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NEW EOCENE DECAPODS (THALASSINIDEA AND BRACHYURA) FROM SOUTHERN CALIFORNIA

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ABSTRACT

A new decapod fauna has been recovered from Eocene rocks of San Diego County, California. Decapod faunas of Eocene age have been rare from California, although they are well described from the northern Pacific coast. Three new species, including *Neocallichirus rhinos*, *Ctenocheles secretanae*, and *Minohellenus inexpressus*, and two new genera and species, *Acanthoportunus buchanani* and *Vegarthron santiago*, are reported from this new fauna. A new genus has been erected to accommodate *Portunites triangulum* and *Portunites granulifer;* both are herein referred to *Maeandricampus*, new genus. *Callianassa matsoni* Rathbun has been reassigned to *Neocallichirus*. Portions of the cephalothorax and abdomen of a species of *Ctenocheles* are described from fossils for the first time. *Orbitoplax weaveri*, previously known from Eocene rocks of California and Oregon, is reported from the Eocene Mission Valley Formation and the Ardath Shale for the first time. In addition, one specimen of a stomatopod of indeterminate genus is noted. The Eocene decapod fauna from California, now containing eighteen genera, has elements common to the northern Pacific coast of North America as well as taxa known only from California; thus, the area appears to have been suited for decapods adapted to a wide variety of temperature and other environmental conditions. Several genera appear to have evolved within the region, whereas others may have been introduced from the Atlantic or Tethys region via the Central American Seaway. The number of Pacific amphitropical genera continues to increase; two portunid genera discussed here display such a pattern, adding to the four already reported for Cretaceous and Tertiary rocks of the region.

Fossil decapod crustacean faunas have been well described from the Pacific Northwest of North America (see Schweitzer, 2001, for summary) and from Baja California (Rathbun, 1930; Squires and Demetrion, 1992; Schweitzer *et al.*, in press); however, Eocene decapods from California have been relatively uncommon. Isolated occurrences of decapods have previously been described from California (Rathbun, 1926, 1932; Squires, 1980, 2001; Bishop, 1988; Tucker *et al.*, 1994). The discrepancy between numbers of Eocene occurrences in California as opposed to areas to the north of that state was speculated to have been a result either of the paucity of Eocene rocks in California or of differential evolutionary rates in the two areas (Schweitzer, 2001). It now appears that as new material is collected and made available for study, the Eocene record will become increasingly robust. The fauna described here is significant because it is one of the few Eocene decapod faunas known from the California coast and brings to at least eighteen the total number of decapod genera now known from the Eocene of California.

The new material described in this report includes two new genera that appear to be endemic to the region as well as a new species of a genus not previously known from the Eocene of the west coast of North America. Further, three species are described here that are referable to genera already well-known from Tertiary rocks of the northern Pacific coast of North America. This mixture of taxa known only to the southern Pacific coast with taxa previously reported from farther north suggests that the California coast was a region where taxa from the cooler northern provinces mixed with taxa derived from tropical regions to the south.

OCCURRENCE OF FOSSILS

A summary of locality information may be found in Table 1. The specimens described here from Localities 4572, 4573, and 4109 were collected from member B of the Santiago Formation of early Uintan (middle Eocene) age (Golz and Lillegraven, 1977). The Santiago Formation is composed of approximately 600 m of yellow sandstone underlying the Sespe and Vaqueros formations and overlying the Silverado Formation (Schoellhammer *et al.*, 1981). The contacts with the underlying and overlying units are in

Table 1. Localities by number, formation, and age. Locality numbers are those used by the San Diego Museum of Natural History Department of Paleontology.

Locality Number	Locality Name	Formation	Age
4109	Rancho Carillo #1	Santiago Formation	middle Eocene
4529	Agouron/Pfizer site	Ardath Shale	middle Eocene
4572, 4573	Ocean Ranch	Santiago Formation	middle Eocene
4606, 4607	I-125 South	Mission Valley Formation	middle Eocene

some places conformable (Gray, 1961). The Santiago Formation is composed of both marine and nonmarine deposits, including some conglomerates and sandstones, and a moderately robust molluscan and foraminiferan fauna that yields a middle Eocene age, the Ulatisian of Mallory (1959) (Schoellhammer *et al.*, 1981).

The specimens at localities 4572, 4573, and 4109 were recovered during construction of the Ocean Ranch commercial development project in the northern part of the city of Oceanside, San Diego County, California. Specimens were collected at two separate localities, located north of Oceanside Boulevard, south of Mesa Drive, west of Avenida del Oro, and west of the now abandoned Silica Sand Quarry. Locality 4573, 33°12′21″N, 117°17′57″W, was found in Lot 2 of the development project area and was discovered during grading of the site; the locality can now be reached along a cul-de-sac in a south-facing slope. The specimens from this locality are preserved in yellow-gray, massive, bioturbated siltstone, which is the basal unit of a fining-upward sequence that terminates in a *Lingula* bed. Faunal elements collected at locality 4573 include ghost shrimps, crabs, molluscs, shark teeth, ray plates and stingers, and articulated fish in shrimp burrows. *Ctenocheleles secretanae* n. sp. was very common at this site, while *Neocallichirus rhinos* n. sp. was rare.

Locality 4572 was found in most of Lot 5 of the development project at 33°12′38″N, 117°17′50″W; the site is no longer accessible. The rocks at this locality include coarse-grained, fossiliferous, yellowish-gray, bioturbated, massive sandstone that underlies the siltstones of Locality 4573. Organisms collected from this site include ghost shrimp, crabs, fish in burrows, molluscs, shark teeth, and ray plates and stingers. *Neocallichirus rhinos* n. sp. was common at this site, whereas *Ctenocheles secretanae* n. sp. was rare.

Locality 4109, the Rancho Carillo #1 site, is located in Carlsbad, north of San Diego. The specimens were recovered from an excavation at Rancho Carillo bounded by Palomar Airport Drive, Melrose Drive, El Fuerte Street, and the community of La Costa to the south. Transitional facies of the Santiago Formation are exposed here, composed of gray-black, laminated siltstones. The locality is at 33°7′30″N and 117°14′15″W and is no longer accessible.

Rocks of the Eocene Ardath Shale of the La Jolla Group are exposed at Locality 4529. This locality occurs at an excavation for the Agouron/Pfizer Pharmaceuticals facility at 10742 Science Center Drive, Torrey Pines Science Center, 32°53′56″N, 117°13′45″W. Science Center Drive is located off Genesee Avenue about 400 m west of Interstate highway 5 (I-5). The fossils were collected from a total of 10 feet of dark gray, laminated and bioturbated siltstone overlying a dark gray massive siltstone. Fossils were collected from both siltstone types. The locality has been covered by a retaining wall and is no longer accessible. The Ardath Shale contains channel deposits of sandstone, siltstone, mudstone, and shale and is underlain by the Torrey Sandstone and overlain by the Scripps Formation (Lohmar *et al.*, 1979). It has been determined to be of lower middle Eocene age (Golz and Lillegraven, 1977; Geological Survey Research, 1980) and corresponds to the Eocene Penutian and Ulatisian stages of Mallory (1959) (Lohmar *et al.*, 1979). The unit has been interpreted to have been deposited on the lower portion of a continental slope (Lohmar *et al.*, 1979).

Localities 4606 and 4607 contain rocks of the middle Eocene (late Uintan) Mission Valley Formation. The rocks are exposed in the city of Lemon Grove in San Diego County, California, at the Interstate-125, Stage 3, Protoreodon Quarry, 32°44′7″N, 117°00′58″W. The rocks were exposed during excavation for the I-125 South Stage 3 construction project. The locality is directly across Old Troy Street from the eastern edge of Palm Middle School and about 300 m west of Sweetwater Road; it is no longer accessible. The fossils were recovered from a poorly indurated, fine-grained sandstone unit about 3 m thick; this sandstone unit yielded both vertebrate and invertebrate fossils. The fossiliferous unit overlies what appears to be a terrestrial or near-shore deposit containing terrestrial snails. The decapod fossils were collected in association with mammals and terrestrial snails, suggesting a nearshore environment for the decapods. The Mission Valley Formation is composed of mudstones and sandstones deposited between delta buildups or in prodelta areas (Schiebout, 1977) on a nearshore shelf (Lohmar *et al.*, 1979) and is composed of both marine and nonmarine deposits (Golz and Lillegraven, 1977). Numerous mammalian fossils are known from this unit (Golz and Lillegraven, 1977; Schiebout, 1977). Prothero *et al.* (1997) correlated the unit with Chrons C19r and C20n of the middle Eocene.

SYSTEMATIC PALEONTOLOGY

Infraorder Thalassinidea Latreille, 1831

Superfamily Callianassoidea Dana, 1852

Remarks.—In their revision of American species of the Callianassidae *sensu lato*, Manning and Felder (1991) subdivided that group into two families, the Callianassidae *sensu stricto* and the Ctenochelidae, and recognized seven subfamilies and several new genera. This work called attention to the importance of the morphology of the first pereiopod in making generic identifications. This extremely important contribution made it possible to relate the classification of the living animals to fossil remains. Prior to their work, principle taxonomic attention had been placed upon the morphology of the third maxilliped and the pleopods and, to a lesser extent, upon the nature of the delicate carapace. Because only the first pereiopods are typically preserved in fossil forms, the latter characters were of little use. Manning and Felder (1991) placed primary attention on the morphology of the merus. They noted the presence or absence of meral hooks and recognized that some meri were slender and others were nearly as high as long. Most importantly, these features were consistent within the genera that had been defined on traditional morphological features of the maxillipeds, pleopods, and carapace. Unfortunately, the morphology of the propodus and dactylus are not as useful in making generic distinctions; therefore, many callianassids known only from these distal elements remain enigmatic. Tudge *et al.* (2000) confirmed much of Manning and Felder's (1991) work in a phylogenetic study based primarily upon soft-part morphology, thus ensuring its continued usefulness; Martin and Davis (2001) recognized six families within the Callianassoidea. Genera continue to be added to the Callianassidae *sensu lato* (for example, Poore, 2000). It is in this context that *Vegarthron* is proposed as a new genus.

Shortly after the publication of Manning and Felder's revision of the Callianassidae *sensu lato*, one of us (RMF) discussed the work at length with Manning, with particular reference to the identification of fossil species. Two points were critical. Identification to the generic level cannot be made confidently unless the merus and carpus are preserved, and the angle of the propodus/carpus joint is significant. This latter feature was not discussed by Manning and Felder (1991) because living forms typically exhibit an articulation oriented at right angles to the long axis of the articles. However, many fossil species, particularly those from Cretaceous to Eocene rocks, exhibit an articulation that lies at a lower angle. These species have historically been grouped into the genus *Protocallianassa* Beurlen, 1930.

Family Callianassidae Dana, 1852

Subfamily Uncertain

Genus ***Vegarthron***, new genus

Type Species.—Vegarthron santiago n. gen. and n. sp.

Other Species.—Vegarthron sp. as *Protocallianassa* sp. Vega, Feldmann, and Sour-Tovar, 1995, p. 343, fig. 3.3.

Diagnosis.—Large callianassid lacking meral hook; triangular carpus; oblique carpus/propodus joint; notch along distal margin of manus absent.

Description.—As for species.

Etymology.—The generic name combines the surname of Dr. Francisco Vega of UNAM and preeminent researcher of Mexican decapods, and the Greek *arthron* = joint, in reference to the oblique carpus/propodus joint and the lack of a notch at the propodus/dactylus joint.

Occurrence.—The type species was collected from the middle Eocene Santiago Formation in southern California. An additional probable occurrence is that of specimens deposited in the Museo de Paleontología, Universidad Nacional Autónoma de México, and in the Carnegie Museum, Pittsburgh, Pennsylvania, as *Protocallianassa* sp. (Vega *et al.*, 1995). These specimens, collected from the Cardenas Formation in east-central México, are Maastrichtian (Late Cretaceous) in age.

Remarks.—Reexamination of the species embraced within *Protocallianassa*, *sensu* Mertin (1941), reveals that, with respect to the morphology of the meri and carpi, the genus contains representatives of what would be several genera using the criteria of Manning and Felder. In an attempt to clarify at least some of the confusion, we reexamined the description and illustrations of the type species of *Protocallianassa*, *Callianassa archiaci* A. Milne-Edwards, 1860b, and herein refine the diagnosis of *Protocallianassa* as follows: merus highest mesially, slightly longer than high; carpus much longer than high, subrectangular, highest at distal margin; propodus/carpus joint oblique to long axis of articles; propodus with manus about as high as long and bearing prominent notch on distal margin below articulation with dactylus. This definition embraces not only the type species but, for example, also characterizes one of the frequently cited species, *Protocallianassa faujasi* (Desmarest, 1822).

