Paleontología Mexicana
Volumen 5, núm. 2, 2016, p. 123-135

New Occurrences of Fossil *Macrocheira* (Brachyura, Inachidae) from the North Eastern Pacific

Torrey Nyborg[1,*], Brant Nyborg[b], Alessandro Garassino[c], Francisco J. Vega[d]

[a] Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92354, U.S.A.
[b] Brant Nyborg, 4400 SW 179th Avenue, Aloha, Oregon 97078, U.S.A.
[c] Alessandro Garassino, Natural History Museum, Palaeontology Department, Corso Venezia 55, 20121 Milano, Italy.
[d] Francisco J. Vega, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, 04510 CDMX, México.

[*] tnyborg06g@llu.edu

Abstract

New specimens of the fossil *Macrocheira* collected from Eocene to Miocene rocks of Canada and western United States increase the fossil record of the Inachidae (MacLeay, 1838). *Macrocheira* is represented by only one extant species, *M. kaempferi*, endemic to Japan and Taiwan. Two fossil species have previously been described from Washington State: *M. longirostra* (Schweitzer and Feldmann, 1999), from the Eocene Quimper Sandstone, and *M. teglandi* (Rathbun, 1926), from the Oligocene Makah Formation. Three new species are reported: *M. jayi* n. sp. from the late Eocene to Oligocene Hesquiat Formation of Vancouver Island, British Columbia, Canada; *M. sullivani* n. sp. from the late Eocene to early Oligocene Keasey Formation of Oregon State, U.S.A.; and *M columbiaensis* n. sp. from the early to middle Miocene Astoria Formation of Washington State, U.S.A. Several *Macrocheira* species have also been reported from the Miocene of Japan; however, their systematic position is tenuous and therefore they are referred to as *Macrocheira* sp. aff. *M. kaempferi*. With the description of three new species of *Macrocheira*, the number of fossil species is increased to five and the genus is now well established in the North Eastern Pacific from the Eocene to Miocene.

Keywords: *Macrocheira*, Hesquiat Formation, Keasey Formation, Astoria Formation, Canada, U.S.A.

Resumen

Nuevos ejemplares fósiles de Macrocheira, colectados en rocas del Eoceno al Mioceno de Canadá y el oeste de Estados Unidos, incrementan el registro de los Inachidae. Macrocheira está representada únicamente por una especie actual, M. kaempferi, endémica de Japón y Taiwán. Dos especies fósiles han sido previamente descritas del Estado de Washington y Macrocheira longirostra Schweitzer y Feldmann, 1999, de la Arenisca Quimper del Eoceno, y M. teglandi (Rathbun, 1926) de la Formación Makah del Oligoceno. En este trabajo, se reportan tres nuevas especies: M. jayi n. sp., del Eoceno tardío al Oligoceno de la Formación Hesquiat, de la Isla Vancouver, Columbia Británica, Canadá; M. sullivani n. sp., del Eoceno tardío al Oligoceno temprano, de la Formación Keasey, Estado de Oregon, E.U.A.; y M. columbiaensis n. sp., del Mioceno temprano a medio de la Formación Astoria del Estado de Washington, E.U.A. Varios ejemplares de Macrocheira se han reportado también en el Mioceno de Japón, pero su afinidad sistemática es incierta, por lo que de forma preliminar, se identifica como Macrocheira sp. aff. M. kaempferi. Con la descripción de tres especies nuevas de Macrocheira, se incrementa a cinco el número de especies fósiles y el género queda ahora bien establecido para el Eoceno al Mioceno del Pacífico Noreste de Norteamérica.

Palabras clave: Crustacea, Inachidae, Macrocheira, Eoceno-Mioceno, formaciones Hesquiat, Keasey, Astoria, Canadá, E.U.A.

1. Introduction

Three new species of *Macrocheira* described herein increase the number of known fossil *Macrocheira* from two to five from the North Eastern Pacific: *M. jayi* n. sp. from the late Eocene to Oligocene Hesquiat Formation of Vancouver Island, British Columbia, Canada; *M. sullivani* n. sp. from the late Eocene to early Oligocene Keasey Formation of Oregon State, U.S.A.; and *M. columbiaensis* n. sp. from the early to middle Miocene Astoria Formation of Washington State, U.S.A. Two fossil species have previously been described from Washington State: *M. longirostra* (Schweitzer and Feldmann, 1999), from the Eocene Quimper Sandstone, and *M. teglandi* (Rathbun, 1926), from the Oligocene Makah Formation.

