PALEOBIOGEOGRAPHY OF CRETACEOUS AND TERTIARY DECAPOD CRUSTACEANS OF THE NORTH PACIFIC OCEAN

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ABSTRACT—Comprehensive analysis of the Cretaceous and Tertiary decapod crustaceans of the North Pacific Rim, focused primarily on the Brachyura, has resulted in additions to our understanding of the evolution and distribution of these animals, both in that region and globally. Hypotheses about changes in climatological and paleoceanographic conditions have not been extensively tested using decapod crustaceans, although they have been well-documented globally and for the North Pacific Ocean by sedimentological and other faunal evidence. Evidence from the occurrences of decapod crustaceans supports hypotheses obtained through these other means. Because the decapod fauna was studied independent of other faunas, it provides a means by which to compare and test patterns derived from molluscan and other faunal data. The brachyuran decapods show distinctive paleobiogeographic patterns during the Cretaceous and Tertiary, and these patterns are consistent with those documented globally in the molluscan faunas and paleoceanographic modeling. Additionally, the changes in the decapod fauna reflect patterns unique to the North Pacific Ocean. The decapod fauna is primarily comprised of a North Pacific component, a North Polar component, a component of Tethyan derivation, an amphitropical component, and a component derived from the high Southern latitudes. The Cretaceous and Tertiary decapod faunas of the North Pacific Ocean were initially dominated by taxa of North Pacific origin. Decapod diversity was highest in the Pacific Northwest of North America during the Eocene, and diversity has declined steadily since that time. Diversity in Japan was relatively low among the Decapoda until the Miocene, when diversity increased markedly due to the tropical influence of the Tethys and Indo-Pacific region. Diversity has remained high in Japan into the present time. The Cretaceous, Eocene, and Miocene were times of evolutionary bursts within the Brachyura and were separated by periods of evolutionary stasis.

INTRODUCTION

Historical perspective.—The late twentieth-century has seen rapid development in the paleontological study of the Tertiary decapod crustaceans of the North Pacific Ocean. The decapod fauna of the Pacific Northwest of North America was originally described in the monumental work of Rathbun (1926), which has been the definitive volume on the fossil decapods of that region. Shorter early contributions include those of Gabb (1824), Dura (1849), Stimpson (1857), Woodward (1896), Whiteaves (1903), Rathbun (1916, 1932), and Withers (1924). Beginning in the 1970s, the decapods of the Pacific Coast of North America have received renewed descriptive attention (Orr and Kooser, 1971; Kooser and Orr, 1973; Richards, 1975; Berglund and Feldmann, 1989; Feldmann, 1989; Tucker and Feldmann, 1990; Feldmann et al., 1991; Berglund and Goedert, 1992, 1996; Squires and Demetrion, 1992; Tucker et al., 1994; Tucker, 1998; Schweitzer Hopkins and Feldmann, 1997; Schweitzer, 2000; Schweitzer and Boyko, 2000; Schweitzer and Feldmann, 1999, 2000a, 2000b, 2000c, 2000d, 2001; and Schweitzer et al., 2000; Schweitzer and Salva, 2000).


Decapod paleobiogeography has recently been described, especially that of the high southern latitudes (Feldmann et al., 1995, 1997). This work has shown that distinctive faunal provinces and distribution patterns can be defined using a variety of criteria encompassing both dispersal and vicariance events. For example, the Tertiary decapod faunas of eastern and western South America were markedly different from one another, due to barriers such as the South American continent and to ocean current patterns (Feldmann et al., 1995, 1997). Feldmann and Maxwell (1990) and Feldmann and McClay (1993) demonstrated a strong similarity between the faunas of Antarctica and New Zealand in the early Eocene. This similarity disappeared over time as New Zealand diverged from Antarctica and the South Polar area, suggesting that tectonic movement resulted in vicariant distributions (Feldmann and McClay, 1993). In other regional studies, Feldmann et al. (1998) demonstrated a strong similarity between Eocene decapod faunas of southern Europe and the east coast of North America, proposing ocean currents as a dispersal mechanism for the decapods from east to west across the Atlantic. This hypothesis was supported by paleoceanographic modeling. In his major work on the decapods of the Tertiary of southwestern Japan, Karasawa (1993) suggested that many of the decapod taxa had a Tethyan distribution, based upon similarities between Eocene faunas of Europe and Japan. This hypothesis was also proposed for the Cretaceous fauna by Collins et al. (1993). A distinctive North Pacific decapod fauna appears to have developed by the early Tertiary, based upon late Oligocene to early Miocene decapods of the Pysht Formation in Washington (Schweitzer Hopkins and Feldmann, 1997; Schweitzer and Feldmann, 1999).

Paleobiogeographic studies of macrofossils of the North Pacific Ocean have primarily focused on the Mollusca (Addicott, 1970; Marincovich, 1984; Oleinik, 1993; Titova, 1994) as have modern biogeographic studies, in which definition of latitudinal provinces based upon climate are included (Schenck and Keen, 1936; Hall, 1964; Valentine, 1966; Jeffers, 1988). Wicksten (1989) analyzed the latitudinal distribution of Recent off-shore decapod crustaceans but did not consider near-shore decapods, those most commonly preserved in the fossil record. Newman (1991, 1992) has provided analyses of modern crustacean biogeography, mostly focused on tropical and Southern Hemisphere patterns. Paleobiogeographic studies of modern faunas of Japan focus largely on the molluscs, although numerous modern studies have interpreted biogeographic distribution of decapods in Recent oceans.

Database.—Because the Cretaceous and Tertiary decapod fauna of the Pacific Northwest and Japan has received comprehensive

systematic attention, the objective now is to synthesize those works in terms of the broader paleobiogeographic and evolutionary patterns in the occurrences of these animals. The database upon which these interpretations are based is robust. Thus, although it is recognized that the strength of statements regarding areas of origin and directions of dispersal is always constrained by the database, the current state of our understanding of decapod occurrences permits drawing conclusions. The geographic areas under discussion have been extensively studied for several years, and the major occurrences of fossil decapods are well known. Most of the types from the Pacific Northwest of North America and Japan as well as many in Great Britain have been examined by the author, which allows systematic decisions to be consistently applied throughout the work.

This analysis uses only decapod crustaceans. While it is well known that the Decapoda have a less robust database than organisms with durable hardparts such as the Mollusca and Brachiopoda, recent advances in our knowledge of the decapod crustaceans have contributed to a substantial database of worldwide occurrences. Use of the decapods provides a means by which to independently test patterns derived by analysis of clams, snails, brachiopods, and other organisms. It also permits the recognition of differences among the paleobiogeographic patterns derived for the decapods as compared to other groups. Use of molluscan and other data in this analysis, because it is so much more robust than that for the decapods, would surely have masked any pattern that the decapods may have exhibited. Furthermore, combining distributional data from diverse taxa would seem to imply that different taxa respond similarly to environmental stresses and distributional opportunities which may not be the case. The distributional patterns within the Decapoda, or any group, bear directly on the evolutionary relationships within that group and are thus important in delineating the evolutionary history of the organism under study. In fact, most paleobiogeographic analyses are conducted using restricted groups, such as single molluscan families. There is considerable precedent in the literature for conducting paleobiogeographic analyses using only fossil decapods (Feldmann, 1981; Karasawa, 1992, 1993, 1999, 2000; Collins, et al., 1993; Feldmann and McLay, 1993; Collins and Jakobsen, 1994; Feldmann et al., 1997, 1998); as well as analyses based only upon molluscs, in some cases sole genera or single families (for example, Sohl, 1987; Marincovich and Gladenkov, 1999; Marincovich, 2000).