These same characters exclude the callianassids from the Santiago Formation, necessitating creation of a new genus. *Vegarthron* n. gen. has a merus that is similar to that in *Protocallianassa*, as is the angle of the propodus/carpus joint. However, the carpus is about as long as high and is triangular in *Vegarthron*, and the distal margin of the propodus lacks any indication of a notch. The carpus in *Protocallianassa* is rectangular and longer than wide, and the

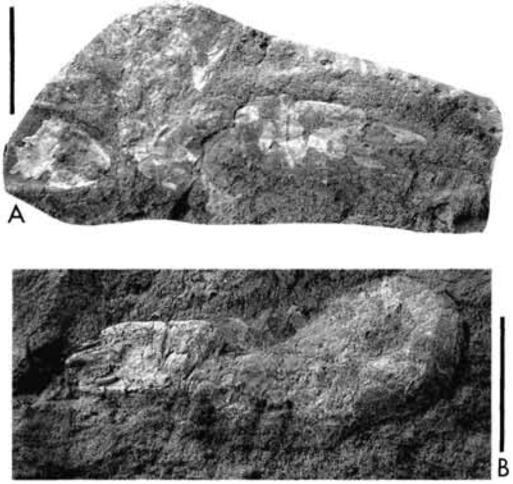

Fig. 1. *Vegarthron santiago* n. gen. and sp. A, lateral view, with well-preserved major cheliped, paratype, SDSNH 81082; B, lateral view of holotype, SDSNH 81078. Scale bars equal to 1 cm.

propodus exhibits a distal notch at the base of the propodus/dactylus articulation. *Vegarthron* is similar in some regards to the callianassid genera *Calliax* de Saint Laurent, 1973; *Eucalliax* Manning and Felder, 1991; and *Anacalliax* de Saint Laurent, 1973. In both *Calliax* and *Eucalliax*, the merus is longer than high, whereas in *Vegarthron*, it is about as long as high. The lower margin of the merus of *Calliax* is serrated, whereas in *Vegarthron*, it is entire. Both *Calliax* and *Eucalliax* have weak indentations in the distal margin of the manus just above the base of the fixed finger; this indentation is not present in *Vegarthron*. The fixed finger of *Anacalliax* is ornamented with a strong spine, whereas the fixed finger of *Vegarthron* is entire. The proximal margin of the manus of *Vegarthron* is positioned at a low angle at the articulation with the carpus, whereas in *Anacalliax*, that margin and articulation lie at right angles. In fact, the inclined angle of the propodus/carpus articulation distinguishes *Vegarthron* from all other known callianassoid genera. These characters are consistent with those identified as being of generic significance by Manning and Felder (1991) and, therefore, constitute firm grounds for establishment of a new genus.

Vegarthron santiago, new species

Figs. 1, 2

Type Material.—The holotype, SDSNH 81078, and paratypes, SDSNH 81080, 81081, and 81110, collected at locality 4573, and paratypes, SDSNH 81079, and 81082, collected from locality 4572, are deposited in the San Diego Natural History Museum, San Diego, California.

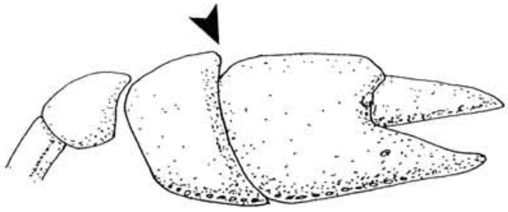

Fig. 2. Line drawing of chela, merus, and carpus of major cheliped of *Vegarthron santiago*. Arrow indicates oblique carpus/propodus articulation.

Diagnosis.—As for genus.

Description.—Moderate-sized callianassid, carapace length estimated to be 12 mm, heterochelous; major cheliped lacking meral hook and bearing triangular carpus and oblique carpus/propodus articulation.

Carapace crushed, lacking detail. Abdomen generally smooth; convex forward anterior and posterior margins, gently and smoothly convex pleural margin; somite 2(?) slightly longer than others. Telson and uropods not observed.

Major cheliped with slender ischium, longer than high; shallow longitudinal sulcus extends along outer surface. Merus nearly twice as long as high; smoothly convex upper and lower margins; smooth, convex outer surface; meral hook absent. Carpus triangular; straight upper margin; proximal margin with concave notch at articulation with merus, curving gently downward and distally into lower margin; lower margin with row of setal pits; distal margin straight, inclined distally from upper to lower margin at about 75 degree angle to long axis of carpus and propodus; outer surface smooth. Propodus stout; manus varies from slightly longer than high to slightly higher than long; rectangular; upper and lower margins straight; outer surface generally with row of setal pits along lower margin. Fixed finger curved slightly upward; triangular; shorter than manus; edentulous. Dactylus curved downward; triangular, length similar to fixed finger; edentulous.

Minor claw with carpus, propodus, and dactylus similar to those of major claw, length of manus about 0.6 that of major claw.

Table 2. Measurements (in mm) taken on specimens of *Vegarthron santiago*, new genus and species. When unspecified, the measurements refer to the major cheliped. L = length; H = height.

	Merus		Carpus		Propodus		Dactylus	
Specimen	L	H	L	H	L	H	L	H
80178 (Holotype)					7.6	5.6	38	2.2
81079 (Minor claw)	4.1	2.2	4.8	5.0	9.1	4.4		
					7.3	3.8		
81080 (Minor claw)					14.0	8.2		
					>13.4	4.8		
81081 (Minor claw)					11.7			
					10.2	4.8		
81082					15.1	9.2		

Measurements.—Measurements taken on specimens of *Vegarthron santiago* are given in Table 2.

Etymology.—The trivial name refers to the Santiago Formation from which the type material was collected.

Occurrence.—The type material was collected from the middle Eocene Santiago Formation at localities 4572 and 4573.

Remarks.—See discussion for genus.

Subfamily Callichirinae Manning and Felder, 1991

Genus *Neocallichirus* Sakai, 1988

Type Species.—*Neocallichirus horneri* Sakai, 1988, by original designation.

Included Living Species.—*Neocallichirus cacahuate* Felder and Manning, 1995; *N. caechabitator* Sakai, 1988; *N. darwinensis* Sakai, 1988; *N. denticulatus* Ngoc-Ho, 1994; *N. grandimanus* (Gibbes, 1850) = *Glypturus branneri* Rathbun, 1900; *N. horneri* Sakai, 1988; *N. indica* (de Man, 1905); *N. jousseaumei* (Nobili, 1906); *N. lemaitrei* Manning, 1993; *N. manningi* Kazmi and Kazmi, 1994; *N. maluccensis* (de Man, 1905); *N. natalensis* (Barnard, 1947); *N. nickellae* Manning, 1993; *N. pachydactylus* (A. Milne-Edwards, 1870); *N. rathbunae* (Schmitt, 1935); *N. raymanningi* Blanco Rambla and Lemaitre, 1999; *N. sassandrensis* (Le Loeuff and Intès, 1974); *N. taiaro* Ngoc-Ho, 1995.

Included Fossil Species.—*Neocallichirus bona* (Imaizumi, 1958), as *Callianassa* (see Karasawa, 1997); *N. grandis* Karasawa and Goda, 1996; *N. matsoni* (Rathbun, 1935), as *Callianassa matsoni*; *N. nishikawai* Karasawa, 1993; *N. okamotoi* Karasawa, 1993; *N. peraensis* Collins, Donovan, and Dixon, 1996; *N. rhinos* n. sp.; *N. sakiae* Karasawa and Fudouji, 2000.

Remarks.—The specimens under consideration here consist of the ischium, merus, carpus, propodus, and dactylus of the major cheliped so that the classification of Manning and Felder (1991) can be applied. The fossils from the Santiago Formation can clearly be assigned to *Neocallichirus*. The merus is very broad; the distance from the upper to the lower margin of the merus is about 0.8 that of the carpus. Furthermore, the lower margin of the merus curves distally and upward and bears a serrated edge, the primary key character for the genus (Manning and Felder, 1991, fig. 4).

There are some additional morphological features exhibited by most, if not all, extant species within the genus that are also found in the fossil form. The carpus, although variable in shape, is not rectangular and typically has a rounded lower margin. The finger of the propodus tends to be edentulous, whereas the dactylus is stout and heavily armed with a triangular or rectangular tooth near the proximal end of the element. This tooth may bear nodes or denticles that would appear to occlude not solely with the fixed finger but also with the thickened and often serrated distal margin of the manus. Although the distal margin of the manus in several callianassids may be thickened, serrations are not commonly observed. Coupled with the strongly armed dactylus, the claw seems to be equipped with a robust grasping and crushing device for grabbing and crushing food resources.

The morphology of the dactylus, in particular, is distinctive and prompts reassignment of *Callianassa matsoni* Rathbun, 1935, to *Neocallichirus*. This assignment is made with caution owing to the absence of the merus in this species; however, the form of the dactylus is so

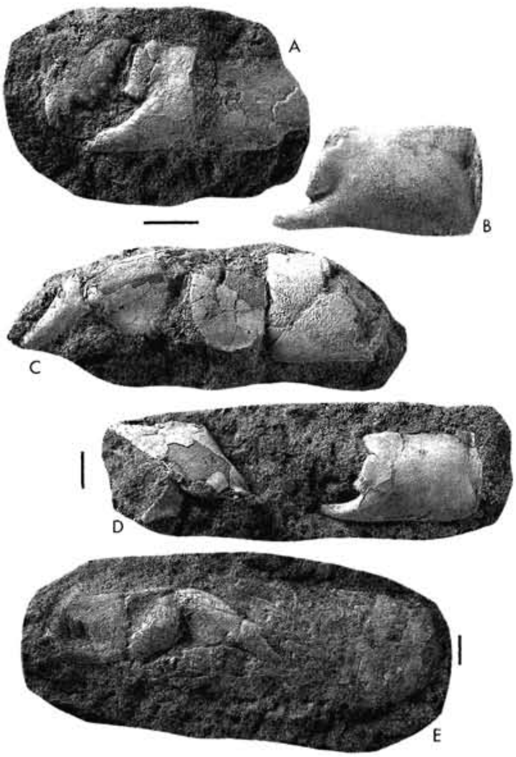

Fig. 3. *Neocallichirus rhinos* n. sp. A, major chela with well preserved movable finger, paratype, SDSNH 81089; B, inner surface of major chela, paratype, SDSNH 81087; C, major cheliped, paratype, SDSNH 81086; D, two left chelae, paratype, SDSNH 81084 (at left) and 81085 (at right); E, crushed specimen retaining carapace and abdomen, holotype, SDHNM 81083. Uppermost scale bar for A, B, and C. Scale bars equal to 1 cm.

much like that of some living forms as to be unmistakable; see for example, *N. nickellae* Manning, 1993.

Neocallichirus rhinos, new species
Figs. 3, 4

Types.—The holotype, SDSNH 81083, and eleven paratypes, SDSNH 81085–81090, 81099–81101, and 81104, are deposited in the San Diego Museum of Natural History, San Diego, California.

Diagnosis.—Extremely large, strongly heterochelate callianassid with edentulous fixed finger and strongly toothed dactylus on major chela that occludes with strengthened, serrated distal surface of manus and fixed finger.

Description.—Cephalothorax preserved on a single specimen; crushed; details obscured.

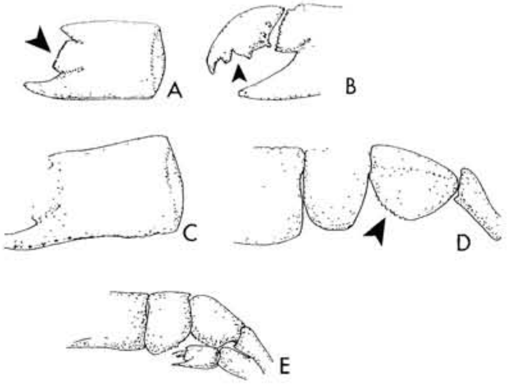

Fig. 4. Line drawings of *Neocallichirus rhinos*. A, outer surface of manus of major chela, SDSNH 81084, arrow indicates thickened, serrate distal margin; B, fingers and distal portion of manus, SDSNH 81089, arrow indicates strongly armed dactylus; C, inner surface of manus of major chela, SDSNH 81087; D, distal portion of ischium, merus, carpus, and proximal portion of manus of major cheliped, SDSNH 81086, arrow indicates serrated lower margin of merus; E, proximal portion of major cheliped and distal portion of minor cheliped, SDSNH 81083.

Major claw of first pereiopod, left on three specimens and right on three specimens, with manus up to 21 mm high and 28.8 mm long. Ischium about 2.4 times as long as maximum height, measured at distal end; about 2.5 times as high distally as proximally; one row of pustules extends from proximal end of upper surface to about midlength and another row of pustules extends entire length along lower margin. Merus about 1.4 times as long as high, rounded triangular, bearing weak keel extending from lower proximal articulation to lower distal articulation; lower margin serrated. Carpus about 0.6 times as long as high; upper and distal margins straight; proximal and lower margins smoothly rounded, punctate; outer surface smooth. Propodus with rectangular manus, about 1.4 times as long as high; upper surface keeled proximally and sharply rounded distally; distal margin nearly straight, at right angles to long axis of manus; lower surface of manus and fixed finger punctate; outer surface smoothly rounded with depressed, lanceolate articular region proximally and inflated distal margin separated from remainder of hand by arcuate, shallow sulcus extending from upper end of fixed finger proximally and upward to lower articulation with dactylus. Inner surface smooth, moderately inflated. Distal margin of manus with inclined upper portion extending downward and proximally to inflated region in midlength bearing coarse to moderately coarse denticles and separated from short, edentulous fixed finger by shallow, rounded notch. Dactylus stout, about 1.9 times as long as high; upper surface smoothly rounded to acute tip; occlusal surface with one triangular denticle between tip and strong projection bearing 4 transverse swellings on lower part of outer surface extending to occlusal surface, which bears nodose denticles.

