HOMOLIDAE DE HAAN, 1839 AND HOMOLODROMIIDAE ALCOCK, 1900 (CRUSTACEA: DECAPODA: BRACHYURA) FROM THE PACIFIC NORTHWEST OF NORTH AMERICA AND A REASSESSMENT OF THEIR FOSSIL RECORDS

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ABSTRACT—New material collected from Cretaceous and Tertiary rocks of the Pacific Northwest of North America has prompted a reevaluation of the fossil record of the Homolidae de Haan, 1839 and the Homolodromiidae Alcock, 1900. The fossil records of the homolid genera *Homola* Leach, 1815; *Homolopsis* Bell, 1863; and *Hoplitocarcinus* Beurlen, 1928 are restricted, and *Latheticocarcinus* Bishop, 1988, which is synonymous with *Eohomola* Collins and Rasmussen, 1992 and *Metahomola* Collins and Rasmussen, 1992, is reinstated as a distinctive genus. Thirteen new combinations resulted from reinstatement of *Latheticocarcinus*: *L. adelphinus* (Collins and Rasmussen, 1992), *L. affinis* (Jakobsen and Collins, 1997), *L. atlanticus* (Roberts, 1962), *L. brevis* (Collins, Kanie, and Karasawa, 1992), *L brightoni* (Wright and Collins, 1972), *L. centurialis* (Bishop, 1992), *L. declinata* (Collins, Fraaye, and Jagt, 1995), *L. dispar* (Roberts, 1962), *L. pikeae* (Bishop and Brannen, 1992), *L. punctatus* (Rathbun, 1917), *L. schlueteri* (Beurlen, 1928), *L. shapiroi* Bishop, 1988, *L. spiniga* (Jakobsen and Collins, 1997), and *L. transiens* (Segerberg, 1900). A new species, *Latheticocarcinus ludvigseni*, is described from Cretaceous rocks of British Columbia. The first fossil occurrence of the extant homolid genus *Paromolopsis*, *P. piersoni* new species, is recorded from Miocene rocks of Oregon. *Paromola pritchardi* Jenkins, 1977 is formally transferred to *Dagnaudus* Guinot and Richer de Forges (1995) as suggested by Guinot and Richer de Forges (1995). The extinct family Prosopidae von Meyer, 1860 is referred to the Homolodromioidea Alcock, 1900, following previous work. *Palehomola gorrelli* Rathbun, 1926 is transferred from the Homolidae to the Homolodromiidae, and the new genus *Rhinodromia* is erected to contain *Homolopsis richardsoni* Woodward, 1896, from Cretaceous rocks of British Columbia. A new terminology is suggested for describing the rostral area in homolodromiids, in an attempt to alleviate considerable confusion over that issue. The morphologic similarity of fossil and extant members in both the Homolidae and the Homolodromiidae suggest that these two brachyuran families are evolutionarily conservative, much as the lobsters are. In addition, the similar paleobiogeographic and evolutionary patterns seen in the two families suggests that either they are closely related or that brachyuran families exhibited similar evolutionary and dispersal trends early in their history.

INTRODUCTION

THE HOMOLIDAE and the Homolodromiidae each have well-recognized although not particularly robust fossil records. The Homolidae is well represented in Mesozoic rocks, but has an abysmally poor record in the Tertiary, perhaps due to a habitat shift into deepwater environments, from which decapods are not well known (Feldmann et al., 1991). The Homolodromiidae, on the other hand, has a sparse fossil record in both the Mesozoic and Cenozoic although the related Prosopidae have a robust Mesozoic record (Müller et al., 2000). Nevertheless, it is clear that the Homolidae and Homolodromiidae, both of which have extant members, are ancient lineages and were among the first brachyuran families to appear. In addition, many of the extant members of these two families appear to be virtually unchanged since the Cretaceous, demonstrated by the numerous similarities in external morphology among extant and fossil forms.

It is the purpose of this paper to examine the fossil record of these two families, each of which have displayed a high level of evolutionary conservatism, at least in terms of hard-part morphology, since they appeared in the Jurassic. It is becoming increasingly clear that many decapod crustaceans exhibit a high degree of conservatism in hard-part morphology, including taxa within the Astacidea Latreille, 1802 and the Thalassinidea Latreille, 1831, as demonstrated by the remarkable similarity of Cretaceous and extant Glypheidae Winkler, 1883; and also the Nephropidae Dana, 1852; Ctenochelidae Manning and Felder, 1991; and Galatheidae Samouelle, 1819 (Schweitzer and Feldmann, 2000, 2001). To this list of conservative reptant forms, the podotrematous Brachyura Latreille, 1802, including the brachyuran families Homolidae and the Homolodromiidae, must be added.

Research for this contribution involved the examination of type material and/or illustrations of nearly all fossil homolid and all

fossil homolodromiid taxa. Thus, all taxonomic reassignments and conclusions are drawn from first-hand observations.

Institutional abbreviations.—GSC, Geological Survey of Canada, Ottawa, Ontario; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UWBM Burke Museum of Natural History and Culture, University of Washington, Seattle.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section PODOTREMATA Guinot, 1977
Superfamily HOMOLOIDEA de Haan, 1839
Family HOMOLIDAE de Haan, 1839

Discussion.—The concept of the Homolidae used in this paper is largely that of Guinot and Richer de Forges (1995), who revised the extant homolids, and Collins (1997) and Schweitzer (2001a), who considered the fossil members of the family. Morphological terminology follows that used by Guinot and Richer de Forges (1995) who also provided labeled illustrations of dorsal carapace morphology of typical members of the family.

Three taxa from North America's west coast have previously been assigned to the Homolidae, including *Homolopsis richardsoni* Woodward, 1896, from the Cretaceous of British Columbia; *Palehomola gorrelli* Rathbun, 1926, from the Oligocene of Oregon; and *Homola vancouverensis* Schweitzer, 2001a, from the Eocene of Washington. *Palehomola gorrelli* is herein placed within the Homolodromiidae, and *Homolopsis richardsoni* is referred to a new genus within the Homolodromiidae, *Rhinodromia*.

Collins (1997) defined fossil members of the Homolidae based primarily upon possession of *lineae homolicae* and the conformation and development of the cervical and branchiocardiac grooves. The *lineae homolicae* are very clear in extant forms,
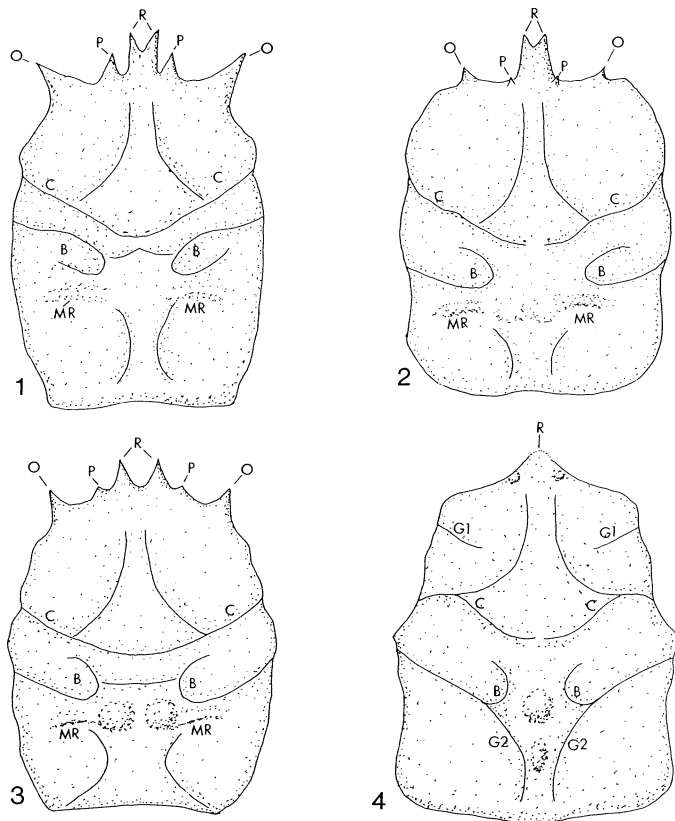
FIGURE 1—Generalized line drawings of four homolid genera, showing the dorsal carapace between the *lineae homolicae* and the shape and orientation of the carapace grooves, ridges, and regions. O = supraorbital spine, P = pseudorostral spine, R = rostrum, C = cervical groove, B = branchiocardiac groove, MR = metabranchial ridge extending from cardiac region, G1 = groove separating protogastric and hepatic region, G2 = groove separating cardiac and branchial regions. *1, Homola*, modified after fig. 1A, Guinot and Richer de Forges, 1995; *2, Hypsophrys*, modified after fig. 1B, Guinot and Richer de Forges, 1995, note that path of branchiocardiac groove has been significantly redrawn here to more closely conform to the morphology of the animal; *3, Latheticocarcinus* sp.; *4, Homolopsis* sp., drawn from fig. 3.1, Collins, 1997.

where the entire dorsal carapace is preserved (see illustrations in Guinot and Richer de Forges, 1995). Glaessner (1969, p. R406, fig. 221.4a, b) illustrated an entire homolid carapace indicating the position of the left *linea homolica*. The carapace breaks along the *lineae homolicae* during molting and often after the death of the animal. In fossils, usually the subhepatic and subbranchial regions, which lie distal to the *lineae homolicae*, are lost. The result is that only the inter-lineal portion of the carapace typically is preserved; this is the portion of the carapace illustrated in Figure 1. A few fossil homolids retain the subhepatic and subbranchial regions, including specimens of *Homolopsis* illustrated by Wright and Collins (1972, pl. 8, fig. 1) and Glaessner (1969, p. R490, fig. 302.3). The illustration of *Tithonohomola* Glaessner, 1933 (Glaessner, 1969, p. R490, fig. 302.2) indicates the portion of the carapace distal to the *lineae homolicae* in dotted lines and the preserved inter-lineal portion in solid lines. These illustrations help to demonstrate why many fossil homolids do not have clear *lineae homolicae* visible; it is because they have broken along the *lineae* and the remainder of the carapace is missing.

In the Homolodromiidae, the *lineae homolicae* are absent. The shape of the dorsal carapace of homolodromiids is remarkably

similar to that of homolids in which the extra-lineal portion is broken and missing (Glaessner, 1969, p. R485, fig. 293.4a, fig. 294). The means by which to distinguish homolids, in which the extra-lineal portion is missing, from homolodromiids is to determine if there are rounded, lateral sides on the carapace. In broken homolids, there are not, because this portion of the carapace is missing. In homolodromiids, these rounded lateral sides are present. In the latter case, one also must look for the *lineae homolicae*, and if none is present, then the specimen is referred to the Homolodromiidae or the related Prosopidae.

The Homolidae first appeared during the Jurassic, and by the Cretaceous was well established in oceanic and epicontinental regions. Jurassic and Cretaceous occurrences include species of *Gastrodorus* von Meyer, 1864; *Lignihomola* Collins, 1997; *Laeviprosopon* Glaessner, 1933; *Tithonohomola* Glaessner, 1933; and *Zygastrocarcinus* Bishop, 1983 (Collins, 1997). *Latheticocarcinus* Bishop, 1988 is known from late Early Cretaceous through Paleocene rocks, while the only fossil species of *Homola*, *H. vancouverensis*, is known from Eocene rocks of Washington, U. S. A. (Schweitzer, 2001a). The early history of the family appears to be characterized by north polar routes of dispersal, while later, the family appears to have dispersed via Tethyan avenues. *Paromolopsis* Wood-Mason *in* Wood-Mason and Alcock, 1891 is known from Miocene occurrences in Oregon, U. S. A., described herein. Other Tertiary occurrences of homolids include the extinct *Prohomola* Karasawa, 1992, from Eocene rocks of Japan and eastern coastal U. S. A. (Karasawa, 1992; Blow and Manning, 1996).

