museum of Natural History, allowed access to the biological collections at that institution and provided helpful discussions about xanthoid taxa. W. Blow, United States National Museum of Natural History, Washington, D.C., kindly loaned type material from that institution. Funding for travel to examine Japanese material was provided by National Geographic Society Grant 6265-98 to Schweitzer and R. M. Feldmann, Kent State University, Kent, Ohio.

#### LITERATURE CITED

- Alcock, A. 1895. The Brachyura Oxyryncha: materials for a carcinological fauna of India, No. 1.—Journal of the Asiatic Society of Bengal 64(II:2): 157–291, pls. 3–5.
- . 1896. The Brachyura Oxystomata: materials for a Carcinological Fauna of India, No. 2.—Journal of the Asiatic Society of Bengal, 65(II:2): 134–296, pls. 6–8.
- Bell, T. 1863. A monograph of the fossil malacostracous Crustacea of Great Britain. Part II. Crustacea of the Gault and Greensand.—Palaeontographical Society Monograph, London. Pp. 1–40.
- Berglund, R. E., and J. L. Goedert. 1992. A new species of *Cancer* (Decapoda: Brachyura) from the Miocene Astoria Formation in Washington.—Burke Museum Contributions in Anthropology and Natural History No. 9: 1–11.

- , and ———. 1996. A new crab (Brachyura: Cancridae) from lower Miocene rocks of the northwestern Olympic Peninsula, Washington.—*Journal of Paleontology* 70: 830–835.
- Beurlen, K. 1928. Die fossile Dromiaceen und ihre Stammesgeschichte.—*Palaeontologie Zeitschrift* 10: 144–183, figs. 1–7.
- . 1930. Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse.—*Fortschritte der Geologie und Palaeontologie* 8: 540–546.
- Bishop, G. A. 1988. New fossil crabs, *Plagiophthalmous izetti*, *Latheticocarcinus shapiro*, and *Sagittiformosus carabus* (Crustacea, Decapoda), from the Western Interior Cretaceous, U.S.A.—*Proceedings of the Biological Society of Washington* 101: 375–381.
- . 1992. Two new crabs, *Homolopsis williamsi* and *Homolopsis centurialis* (Crustacea: Decapoda) from the Western Interior Cretaceous of the United States.—*Proceedings of the Biological Society of Washington* 105: 55–66.
- 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: 1–26.
- Collins, J. S. H. 1997. Fossil Homolidae (Crustacea; Decapoda).—*Bulletin of the Mizunami Fossil Museum* 24: 51–71.
- , J. W. M. Jagt, and R. H. B. Fraaye. 1995. Late Cretaceous anomurans and brachyurans from the Maastriechian type area.—*Acta Geologica Polonica* 40: 165–210.
- , Y. Kanie, and H. Karasawa. 1993. Late Cretaceous crabs from Japan.—*Transactions and Proceedings of the Palaeontological Society of Japan*, N. S. 172: 292–310.
- , and H. W. Rasmussen. 1992. Upper Cretaceous–Lower Tertiary decapod crustaceans from West Greenland.—*Grønlands Geologiske Undersøgelse* 162: 1–46.
- Dana, J. D. 1854. On the geographical distribution of Crustacea.—*American Journal of Science and Arts*, series 2, 18: 1–45, 1 map.
- Eldredge, L. 1980. Two species of *Homola* (Dromiacea, Homolidae) from Guam.—*Micronesica* 16: 271–277.
- Fabricius, J. C. 1793. *Entomologia Systematica Emendata et Aucta Secundum Classes, Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus*.—Hafniae. 519 pp.
- Feldmann, R. M., K. L. Bice, C. Schweitzer Hopkins, E. W. Salva, and K. Pickford. 1998. Decapod crustaceans from the Eocene Castle Hayne Limestone, North Carolina: Paleogeographic implications.—*Journal of Paleontology Memoir* 48 (Supplement to Vol. 73). Pp. 1–28.