Minor chela on first pereiopod with manus about 0.4 times as long as that of major pereiopod; merus long, slender, about 3.7 times as long as high, slightly curved upward; carpus generally rectangular; about 1.3 times as long as high; slightly convex upper and lower margins. Propodus with manus about 1.3 times as long as high; slightly convex upper and lower margins; proximal margin at right angles to long axis of manus; distal margin inclined from upper margin toward short fixed finger; dactylus straight, slender. Details of surfaces on minor chela obscured.

Elements of some of pereiopods 2–5 present, poorly preserved; generally much more delicate than pereiopod 1, elements rectilinear, slender; some with pustulose upper surfaces.

Measurements.—Measurements taken on the type series are given in Table 3.

Etymology.—The trivial name is derived from the Greek word *rhinos* (f.) = snout or beak and alludes to the outline of the dactylus, which is reminiscent of the snout of a rhinoceros or the beak of a parrot.

Occurrence.—The holotype, SDSNH 81083, and paratypes SDSNH 81085 and 81087–81090 were collected from locality 4572. SDSNH 81086 was collected from locality 4573. SDSNH 81099–81101 and 81104 were collected from locality 4529.

Remarks.—*Neocallichirus rhinos* n. sp. differs markedly from the other members of the genus in at least two significant ways. The linear dimensions of major claws and the interpreted size of the carapace of *N. rhinos* are at least twice that of any other known species within the genus (Schmitt, 1935; Manning and Felder, 1991; Manning, 1993; Felder and Manning, 1995). Typical carapace lengths range from 11 mm to 18 mm in extant forms, whereas the estimated carapace length in *N. rhinos* is 45 mm. Lengths of the mani of the major pereiopod in extant forms are up to 10 mm; it is 18 mm in the Pliocene *N. matsoni* and is about 30 mm in *N. rhinos*. In addition to size, the morphology of the distal margin of *N. rhinos* differs from all other species in being more distinctly thickened and bearing strong serrations. Thus, confusion with previously named species of *Neocallichirus* is unlikely.

American species of *Neocallichirus* inhabit nearshore and littoral habitats on the Atlantic coast of Florida (Felder and Manning, 1995) and the Caribbean (Schmitt, 1935; Manning, 1993). Griffis and Suchanek (1991) summarized the relationships between ghost shrimp burrow architecture and feeding style, concluding that the style of burrowing was species-specific. Among the animals studied was *Neocallichirus rathbuni* (as *Callianassa rathbuni*), which they characterized as constructing simple, branching burrows to a depth of about 150 cm, with two burrow openings and lacking seagrass in chambers. The presence of mounds surrounding the openings of the burrows indicated that they are deposit feeders. The burrow diameter of 30 mm (Griffis and Suchanek, 1991: 174) is approximately 1.5 times the carapace length of the holotype of the species (Schmitt, 1935: 17). If that same relationship is applied to *N. rhinos*, the burrow diameter would be in the range of 60 mm, recalling that the determination of the carapace length of the sole specimen with a crushed carapace (SDSNH 81083) is a broad estimate. Although there is no clear evidence of a burrow structure associated with any of the specimens of this species, the form of SDSNH 81083 is compact with the pereiopods extended in advance of the carapace, suggesting that it is oriented in a position much like its presumed life position. The height of the entire specimen is about 40 mm, which must approximate the inside diameter of the burrow.

Family Ctenochelidae Manning and Felder, 1991

Type Genus.—*Ctenocheles* Kishinouye, 1926.

Subfamily Ctenochelinae Manning and Felder, 1991

Genus *Ctenocheles* Kishinouye, 1926

Ctenocheles Kishinouye, 1926, p. 63, fig. 1.
Ischnodactylus Pelseneer, 1886, p. 163, fig. 1.
Non Ischnodactylus Chevrolat, 1877, p. 173.
Non Ischnodactylus Cossmann, 1889, p. 83.

Type Species.—*Ctenocheles balssi* Kishinouye, 1926, by monotypy.

Table 3. Measurements (in mm) taken on specimens of *Neocallichirus rhinos* new species. L = length; H = height.

	Ischium		Merus		Carpus		Manus		Fixed finger		Dactylus	
Specimen	L	H	L	H	L	H	L	H	L	H	L	H
80576	18.5	8.3	21.0	15.0	16.3	22.6	~22	23.3				
80576		(Minor claw)			9.7	8.8	11.6	8.7	6.0	1.4	>7	2.1
80572a							30.1	22.1	12.2	6.7		
80572b							28.9	20.2	11.9	6.3		
80572c							20.3	20.2	10.1	5.0		
8057d							25.4	16.8	>7	4.8		
80573	21.9	9.4	23.8	17.2	16.7	22.3		23.8				
80583								~17.7	11.1	7.1	18.7	10.4
80620											20.5	11.6

Included Fossil Species.—Schweitzer and Feldmann recently (2001b) updated the compilation of fossil species prepared earlier (Feldmann *et al.*, 1995) and named a new species from the late Eocene Hoko River Formation in Washington, *Ctenocheles hokoensis*. Thus, the list will not be repeated here.

Diagnosis.—"Rostral carina and rostral spine present. Dorsal surface of eye flattened. Mxp3 with or without exopod, distal margin of merus usually with spine. Major cheliped with or without proximal meral hook, palm subglobular, fingers elongate, pectinate. Uropodal exopod with lateral incision." (Manning and Felder, 1991: 784)

Remarks.—The genus *Ctenocheles* is a distinctive thalassinid because it bears a major claw that is different from that of any other member of the infraorder. *Ctenocheles* exhibits a bulbous manus with fingers that are much longer than the manus and arrayed with acicular teeth, resembling the teeth of a comb. In their revision of the Callianassidae *sensu lato*, Manning and Felder (1991) recognized several attributes of the carapace, uropods, maxillipeds, and pleopods that separated *Ctenocheles* and the genera *Gourretia*, *Paracalliax*, *Anacalliax*, and *Callianopsis* from the Callianassidae *sensu stricto* and that provided a definitional basis for the erection of a distinct family, the Ctenochelidae. At the same time, they erected a new genus within that family, *Dawsonius*.

Placement of specimens from the Santiago Formation may be done confidently. The major claw, together with the longitudinal carina on the exopod of the uropod, conforms precisely to the definition of that structure in *Ctenocheles* and helps to confirm placement in the genus. Thus, although features of the carapace, maxillipeds, and pleopods are not available for study, the placement is assured.

To our knowledge, the uropodal notch has not previously been observed in fossil representatives of *Ctenocheles*. Although the genus is known to range from the Late Cretaceous to Recent, the specimens described herein represent the first fossils preserving some evidence of the cephalothorax and abdomen.

There has been considerable confusion about the generic placement of fossils that are assignable to *Ctenocheles*. Pelseneer (1886) proposed a new genus *Ischnodactylus*, based upon the type species, *Ischnodactylus inaequidens* Pelseneer, 1886. His description of the genus (1886: 164) included description of carapace features he described as "d'Astacomorphe," clearly indicating that he considered the genus to be a macruran, not an anomuran. The problem, however, was that the type species was represented by a claw that has subsequently been recognized as that of a callianassid ghost shrimp. Rathbun (1935) applied the name *Ischnodactylus* to several claw fragments based upon their resemblance to *I. inaequidens*. She referred those species to the Homaridae. Subsequently, Mertin (1941: 178) placed *Ischnodactylus*, along with several genera of authentic macrurans, in synonymy with *Oncopareia* Bosquet, 1854, principally on the basis of the possession in each of a pereiopod with acicular denticles.

It was apparently Secretan (1964) who first suggested that *Ischnodactylus* was closely related to *Ctenocheles* and that *Oncopareia* as then defined included several unrelated organisms. Glaessner (1969: R478) also noted that *Ischnodactylus* was a callianassid rather than a macruran; however, he did not formalize that observation by placing Pelseneer's genus in synonymy with *Ctenocheles* Kishinouye. Tshu-

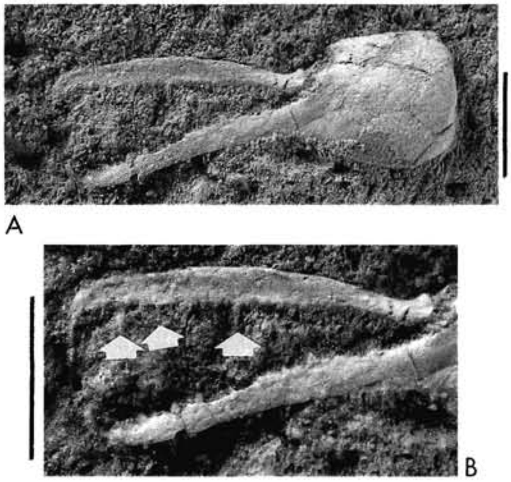

Fig. 5. *Ctenocheles secretanae* n. sp. A, major chela, paratype, SDSNH 81095; B, magnified view of fingers of SDSNH 81095, long spines on fingers indicated by arrows. Scale bars equal to 1 cm.

dy (1993), in an unpublished Ph.D. dissertation, discussed the confusion resulting from the inclusion of this genus in the Macrura and the further complication of Mertin's conclusion that *Ischnodactylus* was synonymous with *Oncopareia*. *Oncopareia* is in fact a nephropid lobster. Tshudy recognized that *Ischnodactylus* was based upon a type species that was clearly assignable to *Ctenocheles* and thus that the two genera were synonymous. Further, the similarity of claw morphologies between *Ctenocheles* and *Oncopareia* was a clear example of convergence. Tshudy and Sorhannus (2000) presented the documentation of the convergence but did not discuss the systematic problems.

None of the above authors seems to have noted that *Ischnodactylus* Pelseneer, 1886, was the junior homonym of *Ischnodactylus* Chevrolat, 1877, a name given for a butterfly, nor that a second junior homonym, *Ischnodactylus* Cossmann, 1889, a name applied to a mollusc, had been erected. This latter name was soon replaced; however, *Ischnodactylus* Chevrolat is the first formally proposed use of the name, and thus Pelseneer's name, although older (1886), cannot be invoked as a senior synonym of *Ctenocheles* Kishinouye, 1926.

***Ctenocheles secretanae*, new species**
Figs. 5–7

Type Material.—The holotype, SDSNH 81091, and paratypes SDSNH 81092–81094 and 81096–81097 were collected from locality 4573, and paratype SDSNH 81095 was collected from locality 4572.

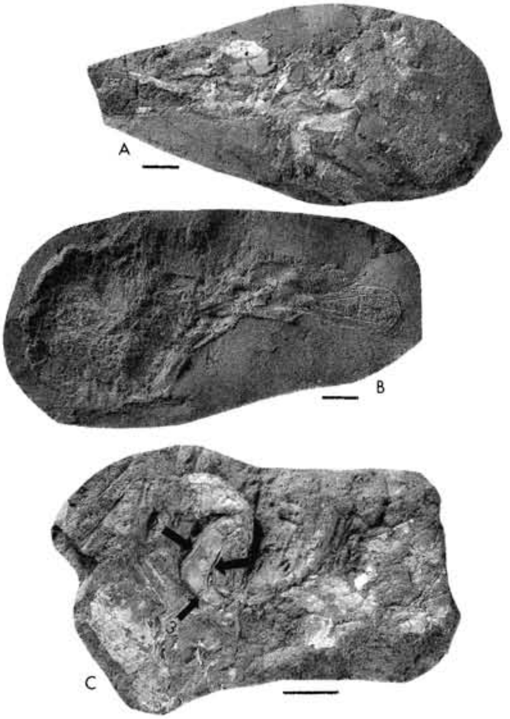

Fig. 6. *Ctenocheles secretanae* n. sp. A, lateral view of carapace, abdomen, and both major and minor chelae, minor chela above major chela, paratype, SDSNH 81094; B, lateral view showing abdomen, carapace, and major chela, holotype, SDSNH 81083; C, uropods, indicated by arrow 1. The diagnostic uropodal notch (arrow 3) and ridge (arrow 2) are well-preserved, paratype, SDSNH 81092. Scale bars equal to 1 cm.

Diagnosis.—Ctenochelid with nearly equidimensional manus on major chela whose upper

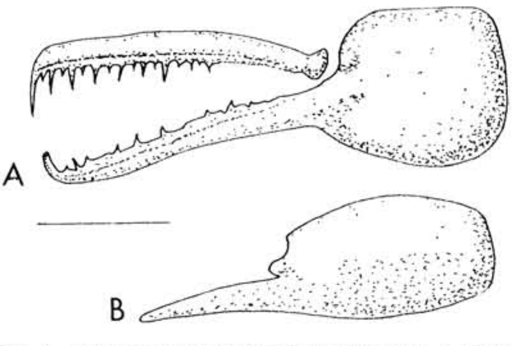

Fig. 7. Line drawings of *Ctenocheles secretanae*. A, major chela, SDSNH 81095; B, minor chela, SDSNH 81094. Scale bar equal to 1 cm.

margin is straight and whose lower margin is only slightly rounded.

Description.—Moderately large for genus; strongly heterochelate, with minor chela about 0.6 times as long as major claw.

Carapace crushed, morphology indeterminable. Abdomen with somites longer than high, with longitudinal pustulose keel on some somites; remainder of abdominal surfaces smooth. Telson crushed. Uropods with smoothly rounded margins; endopod with keeled outer margin; exopod with median longitudinal keel and keeled outer margin; outer margin with deep, narrow incision just in advance of longitudinal keel and extending proximally almost to keel.