Jenkins (1977) had originally described *Paromola pritchardi* from Oligocene and Miocene rocks of Australia. Members of *Paromola* have pseudorostral spines that are only as long as or slightly longer than the rostrum, while in *P. pritchardi*, the pseudorostral spines are much longer than the rostrum. Guinot and Richer de Forges (1995) suggested that the Australian fossil species belonged to either *Dagnaudus* Guinot and Richer de Forges, 1995 or *Mohola* Guinot and Richer de Forges, 1995. We suggest that the species be referred to *Dagnaudus*, based upon the extremely long pseudorostral spines and the dense dorsal carapace ornamentation, both characteristic of *Dagnaudus*. Species of *Moloha* also have long pseudorostral spines, but the dorsal carapace is ornamented with sharp spines, not characteristic of *P. pritchardi*, and lacks dense, large, granular ornament as seen in *P. pritchardi*.

Genus HOMOLA Leach, 1815
Figure 1.1

Type species.—*Homola spinifrons*, Leach, 1815, (subjective synonym of *Cancer barbatus* Fabricius, 1793), by monotypy.

Fossil species.—*Homola vancouverensis* Schweitzer, 2001a.

Diagnosis.—Carapace elongate, rectangular, ornamented with swellings, tubercles, or spines; sub-hepatic and sub-branchial regions usually at right angles to upper surface of dorsal carapace but may be visible dorsally; *lineae homolicae* distinct; rostrum distinctly bifid or bifid only at tip; cervical groove distinctive; branchiocardiac groove always deep near axial regions, U-shaped, anterior segment of "U" may reach lateral margin but does not do so in all species (Fig. 1.1); carapace with pseudorostral and supraorbital spines, and anterolateral spines on sub-branchial region; regions moderately defined by grooves; cardiac region usually with transverse ridge extending laterally onto branchial regions.

Discussion.—The diagnosis is emended from that of Schweitzer (2001a) and reflects the morphology of modern members as well as *Homola vancouverensis*. *Homola* was synonymized with *Hoplitocarcinus*, *Eohomola*, and *Metahomola* by Schweitzer (2001a). However, it now appears clear that *Hoplitocarcinus* is a

distinct, monotypic genus based upon the illustration of the type species in Beurlen (1928). *Eohomola* and *Metahomola* are junior subjective synonyms of *Latheticocarcinus* and are discussed below. Thus, *H. vancouverensis* is the sole fossil member of the genus.

Homola vancouverensis is most similar to *H. barbata* (Fabricius, 1793), with which it shares remarkable similarity in the development of carapace grooves and regions. Both species share possession of a pseudorostral spine, which was not originally described in *H. vancouverensis*, and both have three swellings arranged in a triangular pattern on the cardiac region and transverse ridges extending from the cardiac region onto the branchial regions. The hepatic region in both is rectangular and is oriented obliquely toward the axis of the animal. Thus, it is clear that *H. vancouverensis* is a member of *Homola*, based upon its overall similarity to species of that genus. The two species differ in several important regards. The outline of *H. vancouverensis* as defined by the *lineae homolicae* is more bulbous, sinuous, and convex than that of *H. barbata* and *H. vancouverensis* lacks the spines on the dorsal carapace seen in *H. barbata*.

According to available evidence, the genus first appeared in the eastern North Pacific, based upon the occurrence of *Homola vancouverensis. Homola* was probably derived from *Hoplitocarcinus*, *Latheticocarcinus*, or another closely related taxon; *Latheticocarcinus* was well established in the North Pacific Ocean and the Western Interior Seaway of North America during the Cretaceous. In modern oceans, *Homola* is nearly cosmopolitan (Guinot and Richer de Forges, 1995).

Genus HOMOLOPSIS Bell, 1863
Figure 1.4

Type species.—*Homolopsis edwardsii* Bell, 1863, by original designation.

Included species.—*Homolopsis chilensis* Förster and Stinnesbeck, 1987; *H. edwardsii*; *H. glabra* Wright and Collins, 1972; *H. hachiyai* Takeda and Fujiyama, 1983; *H. williamsi* Bishop, 1992.

Diagnosis.—Carapace longer than wide (width measured between *lineae homolicae*), widest about half the distance posteriorly at marked lateral extension on carapace, granular, ornamented with large tubercles; rostrum poorly known, sulcate, apparently with two small pseudorostral protuberances; orbit without supra-orbital spine; regions very well marked by deep grooves; protogastric and hepatic regions separated by deep, oblique groove (G1, Fig. 1.4) that does not extend to the posterior margin of the protogastric region; cervical groove well developed, sinuous; branchiocardiac groove beginning at margin of metagastric region, curving axially, very deep anteriorly, arcing laterally and extending to lateral margin where it intersects *linea homolica* and continues onto sub-branchial region; cardiac region narrow, with central swelling, distinctly separated from branchial regions by deep groove (G2, Fig. 1.4); sub-hepatic region with large sub-hepatic spine; sub-branchial region with very large, stout antero-lateral spine situated adjacent to epibranchial region.

Discussion.—The genus *Homolopsis* was erected by Bell in 1863 to embrace a Cretaceous homolid similar to modern *Homola*, but differing from it in several important regards, including the shape of the carapace, the development of the branchiocardiac groove, and the development of the carapace regions. Most Cretaceous homoloid species have been referred to *Homolopsis*, to the point that the generic definition of *Homolopsis* has been enlarged so as to have no biological meaning. This commonly happens with decapod, and especially brachyuran, genera; a kind of "generic drift" occurs wherein genera become "catch-alls" for similar species and the definition of the genus becomes hopelessly broad and defined by more recent additions to it than by the

morphology of the type species. For example, most of the North American homoloids have been referred to *Homolopsis* after *H. punctata* (herein referred to *Latheticocarcinus*) was described by Rathbun (1917); in actuality, only one North American homoloid can be embraced by *Homolopsis* sensu stricto, based upon favorable comparison of its morphology to that of the type species.

Guinot and Richer de Forges (1995) suggested that many species then referred to *Homolopsis* were actually more similar to some extant species of *Homola* and *Hypsophrys* Wood-Mason *in* Wood-Mason and Alcock, 1891. Collins (1997) began to address the problem with regard to fossil species by assigning some species of *Homolopsis* to *Eohomola* or *Hoplitocarcinus. Hoplitocarcinus* was defined as possessing a singular rostrum and a metabranchial ridge extending laterally from the cardiac region onto the branchial region, and *Eohomola* was defined as possessing a bifid rostrum and a metabranchial ridge as in *Hoplitocarcinus*. These two genera were distinguishable from *Homolopsis*, which does not have a metabranchial ridge extending from the cardiac region.

In fact, many other features distinguish *Homolopsis* from *Hoplitocarcinus* and *Eohomola* and all other homolids. *Homolopsis* is narrow anteriorly (as measured between the *lineae homolicae*) and has a marked projection from the lateral margin at the mid-length, which species assigned to *Eohomola* and *Hoplitocarcinus* lack. The latter two genera are relatively uniformly narrow along their entire length. *Eohomola* and *Hoplitocarcinus* lack the deep groove (G2) separating the cardiac region from the branchial region, which is so distinctive in *Homolopsis*. The cardiac region of *Homolopsis* is narrow and has a single central swelling, whereas most other homolids including *Hoplitocarcinus* and *Eohomola* have a broader cardiac region with two swellings placed beside one another. *Homolopsis* lacks a supra-orbital spine, which members of *Eohomola* and *Hoplitocarcinus* appear to possess. The cervical groove is very deep and U-shaped in *Eohomola* and *Hoplitocarcinus* whereas in *Homolopsis* it is shallower and sinuous.

Most of the species formerly referred to *Homolopsis* are actually distinct from *Homolopsis* s.s. and are herein referred to *Latheticocarcinus*, as discussed below. *Homolopsis* as now defined embraces the Aptian *H. hachiyai* from Japan; two Albian British species, *H. edwardsii* and *H. glabra*; a Turonian North American Western Interior species, *H. williamsi*; and a Maastrichtian Chilean species, *H. chilensis*. The genus clearly exhibits an amphitropical distribution, and appeared first in the North Pacific region based on current knowledge. It may have dispersed across the Polar region into the North Atlantic and into the Western Interior, all of which could have been facilitated by high sea levels and the ice-free pole during the Late Cretaceous. Alternatively, the Chilean occurrence suggests that the dispersal route may have been Tethyan. The amphitropical distribution, which is also seen in Cretaceous species of *Necrocarcinus* Bell, 1863, may be a result of the breakup of Pangaea during the Cretaceous (Crame, 1993) or may be a relict Tethyan distribution (Newman, 1992).

Van Straelen (1936) described *Homolopsis tuberculata* and *H. spinosa* from Hauterivian and Albian rocks, respectively, of France; however, the illustrations of these taxa make it nearly impossible to determine their generic status without examination of type material. *Homolopsis spinulosa* Glaessner, 1980, from the Cenomanian of Australia is poorly preserved, and examination of type material will be necessary to make a confident generic assignment. *Homolopsis mendryki* Bishop, 1982, was referred to *Zygastrocarcinus* by Bishop (1983). Collins (1997) referred *Homolopsis etheridgei* Woodward, 1892 to a new genus, *Lignihomola*, based upon its rounded carapace narrowing anteriorly, inflated branchial regions, and deep grooves.

Genus HOPLITOCARCINUS Beurlen, 1928

Hoplitocarcinus BEURLEN, 1928, p. 154, text-figs. 3, 4.

Type and sole species.—*Hoplitocarcinus johannesboehmi* Beurlen, 1928, by monotypy.

Discussion.—*Hoplitocarcinus johannesboehmi* was named based upon a single specimen that is very poorly illustrated (Beurlen, 1928, text-figs. 3, 4). Mertin (1941) considered the species to be synonymous with *Dromiopsis gibbosa* Schlüter, 1879. *Dromiopsis gibbosa* clearly does not belong within *Dromiopsis* Reuss, 1859, and so was retained within *Hoplitocarcinus*. Thus, *H. johannesboehmi* became a junior synonym of *H. gibbosa* (Mertin, 1941; Collins, 1997; Collins et al., 2000).

The specimen that Beurlen (1928) referred to *H. johannesboehmi* apparently has very large lateral spines projecting from the margin of the branchial regions, at least as drawn (text-fig. 3), although these spines are not visible in the poor photograph (text fig. 4). The specimens referred by Schlüter (1879) to *D. gibbosa* and as drawn by Mertin (1941) appear to lack these large lateral spines. That *D. gibbosa* is a homolid appears clear; however, it is not clear that *H. johannesboehmi* is synonymous with it. The illustrations of *D. gibbosa* suggest that it could be referable to *Homola*, *Hoplitocarcinus*, or *Latheticocarcinus*, but examination of type material will be necessary to establish its generic position.

Collins et al. (2000) referred specimens from the lower Campanian of Belgium to *Hoplitocarcinus gibbosus*; however, they did not examine type material of either *Dromiopsis gibbosa* or *H. johannesboehmi*. Thus, their material was not appropriately demonstrated as *D. gibbosa*. The specimens that they referred to *H. gibbosus* do appear to be homolids; however, the very convex lateral margins that lack large spines do not fall within the morphological definition of *Homolopsis* sensu Beurlen (1928). Until type specimens of *D. gibbosa* and *H. johannesboehmi* are examined and compared to one another and to the material that Collins et al. (2000) referred to *H. gibbosus*, it seems most prudent to retain *D. gibbosa* and *H. johannesboehmi* as separate species, probably referred to different genera. Confirmation of the generic and specific identity of the material Collins et al. (2000) referred to *H. gibbosus* must await that work.

Genus LATHETICOCARCINUS Bishop, 1988
Figure 1.3

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. 94–95, fig. 1C, plate 1, figs. 2–4, 6; COLLINS, 1997, p. 53, 54, 60, fig. 4.
Homolopsis BELL, 1863 (part). SEGERBERG, 1900, p. 366, pl. 8, figs. 6–8; RATHBUN, 1917, p. 388, pl. 33, figs. 1–3; BEURLEN, 1928, p. 153, fig. 2; ROBERTS, 1962, p. 179, 180, pl. 89, figs. 4, 5; WRIGHT AND COLLINS, 1972, p. 45, pl. 6, figs. 1–7; BISHOP, 1992, p. 59, figs. 3, 4, 5b; BISHOP AND BRANNEN, 1992, p. 319, fig. 1; COLLINS, FRAAYE, AND JAGT, 1995, p. 184, fig. 8a, b; JAKOBSEN AND COLLINS, 1997, p. 92, fig. 1B, pl. 1, figs. 1, 5, 7–14; COLLINS, 1997, p. 53, 54, 56, fig. 3.3, 3.4, 3.5.
Homola LEACH, 1815 (part). SCHWEITZER, 2001a, p. 522.
Metahomola COLLINS AND RASMUSSEN, 1992, p. 18. COLLINS, KANIE, AND KARASAWA, 1993, p. 297, fig. 2.2, 2.3.