The decapod taxa analyzed here are brachyurans, except for three thalassinoid taxa, one hippoid taxon, one porcellanid taxon, and several galatheoid taxa. Macruran decapods including the lobsters, are not considered, because their occurrences are restricted mainly to the Cretaceous (Nagao, 1931; Feldmann, 1974; Karasawa, 1998; Karasawa and Hayakawa, 2000), and taxonomic placement of the macruran taxa along the Pacific Rim has yet to be confirmed. Additionally, numerous taxa have been assigned to Callianassa sensu lato and other thalassinoid genera. However, those generic assignments remain to be confirmed; thus, these taxa were not used. Taxa were used in this study only if represented by dorsal carapace material clearly assignable at the generic level. Because of several inconsistencies and discrepancies within their work, Hu and Tao (1996) was not considered in this report. Authors and dates of taxa are listed in the text only for those taxa not listed in Table 4.

Scope.—Several paleobiogeographic patterns were previously unrecognized. Additionally, revised evolutionary patterns for numerous families, subfamilies, and genera have emerged from this synthesis. Areas such as coastal Alaska; the Kamchatka Peninsula, Russia; Chile; western, southern, and central Mexico; Central America; and Southern Europe should be targeted in order to provide vital evidence from these under-represented areas.
and the Tethys. Two possible dispersal pathways have been identified. First, some taxa appear to have dispersed westward from southern Europe and Tethys to the east coast of North America and subsequently to the West coast of North America, via the Central American Seaway. Second, other taxa appear to have moved eastward from Europe through the Tethys to Japan, sometimes with subsequent dispersal to western North America. Many taxa found in Tertiary strata of western North and Central America appear to have evolved in southern Europe and the Tethys, such as *Calappilia*, *Hepatus*, *Montezumella*, and *Panopeus*. *Portunites* appears to have evolved in southern Europe and dispersed to the North Pacific by moving eastward through the Tethys. Conversely, some taxa appear to have evolved in North America and subsequently dispersed eastward to Europe, a pattern documented by occurrences of *Prehepatus* (Fraaye and Collins, 1987; Vega et al., 1995). These occurrences suggest that faunal exchange between the Pacific Ocean and Atlantic Ocean took place at least as early as the Eocene and continued until at least the Miocene, a time during which the Central American Seaway was still open. *Eriosachila* and *Laeviranina* are known from the Eocene of the east and west coasts of North America, and *Prohomola* is known from the Eocene of eastern North America and Japan, also supporting active faunal exchange via the Central American Seaway. Further, *Viapinnixa*, previously known only from Greenland, occurs in Eocene deposits of southern Mexico (Vega, personal commun.), supporting a dispersal pathway across the Atlantic Ocean. The Eocene decapod faunas of the Castle Hayne Limestone of coastal North Carolina and the Eocene fauna of southern Europe share several genera, demonstrating that decapod occurrences could have resulted from westward dispersal to North America across the Atlantic Ocean during Eocene time (Feldmann et al., 1998).

Many decapod taxa appear to have dispersed eastward from Europe through the Tethyan seas to Japan (Karasawa, 1993, 1999). Collins et al. (1993) described the Cretaceous decapod fauna of Japan as being influenced by the Cretaceous decapod fauna of the Tethys. Karasawa (1992, 1993, 1999) reported a strong Tethyan component of the Paleogene decapod fauna of Japan due to dispersal eastward from Europe and Tethys to Japan, including the genus *Portunites*. Miocene and later occurrences of decapods in Japan are strongly influenced by the Tethyan and Indo-Pacific areas (Karasawa, 1993, 1998, 1999). Dispersal of molluscan genera is similar in that first generic occurrences often occur in the central Tethys with subsequent dispersal to Japan (Masuda, 1990). Numerous molluscan families are known to possess Tethyan distributions similar to that suggested here for the decapods (Kollman and Sohl, 1979).

**Fauna of North Polar origin.**—A small number of taxa found in Tertiary strata of the North Pacific Rim appear to have a North Polar distribution. *Macroacaeana* is distributed among Cretaceous to Eocene rocks of Greenland, the Pacific Northwest of North America, and Japan (Tucker, 1998). *Rogueus* occurs in Paleocene strata of Denmark and Eocene rocks of Washington (Berglund and Feldmann, 1989; Collins and Jakobsen, 1995). *Camarocarcinus* is reported from Paleocene strata of Denmark, Greenland, and North Dakota (Holland and Cvancara, 1958; Jakobsen and Collins, 1979; Collins and Rasmussen, 1992). *Homola* appears to have had a North Polar distribution during the Cretaceous and subsequently achieved a cosmopolitan distribution. *Branchioplax* appears first in Eocene rocks of Japan and is subsequently found in the Pacific Northwest of North America and in Great Britain. Reports of the genus in Senegal (Remy and Tessier, 1954) and Central America (Karasawa, 1992) have not been confirmed, and illustrations of the Senegalese material suggest that it does not belong to *Branchioplax*. Polar areas have previously been suggested to be areas of origin for new taxa (Zinsmeister and Feldmann, 1984; Crame, 1992; Feldmann et al., 1993); therefore,
these genera may have evolved and dispersed within the North Polar region.

Faunal exchange among the northern oceans and polar regions has been facilitated at various time intervals. Faunal exchange between the North Atlantic and North Pacific oceans is well documented during Cretaceous and Plio-Pleistocene times (Marincovich et al., 1983; Gladenkov, 1979; Vermeij, 1991; Dunton, 1992); however, exchange during the Tertiary has not been well-described and possibly did not occur then at all (Marincovich et al., 1983). Polar regions were iceless during the Cretaceous, thus permitting active dispersal across the Arctic. Feldmann (1974) reported occurrences of the macruran genus Hoploparia McCoy, 1849, in the Neocomian (Hauterivian) of Europe and western North America, and Karasawa and Hayakawa (2000) have reported species of Hoploparia from Cretaceous rocks of Japan. This, in addition to Homola and Macroacaena reported here, supports an Arctic dispersal avenue during the Cretaceous. Cretaceous North Polar distributions thus seem to have been readily facilitated.

Marincovich et al. (1990) concluded that the connection between the Arctic Ocean and the Gulf of Mexico, via the Western Interior Seaway of North America was closed by Paleocene time, based upon tectonic, sedimentological, and faunal evidence. However, the Paleocene (Danian) Cannonball Formation of North Dakota in the north-central United States, contains deposits of the most southerly extent of the Tertiary Arctic Ocean (Marincovich et al., 1985, 1990), suggesting that the connection between at least the Western Interior and the North Atlantic remained open into the Paleocene. This connection is supported by paleontological evidence (Cvancara, 1966; Jeletzky, 1971; Feldmann, 1972), and thus Paleocene distributions in the Western Interior and North Atlantic may be the result of faunal exchange via the Arctic Sea.