Major chela large, with acicular denticles on fingers. Manus as long as high, with nearly straight upper and proximal margins and slightly rounded lower margin. Surface moderately vaulted, smooth, with small swollen articulation of dactylus. Fixed finger nearly twice as long as manus, downcurved, with acicular tip curved strongly upward; occlusal surface with numerous acicular denticles. Dactylus blade-like, narrow, circular in cross section proximally, widening and becoming flattened and longitudinally depressed mesially, narrowing abruptly into downturned acicular denticle distally; occlusal surface with numerous acicular denticles that appear to be arrayed in five or six rhythmic series of an intermediate-length denticle flanked by pair of shorter denticles, flanked, in turn, by pair of long denticles.

Minor chela with ovoid manus, about twice as long as high; surface gently vaulted, with subtle longitudinal keel mesially, generally smooth. Fixed finger about 0.6 times length of manus, slightly concave lower margin; occlusal surface poorly preserved, appearing to be smooth. Dactylus not preserved.

Measurements.—Measurements, in millimeters, taken on the chelae of *Ctenocheles secretanae*, are as follows: Holotype, SDSNH 81091, manus length, 13.2; manus height, 11.4; fixed finger length, 25.3; dactylus length, 25.6. Paratype SDSNH 81094, major manus length, 12.6; major manus height, >10; minor manus length, 13.8; minor manus height, 7.9; minor fixed finger length, 10.9. Paratype SDSNH 81095, manus length, 13.1; manus height, 12.9; fixed finger length, 23.7; dactylus length, 23.7. Paratype SDSNH 81096, manus length, 13.8; manus height, 12.9.

Etymology.—The trivial name honors Sylvie Secretan, Muséum National d'Histoire Naturelle, Paris, who first suggested that *Ischnodactylus* was synonymous with *Ctenocheles*.

Remarks.—Fossil species of *Ctenocheles* are distinguished on the basis of morphology of the major chela because that is the only element that is preserved, typically, and is certainly the most distinctive morphological aspect of the genus. *Ctenocheles secretanae* can be readily distinguished from other members of the genus because the manus is equidimensional, rather than longer than high, as it is in all other known species. This attribute is so pronounced that Schweitzer and Feldmann (2001b) considered it to be a diagnostic feature of the genus; thus, the diagnosis for the genus must be emended to reflect possession of a manus that ranges from equidimensional to longer than high. Other aspects of the chela morphology, including inflation of the manus, downcurved orientation of the fixed finger, length of the fingers relative to the manus, and form of the denticles, are similar to those of other species of the genus. The precise pattern of the denticles in terms of their length cannot be determined with certainty. However, the pattern of short, intermediate, and long denticles, in that order and repeated along the length of the finger, seems to be recognizable. Unfortunately, this character cannot typically be observed in fossils because the denticles are broken or obscured.

It is important to note that the presence of fragments of the carapace and parts of the abdomen represents the first such notice in the fossil record and confirms that some of the key characters of the genus have been constant since the Eocene. The weakly keeled abdominal somites and the keeled uropod with a notched margin are distinctive features of *C. secretanae*. This provides independent confirmation of the generic placement of this species and, perhaps, justifies the assignment of isolated claws with morphology similar to that of extant *Ctenocheles* to the genus.

The genus ranges from the Late Cretaceous (Cenomanian–Campanian) of Madagascar (Secretan, 1964) to Recent oceans. Extant species are deep-water forms. Holthuis (1967) summarized the occurrences of the living species then known and reported the shallowest occurrence to be that of *C. maorianus* from a depth of 19–20 fathoms (about 40 m). Other species have been reported from depths up to 800 m

(Holthuis, 1967). Several fossil species have been reported from rocks interpreted to have a shallow-water origin (Feldmann *et al.*, 1995), and the presence of the genus in the Santiago Formation reinforces this observation.

Infraorder Anomura H. Milne Edwards, 1832

Superfamily Paguroidea Latreille, 1802

Family, genus, and species indeterminate

Fig. 8

Material Examined.—Specimen SDSNH 81112.

Description.—Manus about as long as high, ovate; proximal margin nearly straight, with large, rounded projection at lower corner; upper margin convex; lower margin weakly convex; distal margin at 100-degree angle to upper margin; fixed finger short, very high proximally and narrowing dramatically distally, straight; movable finger longer than fixed finger, narrow, weakly arched, with large denticles on occlusal surface.

Measurements.—Length of manus including fixed finger = 12.4; length of manus excluding fixed finger = 8.2; height of manus = 8.7; length of fixed finger = 3.0; length of movable finger = 6.9. All measurements in millimeters.

Occurrence.—Locality 4606.

Remarks.—The manus is referable to the Paguroidea based upon its short and ovate manus, short fixed finger, and long movable finger. However, within the Paguroidea, it is not possible to assign the new specimen to a family or genus without more complete material. Within the Paguroidea, the Parapaguridae Smith, 1882; Pylochelidae Bate, 1888; and the Coenobitidae Dana, 1851, have convex lower margins of the manus. However, in the Pylochelidae, the movable finger is shorter than the fixed finger, and the fixed finger is upcurved; thus, the new specimen is not referable to that family. Within the Parapaguridae, the fixed finger is shorter than the movable finger and the movable finger is deflexed and arched; thus, the new material could be referable to this family. Members of the Coenobitidae also have short fingers and a high, stout fixed finger; thus, the new material could also be assignable to this family. It is less likely that the material is referable to the Coenobitidae because extant representatives are terrestrial. The new specimen does not resemble any of the paguroid taxa previously described from Eocene rocks of the west cost of North America, all of which are referable to the Diogenidae Ortmann, 1892, or the Paguridae Latreille, 1802. Because of these uncertainties, the material is not formally referred to a family, and that decision must await more complete material.

Fig. 8. Paguroidea, family, genus and species indeterminate. Outer surface of manus of first pereiopod, SDSNH 81112.

Infraorder Brachyura Latreille, 1802

Section Podotremata Guinot, 1977

Superfamily Raninoidea de Haan, 1839

Family Raninindae de Haan, 1839

Subfamily Raninoidinae Lörenthey in Lőrenthey and Beurlen, 1929

Genus *Raninoides* H. Milne Edwards, 1837

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

Remarks.—The material described here is referrable to *Raninoides* for several reasons. It exhibits the smooth, relatively featureless carapace and the overall shape and ratio of length to width typical of species of *Raninoides*. The carapace is widest just posterior to the mid-length of the carapace, typical of many species of *Raninoides* including *Raninoides fulgidus* Rathbun, 1926, from the Eocene of Washington. The specimen has no indication of a post-frontal ridge, thus clearly separating it from *Laeviranina* Lörenthey and Beurlen, 1929, a genus to which *Raninoides* is very similar (see Schweitzer *et al.*, 2000, for discussion). Unfortunately, the front, orbits, and rostrum are missing, making confirmed placement difficult. However, because the specimen exhibits the overall carapace features of the genus *Raninoides*,

Fig. 9. *Raninoides dickersoni*? Rathbun, 1926. Dorsal carapace of specimen, SDSNH 81077.

and because *Raninoides* is a common taxon found in Eocene deposits of the Pacific coast of North America, the new material is placed within that genus.

Raninoides dickersoni? Rathbun, 1926
Fig. 9

Material Examined.—The sole specimen, SDSNH 81077, is deposited in the San Diego Museum of Natural History, San Diego, California.

Description of Material.—Rostrum, orbits, and associated spines broken. Carapace about twice as long as wide, widest a little over half the distance posteriorly on carapace; narrowing distally, posterior width about 60 percent maximum carapace width. Anterolateral margins broken. Branchiocardiac groove moderately deep; remainder of carapace smooth, unornamented. Merus of first pereiopods longer than carpus, about twice as long as high; carpus slightly longer than high.

Measurements.—Measurements (in mm) taken on SDSNH 81077 are as follows: maximum length > 46.8; maximum width = 22.5; posterior width = 13.2.

Occurrence.—The specimen was collected from locality number 4573.

Remarks.—Rathbun (1926) described *Raninoides dickersoni* from Eocene rocks of Fresno County, California. That specimen (now deposited in the University of California) exhibits only the ventral surface of the carapace, making direct comparison with the new material impossible. Tucker (1995) confirmed placement of Rathbun's specimen within *Raninoides* based upon the distinctive structure of the sternal plate between the first and second pereiopods.

The new material is poorly preserved, thus making it imprudent to name a new species based upon it. Squires (2001) described *Raninoides slaki* from the Eocene Llajas Formation, but that species has a much more ovoid carapace than the material described here. Because *Raninoides dickersoni* has previously been named from Eocene rocks of California and because the new material is not referable to *Raninoides slaki*, it seems best to refer the new material provisionally to *R. dickersoni* until better material is discovered that could further clarify its placement.

Section Heterotremata Guinot, 1977

Superfamily Portunoidea Rafinesque, 1815

Family Portunidae Rafinesque, 1815

Subfamily Psammocarcininae Beurlen, 1930

Included Genera.—*Acanthoportunus* n. gen.; *Enoplonotus* A. Milne-Edwards, 1860a; *Psammocarcinus* A. Milne-Edwards, 1860a; *Rhachiosoma* Woodward, 1871.

Diagnosis.—Carapace hexagonal, usually much wider than long but may be nearly equidimensional; shallow, circular orbits; extremely produced lateral spine that may or may not be ornamented with smaller spines; and granular or tubercular ornamentation on dorsal carapace.

Remarks.—The new genus described below possesses all of the diagnostic features of members of the Psammocarcininae and is thus placed within that subfamily. The new genus described below also resembles the genus *Colneptunus* Lőrenthey *in* Lőrenthey and Beurlen, 1929, a member of the subfamily Portuninae Rafinesque, 1815. *Colneptunus* has been reported to be relatively difficult to distinguish from *Portunus* Weber, 1795, a Recent member of the Portuninae (Glaessner, 1969), and has the broad, relatively smooth carapace; multispined anterolateral margin; and arcuate ridge extending from the last and longest anterolateral spine typical of the subfamily Portuninae. However, *Colneptunus* also has faint branchial tubercles arrayed in rows oblique to the axis of the carapace reminiscent of the new genus and *Rhachiosoma*, members of the Psammocarcininae. Because *Colneptunus* is in most ways very similar to the Recent *Portunus* and other members of the Portuninae, it seems most appropriate for it to remain in that subfamily. However, the similarity of *Colneptunus* with genera within the Psammocarcininae suggests that the two subfamilies may be closely related.

The Psammocarcininae is an extinct subfamily within the Portunidae and has a geologic range from the early Eocene to the early Oligocene (Glaessner, 1969). The Eocene was a time of radiation within the Portunidae, and genera within three of the five subfamilies flourished at that time (Glaessner, 1969; Schweitzer and Feldmann, 2000b). By the Miocene, primarily only those genera that survive into the Recent are found in the fossil record (Schweitzer, 2001; Schweitzer *et al.*, in press), a pattern similar to that of other decapod families.

The fossil record of both the Psammocarcininae and the Portuninae extends into the Eocene (Glaessner, 1969). The two subfamilies have several features in common, including a carapace that is usually markedly wider than long; a long lateral spine at the anterolateral corner; an arcuate ridge extending from the lateral spine toward the axis of the carapace; and numerous spines on the anterolateral margin. As far as is known for certain, the fifth pereiopod of the Psammocarcininae is paddle-like, which also characterizes the Portuninae. The other subfamilies within the Portunidae differ from these two subfamilies in several ways. For example, the Podophthalminae have very elongate orbits and extremely narrow fronts, not typical of either the Portuninae or the Psammocarcininae. The Polybiinae have carapaces that are not much wider than long, as do members of the Carcininae, and the Carcininae have lanceolate dactyls on the fifth pereiopods instead of paddle-like dactyls.

The earliest portunid known with certainty is from the Paleocene of Argentina (Feldmann *et al.*, 1995), and the family may in fact extend into the Cretaceous (Schweitzer and Feldmann, 2000b). Thus, the common ancestor for all of the portunids probably existed during the Paleocene or before, based upon current evidence for the family (Schweitzer and Feldmann, 2000b). It may be possible that both the Psammocarcininae and the Portuninae arose from a common ancestor during the late Paleocene, probably in the Tethys or southern Europe. The Portuninae and the Psammocarcininae may have diverged from one another sometime after that but before the early Eocene.

The Psammocarcininae appear to have evolved in the Tethys and North Atlantic region in what is now Europe, as most of the occurrences are from that region (Glaessner, 1969). The occurrence of the new genus in southern California suggests a dispersal route across the Atlantic Ocean and through the open Central American Seaway, a dispersal route displayed by many other decapod genera (Schweitzer and Salva, 2000; Schweitzer, 2001; Schweitzer *et al.*, in press). Discovery of fossils referable to the Psammocarcininae in the Caribbean, México, or Central America would help to confirm this observation.