Type species.—*Latheticocarcinus shapiroi* BISHOP, 1988, p. 378, fig. 1E–H, J, M.

Included species.—*Latheticocarcinus adelphinus* (Collins and Rasmussen, 1992), as *Eohomola*; *L. affinis* (Jakobsen and Collins, 1997), as *Eohomola*; *L. atlanticus* (Roberts, 1962), as *Homolopsis*; *L. brevis* (Collins, Kanie, and Karasawa, 1993), as *Metahomola*; *L. brightoni* (Wright and Collins, 1972), as *Homolopsis*; *L. centurialis* (Bishop, 1992), as *Homolopsis*; *L. declinatus* (Collins,

Fraaye, and Jagt, 1995), as *Homolopsis*; *L. dispar* (Roberts, 1962), as *Homolopsis*; *L. pikeae* (Bishop and Brannen, 1992), as *Homolopsis*; *L. punctatus* (Rathbun, 1917), as *Homolopsis*; *L. schlueteri* (Beurlen, 1928), as *Homolopsis*; *L. shapiroi*; *L. spiniga* (Jakobsen and Collins, 1997), as *Homolopsis*; *L. transiens* (Segerberg, 1900), as *Homolopsis*.

Diagnosis.—Carapace longer than wide (width measured between *lineae homolicae*), typically widest just posterior to intersection of cervical groove and *linea homolica* but relatively uniformly wide throughout entire length, surface granular, ornamented with discrete, large tubercles; rostrum bifid or singular, sulcate; often with small pseudorostral spines; usually with supraorbital spine; protogastric, hepatic, mesogastric, and cardiac regions ornamented with large tubercles; grooves defining lateral margins of mesogastric region deeply incised; cervical groove very deeply incised, arcuate, U-shaped, not typically sinuous, separating the carapace into distinctive anterior and posterior portions; branchiocardiac groove very deep anteriorly, beginning about midway between *linea homolica* and axis, extending axially, curving around and extending laterally to intersect *linea homolica*; *lineae homolicae* very well-developed, sub-hepatic and sub-branchial regions rarely preserved; cardiac region with two swellings positioned beside one another, sometimes with lateral ridges extending onto cardiac regions (MR); cardiac region not well differentiated from branchial regions by deep groove.

Discussion.—Schweitzer (2001a) synonymized *Homola* with *Eohomola*, *Hoplitocarcinus*, *Latheticocarcinsus*, and *Metahomola*. As discussed above, *Hoplitocarcinus* is a separate monotypic genus. *Latheticocarcinus*, *Eohomola*, and *Metahomola* are synonymous and distinct from *Homola*; *Latheticocarcinus* is the senior synonym. The grooves of species of *Homola* are not nearly as deeply incised as those of *Latheticocarcinus*. In *Homola*, the branchiocardiac groove begins anteriorly at the intersection with the *linea homolica*, arcs axially, and then extends laterally again and generally terminates before reaching the *linea homolica* (Fig. 1.1). The branchiocardiac groove of species of *Latheticocarcinus* has a distinctly different conformation as discussed above. In addition, the cervical groove of *Homola* does not separate the carapace into distinctive anterior and posterior portions as is typical of *Latheticocarcinus*. Thus, *Homola* and *Latheticocarcinus* are distinctive genera.

Latheticocarcinus is in many ways very similar to *Homola* but is more similar to the extant *Hypsophrys* which has deeply incised grooves and a branchiocardiac groove that has the same general conformation (Fig. 1.2) as that of species of *Latheticocarcinus*. The cervical groove of *Hypsophrys* is very deeply incised and clearly separates the carapace into an anterior and posterior portion as is so distinctive in *Latheticocarcinus*. However, there are many aspects of the carapace, venter, and appendages that cannot be directly compared because the record of fossil homolids, with few exceptions, is limited to only that part of the carapace between the *lineae homolicae*. The appendages are rarely preserved, and the sub-branchial and sub-hepatic regions are fragmentary in most specimens. The venter is rarely, if ever, known. Thus, it is impossible to compare the number of anterolateral spines on the sub-branchial regions, or the number of orbital spines on the sub-hepatic regions. Also, the length and disposition of the appendages, which is important for Recent homolid systematics, cannot be compared. As suggested by Collins and Rasmussen (1992), it seems best at this point to place the fossil species in the exclusively fossil genus *Latheticocarcinus* until more complete material permits more direct comparison with extant genera that may facilitate synonymy of *Latheticocarcinus* with an extant genus. Because of the numerous similarities between *Latheticocarcinus* and both *Homola* and *Hypsophrys*, it seems clear that both are descendants of *Latheticocarcinus*-like stocks.

TABLE *1*—Species assigned herein to *Latheticocarcinus* and their age and geographic range. Much of the information in this table was derived from Bishop (1992) and Collins (1997).

Species	Age	Geographic occurrence
L. adelphinus	U. Campanian-Maastrichtian	Denmark
L. affinis	Danian	Denmark
L. atlanticus	Campanian	eastern coastal USA
L. brevis	Turonian	Japan
L. brightoni	Albian-Cenomanian	Britain
L. centurialis	Campanian	Western Interior, USA
L. declinatus	Maastrichtian	Netherlands
L. dispar	Campanian	eastern coastal USA
L. ludvigseni new species	early Santonian	Coastal British Columbia
L. pikeae	Cenomanian	Western Interior, USA
L. punctatus	Campanian-Maastrichtian	Western Interior, USA
L. schlueteri	Campanian	Northern Europe
L. shapiroi	Maastrichtian	Western Interior, USA
L. spinigus	Danian	Denmark
L. transiens	Danian	Denmark

Most of the species herein assigned to *Latheticocarcinus* were originally referred to *Homolopsis* (Table 1). *Eohomola* and *Metahomola* are now subjective synonyms of *Latheticocarcinus*; thus, all of the species assigned to those two genera are now embraced within *Latheticocarcinus*. The North American species *Homolopsis atlanticus*, *Homolopsis centurialis*, *Homolopsis dispar*, *Homolopsis pikeae*, and *Homolopsis punctatus* all possess a deep, arcuate cervical groove; and the conformation of the branchio-cardiac groove; narrow carapace; transverse metabranchial ridge extending laterally from the cardiac region; and development of carapace regions are typical of *Latheticocarcinus*. *Homolopsis brightoni* has the arcuate, non-sinuous cervical groove; broad cardiac region; transverse metabranchial ridges extending from the cardiac region; and indistinctly separated cardiac and branchial regions typical of *Latheticocarcinus*. *Homolopsis declinata* has well-developed pseudorostral spines, a deep, arcuate cervical groove, and indistinct separation of the cardiac and branchial

regions typical of *Latheticocarcinus* and lacks the projection from the lateral margin marking the point of maximum width as seen in *Homolopsis*. *Homolopsis schlueteri*, although not well illustrated, has the arcuate, deep cervical groove and poor separation of cardiac and branchial regions typical of *Latheticocarcinus*.

Homolopsis spiniga and *H. transiens* differ from typical *Latheticocarcinus*, and for that matter from *Homolopsis*, in being broadest in the anterior portion of the carapace. In all other respects, however, those two species are similar to members of *Latheticocarcinus*. *Homolopsis atlanticus*, *H. brightoni*, and *H. punctatus* are also widest in the anterior portion of the carapace. In addition, these latter three species and *H. transiens* have a more sinuous cervical groove than other species of the genus; however, *H. spiniga* has the smoothly arcuate cervical groove typical of the genus. Because these differences appear to be gradational, these species are placed within *Latheticocarcinus*. With the exception of the minor differences listed in these latter five species, the morphological composition of *Latheticocarcinus* is remarkably conservative and is distinctive and well constrained.

The earliest known species of *Latheticocarcinus* is *L. brightoni* from Albian rocks of Britain. By the middle Late Cretaceous, the genus was well established in the middle to high northern latitudes, either dispersing via Polar routes to Japan and the Pacific coast of North America or via the Atlantic Ocean and Tethys to the Western Interior of the United States (Table 1). Both polar and Tethyan dispersal routes have been well documented for Cretaceous and Paleocene decapod crustaceans (Schweitzer, 2001b).

LATHETICOCARCINUS LUDVIGSENI new species
Figures 2, 3

Homolopsis sp. LUDVIGSEN AND BEARD, 1994, p. 125–126, fig. 96.

Diagnosis.—Carapace longer than wide; rostrum deeply bifid; pseudorostral spines small, triangular; supra-orbital spine broad at base and slender at tip, directed anterolaterally; regions granular and ornamented with large, discrete tubercles; lateral margins weakly convex.

Description.—Carapace longer than wide (width measured between *lineae homolicae*), width about 78 percent length, widest just posterior to cervical groove; *lineae homolicae* well developed; sub-hepatic and sub-branchial regions unknown; regions well defined by deeply incised grooves; surface granular, ornamented with large, discrete tubercles; rostrum and post-rostral area depressed well below level of inflated protogastric regions, carapace thus strongly vaulted longitudinally in anterior quarter of carapace.

Rostrum bifid, spines separated to bases; axially sulcate; rostral

FIGURE 2—*Latheticocarcinus ludvigseni* n. sp., dorsal carapace of holotype, GSC 124842. Scale bar = 1 cm. Note that carapace lacks the portions distal to the *lineae homolicae* due to breakage along the *lineae*.
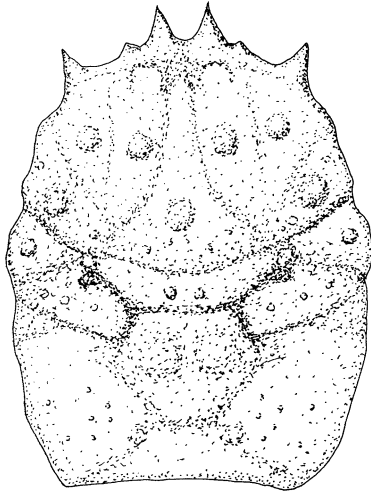
FIGURE 3—Line drawing of *Latheticocarcinus ludvigseni* n. sp.

width, measured at bases of spines about one-quarter maximum carapace width; pseudo-rostral spines small, blunt, triangular. Supraorbital spine broad at base and needlelike at tip, directed slightly anterolaterally, width between supraorbital spines about two-thirds maximum carapace width. Anterolateral and posterolateral margins continuous, sinuous, weakly convex, defined by cleavage at lineae homolicae. Posterior margin weakly convex, about 70 percent maximum carapace width.

Post-rostral region sulcate, depressed; epigastric regions rectilinear, equidimensional, most inflated anteriorly. Protogastric region very inflated, broad, triangular, defined by shallow groove laterally, with two large tubercles placed beside one another and with weak longitudinal sulcus between them. Mesogastric region with long anterior process, process terminating at base of epigastric regions; widened posteriorly, with large central tubercle; two gastric pits just anterior to deep cervical groove which defines convex posterior margin of region. Metagastric region widest of axial regions and widest anteriorly, lateral margins converging posteriorly, with two small swellings axially. Urogastric region very narrow, with constricted lateral margins and weakly concave upper and lower margins. Cardiac region pentagonal, all sides nearly straight; anteriormost side shared with urogastric region, anteriormost lateral sides short, posteriormost lateral sides long; two broad central swellings beside one another. Intestinal region large, depressed, widening posteriorly.