In Japan, *Macrocheira* sp. aff. *kaempferi* is represented in the Miocene (Temminck, 1836; Karasawa and Ohara, 2012), and is the sole extant species found in the waters surrounding mostly the Pacific side of Japan and eastern Taiwan (Sakai, 1976; Huang *et al*., 1990; Ng *et al*., 2008). From the known fossil occurrences of *Macrocheira*, the genus appears to have evolved in the North Eastern Pacific, dispersing sometime during the Miocene to Japan and Taiwan, where it is endemic today (Figure 1).

The extant *M. kaempferi* shows little variation in dorsal carapace size and morphology throughout adulthood with the exception of the chelipeds and walking legs which lengthen considerably as the crab ages (Arakawa, 1964; Okamoto, 2001). Males have longer legs and chelipeds than the females; however, the dorsal carapace remains the same (Arakawa, 1964). All of the *Macrocheira* fossils are based upon a small number of specimens; however, differences in rostral spines, orbital spines, anterolateral spines, and the position and sizes of dorsal carapace tubercles and bulbous areas separate the fossil species amongst themselves and the sole extant species.

2. Geological settings

2.1. Canada (*Macrocheira jayi* n. sp.)

One specimen from the Late Eocene to Oligocene Hesquiat Formation is preserved in a calcareous concretion collected from intertidal zone wave cut benches of the Hesquiat Formation near Escalante Point, along the Hesquiat Peninsula, Vancouver Island, British Colombia, Canada (49°31'35"N, 126°33'59"W). The Hesquiat Formation is 1200 m thick and ranges from basal calcareous sandstone to argillaceous sandstone and siltstone with shale interbeds (Muller, 1977; Jeletzky, 1975). Much of the wave cut benches along the Hesquiat Peninsula consist of concretions within a conglomeratic to mudstone matrix. The concretions lie in random orientation with respect to bedding, having been incorporated into the matrix by submarine channel fill turbidite flows (Cameron, 1971, 1975, 1980) or by more localized slumping and/or mud flows (Jeletzky, 1975; Muller *et al*., 1981) into various ancient subbasins of the Tofino Basin (refer to Johns *et al*., 2012 for detailed stratigraphy and depositional models of the Tofina Basin).

The Hesquiat Formation is part of the Carmanah Group which consists of three formations from oldest to youngest. These are: the Escalante Formation, the Hesquiat Formation, and the Sooke Formation (Jeletzky, 1975; Muller, 1977).

Figure 1. Modern map of the North Pacific Ocean Region showing relative position of *Macrocheira* species.

The Carmanah Group is exposed along western Vancouver Island from Sooke to the Brooks Peninsula (Jeletzky, 1954; Cameron, 1980; Banks *et al*., 1981; Muller *et al*., 1981; Smyth, 1997; Kaiser *et al*., 2015). Foraminifera (Cameron, 1980; Narayan *et al*., 2005), ichthyoliths (Johns *et al*., 2006) and molluscs (Jeletzky, 1975) have been previously described from the Hesquiat Formation. In addition, a pine cone, *Pinus escalantensis* (Banks, Ortiz-Sotomayor, and Hartman, 1981), was reported near the area where the fossil crab described herein was collected. Jeletzky (1975) illustrated a few representative fossil crabs from the Hesquiat Formation but did not formally describe them. This is the first report of a new crab from this formation.

2.2. Oregon (*Macrocheira sullivani* n. sp.)

Three specimens from the late Eocene to early Oligocene Keasey Formation are preserved in calcareous concretions collected from the Smithwick-Haydite abandoned rock quarry, and from river cut exposures along the Nehalem River near the town of Mist, Oregon. The Keasey Formation consists of approximately 700 m of near-shore shelf-slope deposits consisting of deep-marine tuffaceous siltstone and mudstones exposed in river-cuts, road-cuts, and rock quarries in the Nehalem River basin of northwestern Oregon (Warren *et al*., 1945; Warren and Norbisrath, 1945; Van Atta, 1971a, 1971b; Niem and Van Atta, 1973; Niem *et al*., 1994; Prothero and Hankins, 2000). The formation was first described by Schenck (1928) and later divided into three informal members (lower, middle and upper) (Warren *et al*., 1945; Warren and Norbisrath, 1946; Hickman, 1976). The Keasey Formation is disconformably underlain by the middle Eocene Cowlitz and Hamlet formations and disconformably overlain by the lower Oligocene Sage Creek and Pittsburg Bluff formations (Niem *et al*., 1994; Prothero and Hankins, 2000).