Glaessner (1980) referred *Portunites granulifer* Glaessner, 1960, to *Rhachiosoma*, an assignment with which later authors concurred (Feldmann and Maxwell, 1990; Feldmann, 1991; Feldmann and Keyes, 1992). However, that species lacks the extremely elongate lateral spine that characterizes *Rhachiosoma*. The spine in *Rhachiosoma granuliferum* occupies less than about one-quarter the carapace width, whereas in authentic *Rhachiosoma*, the lateral spine occupies half the carapace width. The long lateral spine in confirmed members of *Rhachiosoma* is needle-like, can be ornamented with a small spine, and projects directly laterally or can be recurved posteriorly; the lateral spine of *Rhachiosoma granuliferum* is triangular, unornamented, and curved slightly anterolaterally. In confirmed species of *Rhachiosoma*, there are two or three anterolateral spines that are very broad and greatly produced from the anterolateral margin. In *Rhachiosoma granuliferum*, there are four anterolateral spines that are of moderate size and not greatly produced from the anterolateral margin. In authentic *Rhachiosoma*, there are oblique ridges on the branchial regions of the carapace that are ornamented with tubercles; in *Rhachiosoma granuliferum*, those ridges are absent. Thus, it appears clear that *Rhachiosoma granuliferum* is not a member of *Rhachiosoma* and is referred to the new genus, *Maeandricampus*, to be described below.

Genus ***Acanthoportunus***, new genus

Type Species.—Acanthoportunus buchanani n. sp. by monotypy.

Diagnosis.—As for species.

Fig. 10. *Acanthoportunus buchanani* n. gen. and sp. A, dorsal carapace, holotype, SDSNH 81055; B, dorsal carapace, paratype, SDSNH 81056; C, dorsal carapace, paratype, SDSNH 81057. Scale bars equal to 1 cm.

Description.—As for species.

Etymology.—The generic name is derived from the Greek word *akantha*, meaning "thorn," and the generic name *Portunus*, the type genus for the family Portunidae and a common root name used for generic names within the family. The name refers to the spiny anterolateral margins of the dorsal carapace.

Occurrence.—The genus is known only from middle Eocene (Uintan) rocks of southern California.

Remarks.—The new material is clearly allied with members of the Psammocarcininae but cannot be accommodated within any of the existing genera. The new genus is most like *Rhachiosoma*, to which it is probably very closely related and perhaps from which it was derived. *Acanthoportunus* is, however, distinguishable from *Rhachiosoma* by several means. Within *Rhachiosoma*, the anterolateral margin has two or three spines, whereas in *Acanthoportunus*, the anterolateral margin has six spines not counting the outer orbital spine or the long lateral spine. The mesogastric and cardiac regions of *Rhachiosoma* have one tubercle each, whereas in *Acanthoportunus*, those regions each have two tubercles placed next to one another. The transverse arcuate ridge in *Rhachiosoma* is more poorly developed than that of *Acanthoportunus*, and in *Rhachiosoma*, it is ornamented with a central tubercle that *Acanthoportunus* lacks. The oblique rows on which tubercles are situated in *Rhachiosoma* are much more inflated than those of *Acanthoportunus*, and the tubercles of those rows are larger and more discrete in *Acanthoportunus*. Finally, the long lateral spine of *Rhachiosoma* is unornamented or has one spine, whereas *Acanthoportunus* has at least two spines on the long lateral spine. Thus, the two genera are easily distinguished from one another.

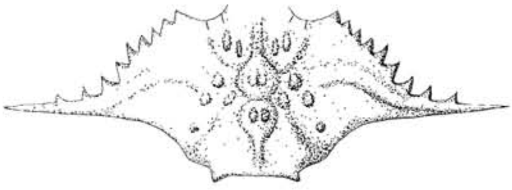

Fig. 11. Composite line drawing of *Acanthoportunus buchanani*.

Acanthoportunus is easily distinguished from *Psammocarcinus* because *Psammocarcinus* is about as wide as long, whereas *Acanthoportunus* is much wider than long. *Psammocarcinus* has much shorter lateral spines than does *Acanthoportunus* and lacks the strongly developed arcuate ridge separating the gastric and branchial regions that characterizes *Acanthoportunus*. *Enoplonotus* possesses rows of small tubercles that extend in oblique lines from the anterolateral margin towards the axis of the carapace, a very distinctive feature that *Acanthoportunus* lacks. Further, the long lateral spine of *Enoplonotus* is serrate along its entire length, whereas the long lateral spine of *Acanthoportunus* has discrete, markedly-spaced spines.

Acanthoportunus buchanani, new species
Figs. 10, 11

Types.—The holotype, SDSNH 81055, and three paratypes, SDSNH 81056, 81057, and 81108, are deposited in the San Diego Museum of Natural History, San Diego, California.

Diagnosis.—Carapace much wider than long including long lateral spines; anterolateral margin with six triangular spines; anterolateral corner with very long, attenuated lateral spine, which is itself ornamented with at least two triangular spines; protogastric, mesogastric, cardiac, and branchial regions ornamented with large, discrete swellings.

Description.—Carapace wider than long, less than twice as wide as long (L/W = 0.61) not including long lateral spine, which is more than twice as wide as long (L/W < 0.45); flattened longitudinally and transversely; regions poorly defined, sparsely granular, ornamented with large, isolated swellings.

Front not known. Orbits moderately wide, circular, shallow, directed forward; with two fissures, similar in length, inner fissure closed, outer fissure open; outer orbital spine triangular, of same general size and form as anterolateral spines, directed forward; fronto-orbital width about half the carapace width measured without lateral spines, less than 40 percent carapace width measured with lateral spines. Anterolateral margin with 6 spines not including outer orbital spine or long lateral spine; triangular; first three directed forward; fourth and fifth directed anterolaterally; sixth curved, directed forward at tip. Long, attenuated lateral spine at anterolateral corner, addition of which nearly doubles the width of the animal; with at least two triangular spines on anterior surface, spines of same form and size as anterolateral spines. Posterolateral margin sinuous, with convex projection in posterior third; posterolateral corner developed into small, distally-projecting, triangular spine. Posterior margin straight, with granular rim; about one-third carapace width measured without lateral spines, less than 20 percent carapace width measured with lateral spines.

Mesogastric region with long, narrow anterior process, process flattened anteriorly and weakly inflated posteriorly; posterior portion of mesogastric region nearly spherical, with two weakly-developed, longitudinal swellings. Urogastric region strongly depressed, poorly developed. Cardiac region subpentagonal, apex directed posteriorly, with two large spherical swellings; region extending posteriorly into long process which becomes more poorly developed posteriorly. Intestinal region very poorly developed.

Protogastric regions small, ovoid, with two longitudinal swellings positioned parallel to anterior process of mesogastric region; weakly inflated. Hepatic region flattened, very poorly defined. Arcuate ridge extending axially from long, lateral spine separates gastric regions from branchial regions. Branchial regions poorly differentiated, anterior two-thirds of branchial regions moderately inflated, with three swellings arranged linearly and positioned at oblique angle to axis of carapace, one elongate swelling on either side of urogastric region; posterior one-third of branchial region flattened.

Venter and appendages unknown.

Measurements.—Measurements (in mm) taken on the dorsal carapace of specimens of *Acanthoportunus buchanani*: SDSNH 81055, width (not including lateral spines) = 24.4; width (including lateral spines) >33.2; length = 15.0, fronto-orbital width = 13.8; posterior width = 7.1. SDSNH 81056, width (not including lateral spines) = 30.6, width (including lateral spines) = 52.8.

Etymology.—The trivial name honors the late William Buchanan, Clallam Bay, Washington, an amateur collector and World War II veteran who helped build the Burma Road in Southeast Asia. He collected and donated many decapod specimens for study during his life.

Occurrence.—Locality 4573.

Remarks.—The specimens are moderately well preserved in siltstone, and both were probably molts because they retain no vestiges of the appendages or ventral surface of the carapace. Unfortunately, the front is missing on both specimens.

Some modern portunids live in silty or muddy environments, burrowing very shallowly into the mud, perhaps to await prey or for camouflage (Warner, 1977). The presence of rays in the deposits enclosing the crabs, which have a similar habit, suggests that this may in fact have been the ecological niche of these crabs.

Subfamily Polybiinae Ortmann, 1893

Included Fossil Genera.—*Maeandricampus*, new genus; *Megokkos* Schweitzer and Feldmann, 2000b; *Minohellenus* Karasawa, 1990; *Portunites* Bell, 1858; *Proterocarcinus* Feldmann *et al.*, 1995.

Genus *Minohellenus* Karasawa, 1990

Cancer Linnaeus, 1758 (part): Philippi, 1887, p. 214, pl. 50, fig. 2.

Portunites Bell, 1858 (part): Glaessner, 1960, p. 33.

Charybdis (*Minohellenus*) Karasawa, 1990, p. 21, pl. 6, figs. 7, 8; Karasawa, 1993, p. 56, pl. 13, figs. 3a, b, pl. 14, figs. 3a–c.

Itoigawaia Karasawa, Sakumoto, and Takayasu, 1992, p. 455, pl. 64; Karasawa, 1993, p. 53, pl. 11, figs. 1–3, pl. 11, fig. 6; Kato, 1996, p. 512–514, figs. 5.11, 6.7–6.12; Karasawa, 1997, p. 48, 49, pl. 11, figs. 9, 11, 13.

Imaizumila Karasawa, 1993, p. 52, pl. 11, figs. 1–3. Karasawa, 1997, p. 48, pl. 11, figs. 8, 12; Schweitzer and Feldmann, 2000b, p. 639, figs. 3–4.

Minohellenus Karasawa, 1990; Kato and Karasawa, 1994, p. 53, fig. 2, pl. 4; Kato and Karasawa, 1996, p. 31, pl. 10; Karasawa, 1997, p. 49, pl. 11, fig. 11, pl. 14, figs. 2–7, pl. 12, figs. 5a–c, pl. 13, figs. 4a–c.

Type Species.—Charybdis (*Minohellenus*) *quinquedentata* Karasawa, 1990.

Other Species.—Minohellenus araucanus (Philippi, 1887), as *Cancer*; *M. chichibuensis* (Kato, 1996); *Minohellenus inexpressus*, new species; *M. macrocheilus* Kato and Karasawa, 1994; *M. minoensis* (Karasawa, 1990); *M. sexdentatus* (Karasawa, 1993); *M. umemotoi* (Karasawa, 1993).

Emendation to Diagnosis.—As in Schweitzer and Feldmann (2000b) with the following additions: Branchial regions may have low, poorly developed arcuate ridge parallel to arcuate ridge separating branchial and gastric regions and extending from base of fifth anterolateral spine toward the axis. Branchial regions without nodose ornamentation.

Remarks.—Schweitzer and Feldmann (2000b) synonymized *Minohellenus* with *Itoigawaia* based upon their indistinguishable carapace shape and ornamentation. At that time, *Portunites triangulum* Rathbun, 1926, was placed within *Minohellenus* but was differentiated from all other species in the genus by its possession of nodes on the branchial regions and keels on the outer surface of the manus. However, possession of these nodes and keels, as well as the observation that members of *P. triangulum* have a longitudinal ridge on the branchial region parallel to the axis of the carapace, suggests that the species does not belong within *Minohellenus*. Reconsideration of that placement and examination of *Rhachiosoma granuliferum* (Glaessner, 1960) indicates that *Portunites triangulum* and *R. granuliferum* should be placed within a separate genus, *Maeandricampus*, to be discussed below.

In their 2000b work, Schweitzer and Feldmann considered *Imaizumila* to be distinguishable from *Minohellenus* based upon the better defined carapace regions and more inflated carapace of *Imaizumila*. Members of *Imaizumila* also have a low, arcuate ridge on the branchial region parallel to the arcuate ridge extending from the base of the last anterolateral spine toward the axis of the carapace. However, examination of the new material described here suggests that these two genera are in fact synonymous. The new material exhibits features intermediate between the two genera. For example, the axial regions of the new specimens are moderately well defined as in *Imaizumila*, whereas *Minohellenus* has more poorly defined carapace regions. However, the new material lacks the low arcuate ridge parallel to the major ridge, which is seen in species of *Imaizumila* but is lacking in species of *Minohellenus*. Because the criteria for differentiating the two genera was already tenuous and because new material has been found that is intermediate between the two, it seems best to synonymize the two genera. *Minohellenus* is the senior synonym, and its diagnosis is herein emended to reflect the possible presence of a low ridge parallel to the branchial ridge separating the gastric and branchial regions.

Minohellenus was known from the Oligocene-Miocene of the North Pacific Rim (Schweitzer and Feldmann, 2000b); however, the synonymy with *Imaizumila* extends its known geologic range to the Eocene-Miocene of Chile. Unfortunately, the age of the Chilean material is very poorly constrained. The new species described below is middle Eocene in age, making it the oldest species with a confirmed age. The evolutionary history of the genus awaits further work on the Chilean material; however, it is clear that *Minohellenus* displayed an amphitropical distribution. Possibly the genus evolved in North America and subsequently dispersed southward to the Southern Hemisphere and westward to Japan via the North Pacific gyre. *Minohellenus* is one of numerous genera that have a North Pacific origin with subsequent dispersal within that realm; however, relatively few other genera are known to have dispersed from the North Pacific to the southern hemisphere (Schweitzer, 2001).

Minohellenus inexpressus, new species

Fig. 12

Types.—The holotype, SDSNH 81058, and paratypes, SDSNH 81059, 81102, and 81103, are deposited in the San Diego Natural History Museum, San Diego, California.

Diagnosis.—Carapace wider than long; regions poorly defined; frontal margin with four spines not including inner orbital spines; inner orbital spines very short; anterolateral margin with four spines not including outer orbital spine, last spine longest; urogastric region defined by deep grooves; carapace smooth and unornamented.