Hepatic regions rectangular, oriented obliquely axially, with large central swelling and several smaller tubercles. Cervical groove deeply incised, continuous across axis, broadly concave, not sinuous, distinctly separating carapace into anterior and posterior portions. Branchiocardiac groove tightly U-shaped, beginning about half the distance axially from lateral margin, arcing very deeply along lateral margin of meta- and urogastric regions and anteriormost cardiac region, then curving anteriorly and extending laterally to margin (Fig. 1.3); nearly straight segments diverge from very deep margin of metabranchial region to form posterior margin of that region.

Epibranchial regions elongate, directed obliquely axially with several large tubercles arranged centremainder of branchial regions undifferentiated; with straight, weak transverse ridge extending laterally from cardiac region; with numerous large granules and large tubercles situated near triple junction of branchial, cardiac, and intestinal regions.

Remainder of carapace, appendages, and ventral aspect of carapace unknown.

Measurements.—Measurements (in mm) of the holotype and sole specimen: maximum width, 10.7, maximum length, 13.7, fronto-orbital width, 6.8, rostral width (measured at base of rostral spines), 2.6, posterior width, 7.6.

Etymology.—The name honors Rolf Ludvigsen, British Columbia, Canada, for his support of amateur paleontology in that region.

Type.—The holotype, GSC 124842, is deposited in the Geological Survey of Canada Type Collections in Ottawa, Ontario, Canada. The specimen illustrated by Ludvigsen and Beard (1994) is deposited in the Vancouver Island Paleontological Museum in Qualicum Beach, British Columbia, Canada.

Occurrence.—The holotype was collected from float along the Trent River, Vancouver Island, B.C., about 7.2 km west of highway 19A on Bayton Main Logging Road at the former site of a logging bridge, at lat. 49°35′30.5″N, long. 124°59′28.4″W, from early Santonian rocks of the lower Haslam Formation. The block in which the holotype was found contained *Polyptychoceras* sp. The specimen illustrated by Ludvigsen and Beard (1994) was collected from late Campanian to early Maastrichtian rocks of Hornby Island.

Discussion.—The sole specimen has a well-preserved rostrum and orbits, which is unusual for fossil specimens of the family. The posterior portion of the carapace lacks cuticle; thus, details about its ornamentation are unknown except that it appears to have been granular.

Latheticocarcinus ludvigseni differs from all other species of the genus in having a strongly bifid rostrum. No other species displays such a distinctly and broadly bifid rostrum. In addition, the new species has well-developed, long supra-orbital spines, not seen in other species of the genus. *Latheticocarcinus ludvigseni* is most like *L. adelphinus* but differs from it in having more convex lateral margins. Those of *L. adelphinus* are nearly straight. The epibranchial regions of *L. pikeae* are much more narrow and ridge-like than those of *L. ludvigseni*. *Latheticocarcinus punctatus* has scabrous ornamentation, especially on the cardiac and branchial regions, which *L. ludvigseni* lacks. *Latheticocarcinus atlanticus* has granular ornamentation on the large tubercles, while those of *L. ludvigseni* are not ornamented. *Latheticocarcinus dispar* has an axially interrupted cervical groove whereas that of the new species is continuous. The carapace grooves of *L. brevis* are more deeply incised than those of *L. ludvigseni*, especially those surrounding the cardiac region. *Latheticocarcinus brightoni* lacks large tubercles on the dorsal carapace; large tubercles are present in the new species. *Latheticocarcinus declinatus* is more narrow and elongate than the new species and has much more poorly developed transverse projections from the cardiac region than does *L. ludvigseni*. The new species differs from *L. spinigus* and *L. transiens* because *L. spinigus* and *L. transiens* are broad anterolaterally whereas *L. ludvigseni* is not.

The occurrence of *Latheticocarcinus ludvigseni* in Santonian (Cretaceous) rocks of British Columbia marks the earliest geologic occurrence of the genus on the Pacific coast of North America. By Turonian time, *Latheticocarcinus* was established in the Northern Atlantic, the northwestern Pacific, and the Western Interior, so that the rootstock for the new species may have invaded the eastern Pacific slope from any one of these areas, as each dispersal pattern has been documented previously for decapods (Schweitzer, 2001b).

Genus PAROMOLOPSIS Wood-Mason *in* Wood-Mason and Alcock, 1891

Paromolopsis WOOD-MASON *in* WOOD-MASON AND ALCOCK, 1891, p. 268; ALCOCK, 1899, p. 11, 1900, p. 160, 1901, p. 65; BOUVIER, 1896, p. 37, 38; ORTMANN, 1901, p. 1156; IHLE, 1913, p. 54, 60, 61, 73;
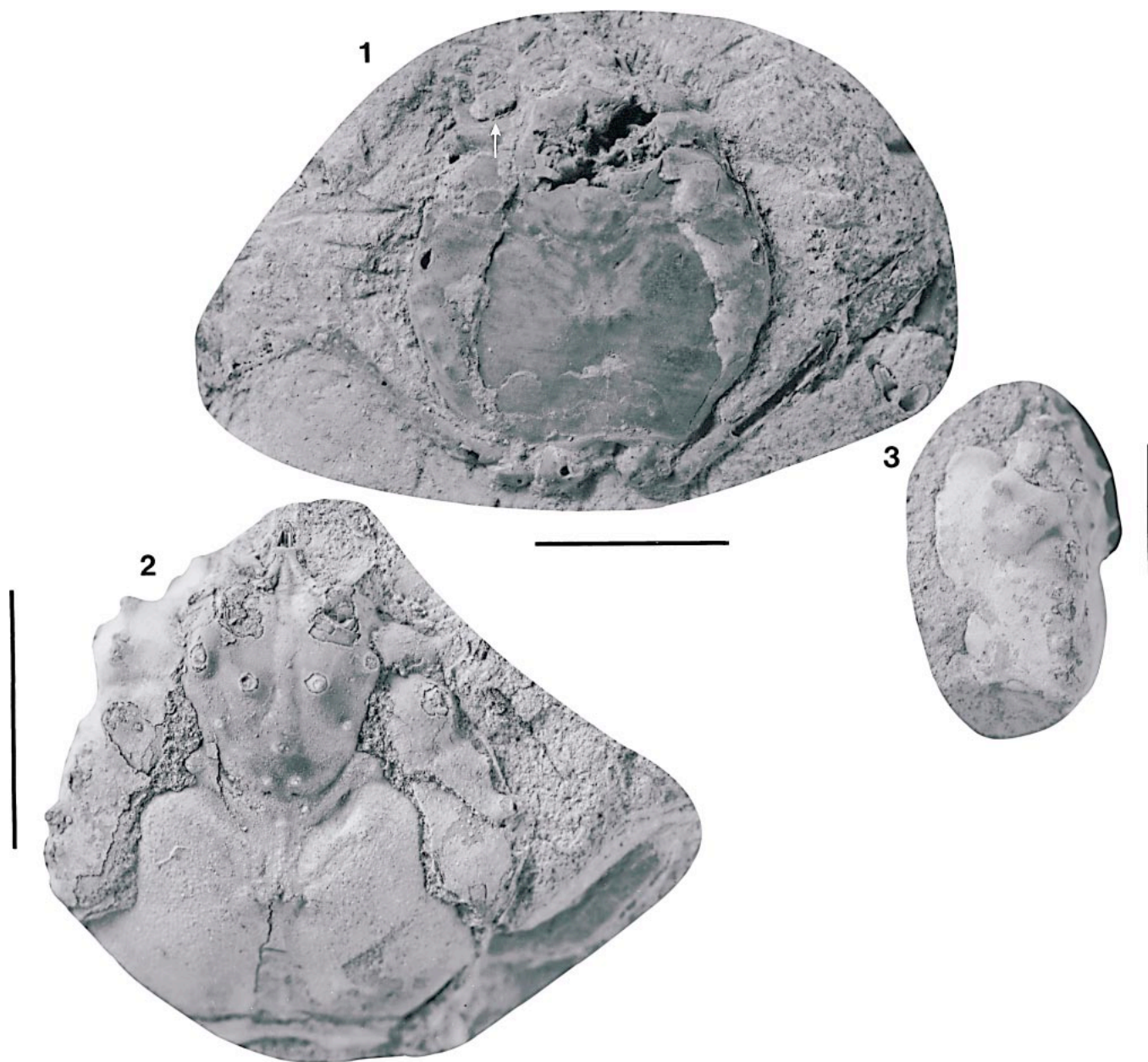
FIGURE 4—*Paromolopsis piersoni* new species. *1,* dorsal view of carapace, paratype UWBM 97179; note breakage along *linea homolica* and thin, long, pereiopod; arrow indicates eye; *2,* dorsal view of carapace of holotype, UWBM 97178; *3,* lateral view of holotype, UWBM 97178. Scale bars = 1 cm.

SERÉNE AND LOHAVANIJAYA, 1973, p. 23, 29; GUINOT, 1979, p. 232; GUINOT AND RICHER DE FORGES, 1981, p. 540.

Type Species.—*Paromolopsis boasi* Wood-Mason *in* Wood-Mason and Alcock, 1891.

Extant Species.—*Paromolopsis boasi* Wood-Mason *in* Wood-Mason and Alcock, 1891, p. 268, fig. 5.

PAROMOLOPSIS PIERSONI new species
Figures 4, 5

Diagnosis.—Carapace urn-shaped, flat, widest across branchial region, ornamented with supra-orbital, subhepatic, and anterolateral spines anteriorly, length about 90 percent total carapace width. Carapace regions well defined anteriorly and laterally, carapace smooth posteriorly. Rostrum simple, composed of single,

triangular, weakly upturned spine. Orbits poorly defined. Eyes hemispherical, basal article short. *Linea homolica* well developed, within the lateral borders. Posterior margin deeply concave. Mesogastric region flask-shaped. Urogastric region triangular, defined by closely spaced, deep cervical and branchiocardiac grooves. Cardiac region very small, weakly pentagonal. Branchial regions weakly inflated, smooth. Cervical and branchiocardiac grooves well defined.

Description.—Carapace subrectangular, urn-shaped, flat; longer than wide, widest across branchial region; length about 90 percent total carapace width; length equal to width without rostrum; anterior and lateral carapace regions well defined by broad, deep grooves, tubercles, and inflated regions; posterior carapace smooth, weakly inflated; carapace surface finely granular becoming densely granular on tubercles. Rostrum simple, triangular,
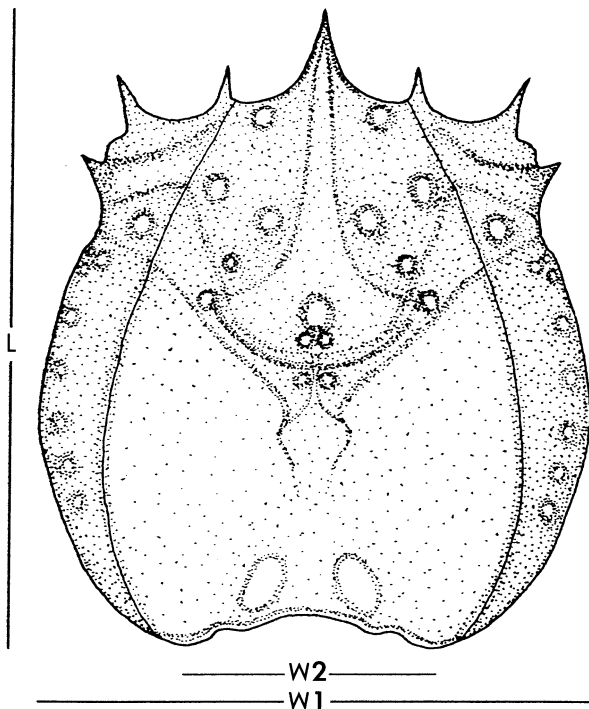
FIGURE 5—Reconstruction of *Paromolopsis piersoni*, with position and orientation of measurements indicated.

composed of one sharp, weakly upturned spine; strongly rimmed laterally and ridged medially. Orbits not well defined, incomplete, weakly sinuous, gently sloping laterally and posteriorly to acute, forward directed, supra-orbital spine and continuing laterally to sharp, forward directed sub-hepatic spine curving weakly laterally. Eyes hemispherical, basal article short; eyes rest in depressed hepatic region.