Exchange may have also included the North Pacific Ocean if oceanic connections existed; exchange between the North Atlantic and North Pacific oceans seems well-documented by the pattern of occurrences of Rogueus and Macroacaena. Taxa may have been introduced from the North Atlantic Ocean to the Western Interior Seaway during the Late Cretaceous and subsequently established in the North Pacific Ocean; however, the latest paleogeographic reconstructions (Scotese, 1997) do not show a connection between the Western Interior and the Pacific Northwest. Thus, further investigation is necessary to resolve the origin of the Paleocene North Polar distributions.

The presence of an Eocene North Polar taxon (Branchioplax) is problematic. It suggests that a connection between the North Atlantic and North Pacific oceans may have been open longer than postulated by Marincovich et al. (1990). Alternatively, this taxon may lack a fossil record documenting its presence in the North Pacific before the Eocene. The Eocene North Polar taxon could also be a result of dispersal between the Atlantic and Pacific oceans via the Central American Seaway; however, there are no fossil occurrences in Mexico, Central America, or the east coast of the United States to support this hypothesis. More importantly, examination of plates of the European material suggests that it may not be congeneric with the North Pacific taxa; thus, Branchioplax could be simply another North Pacific taxon. Examination of type material in Europe will be necessary to further clarify the matter.

Fauna of high southern latitude origin.—Zinsmeister and Feldmann (1984) and Feldmann et al. (1997) suggested that the high southern latitudes may have been an area of origin for decapod taxa that currently inhabit low latitude or northern hemisphere settings. Additionally, the Cretaceous and Tertiary decapod faunas of Antarctica had a strong influence on subsequent decapod faunas of the circum-Pacific region (Zinsmeister and Feldmann,
Several taxa that occur in Tertiary rocks of the North Pacific Rim document this view. The earliest known occurrence of *Palaeopinnixa* is in Paleocene rocks of Argentina (Feldmann et al., 1995). Subsequent occurrences of that genus are in Eocene to Oligocene rocks of northern South America, the Caribbean, Central America, and the west coast of North America (Schweitzer et al., 2000), suggesting a northward dispersal of the genus. Further, *Chasmocarcinus* and *Calappa* are recorded from Eocene rocks of Antarctica (Feldmann and Zinsmeister, 1984; Feldmann and Wilson, 1988). *Chasmocarcinus* is currently known from the east and west coasts of North America and the Caribbean (Schweitzer and Feldmann, 2001), and *Calappa* has a worldwide distribution (Schweitzer and Feldmann, 2000a). Finally, *Asthenognathus* first occurs in Eocene rocks of Argentina and is found in Oligocene to Miocene deposits of the North Pacific Rim and the Recent Atlantic and Pacific oceans (Schweitzer and Feldmann, 1999, 2001). All three of these genera exhibit distribution patterns in which the taxon originated in the high southern latitudes and subsequently dispersed northward. This distribution pattern may be a result of dispersal or of fragmentation of formerly widespread distributions with subsequent extinction in the high southern latitudes. Molluscan taxa are known which originated in the high southern latitudes and subsequently dispersed to lower latitude seas (Crame, 1992, 1996), a pattern that seems to apply to the decapods *Calappa* and *Asthenognathus*, currently found in warm-water areas.

**Amphitropical fauna.**—In addition to the four biogeographic components described above, there appears to be an amphitropical component in the Cretaceous and Tertiary decapod fauna of the Pacific Ocean. The Cretaceous genus *Eodorippe* is known from Australia (Glaessner, 1980), Japan (Collins et al., 1993), and from unpublished occurrences in Oregon (T. Nyborg, personal communication). The Cretaceous to early Tertiary *Necrocarcinus* is found in temperate localities in the Northern Hemisphere and in Antarctica in the Southern Hemisphere (Schweitzer and Feldmann, 2000a).

The Portunidae display an amphitropical distribution early in their history, occurring in Paleocene and Eocene rocks of Argentina and Eocene rocks of the North Atlantic and North Pacific oceans (Feldmann et al., 1995; Schweitzer and Feldmann, 2000b). Portunids are cosmopolitan in modern oceans. The portunid genus *Imaizumia* occurs in Oligocene deposits of Japan and Oligocene to Miocene deposits of Chile (Karasawa, 1993; Schweitzer and Feldmann, 2000b).

The cancrid genus *Metacarcinus* has an amphitropical distribution, reported from north and south temperate latitudes, in Oligocene to Recent oceans (Feldmann and McLay, 1993; Schweitzer and Feldmann, 2000c). Further, the Cancrini (Cancridae) has had a north and south temperate distribution during its entire geological record (Schweitzer and Feldmann, 2000c). *Mursia* first occurred in the Eocene of the North Pacific (Schweitzer and Feldmann, 2000a), and unpublished reports document it in Chile in the Miocene (Chirino-Gálvez, 1993). Further, unpublished reports indicate that *Trichopeitum* occurred in the Oligocene of the Pacific Northwest of North America (Schweitzer and Feldmann, 1999), had reached Chile by the Miocene (Chirino-Gálvez, 1993). Both *Mursia* and *Trichopeitum* are widespread in modern oceans. Ongoing work on Chilean and Argentinian material should begin to explain this amphitropical distribution pattern and may suggest dispersal patterns.

Théel (1911) and Valentine (1984) suggested that amphitropical distributions, at least in modern faunas, may result because more derived forms force primitive forms from the tropics to higher latitudes. Newman and Foster (1987) noted that geologically younger and more advanced groups often inhabit the tropics while older groups tend to inhabit areas peripheral to the tropics. This results in amphitropical distributions. Newman (1992) suggested that modern amphitropical distributions may be relics of formerly Tethyan distributions in which the tropical component no longer remains.

The Cretaceous amphitropical decapod distributions are most likely a result of the break-up of Pangaea, in which formerly
widespread distributions were fragmented (Crame, 1993). The Cenozoic amphitropical taxa in the North Pacific seem to have an altogether different origin than those discussed by Newman (1992), since they appear to have originated in temperate regions with subsequent dispersal to temperate latitudes in both the northern and southern hemispheres. Perhaps those taxa that evolved in temperate areas were able to move across equatorial areas by submergence, inhabiting deep, cool water in those areas (Wicksten, 1989). However, Crame (1993, 1996) suggested that many amphitropical or bipolar distributions cannot be explained by this mechanism since most organisms exhibiting an amphitropical distribution are adapted to shallow water conditions. Amphitropical distributions could have been initiated during the Cretaceous because of the opening of the Atlantic Ocean, fragmenting continental populations into northern and southern components. The resulting vicariant distribution could then have been further modified by dispersal within the two regions (Crame, 1993). This hypothesis cannot be applied to the taxa herein which have Pacific amphitropical distributions because the Pacific Ocean was already open and not subject to vicariant events because of continental break-up. Kaufmann (personal commun.) suggests that these amphitropical distributions could have been caused by new circulation patterns initiated by the break-up of Pangaea.

The late Eocene and Oligocene were times of global oceanic cooling (Fischer, 1982); thus, widespread dispersal of taxa may have occurred during that time because of more equitable, cooler, global ocean temperatures. The ranges may have been separated into amphitropical components due to subsequent warming during the Miocene, restricting the taxa to cooler higher latitude waters (Crame, 1993, 1996). The amphitropical distribution of the Pacific taxa which originated in the Eocene and Oligocene may have originated from these global oceanic temperature changes. The amphitropical distribution could also be the result of extinction in the tropics of originally cosmopolitan taxa; however, the known fossil record does not support extinction in the tropics.