Description.—Carapace wider than long, L/W = 0.64; regions poorly defined by shallow grooves; carapace relatively smooth; flattened both longitudinally and transversely.

Frontal margin with four spines not including inner orbital spines, frontal width 28 percent maximum carapace width; inner two spines closely spaced, outer two separated from inner spines by broad, smoothly concave margin. Orbits shallow, with two closed orbital fissures of about same size; fronto-orbital width about half maximum carapace width; inner orbital spine short, triangular, projected forward; outer orbital spine longer than inner orbital spine, triangular, about same size as anterolateral spines, directed forward. Anterolateral margin with four spines not including outer orbital spine; broad at bases, triangular; last spine longest; spines 1–3 directed anterolaterally; last anterolateral spine directed weakly anterolaterally. Posterolateral margin sinuous, entire. Posterolateral corner and posterior margin poorly known.

Epigastric regions nearly square, most inflated anteriorly. Protogastric regions weakly inflated. Mesogastric region with long anterior process, process becomes poorly developed and disappears at base of epigastric regions; posterior portion of region diamond-shaped, well-delimited on convex posterior margin by muscle pits. Urogastric region narrow, with deeply defined, concave lateral margins. Cardiac region not well known but appearing to be weakly defined. Intestinal region not known.

Hepatic region flattened, depressed. Arcuate ridge curves anteriorly from base of last anterolateral spine, poorly developed. Branchial regions undifferentiated, weakly inflated anteriorly.

Major chela stout, longer than high; fingers with blunt tubercles on occlusal surfaces. Remainder of appendages and venter unknown.

Measurements.—Measurements (in mm) taken on the dorsal carapace of SDSNH 81058: maximum width = 46.4; maximum length = 29.5; fronto-orbital width = 23.0; frontal width = 12.8.

Etymology.—The trivial name is derived from the Latin word prefix "*in-*," meaning without, and the Latin word "*expressus*," meaning clear and distinct, in reference to the lack of distinctive ornamentation and the poorly defined regions of the carapace.

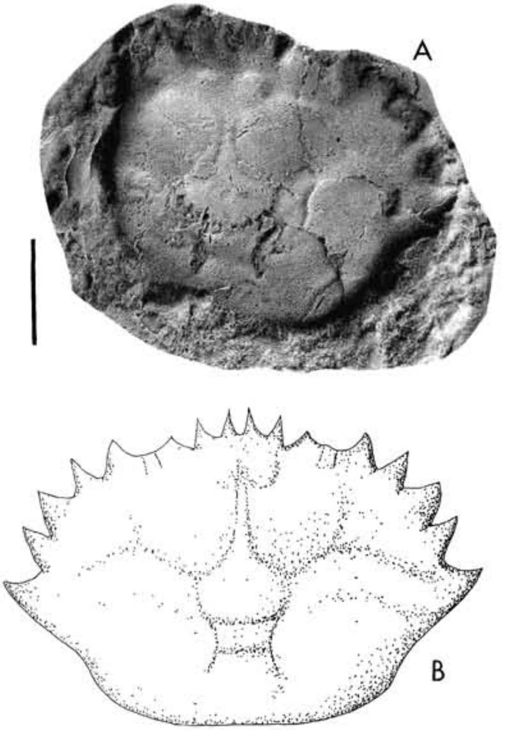

Fig. 12. *Minohellenus inexpressus* n. sp. A, silicone cast of dorsal carapace of holotype, SDSNH 81058, scale bar equal to 1 cm; B, line reconstruction.

Occurrence.—The holotype, SDSNH 81058, and paratypes 81102 and 81103 were collected from locality 4572; paratype SDSNH 81059 was collected from locality 4573.

Remarks.—Only four fragmented specimens are known; thus, the posterior margin in Fig. 13 is inferred. However, the most important dorsal carapace features, including the front, orbits, anterolateral margins, gastric regions, and arcuate ridge, are observable. The new species conforms to all of the diagnostic aspects of *Minohellenus*. It differs from all other species within the genus in having very small inner orbital spines and a very poorly defined arcuate ridge separating the gastric and branchial regions of the carapace. Better understanding of the ecology and life habits of the organism will be possible only with the addition of new material including the pereiopods and ventral aspect.

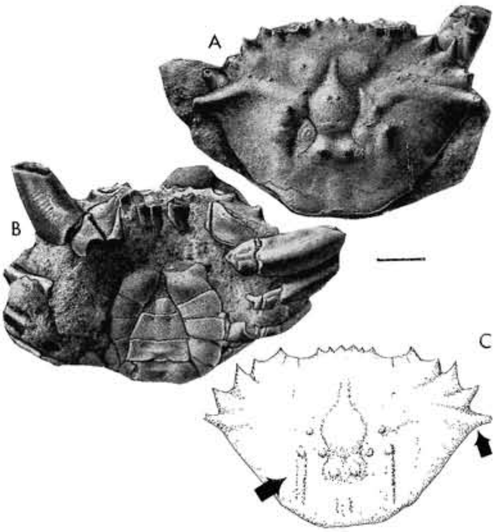

Fig. 13. *Maeandricampus* n. gen. A, dorsal carapace of *Maeandricampus triangulum* (Rathbun, 1926); B, ventral surface of *Maeandricampus triangulum*; C, line drawing of *Maeandricampus*, arrows indicate key generic features including long anterolateral spine and branchial ridge. A and B are digital images of pl. 17, fig. 5 and 6 respectively from Rathbun (1926). Scale bar = 1 cm.

Another portunid taxon assignable to a genus closely related to *Minohellenus*, *Portunites insculpta* Rathbun, 1926, has been described from the Eocene Llajas Formation (Squires, 2001). However, the new material is not referable to that taxon because *Portunites insculpta* possesses deeply incised grooves and well-defined regions, whereas *Minohellenus inexpressus* has poorly defined carapace regions.

Genus ***Maeandricampus***, new genus
Fig. 13

Portunites Bell, 1858 (part): Rathbun, 1926, p. 68, pl. 17, figs. 3–6; Schweitzer and Feldmann, 1999, p. 245, fig. 8.
Rhachiosoma Woodward, 1871 (part): Glaessner, 1980, p. 187, fig. 14, 14A; Feldmann and Maxwell, 1990, p. 788, figs. 9.1–9.5, 10; Feldmann, 1991, p. 21, figs. 12, 13; Feldmann and Duncan, 1992, p. 460, figs. 4–6.
Minohellenus Karasawa, 1990 (part): Schweitzer and Feldmann, 2000b, p. 643, fig. 6.

Type Species.—Portunites triangulum Rathbun, 1926, by original designation.

Other Species.—Maeandricampus granuliferus (Glaessner, 1960), as *Portunites*.

Diagnosis.—Carapace wider than long, L/W = 0.6–0.7, widest at position of last anterolateral spine; regions moderately defined; arcuate ridge extending from last anterolateral spine to axis of carapace, may be ornamented with tubercles; front with four spines not including inner orbital spine; orbits circular, with two closed fissures, inner-orbital spine small, outer-orbital spine as large as anterolateral spines; anterolateral spines 1–3 triangular, flattened, directed forward or weakly anterolaterally, tips sharp; last anterolateral spine longest, twice as long as other anterolateral spines, directed laterally, more needle-like and circular in cross-section than other spines. Branchial regions with longitudinal ridge extending from position lateral to urogastric region to posterior margin, may be ornamented with tubercles; remainder of regions relatively unornamented.

Etymology.—The name is derived from the Latin words "*Maeander*," the name of a river in Asia Minor with a winding course, and "*campus*," a Latinization of the Greek "*kampos*," a sea animal. The name alludes to the difficulty and resultant meandering path taken in making a generic placement for both of the included species.

Occurrence.—The new genus is known from Oligocene-early Miocene rocks of Washington (Schweitzer and Feldmann, 1999, 2000b) and the Eocene of New Zealand (Glaessner, 1960, 1980; Feldmann and Maxwell, 1990; Feldmann and Duncan, 1992).

Remarks.—Rathbun (1926) described *Portunites triangulum* from Oligocene rocks of the west coast of North America, placing it within *Portunites* based upon its large orbits, dentate front, flattened carapace, and longitudinal ridge on the branchial region. Schweitzer and Feldmann (1999) concurred with Rathbun, but later (Schweitzer *et al.*, 2000b), they provided compelling evidence that *P. triangulum* is not referrable to *Portunites sensu stricto*. In the later work, Schweitzer *et al.* placed *P. triangulum* in *Minohellenus* based upon the dimensions of the carapace, anterolateral spines, and general carapace region arrangement. However, new material described above indicates that *Minohellenus* cannot accommodate species with nodose ornamentation or with longitudinal branchial ridges. Thus, a new genus must accommodate *P. triangulum*.

Glaessner (1960) described *Portunites granulifer* from Eocene rocks of New Zealand. At that time, he noted that the new species was most like *P. triangulum* in the ornamentation and shape of the carapace. Later, he referred that species to *Rhachiosoma* (Glaessner, 1980) because of the long lateral spines on the carapace of *P. granulifer*, which members of *Rhachiosoma* also possess. However, species of *Rhachiosoma* are very different from *P. granulifer*. In *Rhachiosoma sensu stricto*, the lateral spine is half the length of the carapace and in some cases is directed posterolaterally at its tip. The long spine itself can be ornamented with small spines in *Rhachiosoma*. In *Rhachiosoma*, the anterolateral margin has two or three broad, produced, triangular spines separated by large, deep, concave reentrants. The branchial regions of *Rhachiosoma* have an oblique ridge that extends from the posterolateral margin to the urogastric region and that is ornamented with large tubercles.

Portunites granulifer possesses none of the diagnostic features of *Rhachiosoma* and in fact is very similar to *P. triangulum*, as Glaessner (1960) originally noted. Both species have four frontal spines not including the inner orbital spine; a very small inner orbital spine; circular orbits with two fissures; a fronto-orbital width of about 50 percent; four anterolateral spines not including the outer-orbital spine, the last of which is longest; a poorly developed arcuate ridge separating the gastric and branchial regions; a longitudinal ridge on the branchial regions that is ornamented with tubercles; and poorly defined carapace regions. Thus, the two species clearly belong to the same genus and are herein placed within the new genus *Maeandricampus*.

The new genus is most similar to *Parathranites* Miers, 1886, but may be distinguished from it in several ways. *Parathranites* has five anterolateral spines, whereas *Maeandricampus* has four. In *Parathranites*, the posterolateral corner has huge, sharp spines directed posteriorly, which *Maeandricampus* lacks. *Parathranites* lacks the distinct ridge on the branchial regions and instead has an array of tubercles in that location, and the cardiac region of *Parathranites* is much more inflated and better developed than that of *Maeandricampus*.

The earliest known occurrence of the genus is in Eocene rocks of New Zealand; the genus is subsequently known from Oligocene to early Miocene rocks of Washington, U.S.A. The genus was apparently amphitropical, as were many other Tertiary portunids (Schweitzer and Feldmann, 2000b) including *Minohellenus* (Schweitzer, 2001).

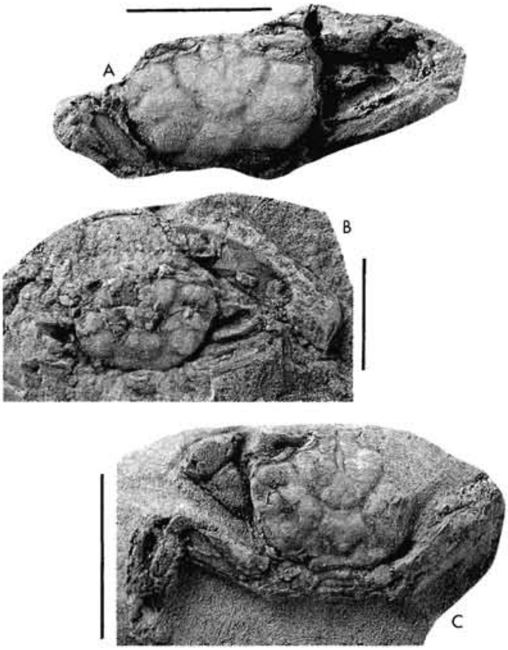

Fig. 14. *Orbitoplax weaveri* (Rathbun, 1926). A, dorsal carapace, SDSNH 81065; B, dorsal carapace and appendage fragments, SDSNH 81062; C, SDSNH 81063. Scale bars equal to 1 cm.

Superfamily Xanthoidea MacLeay, 1838

Family Goneplacidae MacLeay, 1838

Genus *Orbitoplax* Tucker and Feldmann, 1990

Type Species.—*Orbitoplax plafkeri* Tucker and Feldmann, 1990.

Other Species.—*Orbitoplax tuckerae* Schweitzer, 2000; *Orbitoplax weaveri* (Rathbun, 1926).

Orbitoplax weaveri (Rathbun, 1926)
Figs. 14, 15

Material Examined.—Specimens SDSNH 81060–81076 and 81105–81107 are deposited in the San Diego Natural History Museum, San Diego, California.

Emendation to Description.—As in Schweitzer (2000) with these additions: Intra-orbital projection blunt or sharp. Fixed finger of major chela deflexed at about 170-degree angle to lower margin of manus; long, slender; with small, sharp denticles on occlusal surface. Movable finger strongly deflexed; very long, slender; with larger, sharp and blunt denticles on occlusal surface. Fixed finger of minor chela more weakly deflexed than in major chela, stouter than fixed finger of major chela.