- , A. B. Tucker, and R. E. Berglund. 1991. Paleobathymetry of decapod crustaceans, Washington.—*National Geographic Research and Exploration* 7: 352–363.
- Glaessner, M. F. 1969. Decapoda. Pp. R400–R533 in R. C. Moore, ed. *Treatise on Invertebrate Paleontology, Part R, Arthropoda* 4(2). Geological Society of America and University of Kansas Press, Lawrence.
- . 1980. New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand.—*Transactions of the Royal Society of South Australia* 104: 171–192.
- Guinot, D. 1989. Le genre *Carcinoplax* H. Milne Edwards, 1852 (Crustacea, Brachyura: Goneplacidae). Pp. 265–345 in J. Forest, ed. *Résultats des Campagnes MUSORSTOM*. Vol. 5. *Mémoires du Museum National d'Histoire Naturelle, Zoologie* 144.
- , and B. Richer de Forges. 1995. Crustacea Decapoda Brachyura: Révision de la famille des Homolidae de Haan, 1839. Pp. 283–517 in A. Crosnier, ed. *Résultats des campagnes MUSORSTOM*. Vol. 13. *Mémoires du Museum National d'Histoire Naturelle, Zoologie* 163.
- Haan, W. de. 1833–1850. Crustacea. Fasc. 1–8: I–XVII, I–XXXI, 1–243, pls. 1–55, A–J, L–Q. in P. F. von Siebold, ed. *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepit, Annis 1823–1830 Collegit, Notis, Observationibus e Adumbrationibus Illustravit*. Lugduni-Batavorum, Leiden.
- Henderson, J. R. 1888. Report on the Anomura collected by H. M. S. Challenger during the years 1873–1876.—*Reports of the Scientific Research Voyage of the H. M. S. Challenger* 27: 1–XI, 1–221, pl. 1–21.
- Jakobsen, S. L., and J. S. H. Collins. 1997. New middle Danian species of anomuran and brachyuran crabs from Fakse, Denmark.—*Bulletin of the Geological Society of Denmark* 44: 89–100.
- Karasawa, H. 1992. Fossil decapod crustaceans from the Manda Group (Middle Eocene), Kyushu, Japan.—*Transactions and Proceedings of the Palaeontological Society of Japan*, N. S. 167: 1247–1258.
- . 1993. Cenozoic decapod Crustacea from Southwest Japan.—*Bulletin of the Mizunami Fossil Museum* 20: 1–92, 24 pls.
- , and H. Kato. 1996. *Daldorfia* Rathbun, 1904 (Crustacea, Decapoda) from the Neogene of Japan.—*Proceedings of the Biological Society of Washington* 109: 44–52.
- Leach, W. E. 1815. A tabular view of the external characters of four classes of Animals, which Linné arranged under Insecta: with the distribution of the genera composing three of these classes into orders, and descriptions of several new genera and species.—*Transactions of the Linnean Society of London* 11: 306–400.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Edition 10, volume 1, Holmiae. Pp. iii + 1–824.
- 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 A. Smith, ed. *Illustrations of the Zoology of South Africa, Invertebrate*. Smith, Elder, and Co., London.
- Mertin, H. 1941. Decapode Krebse aus dem subhercynen und Braunschweiger Emscher und Untersenon.—*Nova Acta Leopoldina* 10: 152–264.
- Milne Edwards, A. 1880. Etudes préliminaires sur les Crustacés, 1<sup>re</sup> Partie. Reports on the Results Dredging under the Supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the U. S. Coast Survey steamer "Blake," Lieutenant-Commander C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., Commanding, VIII.—*Bulletin of the Museum of Comparative Zoology, Harvard*, 8: 1–68, pls. 1, 2.
- Milne Edwards, H. 1852. Observations sur les affinités zoologiques et la classification naturelle de Crustacés.—*Annals du Science Naturelle (Zool.)*, 3, 18: 109–166, pls. 3, 4.