**Biogeographic Distribution in Time**

**Overview.**—The Cretaceous and Tertiary decapod faunas of the North Pacific Ocean were initially dominated by taxa of North Pacific origin. Diversity was highest in the Pacific Northwest of North America during the Eocene, and diversity has declined steadily since that time. Diversity in Japan was relatively low until the Miocene, when diversity increased markedly due to the tropical influence of the Tethys and Indo-Pacific region. Diversity has remained high in Japan into the present time.

**Cretaceous and Paleocene.**—The brachyuran fauna of the Pacific Northwest of North America is characterized by low abundance and diversity during the Cretaceous and early Tertiary. Only four genera in four families are known from Cretaceous rocks of the area (Fig. 2). Of these, Longusorbis and Pristinaspina were endemic, Archaeopus had a North Pacific distribution, and Eodorippe appears to have had a Pacific amphitropical distribution. There are no decapods known from Paleocene rocks (Fig. 3). The small number of fossils in Cretaceous and Paleocene deposits is undoubtedly related to the paucity of rocks of that age exposed and collected in the Pacific Northwest; therefore, the known fauna has apparent low abundance and diversity. The lack of decapods in Paleocene rocks could also be due to extinctions resulting from the end-Cretaceous event(s).

The Cretaceous brachyuran fauna of Japan is somewhat more robust, including nine genera in nine families (Fig. 2). Only two genera are shared between Japan and the Pacific Northwest of North America, Archaeopus (Collins et al., 1993) and Eodorippe, which is known from North America from unpublished data (T. Nyborg, personal commun.). Homola is distributed among Japan, the Western Interior of the United States, and Great Britain. Necrocarcinus has a nearly cosmopolitan distribution, recorded in Japan, Great Britain, the Western Interior of the United States, the Tethys, and Antarctica. Eodorippe has a Pacific amphitropical distribution. Notopocorystes, Pithonoton, and Diaulax were distributed in the North Atlantic, the Tethys, and Japan, suggesting that...
they reached Japan via the Tethys. Paki and Luisogalathea are endemic to Japan. Therefore, the Cretaceous brachyuran fauna of Japan appears to be strongly influenced by the biota of the North Atlantic Ocean and Tethys and includes a considerable component of the North Pacific fauna. There are no decapods reported from Paleocene rocks of Japan, undoubtedly due to the paucity of exposed and investigated deposits of that age (Fig. 3).

**Eocene.**—The Eocene was a time of high diversity in the Pacific Northwest of North America. Twenty-six genera in 17 decapod families are now recorded from Eocene rocks of that area, 11 of which are first occurrences for the genera in the rock record (Fig. 4). Of these, at least 56 percent are known only from the North Pacific Ocean. The Eocene decapod fauna of Japan includes 25 percent North Pacific taxa. Thus, a strong North Pacific faunal component appears to have developed by Eocene time.

Additionally, 15 percent of the decapod genera of the Pacific Northwest and 25 percent of those from Japan have North Polar distributions. The remainder of the decapod fauna of the Pacific Northwest of North America and Japan is dominated by taxa that have Tethyan distributions. Following Feldmann et al. (1998), Schweitzer and Salva (2000) and Schweitzer and Feldmann (2000a) suggested that faunal affinities between southern Europe, eastern North America, and the North Pacific Ocean could have been facilitated by exchange via the Central American passage-way. Bice et al. (2000) support an open Central American passageway into the Miocene. It is now clear that the Tethyan fauna had a significant influence on the composition of the decapod biota of the North Pacific Rim by Eocene time.

The high diversity of the Eocene decapod fauna of the Pacific Northwest can be attributed to a variety of factors. First, there are abundant and well collected marine deposits of Eocene age in that area, providing ample opportunity to collect Eocene decapods. Second, the climate during the Eocene appears to have been warmer than at any subsequent time (Fischer, 1982). This is supported by the presence of Tethyan and subtropical decapod taxa in the Pacific Northwest, which is now cool temperate. Third, Central America was largely submerged during this time (Scotese, 1997; Bice et al., 2000), allowing the decapods to move from one ocean to another.

The low diversity of the Eocene decapod fauna of Japan is more difficult to explain but may be attributable to several factors. First, the Eocene decapod fauna from Japan appears to be restricted to very few outcrops, perhaps because rocks of Eocene age appear to be rare in Japan. Second, the Eocene decapod fauna of Japan was very similar to that of the Pacific Northwest, and many of the taxa in Japan were part of the North Pacific fauna. Third, the Miocene and post-Miocene faunas of Japan were strongly influenced by the Tethys and Indo-Pacific realm, while the faunas of the Eocene and Oligocene were less strongly influenced. This suggests that it may have been too cool in Japan during the Eocene for many of the primarily warmer water Tethyan taxa to successfully establish, thus limiting the diversity of the fauna during that time. Additionally, during the Eocene and Oligocene, equatorial ocean currents were essentially circumglobal, so that tropical waters never reached Japan. Thus, it was isolated from Tethyan and Tropical influence (Bice, unpublished data).

**Oligocene.**—The Oligocene decapod fauna of the Pacific Northwest remained relatively diverse, comprised of seventeen genera in twelve families, while that of Japan remained low; six genera in five families (Fig. 5). The fauna of the Pacific Northwest was dominated by taxa with North Pacific distributions, 35 percent. About half of the taxa were found in both Eocene and Oligocene deposits. Minor components consist of those genera with a Tethyan origin; amphitropical genera; endemic genera; and tropical and cosmopolitan genera. The decapod fauna of Japan...
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Figure 6—Composition of the Miocene decapod fauna of the North Pacific Ocean. Dispersal avenues identifiable during this time interval are shown with large arrows. Base map from Scotese (1997, 20 Ma) and paleocurrent data from Bice (unpublished data, 20 Ma).

The Miocene was a time of dramatic change in the decapod faunas of the Pacific Northwest and Japan (Fig. 6). A marked decrease in diversity characterizes the decapod fauna of the Pacific Northwest of North America, which is composed of 12 genera in 10 families. Of these, 58 percent had North Pacific distributions, suggesting that during the Miocene, the decapod fauna of the Pacific Northwest became increasingly isolated from faunas of other regions. Even so, three of the genera had Tethyan distributions and two were distributed along both the east and west coasts of North America. This indicates that the Central American Seaway was still open at least in the early Miocene to facilitate faunal exchange, which is supported by Bice et al. (2000).

By contrast, the decapod fauna of the Miocene of Japan was incredibly diverse, composed of at least 45 genera in 23 families (Fig. 6). About 20 percent of these genera had North Pacific distributions; two were amphitropical; two were cosmopolitan in the northern hemisphere; several were endemic; and two were cosmopolitan in tropical areas. The vast majority of taxa were Tethyan-Indo-Pacific. Clearly, the Tethys, the Indo-Pacific, and Japan were experiencing considerable faunal exchange during this time.