The Keasey Formation is highly fossiliferous including extensive molluscan faunas (Dall, 1909; Hickman, 1969, 1976, 2014); benthic foraminifera (Schenck, 1928; Cushman and Schenck 1928; McDougall, 1975); articulated echinoids, asteroids and ophiuroids (Zullo *et al*., 1964); crinoids (Moore and Vokes, 1953; Burns *et al*., 2005); corals (Durham, 1942; Zullo *et al*., 1964); sharks (Welton, 1972, 1973); and plant material (Moore and Vokes, 1953). Fossil crabs have been mentioned informally from the Keasey Formation (Warren *et al*., 1945; Steere, 1957). This is the first report of a formally described fossil crab species from this formation.

Recent studies on the magnetic stratigraphy, combined with the biostratigraphy of benthic foraminifera and molluscan faunas, constrain the age of the Keasey Formation to Chron C15r-C12r (35.0 – 33.0 Ma) (Prothero and Hankins, 2000).

2.3. Washington (*Macrocheira columbiaensis* n. sp.)

One specimen from the early to middle Miocene Astoria Formation of Washington is preserved in a calcareous concretion collected from wave cut terraces along the north shore of the Columbia River at Pigeon Bluff, near the town of Altoona, Washington. This locality is part of a sequence of early to middle Miocene, continental and marine beds of conglomerate, sandstone, and siltstone, exposed in the southwestern-most portion of Washington, tentatively correlated with the Astoria Formation of Oregon on the basis of their contained fauna, their stratigraphic position, and their lithologic characteristics (Rau, 1948; Snaveley *et al*., 1958). Fossil crabs are limited to southwestern-most Washington, in exposures along the Columbia River and a tributary of the Naselle River within Wahkiakum County, and in southwestern Washington in the Montesano and Willapa Hills area. Age control for the Astoria Formation in Washington is based upon mineral isotope composition (Wolfe and McKee, 1972), molluscan (Moore and Addicott, 1987), and foraminiferan (Rau, 1948) biostratigraphic distribution. The Astoria Formation of Washington interfingers with the Grande Ronde Basalt and the Wanapun Basalt of the Columbia River Basalt Group, which have been dated at near the boundary between the early and middle Miocene (Walsh *et al*., 1987). Fossil crabs collected from the Astoria Formation of Washington appear to represent that part of the Astoria Formation below these basalt flows, placing the fossil crabs within the early Miocene. In southwestern Washington, rocks referred to the Astoria Formation unconformably overlie the upper Eocene-upper Oligocene Lincoln Creek Formation and are unconformably overlain by the upper Miocene Montesano Formation (Weaver, 1912; Etherington, 1931; Rau, 1967; Moore and Addicott, 1987; Prothero, 2001; Prothero *et al*., 2001).

2.4. Abbreviations

CDM, Courtenay and District Museum Palaeontology Centre, Vancouver Island, British Columbia, Canada; CMNH, Condon Museum of Natural History, Eugene, Oregon, U.S.A.; LACMIP, Department of Invertebrate Paleontology, Natural History Museum of Los Angeles County, California, U.S.A.; UWBM, The Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington State, U.S.A.; lcxp: length of carapace (including rostral spines); wcxp: width of carapace; s: sternite.

3. Systematic Paleontology

Superfamily Majoidea Samouelle, 1819
Family Inachidae MacLeay, 1838
Genus *Macrocheira* De Haan, 1839

Type species. *Maja kaempferi* Temminck, 1836, by monotypy.

Extant Species. *Macrocheira kaempferi* (Temminck, 1836).