Anterolateral margin short, sinuous; acute anterolateral spine situated about midwidth; remainder of margin deeply concave. Posterolateral margin continuous, rounded. Posterior margin sinuous, strongly rimmed, centrally deeply concave. *Linea homolica* well developed, well within the lateral borders; terminating anteriorly at inner base of outer-orbital spine. *Linea homolica* and supra-orbital region situated anterior of anterolateral spine.

Epigastric and protogastric regions poorly differentiated, inflated, especially anteriorly; ornamented with four tubercles; first centered, proximal to orbital rim; second parallel to anterolateral spine and adjacent to *lineae homolica*; third just posterior to first, proximal to mesogastric region; fourth small, medially situated, proximal to mesogastric-cervical groove constriction. Mesogastric region flask-shaped; very narrow anteriorly, forming ridge from tip of rostrum, extending posteriorly, where it becomes triangular, rounded; with one large conical tubercle, centered posteriorly and two small tubercles just posterior and on either side to first; separated laterally by shallow depressions and posteriorly by deep cervical groove. Urogastric region triangular, apex directed posteriorly, not differentiated from cardiac region; defined by closely spaced, deep cervical and branchiocardiac grooves; ornamented with large tubercle on lateral corners, proximal to *linea homolica*. Cardiac region very small, weakly pentagonal; extending, without separation, from urogastric region to weakly elevated ridge at about midwidth of epibranchial region; depressed anteriorly, with no separation from branchial region. Intestinal region depressed, not well differentiated.

Hepatic region small, inflated, with sharp anterolateral spine directed laterally; hepatic region combined with subhepatic region, horseshoe shaped; ornamented with numerous spines arranged in a semi-circle starting with the anterolateral spine and terminating with the subhepatic spine. Epibranchial region inflated, weakly triangular, apex directed laterally; ornamented with one large centrally placed tubercle; separated from hepatic and branchial regions by deep cervical and branchiocardiac grooves. Mesobranchial region anteriorly inflated, flattened posteriorly; ornamented laterally with numerous tubercles paralleling and curving posteriorly along anterolateral margin. Metabranchial region, a small swelling situated on either side of intestinal region.

Fifth pereiopod partially preserved; merus very long, terminating in an upper marginal, triangular spine. Remainder of appendages and venter unknown.

Etymology.—The trivial name honors Guy Pierson, of Oregon, U. S. A., an avid amateur paleontologist, who collected one of the specimens.

Types.—The holotype, UWBM 97178, and paratypes UWBM 97179 and 97180, are deposited at the Burke Museum of Natural History and Culture, University of Washington, Seattle, U.S.A.

Measurements.—Measurements (in mm) taken on the dorsal carapace of the holotype UWBM 97178 are: L, length of dorsal carapace = 20.6; and W1, maximum carapace width = 18.1. Measurements (in mm) taken on the dorsal carapace of the paratype UWBM 97179 are: W1, maximum carapace width = 20.4; and W2, posterior width = 9.5. Position and orientation of measurements are shown in Figure 5.

Occurrence.—The holotype and paratypes were collected from upper part of the Astoria Formation in the SE¼, sec. 19, T10S, R11W of the Yaquina Quadrangle, Lincoln County, Oregon; 15 minute series topographic map. At this locality, fossil decapods are preserved within calcareous nodules, mainly within lenses along the wave-cut bench exposures or as float. Stratigraphically, this part of the Astoria Formation lies above a two meter tuff unit that has been dated to ±16.6 Ma, near the top of paleomagnetic Chron C5Cn3 (Prothero et al., 2001, p. 280). It is overlain by the Cape Foulweather (Gingko) basalt flow of the Columbia River Basalt Group, which has been dated at 15.4 ± 0.3 Ma (Prothero et al., 2001). This would place the fossil decapod crustaceans at this locality within the late early to early middle Miocene.

Discussion.—The new species is based upon three well- to moderately well-preserved specimens. The holotype UWBM 97178, consists of a well-preserved dorsal carapace. The paratype UWBM 97179, preserves the posterior portion of the dorsal carapace, preserving part of the eye, eyestalks, and antennae. It also preserves part of the fifth pereiopod, and the distinct *linea homolica*. The paratype UWBM 97180, appears to represent a molt of *P. piersoni*, preserving the dorsal carapace of all except for the frontal region and the lateral and subhepatic portions of the carapace.

Paramolopsis piersoni is referred to the family Homolidae based upon its possession of a *linea homolica*, which is diagnostic for the family. *Paramolopsis piersoni* is referred to the genus *Paramolopsis*, based upon a length to width ratio of 89 percent, and a length equal to width, when measured without the rostrum; a flat, urn-shaped carapace, that is weakly ornamented by tubercles and spines; well-defined *lineal homolicae* and cervical groove; supra-orbital region that is situated anterior of the anterolateral spine; a simple, triangular rostrum; and a similar configuration of spines along the frontal margin as described for the genus. Only the genus *Paramolopsis* possesses these combined dorsal carapace morphological characteristics.

The genus *Paramolopsis* was designated based upon one extant species, *P. boasi*, known today from the Indian and the Western Pacific Oceans (Wood-Mason *in* Wood-Mason and Alcock, 1891; Guinot and Richer de Forges, 1995). Guinot and Richer de Forges

(1995, p. 366) questioned the validity of just one species from all of the known localities of *P. boasi*, pointing out differences in the dorsal carapace ornamentation from virtually smooth, to having scattered, small tubercles, and bearing frontal spines of different sizes. They believed that *P. boasi* most likely comprises more than one species.

Paramolopsis piersoni can be distinguished from *P. boasi* in having well-defined tubercles on the protogastric and mesogastric regions, and a longitudinal row of tubercles paralleling the lateral margin. In addition, *P. piersoni* can be distinguished from *P. boasi* in having a much more reduced cardiac region and two swellings on either side of the intestinal region.

Superfamily HOMOLODROMIOIDEA Alcock, 1900

Included families.—Homolodromiidae Alcock, 1900; Prosopidae von Meyer, 1860.

Discussion.—Numerous authors have compared the Homolodromiidae to the Prosopidae, some suggesting that the Prosopidae is the ancestral form (Glaessner, 1969; Guinot, 1978, 1995; Förster et al., 1985; Müller et al., 2000). Other authors have previously referred the Prosopidae to the Homolodromioidea without discussion (Glaessner, 1980; Collins, Kane, and Karasawa, 1993; Via and Sequeiros, 1993). Glaessner (1969) went as far as to classify the Homolodromiinae as a subfamily of the Prosopidae, and Müller et al. (2000) suggested that the Homolodromiidae were the direct descendants of the Prosopidae. Guinot (1995, p. 265) suggested that fossil taxa referred to the Prosopidae may be referable to the Homolodromiidae but that a decision must await discovery and examination of ventral material and appendages of prosopids. As it stands now, each family has a fossil record extending into the Jurassic, but only the Homolodromiidae is represented in modern oceans. It seems quite possible that as studies on these groups continue, the Prosopidae and the Homolodromiidae may be considered synonymous. At the least, the Prosopidae must be referred to the Homolodromioidea, demonstrating the affinity between the two families.

Family HOMOLODROMIIDAE Alcock, 1900

Type genus.—*Homolodromia* A. Milne Edwards, 1880.

Included genera.—*Antarctidromia* Förster, Gaździcki, and Wrona, 1985 (fossil only); *Dicranodromia* A. Milne Edwards, 1880 (fossil and extant); *Eoprosopon* Förster, 1986 (fossil only); *Homolodromia* A. Milne Edwards, 1880 (fossil and extant); *Palehomola* Rathbun, 1926 (fossil only); *Rhinodromia* new genus (fossil only).

Diagnosis.—Carapace longer than wide; lacking well-defined orbits; eyes resting in concavity formed by orbital spines or by subhepatic region; two forward-directed lateral rostral spines positioned at base of central rostral spine if present, sometimes fused into a single bifid structure, lateral rostral spines appear to originate on dorsal carapace; central rostral spine variable, may be absent, tiny, downturned, or attenuated; subhepatic region inflated, sometimes markedly so; other subdorsal areas may be well-developed; cervical and branchiocardiac grooves moderately well defined, parallel to one another; regions indistinct in extant forms and well developed in most fossil forms; appendages typically slender, sometimes long, pereiopod 5 usually carried dorsally; abdominal somites with flangelike pleurae.

Discussion.—The Homolodromiidae has a well-established fossil record; in fact, all of the referred genera are known as fossils. Guinot (1995) examined all of the known fossil genera and added *Eoprosopon* based upon the resemblance of its abdomen, pereiopods, and dorsal carapace to extant *Homolodromia*. Homolodromiids are fairly distinctive, primitive crabs which superficially resemble homolids but which lack *lineae homolicae*. The carapace is longer than wide and lacks distinctive anterolateral and posterolateral margins; instead, they are confluent. Homolodromiids lack well-defined orbits; the eyes arise from the area ventral to the rostrum, and they typically rest in a concavity that can be formed by outer-orbital and suborbital spines or by the subhepatic region. Homolodromiids often have well-developed subhepatic regions, and especially in fossils, have well-developed subbranchial regions. In modern forms, the cervical and branchiocardiac grooves are parallel to one another and extend across the carapace at nearly right angles to the axis; in fossil forms, the two grooves are sometimes oriented at more oblique angles, as in *Antarctidromia*, *Palehomola*, and *Rhinodromia* new genus. Carapace regions can be distinct, especially in fossil forms, but extant taxa usually have subdued development of regions. In addition, extant forms differ from fossils forms in having a soft, fragile, poorly-calcified carapace (Guinot, 1995) and typically have long, slender legs; both of these may be adaptations to deepwater environments in which extant taxa live (Feldmann and Wilson, 1988; Báez and Martin, 1989; Guinot, 1995). Feldmann and Wilson (1988) suggested that the family may have arisen in shallow-water environments, based upon the occurrence of the Eocene *Homolodromia chaneyi* Feldmann and Wilson, 1988 in shallow-water sediments. Müller et al. (2000) also demonstrated that early primitive crabs, specifically the Prosopidae, inhabited shallow water environments in northeastern Europe. *Homolodromia chaneyi*, as well as the Cretaceous *Rhinodromia richardsoni* (Woodward, 1896) new combination discussed below, have stouter, shorter appendages that might be better adapted to shallow-water environments. The move to deeper water environments, and thus evolution of longer, more slender appendages, appears to have occurred later in the Tertiary, possibly in the Oligocene, as *Palehomola gorrelli* and *Antarctidromia inflata* Förster et al. (1985) have relatively long, slender appendages.