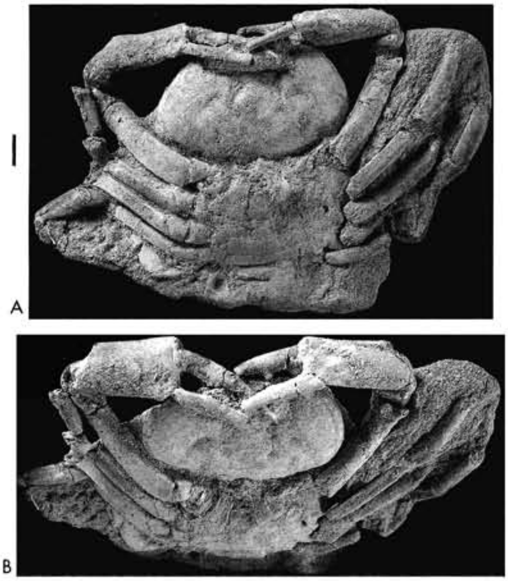

Fig. 15. *Orbitoplax weaveri* (Rathbun, 1926), SDSNH 81060. A, dorsal carapace and venter of molt; B, oblique anterior view of molt showing chelipeds. Scale bar equal to 1 cm.

Movable finger of minor chela stouter than that of major chela, with at least a few large, blunt denticles on occlusal surface.

Occurrence.—Four specimens, SDSNH 81062–81065, were collected from Locality 4529, and fifteen specimens, SDSNH 81060, 18061, 81066–81076, 81105, and 81106, were collected at Locality 4606. SDSNH 81107 was collected from locality 4607.

Remarks.—Schweitzer (2000) referred *Plagiolophus weaveri* Rathbun, 1926, to *Orbitoplax* and provided a detailed description of the species based upon very well-preserved material from Eocene rocks of Oregon. The specimens reported here exhibit all of the diagnostic features of the genus and species and are clearly referrable to *O. weaveri*. The material collected from San Diego County is rather poorly preserved, but the fingers of the major and minor chelae are better preserved than in either Rathbun's (1926) or Schweitzer's (2000) material.

Contained within the San Diego material is a spectacular specimen, SDSNH 81060, preserved in the process of molting (Fig. 15). The specimen is badly weathered, and the cuticle is completely lacking. The relative shape of the carapace, the definition of regions where visible, and the unusual shape of the chela suggest that referral to *O. weaveri* is warranted. The chelae of *O. weaveri* widen markedly distally, and the fingers are narrow and acute; the molted specimen possesses chelae of this nature. A rather perplexing feature of the molted specimen is that it is one-third larger than other known specimens of the species. Also, the large specimen is preserved in sandstone, whereas the others are preserved in shale. Perhaps the difference in environment or substrate permitted the molted specimen to achieve a larger size. It might be expected that animals living on a soft substrate such as mud would be smaller, and thus more easily supported, than animals living in a sandy, presumably more energetic environment. Larger size in a sandy, higher energy environment could protect the animal from abrasion.

Family Hexapodidae Miers, 1886

Genus *Palaeopinnixa* Via, 1966

Type Species.—*Palaeopinnixa rathbunae* Schweitzer, Feldmann, Tucker, and Berglund, 2000. Originally *Pinnixa eocenica* Rathbun, 1926; see Schweitzer *et al.* (2000) for discussion.

Other Species.—*Palaeopinixxa eocenica* (Woods, 1922); *P. intermedia* (Collins and Morris, 1976); *P. mytilicola* Via, 1966; *P. perornata* Collins and Morris, 1976; *P. prima* (Rathbun, 1918); *P. rocaensis* (Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995); *P. rotundus* Schweitzer and Feldmann, 2001a.

Palaeopinnixa granulosa, new species
Figs. 16, 17

Types.—The holotype, SDSNH 81052, and two paratypes, SDSNH 81053 and 81054, are deposited in the San Diego Museum of Natural History, San Diego, California.

Diagnosis.—Carapace small for genus, rectangular, strongly vaulted along anterior and posterior margins; carapace regions weakly defined, gastric and branchial regions granular except axial regions, which are pitted.

Description.—Carapace rectangular, wider than long, L/W = 0.62, widest about two-thirds the distance posteriorly on carapace; regions poorly defined by weakly developed grooves; moderately vaulted longitudinally, especially along anterior and posterior margins; flattened trans-

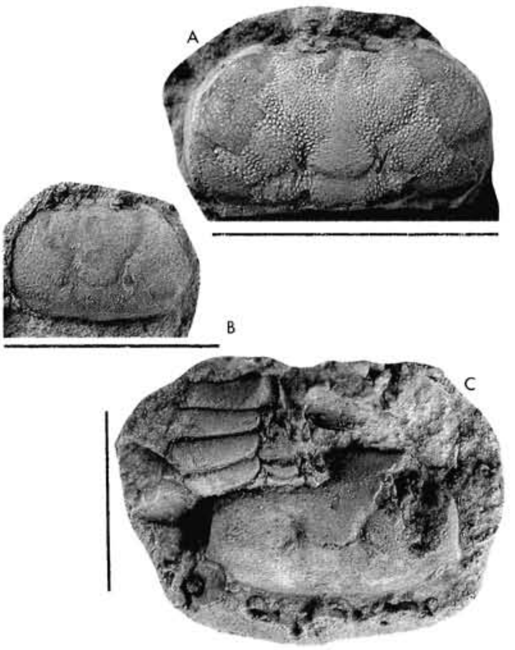

Fig. 16. *Palaeopinnixa granulosa* n. sp. A, dorsal carapace showing granular texture of carapace, holotype, SDSNH 81052; B, dorsal carapace, paratype, SDSNH 81054; C, dorsal carapace and partial ventral surface of molted specimen, paratype, SDSNH 81053. Scale bars equal to 1 cm.

versely; regions densely granular except axial regions, which are pitted.

Front widening distally, weakly sulcate axially, about 15 per cent maximum carapace width, lateral margins concave. Orbits square, directed forward; upper orbital margin sinuous, entire; fronto-orbital width about half maximum carapace width. Anterolateral and posterolateral margins confluent, entire; large reentrant at posterolateral corner, posterior margin entire, weakly convex, about 80 percent maximum carapace width.

Epigastric regions small, square, weakly inflated. Mesogastric region with long anterior process, widening distally, with convex posterior margin, length of entire mesogastric region about two-thirds length of carapace. Urogastric region poorly developed. Cardiac region ovoid, weakly inflated. Intestinal region flattened, poorly defined, deflected down towards posterior margin.

Protogastric regions weakly defined, densely granular. Hepatic region broad, long, granular, weakly defined. Branchial regions not differentiated, sloping steeply to posterior margin.

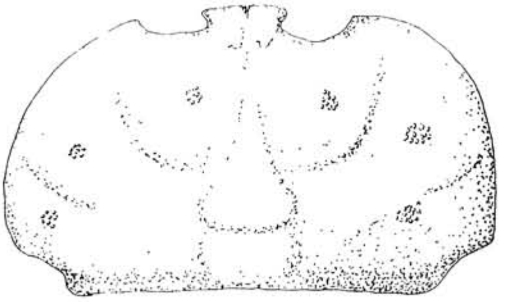

Fig. 17. Composite line drawing of *Palaeopinnixa granulosa* n. sp. Protogastric, hepatic, and branchial regions are entirely covered by granules; only a small portion of the granules are drawn.

Sternum ovate, widest at position of fifth sternite; sternites 4 and 5 directed anterolaterally; sternite 6 directed laterally; sternite 7 directed weakly posterolaterally; upper and lower margins of sternites nearly straight.

Male abdomen narrow, widest at position of first few somites. Remainder of ventral surface unknown.

Measurements.—Measurements (in mm) taken on the dorsal carapace of specimens of *Palaeopinnixa granulosa* (W1 = maximum width, W2 = fronto-orbital width, W3 = posterior width, W4 = frontal width): SDSNH 81052, L = 6.1, W = 10.9, W2 = 5.2, W3 = 8.3, W4 = 1.5; SDSNH 81054, L = 5.6, W1 = 7.8, W2 = 4.5, W3 = 6.2, W4 = 1.3; SDSNH 81053, L = 13.8, W1 = 7.9, W2 = 11.0.

Etymology.—The trivial name is derived from the Latin word *granum*, meaning seed or grain, in reference to the granular nature of the dorsal carapace.

Occurrence.—The specimens were collected at Locality 4529.

Remarks.—Schweitzer and Feldmann (2001a) provided a diagnosis for the genus *Palaeopinnixa*, and the new specimens correspond in all regards to the diagnostic characters of the genus. *Palaeopinnixa granulosa* differs from all other species of the genus in its densely granular ornamentation on the gastric and branchial regions and pitted ornament on the axial regions. In addition, the dorsal carapace of *Palaeopinnixa granulosa* is more steeply vaulted along the posterior margin than any other species in the genus. *Palaeopinnixa granulosa* lacks the triangular arrangement of small nodes on the

Fig. 18. Stomatopoda, Unipeltata, family, genus, and species indeterminate. Finger of holotype, SDSNH 81098. Scale bars equal to 1 cm.

cardiac region that is present on many species of the genus, and the mesogastric region in *Palaeopinnixa granulosa* is longer than that of any other species of the genus.

Palaeopinnixa aff. *P. rathbunae* Schweitzer *et al.* (2000) has been reported from the Eocene Llajas Formation of southern California (Squires, 2001); however, new material is clearly not referrable to *P. rathbunae* because of its granular ornamentation. Other species of *Palaeopinnixa* have been reported from Paleocene rocks of Argentina and Eocene rocks of Peru, Washington, and Oregon (Woods, 1922; Schweitzer and Feldmann, 2001a); Oligocene rocks of Panama (Rathbun, 1918); and Miocene rocks of Trinidad and Spain (Via, 1966; Collins and Morris, 1976). Thus, the occurrence in Eocene rocks of California would be expected, as it appears that the genus evolved during the Paleocene in the high southern latitudes and subsequently dispersed to the northern hemisphere and moved northward up the Pacific coast of North America.

Order Stomatopoda Latreille, 1817

Suborder Unipeltata Latreille, 1825

Family, genus, and species indeterminate
Fig. 18

Studied Material.—The sole specimen, SDNHM 81098, is deposited in the San Diego Museum of Natural History, San Diego, California.

Description.—Raptorial claw with large, nearly complete dactylus and occlusal surface of propodus. Propodus fragment bears thickened, pectinate occlusal surface along midlength; otherwise broken and obscure. Dactylus smooth; elongate; 22.9 mm long; tapering distally to upturned, sharp distal termination; not inflated proximally. Occlusal surface with at least five short, pointed, distally-directed spines along proximal half of length; apparently lacking spines on distal half of length.

Occurrence.—The sole specimen was collected from locality 4573.

Remarks.—Stomatopoda, or mantis shrimp, comprise a diverse assemblage of malacostracans arrayed in as many as 20 families in seven superfamilies, principally as a result of the work of Manning and his associates (Ahyong and Harling, 2000; Ahyong, 2001; Martin and Davis, 2001). Suprageneric characters include details of the rostral region, telson, and claws. Of these characters, the morphology of the claws seems to be least definitive, unless the claws are in some way unique or remarkable (Cees Hof, personal communication). For example, the sole specimen known from the Eocene rocks under consideration has been compared with dactyli from a broad range of genera, and similar, but not identical, forms can be found within three genera: *Squilla*, *Eurysquilla*, and *Lysiosquilla*. These genera are arrayed in three separate families in three separate superfamilies. Thus, it seems inappropriate to attempt to identify the specimen any more specifically than to refer it to the Suborder Unipeltata.

Rathbun (1926) described two species of stomatopods from California: *Clorida sonomana* (Rathbun), as *Chloridella sonomana*, from the ?Pliocene of Sonoma County, and *Pseudosquilla adelaidensis* Rathbun from the Miocene Monterey Formation of San Luis Obispo County. Each is characterized by single specimens of partial abdomina and telsons and therefore cannot be compared to the specimen at hand. However, both *Clorida* and *Pseudosquilla* exhibit raptorial claws bearing three teeth on the dactylus that increase in length distally, quite unlike the dactylus from the Santiago Formation, precluding placement in either of these genera.

ICHNOFOSSILS

Arthropod Burrows
Fig. 19

Material Examined.—Several specimens are preserved in burrows, including SDSNH 81079, 81099, 81109, 81110, and 81111. SDSNH 81109 and 81111 include fish scales.

Remarks.—Although no "typical" arthropod burrows, those referred to *Ophiomorpha* or *Thalassinoides*, are noted from the Eocene rocks under consideration, four specimens do appear to represent burrows produced by callianassids. Two of the burrows contain identifiable remains of the tracemaker.

A single burrow from the Ardath Shale, specimen SDSNH 81099 collected at locality 4529, encloses a nearly complete specimen of *Neocallichirus rhinos* (Fig. 19B). It should be noted that all other described specimens of this species are known from the Santiago Formation. The burrow consists of two elements. The presumed upper part of the burrow has a diameter of about 21 mm and is distinguished only because it contains the major and minor chelae as well as fragments of other pereiopods. There is no apparent demarcation between the burrow and the surrounding matrix. It must be noted that the orientation of the structure is inferred, for the sediment lacks detectable laminations; and upper and lower parts of the burrow are inferred from the orientation of the callianassid and the overall morphology of the burrow. The lower part of the burrow consists of a swelling, which is chordate in longitudinal-section and presumably circular in cross-section with a diameter of about 43 mm. Badly fragmented remains of the abdomen and probably the cephalothorax are preserved therein. This part of the concretion appears to be lined, because there is a dark aureole surrounding the animal and extending upward into the narrower part of the burrow for a short distance. Some callianassids are known to have expanded chambers within their burrows, and in some cases, these chambers are lined with plant material (Griffis and Suchanek, 1991). Presence of plant material would explain the dark stain in the chamber region.