This pattern is documented in molluscan faunas as well (Chinzei, 1991). However, the North Pacific fauna was still a strong component of the fauna of Japan, comprising 20 percent. Thus, the Miocene was a time of marked influx of tropical taxa into the oceans surrounding Japan. The North Pacific fauna became a less significant component of the decapod fauna, a pattern that has continued into the present. The increase in Indo-Pacific and Tethyan taxa in the Miocene and subsequent faunas of Japan may have been in response to warming events in the North Pacific Ocean (Karasawa, 1993) or to an increasingly strong gyre bringing warm water from the equator to Japanese coasts. The disruption of the circum-equatorial current during the Miocene, because of the movement of India into the Tethyan seaway, permitted the initiation of a North Pacific gyre (Bice, unpublished data). High generic diversity in the Miocene of Japan may have been related to increased influx of warm water and therefore warm water species to Japan from the Indo-Pacific. However, the effect of a stronger North Pacific gyre would have been mitigated in North America, because the water would have undergone sufficient cooling to eliminate tropical taxa by the time it reached the North American coast.

Post-Miocene fossil occurrences.—Post-Miocene deposits on the west coast of North America are not abundant, and only four genera in two families are reported from those deposits. Three of those genera are cancrids, which are abundant on the west coast of North America in modern oceans. Clearly, the decapod fauna of the Pacific Northwest experienced a post-Oligocene decline in diversity. At least 24 genera from 12 families are reported from post-Miocene deposits of Japan, approximately half of which were known from Tethyan, Indo-Pacific, and Japanese occurrences. About one-quarter were distributed among tropical regions worldwide. Only two of those taxa had North Pacific distributions, showing a continued stronger tropical influence on the Japanese decapod fauna and a weakening of the North Pacific fauna in Japan.

Recent occurrences.—The modern decapod fauna of the west coast of North America is not particularly diverse when compared with that of Japan. Of all of the decapod genera reported from fossil occurrences on the North Pacific Rim, only ten, in seven
families, inhabit modern oceans of the Pacific Northwest of North America. Hart (1982) reported 30 nonbrachyuran genera in 12 families from waters off British Columbia, and 19 brachyuran genera in seven families. Schmitt (1921) described 30 nonshrimp, nonbrachyuran taxa in nine families and 43 brachyuran genera in seventeen families from the coast of California. Jensen (1995) reported 38 brachyuran taxa from the Pacific Northwest of North America, and Wicksten (1989) reported five brachyuran genera among the offshore decapods of the Pacific Northwest. Thus, the decapod fauna of the Pacific Northwest appears to have declined in diversity since the Eocene, when 26 brachyuran genera were recorded. The Eocene record is not markedly lower than modern reports, especially keeping in mind the probable incompleteness of the fossil record. This decline may be attributed to a variety of factors. The climate of the Pacific Northwest in modern oceans is now too cool to accommodate taxa that are subtropical to tropical. The closing of the Straits of Panama by the end-Miocene appears to have effected a marked decline in the diversity of the decapod fauna of the Pacific Northwest of North America.

By contrast, the modern decapod fauna of Japan is incredibly diverse. Of all of the brachyuran genera reported from fossil occurrences on the Pacific rim, 39 genera in 23 families inhabit modern oceans surrounding Japan. Sakai (1976) reported 337 brachyuran and lophodiid genera in 40 families from the modern oceans surrounding Japan, an order of magnitude higher than the number inhabiting the Pacific Northwest of North America. The vast majority of these taxa have Tethyan and Indo-Pacific or tropical cosmopolitan distributions. The modern fauna of Japan is strongly influenced by warm water currents from equatorial regions and the warm climate of Japan today, allowing tropical and subtropical taxa to survive. Interestingly, in a study of decapod crustaceans from Hokkaido, Northern Japan, Takeda and Hayashi (1990) reported a strong affinity with the faunas of the northern North Pacific, suggesting that the North Pacific fauna remains a significant part of the fauna along the northern-most areas of the North Pacific rim and therefore northern Japan. This is probably due to the cold Oyashio Current flowing from the high northern seas (Kotaka, 1986), whose influence is diminished in southern Japan, which receives significant tropical influence due to the warm Kuroshio Current (Kotaka, 1986). Additionally, marine faunas of the western margins of both the Atlantic and Pacific Oceans are typically more diverse than the eastern margins because of the warm tropical influence in both areas (Newman, 1992). This pattern obtains for the late Cenozoic and modern decapod faunas of the North Pacific Rim.

**AREAS OF ORIGIN FOR NORTH PACIFIC GENERA**

Based upon the work of Karasawa (1993, 1997), Schweitzer and Feldmann (2000a, 2000b, 2000c, 2000d, 2001), and other authors, it appears that several genera, and two families may have originated in the North Pacific Ocean (Tables 2, 4). The geologic range for several taxa has been extended as a result of this work, and it now appears that the North Pacific Ocean may have been an area in which several brachyuran taxa evolved (generic first occurrences are indicated in Table 4 with an asterisk). An important caveat is that as more fossils are recovered and studied, the geologic ranges of more and more taxa may be extended. The areas of origin correspondingly change to reflect these new discoveries. The following conclusions are based upon current evidence.


The Northwestern Pacific Ocean also appears to have been a region where numerous genera evolved. The earliest known occurrence of *Homola* is in Cretaceous rocks of Japan (Takeda and Fujiyama, 1983; Schweitzer, 2001). Eocene first occurrences in Japan include *Branchioplax*, *Callianopsis*, and *Prohomola* (Karasawa, 1992; Schweitzer Hopkins and Feldmann, 1997). Oligocene first occurrences include *Collinsius* (Karasawa, 1993). Several genera appeared during the Miocene of Japan, including *Canzer s.s.*, *Hexapus*, and *Platepistoma* as well as numerous xanthoid taxa (Imaizumi, 1959; Karasawa, 1993; Schweitzer and Feldmann, 2001). There are fewer first occurrences in Japan than in the Pacific Northwest of North America. This suggests that the Japanese decapod fauna is largely a result of dispersal events which introduced taxa from the Tethys, Europe, the eastern Pacific Ocean, and to a lesser extent, the North Atlantic Ocean.

Some families appear to have originated in areas outside of the North Pacific Rim based upon the revisionary work done by Schweitzer (2000, 2001), Schweitzer and Feldmann (2000a, 2000b, 2000c, 2001), Schweitzer and Salva (2000), and Schweitzer et al. (2000) (Table 2). The referral of *Montezumella* to the Cheiragnididae Ortmann suggests that the family arose in the Tethyan region of southern Europe and subsequently dispersed to the east coast of North America, Central America, and the Pacific Ocean, areas which members currently inhabit (Schweitzer and Salva, 2000). Schweitzer et al. (2000) referred several genera previously assigned to the Xanthidae s.l. in the paleontological literature to the Carpiidae, including *Carpiulus*, *Eocarpilius* Blow and Manning, 1996; *Harpaactoxanthopsis* Via, 1959; *Ocalina* Rathbun, 1929; *Palaeocarpilius* A. Milne Edwards, 1862; and *Proxcarpiulus* Collins and Morris, 1978. Based upon this reappraisal of the fossil record of the Carpiidae, the family now appears to have evolved in southern Europe, where the earliest known members have been recovered.