The rostral area of homolodromiids is quite distinctive and variable. Unfortunately, there have been at least four separate sets of terminology used to define structures of this area. Garth (1973) originally called the two prominent spines at the base of the rostral area in *Homolodromia* rostral "horns." Báez and Martin (1989) described the front of *Homolodromia* as bifid, referring to the two "horns." Guinot (1995) noted that there are two types of rostral areas in the family; she described the *Homolodromia*-type as lacking a rostrum and possessing two pseudorostral spines ("horns" of Garth and bifid rostrum of Báez and Martin). *Dicranodromia* was described by Guinot (1995) as having a tiny rostrum, which is essentially a small spine, and two pseudorostral spines ("horns" of Garth); the rostrum lies below the level of the pseudorostral spines. Förster et al. (1985) described the front of *Antarctidromia* as having a frontal spine (rostrum of Guinot, 1995) below the level of two pre-orbital spines ("horns" of Garth and pseudorostral spines of Guinot). All of this miscellaneous terminology refers to the same general structures, all of which we consider to be part of the rostral area. The term "horns" is an apt descriptor, as the two spines give the animal the appearance of a horned owl. However, "horns" is colloquial and may be confusing to non-English speakers. The term "pseudorostral" suggests that the spines are not part of the rostrum, thus we do not believe that it is an appropriate term, and "pre-orbital" is not appropriate either as there is no true orbit in homolodromiids. It is suggested that the term "lateral rostral spines" be used for the two lateral structures, as it is the most descriptive term for the structures. We suggest the term "central rostral spine" for the axial spinelike structure described as "rostrum" by Guinot (1995) and described as "frontal spine" by Förster et al. (1985). We believe that this is the least confusing and most consistent method by which to described these rostral structures. This discussion is intended to clarify this terminology, and it would be helpful if
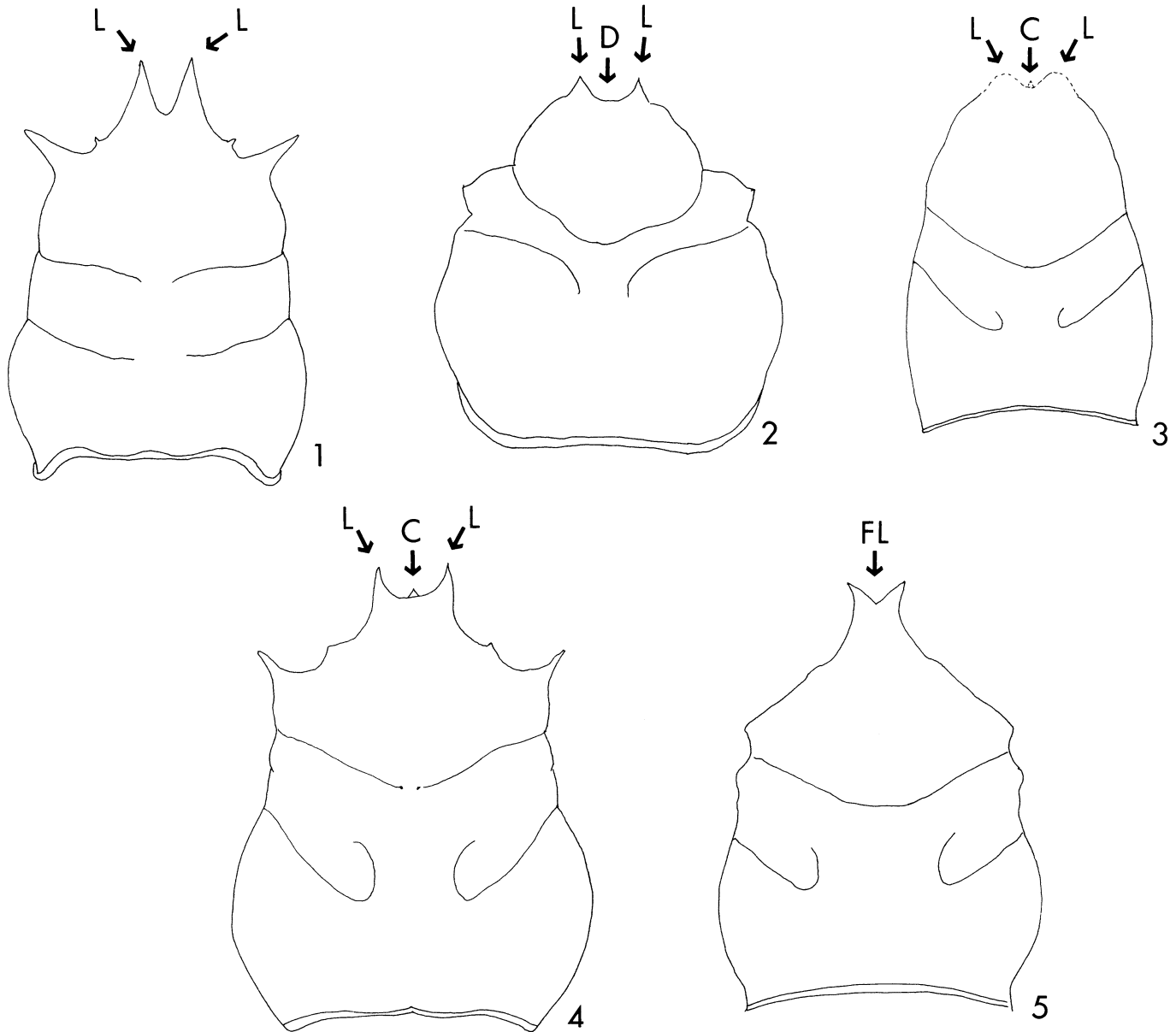
FIGURE *6—1,* Generalized line drawings of five homolodromiid genera, showing the dorsal carapace and the position of the lateral and central rostral spines. Note the lack of *lineae homolicae*. C = central rostral spine, D = down-turned central rostral spine not visible in dorsal view, FL = fused lateral rostral spines, L = lateral rostral spines. *1,* Outline of *Antarctidromia inflata* redrawn from Förster et al. (1985, fig. 4); *Dicranodromia* also exhibits this rostral area type; *2, Palehomola gorelli*, note presence of down-turned cental rostral spine not visible in dorsal view; *3, Eoprosopon klugi* Förster, 1986, redrawn from Förster (1986, figure 1); *4, Homolodromia* spp., redrawn from Guinot (1995, fig. 2B); *5, Rhinodromia richardsoni.*

consistent terminology was used for this area of the carapace. Note that the terminology used for the rostral area of the Homolidae is different than that used for the Homolodromiidae.

Based on evaluation of this terminology and the material redescribed herein, there are three rostral-area types within the Homolodromiidae. One rostral type is characterized by two forward projecting lateral rostral spines which originate in some cases on the dorsal carapace, and lack of a central rostral spine (Fig. 6.1) as seen in *Homolodromia*. The second rostral type has a central rostral spine, which may be tiny, downturned, attenuated, in addition to the two lateral rostral spines (Fig. 6.4) as seen in *Antarctidromia*, *Dicranodromia*, and *Palehomola*. This type of rostral area was inferred by Förster (1986) for *Eoprosopon* (Fig.

6.3). *Palehomola gorrelli* exhibits a downturned, sulcate, triangular central rostral spine and two lateral rostral spines (Fig. 6.2). The third rostral type is characterized by the absence of a central rostral spine and possession of lateral rostral spines that are fused into a bifid structure (Fig. 6.5). *Rhinodromia* exhibits this type.

The only other family with which members of the Homolodromiidae may be confused is the Poupiniidae Guinot, 1991. Members of the Poupiniidae resemble homolodromiids in possessing distinctive carapace grooves, an elongate carapace, and spines in the rostral area. However, members of the Poupiniidae have more ovate carapaces, much better-developed rostral and anterolateral spines, and narrower orbital regions than members of the Homolodromiidae (Feldmnan et al., 1993).

The earliest known homolodromiid is *Eoprosopon* from the late early Jurassic of Germany (Förster, 1986). *Rhinodromia* was collected from Cretaceous rocks of coastal British Columbia. *Homolodromia* is an extant genus also known from Eocene rocks of Seymour Island, Antarctica (Feldmann and Wilson, 1988), and *Antarctidromia* is known from Miocene rocks of King George Island, South Shetland Islands (Förster et al., 1985). *Dicranodromia* sp. has been reported from Miocene rocks of Japan (Takeda et al., 1986). The referral of the Oligocene *Palehomola* to the family does not extend its geologic range but does extend its geographic range to the western coast of North America. Thus, the family appears to have arisen in epicontinental Europe during the Jurassic. Dispersal to the Pacific Northwest of North America during the Mesozoic may have resulted from Arctic dispersal routes, as the pole was ice-free during much of this time. The overall bipolar distribution of the family in Tertiary rocks could be a result of the breakup of Pangaea, separating formerly continuous populations (Crame, 1993, 1996). A similar paleobiogeographic pattern in the Mesozoic is seen in the closely related Homolidae as well as many other decapod taxa (Schweitzer, 2001b; Schweitzer et al., 2002).

Genus PALEHOMOLA Rathbun, 1926

Palehomola RATHBUN, 1926, p. 86, pl. 21, figs. 1, 2. GLAESSNER, 1969, p. R490; COLLINS, 1997, p. 64; SCHWEITZER, 2001a, p. 522.

Type and sole species.—*Palehomola gorrelli* Rathbun, 1926, by monotypy.

Diagnosis.—As for species.

Description.—As for species.

Discussion.—The systematic placement of *Palehomola gorrelli* has been troublesome. Rathbun (1926, p. 86) described the *linea homolica* as "partially visible on left side." Glaessner (1969) questionably placed the genus within the Homolidae. Collins (1997) also placed *Palehomola* within the Homolidae, but subsequently Schweitzer (2001a) suggested that *Palehomola* should be removed from the Homolidae based upon its lack of *lineae homolicae*. Nyborg (2002) concurred with Collins (1997) in believing it to possess *lineae homolicae*. Reexamination of the holotype by two of us (CS and RF) leads to the conclusion that *P. gorrelli* lacks *lineae homolicae* and should thus be removed from the Homolidae.

The dorsal carapace of the sole specimen of *Palehomola gorrelli* was crushed, probably just before or during burial, and the resulting cracks and displaced areas are suggestive of, and superficially similar to, *lineae homolicae*. On the left side, as mentioned by Rathbun (1926), the carapace is fractured beginning approximately 2 mm ventral to the left rostral spine and extending posteriorly, essentially paralleling the lateral margin of the carapace. At about two-thirds the distance posteriorly, the fracture makes a right angle turn axially and then turns again sharply to continue in a sinuous path to the posterior margin. Such a path is not consistent with any known *lineae homolicae* in confirmed homolids. Further, the left branchial region posterior to the right angle turn of the fracture, where the linea would be expected to extend, is entire and shows no evidence of a *linea* (Fig. 7.1, left arrow, Fig. 7.3, arrow). On the right side of the carapace, a fracture begins approximately 3 mm ventral to the right rostral spine and extends posteriorly, taking a very similar path to the fracture of the left side, until it terminates about two-thirds of the distance posteriorly in the middle of the branchial region. The remainder of the branchial region is entire and shows no evidence whatsoever of a fracture that breaks through the entire cuticle or a *linea*. Further, the anterior portion of the right fracture, where it is similar to that of the left fracture, exhibits conchoidal fracture of the dorsal carapace material which is preserved as a black, possibly

manganiferous, substance. This conchoidal fracture, when examined under a binocular microscopic, does not appear to penetrate the entire dorsal carapace. Thus, the path of the right fracture is in part an artifact of the conchoidal fracturing of the dorsal carapace material. In addition, the appearance that the left and right fractures take the same path, at least anteriorly, may be an illusion, because the left portion of the carapace, ventral to the fracture, seems to have been displaced and pushed up and under the dorsal carapace somewhat. All of this evidence strongly indicates that this animal lacked *lineae homolicae*.

There are other aspects of the dorsal carapace that do not resemble those of typical homolids. The subhepatic region is usually developed in homolids, but it is not usually as large or as prominent as in *Palehomola gorrelli*. The rostrum in homolids is usually bifid, while that of *P. gorrelli* is characterized by two lateral rostral spines and a downturned, central rostral spine. Homolids usually do not have the marked lateral rostral spines as in *P. gorrelli*. *Palehomola* is actually much more easily embraced by the Homolodromiidae, a family similar to, but with significant differences from, the Homolidae. Homolodromiids lack *lineae homolicae*, probably the biggest single feature separating the two families. Homolodromiids, especially the fossil forms, often have large, inflated subhepatic and other subdorsal regions, as seen in *P. gorrelli*. Many homolodromiids have two lateral rostral spines and a central rostral spine, which *P. gorrelli* exhibits. The abdominal somites of homolodromiids often have pronounced pleurae, which are seen in *P. gorrelli*, and which do not appear to be prominent in homolids, based upon examination of illustrations in Guinot and Richer de Forges (1995). Thus, placement of *P. gorrelli* within the Homolodromiidae is well justified.

Palehomola differs from all other homolodromiids in its ovate, nearly equant shape, its very large and inflated subhepatic regions, its oblique cervical and branchiocardiac grooves, and its frontal area with a downturned, axially sulcate central rostral spine and two lateral rostral spines. No other homolodromiid exhibits this combination of features. *Palehomola* is most similar morphologically to *Antarctidromia*. *Antarctidromia* possesses distinct carapace regions, including well-developed subhepatic and sub-branchial regions as in *Palehomola*. The configuration of the front in *Antarctidromia* is similar to that of *Palehomola*, but the rostrum of *Antarctidromia* is quite attenuated. The cervical and branchiocardiac grooves of *Antarctidromia* are oriented oblique to the axis as in *Palehomola*, but the branchiocardiac groove is much deeper and better developed in *Antarctidromia* than in *Palehomola*.