Three other structures, specimens SDSNH 81109–81111 from the Santiago Formation, are distinctly different from the burrow structure in the Ardath Formation. These structures are ovoid, about twice as long as high, and are lined with fish scales (Fig. 19C). No other remains of fish are identifiable within the structures. Two of the specimens, SDSNH 81079 (Fig. 19A) and 81110, contain major claws, and one, SDSNH 81111, also preserves part of the abdomen of *Vegarthron santiago*. There is no evidence of the outline of the burrow, and therefore, reference to it as a burrow structure must be inferred from the presence of surrounding fish scales, interpreted to be a lining. To our knowledge, although callianassids are not known to aggressively seek live fish as food, it is quite possible that they might scavenge fish remains and utilize the scales as a burrow lining material. We know of no previous reference to this architectural technique, however, and the interpretation of these structures as burrows must be considered conjectural. If not burrows, they may simply be accumulations of callianassid and fish debris in swales on the sea floor.

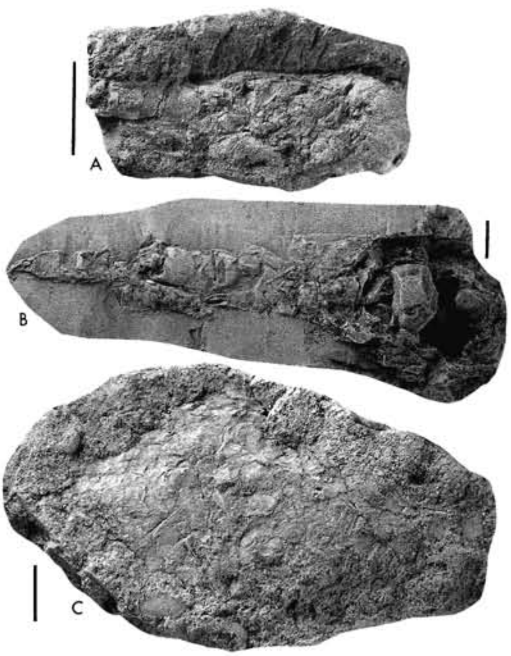

Fig. 19. Arthropod burrows. A, *Vegarthron santiago* n. gen. and sp. preserved within burrow, SDSNH 81079; B, *Neocallichirus rhinos* n. sp. preserved in burrow, SDSNH 81099; C, burrow with fish scales within, SDSNH 81109. Scale bars equal to 1 cm.

Discussion

Rathbun (1926) reported ten genera from Eocene rocks in California, many of which were also found in Eocene rocks in Oregon and Washington. Twenty genera were previously known solely from Eocene rocks from Oregon northward (Schweitzer, 2001). Only two genera were previously known solely from the Eocene of California. Three genera ranged between Oregon or Washington and California. Of the eighteen genera now known from California (Tables 4, 5), five—*Neocallichirus*,

Table 4. Systematic list of fossil decapods currently known from the Cretaceous through Pliocene of California. Taxa known only from claw fragments are not included, except *Callianassa sensu lato*, because of the occurrence of this taxon in great numbers. * Indicates taxa described or discussed in this contribution.

Infraorder Thalassinidea Latreille, 1831
Superfamily Callianassoidea Dana, 1852
Family Callianassidae Dana, 1852
Unknown Subfamily
*Genus *Vegarthron*, new genus
**Vegarthron santiago*, new species
Subfamily Callianassinae Dana, 1852
Genus *Callianassa* Leach, 1814
Callianassa spp. (See Rathbun, 1926)
Subfamily Callichirinae Manning and Felder, 1991
Genus *Neocallichirus* Sakai, 1988
**Neocallichirus rhinos*, new species
Family Ctenochelidae Manning and Felder, 1991
Subfamily Ctenochelinae Manning and Felder, 1991
Genus *Ctenocheles* Kishinouye, 1926
**Ctenocheles secretanae*, new species
Infraorder Anomura H. Milne Edwards, 1832
Superfamily Paguroidea, Latreille, 1802
Family Diogenidae Ortmann, 1892
Genus *Paguristes* Dana, 1852
Paguristes subaequalis (Rathbun, 1926), as *Dardanus*
Paguroidea indeterminate
Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Superfamily Raninoidea De Haan, 1839
Family Raninidae De Haan, 1839
Subfamily Ranininae De Haan, 1839
Genus *Ranina* Lamarck, 1801
Ranina tejoniana Rathbun, 1926
Subfamily Raninoidinae Lőrenthey *in* Lőrenthey and Beurlen, 1929
Genus *Raninoides* H. Milne Edwards, 1837
**Raninoides dickersoni* Rathbun, 1926
Raninoides slaki Squires, 2001
Section Heterotremata Guinot, 1977
Superfamily Calappoidea De Haan, 1833
Family Necrocarcinidae Förster, 1968
Genus *Necrocarcinus* Bell, 1863
Necrocarcinus hannae Rathbun, 1926
Superfamily Majoidea Samouelle, 1819
Family Majidae *sensu lato* Samouelle, 1819
Genus *Loxorynchus* Stimpson, 1857
Loxorynchus grandis Stimpson, 1857
Superfamily Parthenopoidea MacLeay, 1838
Family Parthenopidae MacLeay, 1838
Genus *Branchiolambrus* Rathbun, 1908
Branchiolambrus altus Rathbun, 1908
Superfamily Cancroidea Latreille, 1802
Family Cancridea Latreille, 1802
Subfamily Cancrinae Latreille, 1802
Genus *Cancer sensu lato* Linnaeus, 1758
Cancer fissus Rathbun, 1926
Genus *Romaleon* Gistl, 1848
Romaleon urbanus (Rathbun, 1917)
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Carcininae MacLeay, 1838
Genus *Carcinus* Leach, 1814

Table 4. Continued.

Carcinus minor (Rathbun, 1926)
Subfamily Polybiinae Ortmann, 1893
Genus *Minohellenus* Karasawa, 1990
**Minohellenus inexpressus*, new species
Genus *Portunites* Bell, 1858
Portunites insculptus Rathbun, 1926
Subfamily Psammocarininae Beurlen, 1930
Genus *Acanthoportunus*, new genus
**Acanthoportunus buchanani*, new species
Superfamily Retroplumoidea Gill, 1894
Family Retroplumidae Gill, 1894
Genus *Archaeopus* Rathbun, 1908
Archaeopus antennatus Rathbun, 1908
Superfamily Xanthoidea MacLeay, 1838
Family Goneplacidae MacLeay, 1838
Genus *Coeloma* A. Milne-Edwards, 1865
Coeloma martinezensis Rathbun, 1926
Genus *Cyclocorystes* Bell, 1858
Cyclocorystes aldersoni Squires, 1980
Genus *Orbitoplax* Tucker and Feldmann, 1990
**Orbitoplax weaveri* (Rathbun, 1926), as *Plagiolophus*
Genus *Speocarcinus* Stimpson, 1859
Speocarcinus berglundi Tucker, Feldmann, and Powell, 1994
Family Hexapodidae Miers, 1886
Genus *Palaeopinnixa* Via, 1966
Palaeopinnixa rathbunae Schweitzer, Feldmann, Tucker, and Berglund, 2000
**Palaeopinnixa granulosa*, new species
Family Panopeidae Ortmann, 1893
Panopeus soledadensis (Rathbun, 1926), as *Pilumnoplax*
Family Xanthidae *sensu lato* MacLeay, 1838
Genus *Xandaros* Bishop, 1988
Xandaros sternbergi (Rathbun, 1926)
Genus *Zanthopsis* McCoy, 1849
Zanthopsis hendersonianus Rathbun, 1926

Vegarthron, *Necrocarcinus*, *Carcinus*, and *Acanthoportunus*—occur on the west coast of North America only in that state. Of these five genera, *Acanthoportunus* and *Vegarthron* are known only from this occurrence and thus yield no ecological information. *Neocallichirus* is found in modern oceans in subtropical to warm-temperate areas (Manning and Felder, 1991), and *Carcinus* appears to be widespread (Glaessner, 1969). The extinct *Necrocarcinus* and *Palaeopinnixa* are known from areas thought to have been temperate or cool temperate (Schweitzer and Feldmann, 2000a). These five taxa may have been adapted to somewhat warmer conditions than the northern taxa known only from Oregon northward, although the equable conditions during the Eocene suggest that the waters along the entire coast may have been fairly warm. A more likely explana-

Table 5. Fossil decapods known from the Cretaceous–Pliocene of California, listed by age. Number in parentheses indicates number of taxa known from that time period.

Age	Taxa		
Cretaceous (3)	*Callianassa* spp.	*Archaeopus antennatus*	*Xandaros sternbergi*
Paleocene (1)	*Cyclocorystes aldersoni*		
Eocene (18)	*Vegarthron santiago*	*Callianassa* spp.	*Neocallichirus rhinos*
	Ctenocheles secretanae	*Ranina tejoniana*	*Raninoides dickersoni*
	Raninoides slaki	*Necrocarcinus hannae*	*Carcinus minor*
	Minohellenus inexpressus	*Portunites insculptus*	*Acanthoportunus buchanani*
	Coeloma martinezensis	*Orbitoplax weaveri*	*Palaeopinnixa rathbunae*
	Palaeopinnixa granulosa	*Panopeus soledadensis*	*Zanthopsis hendersonianus*
Miocene (3)	*Paguristes subaequalis*	*Branchiolambrus altus*	*Speocarcinus berglundi*
Pliocene (3)	*Loxorynchus grandis*	*Cancer fissus*	*Romaleon urbanus*

tion is that the dispersal routes or mechanisms taken by these five genera simply did not carry the taxa farther to the north.

Twelve of the Eocene genera known from California are distributed farther to the north along the Pacific Coast; one of these genera is known from occurrences as far north as Alaska (*Orbitoplax*). The occurrence of these taxa along the entire coast supports the notion that the warm climate of the Eocene made it possible for the animals to survive across a broad range of latitudes and temperature regimes that would not be as likely in other, less climatically moderate times.

Three of the Eocene genera occurring in California appear to have evolved during that epoch within the region, based upon known first occurrences; these genera include *Acanthoportunus*, *Neocallichirus*, and *Minohellenus*. Rathbun (1926) reported *Cancer sensu lato* from the Eocene of California; however, that taxon is known only from a claw fragment, making it nearly impossible to verify generic or even family placement. If this taxon does in fact belong to the Cancridae, it would be one of the earliest known occurrences of the family. The Cretaceous genus *Xandaros* is known only from the Pacific coast of California and Baja California Norte, México (Schweitzer *et al.*, in press), and the Miocene genus *Branchiolambrus* is known only from occurrences in California. *Loxorhynchus* appears to be restricted to the Pacific coast of North America and apparently evolved there during the Pliocene (Glaessner, 1969). *Cyclocorystes* is known from Paleocene rocks of Denmark and California; thus, its dispersal pattern is not resolvable at this time. *Vegarthron* has its earliest occurrence in the Cretaceous of northeastern México and subsequently occurs in Eocene rocks of California.

Both *Minohellenus* and *Maeandricampus* exhibit amphitropical Pacific distributions. These two genera are both members of the Portunidae, a family known to have had an amphitropical distribution during the Eocene (Schweitzer and Feldmann, 2000b). The earliest confirmed occurrence of *Minohellenus* is from Eocene rocks of California, whereas *Maeandricampus* is first known from Eocene rocks of New Zealand. *Minohellenus* later occurs in presumably younger rocks of Chile, whereas *Maendricampus* is known in younger Tertiary rocks of Washington. Some other genera found on the Pacific coast of North America display a similar amphitropical pattern in rocks of Cretaceous through Miocene age (Schweitzer, 2001). The mechanism or conditions producing these amphitropical distributions thus appear to have operated both north–south and south–north, based on all available evidence. This may have been the result of cooling during the Oligocene and subsequent warming in the Miocene, which could have separated populations adapted to cooler conditions because of warming at the equator (Crame, 1993, 1996). *Palaeopinnixa* appears to have evolved in the high southern latitudes during the Paleocene and subsequently dispersed to the northern hemisphere, becoming extinct in the southern hemisphere. This supports the notion of south–north dispersal routes.

Zanthopsis sensu stricto and *Necrocarcinus* appear to have reached the area via the Central American Seaway, as both have pre-Eocene records in Europe and, in the case of *Necrocarcinus*, also in Antarctica and the Western Interior Seaway. This dispersal process has been well documented within the Decapoda (Schweitzer, 2001). *Coeloma* is known first from early Eocene rocks of Europe; thus, it likely dispersed to North America sometime in the early Eocene. *Ranina*, *Raninoides*, and *Ctenocheles* each have widespread distributions by the Eocene, and it is difficult to speculate as to where they may have arisen. However, the new material makes clear that *Ctenocheles* is an ancient genus, with well-known living representatives surviving in modern oceans.

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