Several decapod families and subfamilies may have originated in the high southern latitudes. The subfamily Polybiinae, which contains the oldest known members of the Portunidae, and the Geryonidae are recorded from Paleocene and Eocene rocks respectively in southern Argentina (Feldmann et al., 1995; Schweitzer and Feldmann, 2000b). The pinnootherid subfamily Asthenognathae is first recorded from Eocene rocks of southern Argentina as well (Schweitzer and Feldmann, 2001). This is one of the earliest occurrences for the Pinnootheridae, a family whose fossil record is in great need of reexamination.

The evidence for the area of origin for the Hexapodidae and the Cancridae is less conclusive. Schweitzer and Feldmann (2001) demonstrated that the earliest known occurrence of the Hexapodidae was either in Paleocene rocks of Argentina or Paleocene rocks of India, then located far to the south of its current position (Glassner and Rao, 1960). The age of the Indian material must...
be verified before conclusions are drawn. The earliest known members of the Cancridae occur in Eocene rocks of Argentina which yielded a member of the Cancrinae (Schweitzer and Feldmann, 2000c) and in Eocene rocks of southern Europe in which genera referable to the Lobocarcininae are found. Interestingly, each occurrence is assignable to a separate subfamily within the Cancridae. Feldmann and Keyes (1992) and Feldmann and McLay (1993) reported a single cheliped referable to the Cancrinae in Oligocene rocks of New Zealand, further suggesting a southern hemisphere origin for the Cancrinae and possibly the Cancridae. Therefore, the Cancridae arose either in the high southern latitudes or in the Tethys; however, no conclusions can be drawn until more evidence is recovered.

Some patterns of origination described in the revisionary work leading to this study corroborate previously known or inferred areas of origin. Feldmann and Fordyce (1996) reported that the cancrid subfamily Lobocarcininae originated in southern Europe and dispersed eastward throughout the Tethys and to New Zealand. A reevaluation of that subfamily supports that view (Schweitzer and Feldmann, 2000c). The Necrocarcinidae appear to have evolved in the North Atlantic and subsequently dispersed worldwide during the Cretaceous. The Hapalidae and Matutidae also appear to have evolved in the North Atlantic and Southern Europe respectively (Schweitzer and Feldmann, 2000a).

Data on first occurrences is always subject to change based upon new discoveries. At this time, it appears that the Pacific Northwest of North America was an area of evolutionary innovation within several families of the Decapoda during the Eocene. The Tertiary decapod fauna of Japan appears to have been highly influenced by taxa introduced by dispersal events and less dominated by taxa that evolved within Japan; a marked evolutionary burst is recorded in Miocene rocks of Japan documented by a large number of first occurrences.

**EVOLUTION AND EXTINCTION PATTERNS**

Occurrences of the Cretaceous and Tertiary decapod faunas of the North Pacific Rim appear to correspond with well-documented patterns of radiation and extinction (Fig. 7, Table 3). The Cretaceous decapod fauna contained 11 genera, 9 of which (82 percent) appear to have become extinct by the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.). The decapod record for the North Pacific thus far supports a major extinction event at the end of the Cretaceous. Two decapod genera survived well into the Tertiary and one of these survives in modern oceans, as would be typical of ecological generalists that may have preferentially survived the K/T event (Kauffman, personal commun.).
found on the North Pacific Rim that originated during the Eocene, or 38 percent, persist into the Recent, indicating that Eocene times saw the appearance of many modern decapod genera worldwide. Only six genera (21 percent) became extinct during the Eocene, suggesting that Eocene times can be characterized as a time of high evolution and low extinction rates within the Decapoda.

Twenty-four genera are known from Oligocene rocks of the North Pacific Rim. Twenty-nine percent of these originated during the Oligocene, fewer than half the percentage for the Eocene. Additionally, 42 percent of the genera became extinct by the end of the Oligocene, twice the percentage for the Eocene. Of the genera that originated in the Oligocene, 57 percent survive into the Recent. The Oligocene appears to have been a time of greater extinction and more restricted evolutionary innovation as compared with previous Eocene and subsequent Miocene times.

At least 49 genera are recorded from Miocene rocks of the North Pacific Rim, most of which are known from Japan. At least 60 percent and possibly more of these genera originated in the Miocene, and 90 percent of the total number of genera originating along the North Pacific Rim during the Miocene survive into the Recent. About 15 percent of the total number of genera became extinct during the Miocene. The Miocene appears to have been a time of evolutionary innovation and reduced extinction. Many genera that first appeared in the Eocene and Oligocene survived into the Miocene but did not survive beyond Miocene times. The Miocene appears to have been a “crossroads,” wherein many of the early Tertiary genera persisted, and modern taxa began to appear with higher and higher frequency. Post-Miocene fossil decapod occurrences are exclusively comprised of genera that survive in modern oceans.

The overall pattern of evolution and extinction of genera is therefore congruent with that reported for other groups. The Cretaceous is marked by a radiation of decapod taxa (Glaessner, 1969) and terminated in an extinction event that appears to have affected many decapod genera (Feldmann et al., 1995). However, one genus, Homola, and eight families present in the North Pacific at that time survive into the Recent. The Eocene was a time of rapid evolution within the Decapoda, in which numerous new genera appeared, corroborating Glaessner’s (1969) assertion that the early Tertiary was a time of radiation for decapod taxa worldwide. Some North Pacific taxa survived into the modern decapod fauna and some became extinct by the end of the Miocene. The late Eocene-Oligocene marked the end of the most recent “Greenhouse stage,” leading to the initiation of the current “Icehouse stage” and a correlated decline in the fauna (Fischer, 1982). This biotic crisis documented by the decreased diversity and increased extinction of decapods occurs during the Oligocene in the North Pacific Ocean. The Miocene was another time of great evolutionary radiation, in which many new genera appeared, corroborating the conclusions of Glaessner (1969) for decapod taxa worldwide. The Miocene was also a crossroads, in which modern decapod genera and genera typical of the early Tertiary coexisted. During the Miocene, temperature gradients between equatorial regions and the poles increased and have remained stable into the present (Crame, 1993). The Miocene fauna, adapted to those climatic conditions and temperature gradients, survived into the present. Post-Miocene deposits contain only genera that survive into modern oceans, suggesting that the end of the Miocene marks the end of the early Tertiary decapod fauna and a continued expansion of the modern decapod fauna.

LATITUDINAL GRADIENTS AND PROVINCES

Latitudinal diversity gradients have been studied for a variety of groups for Tertiary to Recent faunas of the North Pacific Ocean, resulting in numerous schemes for faunal provinces of the region based upon isopods (Kussakin, 1990), nautiloids (Jefferts, 1988), molluscs (Hall, 1964; Valentine, 1966, includes overview), and offshore decapods (Wicksten, 1989). Most or all of the studies have been at the species level (Schenck and Keen, 1936; Hall, 1964; Valentine, 1966; Jefferts, 1988; Wicksten, 1989; Kussakin, 1990). Modern faunas may be divided into numerous provinces (Schenck and Keen, 1936; Hall, 1964; Valentine, 1966) because of the steep climatic gradient that prevails in modern oceans (Valentine, 1966; Addicott, 1970). Regardless of the group studied, most provincial schemes include Arctic, Aleutian, Oregonian, Californian, and Panamic zones, each with varying latitudinal ranges and minor provinces (Valentine, 1966).