- Müller, P. 1984. Decapod Crustacea of the Badenian.—*Geologica Hungarica, Series Palaeontologica* 42: 1–317.
- Noetling, F. 1881. Über einige Brachyuren aus dem Senon von Maestricht und dem Tertiär Norddeutschlands.—*Zeitschrift der deutschen Geologie Gesellschaft* 33: 357–371, pl. 20.
- Ortmann, A. 1892. Die Decapoden-Krebse des Strassburger Museums. V. Theil. Die Abteilungen Hippidae, Dromiidae, und Oxystomata.—*Zoologische Jahrbuche* 6: 532–588, pl. 26.
- Rathbun, M. J. 1904. Some changes in crustacean nomenclature.—*Proceedings of the Biological Society of Washington* 17: 169–172.
- . 1916. Description of a new genus and species of fossil crab from Port Townsend, Washington.—*American Journal of Science* 41: 344–346.
- . 1917. New species of South Dakota Cretaceous crabs.—*Proceedings of the United States National Museum* 52: 385–391, pls. 32, 33.
- . 1926. The fossil stalk-eyed Crustacea of the Pacific Slope of North America.—*United States National Museum Bulletin* 138: 1–155.
- Roberts, H. B. 1962. The Upper Cretaceous decapod crustaceans of New Jersey and Delaware. Pp. 163–191, pls. 80–89 in H. G. Richards, ed. *The Cretaceous Fossil of New Jersey Bulletin* 61. State of New Jersey Department of Conservation and Economic Development Paleontology Series, Trenton, New Jersey.
- Sakai, T. 1979. Description of three new species of crabs of the family Homolidae from Japan.—*Researches on Crustacea* 9: 1–8 (English), 8–12 (Japanese), figs. 1–3, 1 frontispiece.
- Samouelle, G. 1819. *The Entomologist's Useful Compendium, or an Introduction to the Knowledge of British Insects, etc.* London. Pp. 1–496.
- Schlüter, C. A. von. 1879. Neue und weniger bekannte Kreide- und Tertiärkrebse des nördlichen Deutschlands.—*Zeitschrift der deutschen Geologie Gesellschaft* 31: 586–615, pls. 13–18.
- Schweitzer, C. E. 2000. Tertiary Xanthoidea (Crustacea: Decapoda: Brachyura) from the West Coast of North America.—*Journal of Crustacean Biology* 20: 715–742.
- , and C. B. Boyko. 2000. First report of the genus *Lophomastix* Benedict, 1904 (Crustacea: Decapoda: Albuneidae) in the fossil record and a reappraisal of the status of *Blepharipoda brucei* Rathbun, 1926.—*Journal of Paleontology*, 74: 631–635.
- , and R. M. Feldmann. 1999. Fossil decapod crustaceans from the late Oligocene to early Miocene Pysht Formation and late Eocene Quimper Sandstone, Olympic Peninsula, Washington.—*Annals of Carnegie Museum* 68: 215–273.
- , and ———. 2000a. New species of calappid crabs from Western North America and reconsideration of the Calappidae sensu lato.—*Journal of Paleontology* 74: 230–246.
- , and ———. 2000b. New fossil portunids from Washington, USA, and Argentina and a reevaluation of generic and family relationships within the Portunoidea Rafinesque, 1845 (Decapoda: Brachyura).—*Journal of Paleontology* 74: 636–653.
- , and ———. 2000c. Reevaluation of the Cancridae Latreille, 1802 (Decapoda: Brachyura) including three new genera and three new species.—*Contributions to Zoology* 69: 223–250.
- , and ———. (In press.) Differentiation of the fossil Hexapodidae Miers, 1886 (Decapoda: Brachyura) from similar forms.—*Journal of Paleontology*.
- , ———, A. B. Tucker, and R. E. Berglund. 2000. Eocene decapod crustaceans from Pullali Point, Washington.—*Annals of Carnegie Museum* 69: 23–67.
- , and E. W. Salva. 2000. First recognition of the Cheiragonidae (Decapoda) in the fossil record and comparison of the family with the Atelecyclidae.—*Journal of Crustacean Biology* 20: 285–298.
- Stebbing, T. R. R. 1920. South African Crustacea (Part X of S. A. Crustacea, for the Marine Investigations in South Africa).—*Annals of the South African Museum* 6: 231–593, figs. 1–34.
- Stimpson, W. 1857–1860. *Prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Crustacea Maiioidea.*—*Proceedings of the Academy of Natural Sciences, Philadelphia* 9: 216–221.
- . 1858. *Prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars IV. Crustacea Cancroidea et Corystoidea.*—*Proceedings of the Academy of Natural Sciences, Philadelphia* 10: 93–110.
- Straelen, V. Van. 1933. Sur des Crustacés Décapodes cénozoïques du Venezuela.—*Bulletin du Musée royal d'Histoire Naturelle de Belgique* 9: 1–14.
- Takeda, M., and I. Fujiyama. 1983. Three decapod crustaceans from the Lower Cretaceous Miyako Group, Northern Japan.—*Bulletin of the National Science Museum, Tokyo, Series C* 9: 129–136.
- Tavares, M. S. 1991. Espèces nouvelles de Cyclodorippoidea Ortmann et remarques sur les genres *Tymolus* Stimpson et *Cyclodorippe* A. Milne Edwards (Crustacea, Decapoda, Brachyura).—*Bulletin du Muséum National d'Histoire Naturelle, Paris, (4)* 12: 623–648.
- . 1992a. Sur la position systématique du genre Éocène Américain *Falconoplax* Van Straelen, 1933 (Crustacea, Decapoda, Brachyura).—*Annales de Paléontologie (Vert.-Invert.)* 78: 73–81.
- . 1992b. Tendances évolutives chez les Crabes primitifs, avec la description d'un nouveau type de chambre incubatrice (Crustacea, Decapoda: Cyclodorippinae Ortmann, 1892, et Xeinostominae subfam. nov.).—*Comptes Rendus de l'Académie des Sciences Paris* 314: 509–514.
- . 1993. Crustacea Decapoda: Les Cyclodorippidae et Cymonomidae de l'Indo-Ouest-Pacifique à l'exclusion du genre *Cymonomus*.—*Mémoires du Muséum National d'Histoire Naturelle, Paris* 156: 253–313.
- Tucker, A. B. 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.
- , 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.
- , ———, F. D. Holland, Jr., and K. F. Brinster. 1987. Fossil crab (Decapoda: Brachyura) fauna from the late Cretaceous (Campanian-Maastrichtian) Pierre Shale in Bowman County, North Dakota.—*Annals of Carnegie Museum* 56: 275–288.



- Woods, J. T. 1953. Brachyura from the Cretaceous of Queensland.—Memoirs of the Queensland Museum 13: 155–175.
- Woodward, H. 1896. On some podophthalmous Crustacea from the Cretaceous formation of Vancouver and Queen Charlotte Islands.—Quarterly Journal of the Geological Society of London 52: 221–228.
- Yokoyama, M. 1911. Some Tertiary fossils from the Miike Coalfield.—Journal of the Collections of Science, Imperial University of Tokyo 27: 1–16, 3 pls.

RECEIVED: 1 December 1999.

ACCEPTED: 12 August 2000.