Homolodromia spp. are more rectangular than *Palehomola* and they have cervical and branchiocardiac grooves that are nearly perpendicular to the axis. In addition, the subhepatic regions of *Homolodromia* are not nearly as inflated as those of *Palehomola*, and the front of *Homolodromia* has two lateral rostral spines and no axial rostrum. Members of *Dicranodromia* have a small, spine-like central rostral spine that differs significantly from the downturned, triangular, sulcate central rostral spine of *Palehomola*, and the gastric regions of *Dicranodromia* are much longer and occupy more of the carapace than do those of *Palehomola*, in which the branchial regions are large. The carapace of *Eoprosopon*, although not well preserved, is broadly triangular in shape, heavily ornamented, and has a deep cervical groove; none of these features characterize *Palehomola*. Thus, *Palehomola* is a distinct, monotypic genus.

PALEHOMOLA GORRELLI Rathbun, 1926
Figure 7

Palehomola gorrelli RATHBUN, 1926, p. 86, pl. 21, figs. 1, 2. COLLINS, 1997, p. 64; SCHWEITZER, 2001a, p. 522.

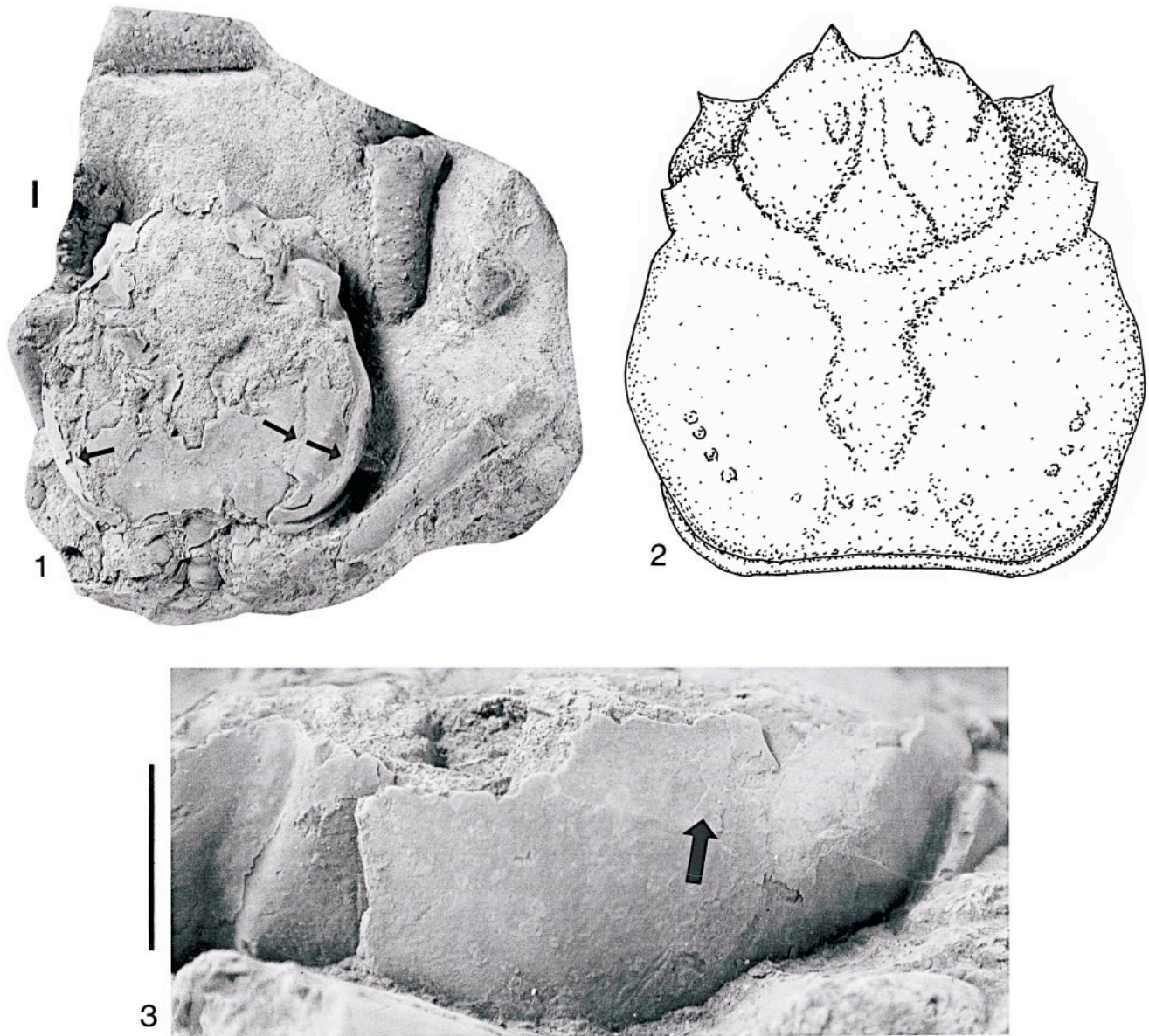*Diagnosis.*—Carapace slightly longer than wide, W/L about

FIGURE 7—*Palehomola gorrelli*, holotype, USNM 352912. *1,* dorsal carapace, arrows indicate position of fractures or conchoidal breaks that superficially resemble *lineae homolicae*; *2,* line drawing, emphasizing lateral rostral spines and other diagnostic features; *3,* oblique posterolateral view of holotype, arrow indicates position where *lineae homolicae* would be expected if it were present. Scale bars = 1 cm.

0.90, ovate; branchial regions bulbous and convex; lateral sides steep, rounded; central rostral spine downturned, sulcate, triangular; lateral rostral spines stout, directed forward; subhepatic region large, inflated, with large triangular spine; subepibranchial region inflated, with large tubercle; cervical groove moderately well developed; branchiocardiac groove weakly developed; appendages long, slender, granular; male abdominal somites with pleurae.

Description of holotype.—Carapace slightly longer than wide, W/L = 0.90, widest about two-thirds the distance posteriorly on carapace; ovate; branchial regions bulbous and convex; lateral sides steep, rounded, no indication of *lineae homolicae*; carapace surface crushed.

Rostral area with downturned triangular central rostral spine; two stout lateral rostral spines at base of rostrum but on dorsal surface of carapace, directed forward; width between outer bases of lateral rostral spines about one quarter maximum carapace width. Anterolateral margin and posterolateral margins confluent; sinuous; small triangular spine distal to lateral rostral spines; extending from orbital area laterally to large, stout subhepatic spine, then extending posteriorly, small spine on subepibranchial region; remainder of lateral margin convex and inflated to posterolateral corner. Posterior margin concave, markedly rimmed, about 80 percent maximum carapace width.

Protogastric regions small, triangular, with oblong swelling positioned longitudinally, not well defined; mesogastric region with long anterior process, widening distally, with convex posterior margin; metagastric region wide, widest anteriorly, short, merging with urogastric region which is narrow and poorly defined; cardiac region appearing to be triangular, very poorly defined; intestinal region long and wide; flattened, with tubercles arrayed transversely.

Hepatic region rectangular, situated at oblique angle to axis, paralleling outer margin of protogastric region and epibranchial region. Subhepatic region large; inflated; with large stout triangular spine centrally, carapace quite wide at position of subhepatic region, width at widest points of subhepatic regions about 80 percent maximum width. Epibranchial region separated from hepatic region by moderately deep cervical groove and from branchial region by weakly defined branchiocardiac groove; epibranchial region narrow, oblong, oriented at oblique angle to axis; subepibranchial region triangular, apex directed ventrally, with one large and few small tubercles. Remainder of branchial regions undifferentiated, inflated, with linear array of tubercles parallel to lateral margin; subbranchial regions steep, rounded, relatively smooth.

Appendages long and slender; first pereiopod stoutest, manus of chela longer than high, granular, fixed finger may be slightly downturned; pereiopods 2–4 much more slender than first; bases of fifth pereiopod suggest it was carried dorsally.

Abdomen of male narrow; somite 1 narrow, positioned between bases of fifth pereiopod; somite 2 with lateral projections and central swelling.

Measurements.—Measurements, in mm, taken on the holotype and sole specimen of *Palehomola gorrelli*: maximum width, 38.4; maximum length (including lateral rostral spines), 42.6; width between bases of lateral rostral spines, 9.5; width at widest point of subhepatic regions, 30.2; posterior width, 30.9; length to position of maximum width, 27.3.

Material examined.—The holotype, USNM 352912, is deposited in the United States National Museum, Smithsonian Institution, Washington, D.C.

Occurrence.—The specimen is reported to have been collected from Oligocene rocks at Judkins Ridge, near Eugene, Oregon (Rathbun, 1926).

Discussion.—The holotype and sole specimen of *Palehomola gorrelli* is unfortunately poorly preserved, undoubtedly contributing to the debate over the family-level placement of the genus. The carapace is badly crushed, and most of the axial area and the protogastric and hepatic areas are missing. However, the fine sand forming the internal mold of the carapace records faint imprints of where the grooves separating some of these regions should be. Thus, the outline of the protogastric region and the cervical groove as drawn in Figure 7.2 are based upon these imprints; however, the remainder of the regions could not be differentiated from the badly crushed specimen. The specimen was probably a living animal, and not a molt, when it was buried, which is suggested by the presence of some of the abdominal somites and elements of the appendages.

Genus RHINODROMIA new genus

Homolopsis BELL, 1863 (part). WOODWARD, 1896, p. 224, text-fig. 3; WHITEAVES, 1900, p. 266, text-fig. 13; RATHBUN, 1926, p. 86, pl. 20, fig. 3.
Palehomola RATHBUN, 1926 (part). COLLINS, 1997, p. 64, fig. 8.

Type and sole species.—*Homolopsis richardsoni* Woodward, 1896.
Diagnosis.—As for species.
Description.—As for species.
Etymology.—The generic name is derived from the Greek *rhino*, meaning nose or snout, in reference to the long bifid rostral structure, and the generic name *Dromia*, upon which most of the generic names in the family are based.
Discussion.—Woodward (1896) originally described *Homolopsis richardsoni* from Cretaceous rocks of the Queen Charlotte Island, British Columbia, and later Rathbun (1926) concurred with placement in *Homolopsis*. However, the species clearly fits neither the diagnosis of *Homolopsis* as given above, nor of the

Homolidae, because it lacks *lineae homolicae*. The holotype and sole specimen has no indication whatsoever of *lineae* or fractures or cracks that could be construed as *lineae*. Thus, we have removed the species from both the family and the genus, placing it into the new genus *Rhinodromia* within the Homolodromiidae.

The species is referable to the Homolodromiidae for several reasons. It has a longer than wide carapace; well-developed cervical and branchiocardiac grooves; an inflated subhepatic region with a spine which might protect the eye; moderately developed subdorsal regions; and moderately developed carapace regions. It lacks well-defined orbits. The rostral area of *Rhinodromia richardsoni* differs somewhat from that of other homolodromiids. It lacks a central rostral spine and possesses lateral rostral spines; however, the lateral rostral spines are fused at the base and bifurcate after extending anteriorly for about 3 mm. We believe that this fused lateral rostral spine is of the same origin as the lateral rostral spines of other homolodromiids.

The possession of the fused lateral rostral spines is sufficiently distinctive to warrant the creation of a new genus to accommodate *Homolopsis richardsoni*. *Rhinodromia* is most like *Eoprosopon* from the Jurassic of Germany. Both genera possess triangular carapaces that widen distally; granular, well-ornamented carapaces; and a well-developed cervical groove and moderately developed branchiocardiac groove, both of which are oblique to the axis. It differs from *Eoprosopon* in having shorter, stouter appendages. *Rhinodromia* differs significantly from the other homolodromiid known from the Pacific Northwest, *Palehomola*, which has an ovate carapace; large, inflated subhepatic regions.