The Tertiary decapod fauna of the Pacific Coast of North America is much more diverse at the generic level in southern latitudes than in southern areas. The Eocene decapod fauna contains eight genera restricted to occurrences in Washington, eight found in either Washington or Oregon, and five ranging from Alaska to Oregon, one of which extends to California. Only five genera were known solely from areas south of Oregon, two of which are distinctively subtropical genera. The Oligocene record is similar: seven genera were known only from Washington, five range from Alaska to Oregon or Washington, two were found in Washington and Oregon, and one was known only from Oregon. One genus was reported from Alaska to California, and one from Washington to California. In the Oligocene fauna, there were no distinctly subtropical taxa, and again, the most diverse fauna is located in northern areas. The Eocene was a time of high diversity for the molluscan fauna, while the Oligocene fauna was less diverse, reflecting probable cooler water conditions (Addicott, 1970), similar to the pattern demonstrated by the decapod fauna.

Miocene occurrences echo that of the Eocene and Oligocene: six genera were reported solely from Washington, one genus ranged from Alaska to Washington, and one was known from Washington to Oregon. One endemic genus has been described from Oregon, and two distinctly subtropical or warm-temperate genera have been reported from California. The area north of Oregon appears to have been conducive to rapid evolution within the Decapoda; alternatively, this record may be an artifact of the studied occurrences, most of which are from well-collected areas in Washington state. Additionally, Eocene to Miocene rocks are particularly abundant and well exposed in coastal areas of Washington, contributing to the abundance of decapods recovered from those rocks.

Tertiary molluscan faunas are divisible into fewer provinces than the Recent fauna because of the warmer, more equalized climate of that time (Addicott, 1970). The decapod fauna, analyzed at the generic level, of the Pacific Northwest of North America appears to support that view. The Tertiary decapod fauna of the Pacific Coast of North America appears to be provincial, but only two major provinces can be suggested. A distinctive, diverse decapod fauna inhabited the area north of Oregon during the Eocene through Miocene, and another distinctly sub-tropical to warm temperate fauna appears to have inhabited the coast of southern California. This observation corresponds to the general faunal zones in modern oceans and those suggested by Addicott (1970) for Tertiary molluscan faunas.

Tertiary molluscan faunas of the temperate North Pacific were dominated by taxa which now live in warmer areas (Addicott, 1970). Some decapod taxa can be interpreted to display this pattern. Lophomastix appears to have originated in Washington and is now found from California to Mexico and in Japan. Trichopelarion and Carpilius, also originating in Washington, are now found in sub-tropical to warm temperate regions. Calappa, originally recovered from north and south temperate sites (Schweizer and Feldmann, 2000a), now inhabits primarily tropical locales. However, Callianopsis, Cancer s.s., Glebocarcinus, and Metaecarcinus inhabit coastal Alaska to California, Romaleon inhabit
coastal British Columbia to Mexico, and Panopeus may be found on the east and west coasts of North America. These ranges are similar to their distribution in the fossil record. Ranina, Macrophieria, Raninoides, and Asthenognathus all appear to occupy similar habitats in modern oceans as during the Tertiary. Therefore, many of the decapod taxa do not appear to demonstrate marked shifts in habitat preference from Tertiary to Recent times.

It is difficult to speculate on faunal provinces and diversity gradients for the Tertiary of Japan, because fossil occurrences have been highly regional. For example, most of the Miocene and post-Miocene occurrences are known from southwestern Japan (Karasawa, 1993), and most Eocene occurrences are from southern Japan. However, the Miocene decapod fauna from central Japan appears to have been similar to the generic level to faunas from southwestern Japan. Strictly tropical species were absent, suggesting possible provinciality in the decapod fauna (Kato, 1996). Deposits from northern Japan are less well studied and include only Cretaceous occurrences (Collins et al., 1993).

DISTRIBUTION OF FAMILY AND HIGHER LEVEL TAXA

Overview.—Brachyurans may be separated into three major groups, the Podotremata, Heterotremata, and Thoracotremata, based upon the position of the genital openings in males and females (Guinot, 1977; Guinot and Richer de Forges, 1997). In the most primitive brachyuran group, the Podotremata, the genital openings are located on the appendages in both males and females. Podotremes are the first brachyuran taxa to be found in the fossil record, dating to the Jurassic and Cretaceous (Glaessner, 1969). The Heterotremata comprise a more derived group, in which the genital openings of the males are on the appendages and those of the females are on the thorax. Members of the Heterotremata first appeared in the fossil record during the Cretaceous (Glaessner, 1969; Schweitzer Hopkins et al., 1999). Finally, the most derived brachyurans, the Thoracotremata, can be characterized by possession of genital openings on the thorax in both males and females and are now restricted to only four families, the Grapsidae, Ocyopidae, Mictyridae, and Gecarcinidae (Guinot and Richer de Forges, 1997). Thoracotremes are abundant in the fossil record beginning in the Miocene (Glaessner, 1969).

The decapod fauna of the Pacific coast of South America was comprised of relatively more podotreme and heterotreme brachyurans than the fauna of the Atlantic coast during the Cretaceous, and this difference in relative proportions has remained stable since that time (Feldmann et al., 1997). Occurrences of high proportions of podotremes and heterotremes in Australia and New Zealand during the Cretaceous and Paleogene were interpreted to suggest that faunas of temperate to polar high latitude areas might be comprised of more primitive brachyurans (Feldmann et al., 1997). Since that publication, at least three taxa belonging to the Heterotremata have been described from Argentina (Schweitzer and Feldmann, 2000b, 2000c, 2001), suggesting that these relative proportions may change as more data become available.

Pacific Northwest.—In Cretaceous deposits, one-third of the decapod genera are referable to the Podotremata and two-thirds are referable to the Heterotremata (Fig. 8). During the Eocene, thirty-two percent of the brachyuran genera are referable to the Podotremata; the majority of these genera are members of the Raninidae. This percentage shows a steady decline throughout the Cenozoic; only 19 percent of the Oligocene fauna and 9 percent of the Miocene genera are referable to the Podotremata. This is primarily due to the decline and eventual disappearance of the Raninidae in these deposits. The percentage of the modern brachyuran fauna comprised of members of the Podotremata is very low. Hart (1982) and Jensen (1995) listed no podotremes and Schmitt (1921) reported only seven percent of the brachyuran fauna of California as referable to families now placed within the Podotremata.

Members of more derived families referable to the Heterotremata comprised about 68 percent of the brachyuran population of the Pacific Northwest during the Eocene. That proportion showed a small but continuous increase through the Oligocene (81 percent), Miocene (91 percent) and post-Miocene (100 percent) deposits. None of the fossil faunas of the Pacific Northwest included a member of the Thoracotremata; however, thoracotremes include shore crabs which have an extremely poor preservation potential which may account for the paucity of thoracotreme fossils.

The modern decapod fauna of the Pacific Northwest is dominated by taxa within the Heterotremata and Thoracotremata. For example, out of nineteen brachyuran genera reported for British Columbia, 89 percent belong to the Heterotremata and 11 percent to the Thoracotremata (Hart, 1982). Schmitt (1921) reported a modern brachyuran fauna for coastal California comprised of 79 percent heterotremes and 14 percent thoracotremes. Out of thirty-eight nearshore brachyuran taxa of the Pacific coast of Canada and the United States discussed by Jensen (1995), 89 percent are referable to the Heterotremata and 11 percent belong to the Thoracotremata.