Rhinodromia richardsoni is the only known species of the genus. It is one of the earliest known homolodromiids; only *Eoprosopon* is older. It appears possible that rootstock for *Rhinodromia*, perhaps derived from or closely related to, *Eoprosopon*, dispersed from epicontinental Europe to the Pacific Northwest of North America via the Polar Seas, which were open during the Cretaceous. This pattern is becoming increasingly well documented for decapod taxa (Schweitzer, 2001b; Schweitzer et al., 2002).

RHINODROMIA RICHARDSONI (Woodward, 1896)
Figures 8, 9

Homolopsis richardsoni WOODWARD, 1896, p. 224, text-fig. 3. WHITEAVES, 1900, p. 266, text-fig. 13; RATHBUN, 1926, p. 86, pl. 20, fig. 3; SCHWEITZER, 2001a, p. 522.

Diagnosis.—Carapace triangular, widening distally, coarsely granular, widest about 80 percent distance posteriorly on carapace; central rostral spine absent; lateral rostral spines fused basally and diverging distally into bifid tip; suborbital spine acicular, forming receptacle in which eye might rest; cervical groove deep; branchiocardiac groove moderately deep; subhepatic region weakly developed, with one spine; hepatic region with lateral spine; first pereiopod stout.

Description.—Carapace longer than wide, maximum width about 80 percent maximum length, widening distally, widest at about 80 percent distance posteriorly; carapace regions moderately well defined; surface coarsely granular; strongly vaulted transversely and moderately vaulted longitudinally; lateral sides (subdorsal) steep.

Frontal area narrow; central rostral spine absent; lateral rostral spines fused at base, then diverging anteriorly into long, bifid projection; suborbital spine acicular, directed anterolaterally. Lateral margins sinuous anteriorly, with hepatic, subhepatic, and two epibranchial spines; posteriormost portion of lateral margin weakly convex, bordered by granules.

Protogastric region not well differentiated from hepatic region, protogastric area flattened, hepatic area inflated; mesogastric region with long anterior process, widening distally, with two large
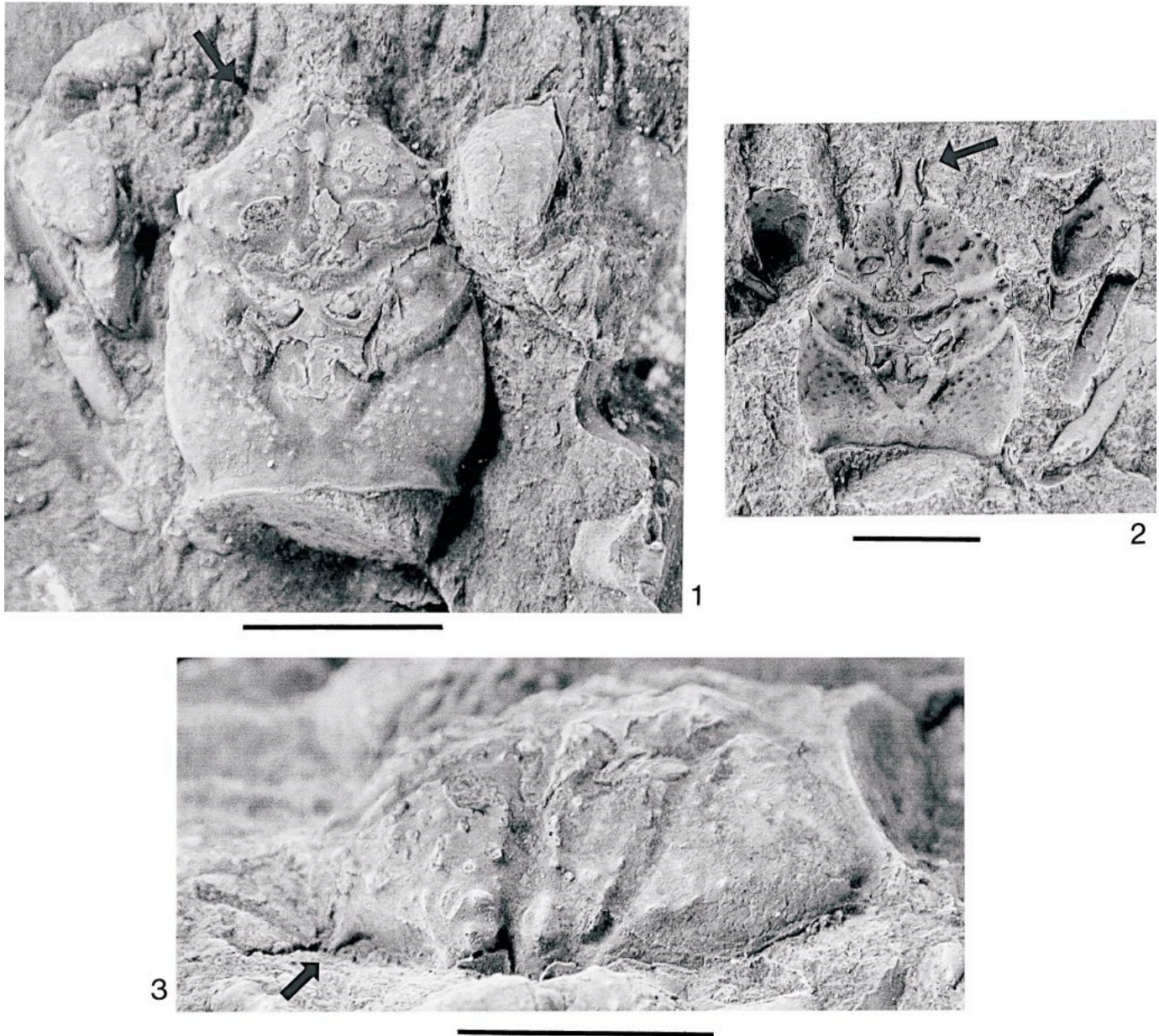
FIGURE *8—Rhinodromia richardsoni* n. gen. and new comb., holotype, GSC 5995 and 5995a. *1,* dorsal carapace, GSC 5995, arrow indicates suborbital spine; *2,* counterpart (GSC 5995a) of holotype, arrow indicates bifid, fused, lateral rostral spines; *3,* lateral view of holotype, GSC 5995; arrow indicates suborbital spine. Scale bars = 1 cm.

swellings posteriorly, posterior margin convex; metagastric region broadest anteriorly and narrowing posteriorly, not well differentiated from poorly defined, narrow urogastric region; cardiac region triangular, axis directed posteriorly; intestinal region short, widening posteriorly, flattened.

Subhepatic region small, inflated, with small triangular spine projecting anterolaterally; remainder of subdorsal areas moderately differentiated, not inflated; cervical groove wide, deeply incised; branchiocardiac groove wide, deeply incised, parallel to cervical groove until curving around cardiac region. Epibranchial and mesobranchial regions lie between cervical and branchiocardiac grooves; each consists of a granular ridge roughly parallel to one another and grooves, ridges separated by overall depressed but irregular surface; metabranchial region inflated, uniformly coarsely granular.

Pereiopod 1 short, coarsely granular; pereiopods 2 and 3 longer and more slender than pereiopod 1. Remainder of animal unknown.

Measurements.—Measurements (in mm) taken on the dorsal carapace of *Rhinodromia richardsoni*: maximum length, 19.4; maximum width, 15.3; length to point of maximum width, 15.7; posterior width, 12.7.

Material examined.—The holotype and sole specimen, GSC5995 (part) and 5995a (counterpart) is deposited in the Museum of the Geological Survey of Canada, Eastern Paleontology, Ottawa, Canada.

Occurrence.—The specimen was collected from Cretaceous rocks of Skidegate Inlet, west of Alliford Bay on Queen Charlotte Island, British Columbia, Canada (Rathbun, 1926).

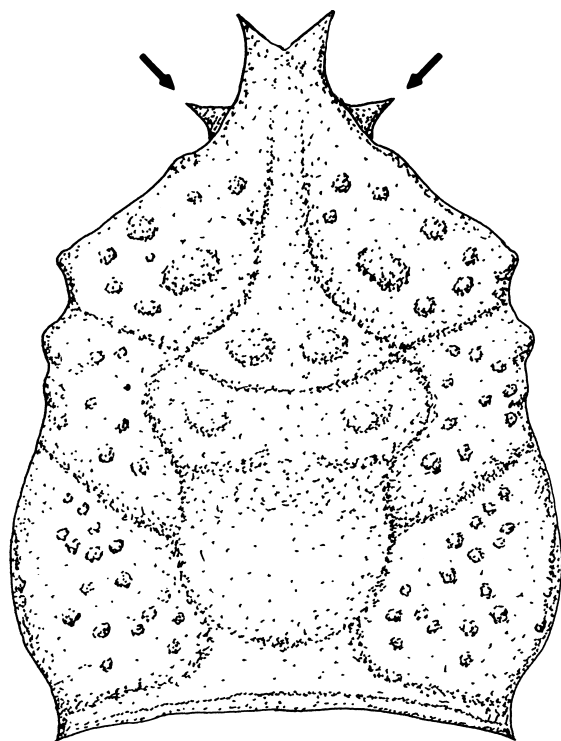*Discussion.*—*Rhinodromia richardsoni* is represented by only

FIGURE *9*—Reconstruction of *Rhinodromia richardsoni*, showing fused, bifid lateral rostral spines. Arrows indicate suborbital spines. Note absence of *lineae homolicae*.

one specimen, which is moderately well preserved. Preparation of both the part and counterpart revealed the fused lateral rostral spines, suborbital spines, and lateral spines which were unknown to Woodward (1896) or Rathbun (1926) (Figs. 8.2, 9). Observation of those features has made it possible to place the specimen within the Homolodromiidae. The species exhibits shorter pereiopods than extant homolodromiids which might suggest a shallow water habitat; however, confirmation of that environment must await sedimentological and faunal analysis of the associated rocks.

DISCUSSION

Both the Homolidae and the Homolodromiidae appear to have originated during the Jurassic in epicontinental Europe and had North Polar distributions early in their history. Later fossil occurrences of the Homolodromiidae are nearly all in high-latitude regions, exhibiting an amphitropical distribution, while homolids are later found over a broad latitudinal range. It is important to note that there may be a collecting bias towards Europe, thus giving the appearance that the group evolved in that region. As discussed by Müller et al. (2000), the Prosopidae, which is another primitive, related family, is also known from areas in Europe near locations of well-established universities. It is quite possible that with collecting in Jurassic and Cretaceous rocks in other geographic areas, ideas about the area of origin for these three families may change.

Extant Homolodromiidae inhabit deep water, and thereby cold environments. Homolodromiid fossils exhibit both long and short pereiopod forms. Pereiopod length in the homolodromiids may be a useful indicator for paleoenvironment; long, slender legs may be especially useful to support the carapace on soft, muddy substrates typical of deepwater habitats. Homolodromiids appear to have exhibited a variety of depth preferences early in the history

of the family, at least as is indicated by pereiopod length, but always have inhabited high latitude, and therefore cooler environments. Thus, although competitive exclusion may have played a role, it seems reasonable to suggest that the distribution of the family has been controlled more by temperature, rather than depth, preference. Amphitropical distributions for taxa that appear to have preferred cool water conditions have previously been reported for many molluscan and decapod groups during the Cretaceous and Eocene (Feldmann and Zinsmeister, 1984; Feldmann, 1991; Crame, 1993, 1996; Schweitzer, 2001b).

Homolids are also known primarily from deepwater occurrences in modern oceans; however, the move to deeper water seems to have occurred early in the history of the family. Post-Cretaceous homolids are rare in the fossil record, and those that are known almost always have been recovered from rocks deposited in deep continental slope environments. Extant homolids are almost exclusively outer continental shelf and slope animals (Jenkins, 1977; Guinot and Richer de Forges, 1995; Collins, 1997). Unfortunately, deepwater decapod fossils are rare (Feldmann et al., 1991). Thus, the paucity of post-Cretaceous homolid fossils suggests that this group moved to deepwater environments sometime after the Cretaceous, possibly as a response to the end-Cretaceous event(s) or to changing sealevels and/or temperatures in the post-Cretaceous world. This pattern is echoed in the lobsters.

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