Japan.—During the Cretaceous in Japan, the decapod fauna was dominated by podotreme decapod families, which comprised two-thirds of the decapod fauna (Fig. 9). The fauna of the Eocene contained 57 percent podotremes and 43 percent heterotremes. The Oligocene fauna lacked podotremes and showed an increase in heterotreme genera which comprised 75 percent of the fauna. The Oligocene fauna was comprised of 25 percent thoracotremes. The Miocene decapod fauna of Japan was comprised of 5 percent podotremes, 84 percent heterotremes and 11 percent thoracotremes. Nine percent of the modern fauna is referable to the Podotremata and fifteen percent is referable to the Thoracotremata.

Summary.—The decapod faunas of Japan and the Pacific Northwest display patterns of evolution that are consistent with the evolutionary history of the Podotremata, Heterotremata, and Thoracotremata. The Podotremata is comprised of the most primitive decapods so the abundance of those forms in the Cretaceous fauna of Japan and the Eocene deposits of both Japan and the Pacific Northwest is not surprising. Additionally, the steady increase in the number of heterotremes throughout the Eocene to Miocene is also consistent, because most heterotreme families made their first appearance in the Cretaceous and Paleogene.

![Graph showing distribution of higher level taxa of the Pacific Northwest](image-url)
est in the Recent; however, this is undoubtedly biased by the incompleteness of the fossil record. The decapod fauna of Japan was low in diversity during the early Tertiary, and diversity and the number of genera increased dramatically in the Miocene and remain high in modern oceans. Several genera and one family appear to have originated in the North Pacific Ocean, which heretofore has not been considered to be a hotbed of decapod evolution. Additionally, the results of this study indicate that the high southern latitude region was an area of origin for several genera and families of decapods. These conclusions corroborate those of Zinsmeister and Feldmann (1984), Zinsmeister et al. (1989), and Crame (1992, 1996) who proposed that many taxa may have originated in high latitude areas with subsequent dispersal to temperate or tropical regions. Southern Europe and Tethys also appear to have been areas in which many families originated.

Several decapod taxa appear to have become extinct at the end of the Cretaceous (Feldmann, 1998); however, the range of some taxa straddles the K/T boundary, corroborating Feldmann et al.’s (1995) assertion that not all Decapoda were dramatically affected by the end Cretaceous event. This is corroborated by Collins and Jakobsen (1994). Some North Pacific taxa became extinct and others ranged from the Cretaceous well into the Tertiary and even into the Recent. Eight families present along the North Pacific Rim survive into the Recent. The Eocene was a time of evolutionary radiation within the Decapoda (Glaessner, 1969; Warner, 1977; Schram, 1986), a trend clearly demonstrated by the fauna of the North Pacific. Many of the taxa that originated in the Eocene became extinct during the Tertiary, but a significant proportion, about one-third, survived into the Recent. Oligocene time showed an overall decline in diversity and number of genera, and many taxa became extinct at the end of the Oligocene, perhaps as a response to global cooling (Kennett, 1982). The Miocene was again a time of evolutionary radiation (Glaessner, 1969; Warner, 1977), due to overall warming of the oceans, and the vast majority of taxa that originated during the Miocene have modern congeners. The closure of both the Tethyan Seaway and the Central American Seaway during the Miocene dramatically affected ocean circulation so that warm water was pumped into higher latitudes instead of remaining circum-equatorial (Kennett, 1982); this led to the evolutionary explosion and increase in diversity during the Miocene. Additionally, the end Miocene marks the extinction of several decapod taxa, suggesting that the Miocene was a crossroads in which the last of the early Tertiary decapods and the modern Miocene decapod fauna coexisted.

The decapod fauna of the Pacific Northwest of North America shows a very general latitudinal distribution, divisible into three broad regions. This latitudinal distribution persists through the Cenozoic. Several taxa display a primarily northern distribution, ranging from Alaska to Washington or occurring only in Alaska, or British Columbia, or Washington. An intermediate group of decapod ranges from Washington to California, or Washington to Oregon, or Oregon to California, or only in Oregon. Finally, a southern province is defined by a few decapod taxa known only from central to southern California. Such a latitudinal distribution echoes that seen in other taxa in both the fossil record and in modern oceans.

The distribution of the Podotremata, Heterotremata, and Thoracotremata along the North Pacific rim is consistent with the evolutionary history of the three groups. The podotremes, which appeared in the Jurassic and Cretaceous, are most abundant in the Cretaceous decapod faunas of the region. The heterotremes are most derived group of decapods, thoracotremes, appear in the fossil record beginning in the Miocene.

The relative proportion of podotremes, heterotremes and thoracotremes reached modern levels by the Miocene in Japan and has remained relatively stable since then. This is probably due to the fact that the Miocene marks a major radiation of decapods, most of which have survived into modern oceans. Interestingly, the proportion of podotremes and thoracotremes is slightly higher in modern seas of Japan than of the Pacific Northwest. This may be due to the warm, tropical influence that Japan receives from the Indo-Pacific and equatorial regions, so that the diversity of decapods is high as compared to the cold-water influenced fauna of the Pacific Northwest. In spite of this slight difference, the overall similarity in relative proportions of the three groups of brachyurans in both Japan and the Pacific Northwest suggests that latitudinal and regional position does not itself control the distribution of the Podotremata, Heterotremata, and Thoracotremata.

**SUMMARY**

The decapod fauna of the Tertiary North Pacific region can be assigned to five major areas of origin that are well supported by the decapod data as well as by other taxa: a fauna of North Pacific origin, a fauna of Tethyan origin, a fauna of North Polar origin, a fauna derived from the high southern latitudes, and an amphi-tropical fauna. Relative proportions of these five major components change over time. Taxa of North Pacific and North Polar origin were most dominant during the Cretaceous and early Tertiary in both the eastern and western North Pacific. Taxa of Tethyan origin became increasingly dominant throughout the Cenozoic until the Recent, where they dominate the fauna of the western North Pacific. Taxa derived from the high southern latitudes invaded the North Pacific during the middle to late Tertiary and have subsequently become extinct in the Southern Hemisphere.

The diversity of the Cretaceous decapod fauna in both the eastern and western North Pacific was relatively low, a record at least in part influenced by the paucity of Cretaceous marine deposits along the North Pacific rim. The decapod fauna of the Pacific Northwest of North America was very diverse during the Eocene, and diversity as well as the number of genera recorded declined until the Recent. The diversity and the number of genera increased during the early Tertiary, and diversity and the number of genera increased dramatically in the Miocene and remain high in modern oceans.
paralleling their global appearance in abundance during the Miocene.

Comprehensive analysis of the Cretaceous and Tertiary decapods of the North Pacific Rim, especially the Brachyura, has resulted in a major advancement in our understanding of the evolution and distribution of those animals. These conclusions expand upon those already drawn by Feldmann, Vega, and others for Mexican, Central American, and southern hemisphere decapods and Karasawa (1993, 1999) for western North Pacific decapods and provide several new insights on decapod distribution and evolution. Continued analysis of decapod occurrences from both the North and South Pacific, currently underway by Feldmann, Schweitzer, and Vega, as well as from other key areas such as Mexico, southern Europe, Central America, South America, and eastern Russia, will be necessary to expand the global view of the evolutionary and paleobiogeographic history of the decapod crustaceans.

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