Fossil species. *Macrocheira yabei* (Imaizumi, 1957) (Miocene, Japan), represented by juveniles (Imaizumi, 1965), referred to as *Macrocheira* sp. aff. *M. kaempferi* by Karasawa and Ohara (2012); *M. ginzanensis* Imaizumi, 1965 (Miocene, Japan), based upon a portion of chela considered junior synonym of *M. kaempferi* by Karasawa and Ohara (2012); *M. columbiaensis* n. sp., reported herein (Miocene Astoria Formation of Washington State, U.S.A.); *M. teglandi* (Rathbun, 1926) (Schweitzer, 2001) (Oligocene Makah Formation, Washington State, U.S.A.); *M. sullivani* n. sp., reported herein (late Eocene to early Oligocene, Keasey Formation of Oregon State, U.S.A.); *M. jayi* n. sp., reported herein (late Eocene to Oligocene, Hesquiat Formation of Vancouver Island, British Columbia, Canada); and *M. longirostra* Schweitzer and Feldmann, 1999 (Eocene, Quimper Sandstone, Washington State, U.S.A).

Diagnosis. Carapace pyriform, longer than wide, widest at midwidth of branchial region; bifid rostrum, rudimentary orbital eave; orbit poorly developed, separated by preorbital, intercalated, and post-orbital spines; carapace surface ornamented with numerous tubercles and bulbous regions of various sizes; inflated epi-, mesobranchial, and protogastric regions; flask-shaped mesogastric region; U-shaped metagastric region; depressed urogastric region; long, diamond-shaped cardiac region.

Discussion. *Macrocheira* was erected by De Haan, 1839, for the sole extant species *M. kaempferi* (Temminck, 1836) endemic to Japan and Taiwan. *Macrocheira kaempferi* is also known from the Miocene of Japan (Karasawa and Ohara, 2012). The extant and sole species *M. kaempferi* differs from the fossil forms in having much shorter rostral elements that are directed anterolaterally (Figure 2). In addition, the frontal, protogastric, and mesogastric regions are smoother and ornamented only with a few tubercles separated by very shallow grooves (Figure 2). In the North Eastern Pacific specimens, these regions are much more

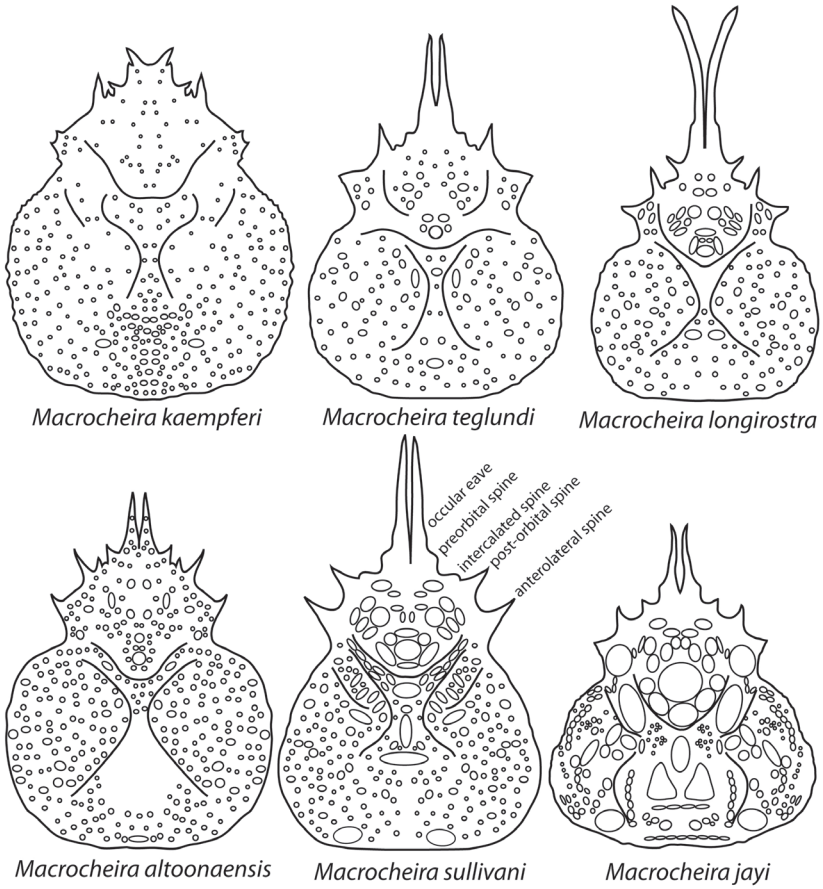

Figure 2. Idealized line drawings of the known fossil and one extant species of *Macrocheira*. *Macrocheira sullivani* shows position of spines discussed in text.

inflated and ornamented with numerous tubercles and bulbous regions separated by distinct grooves (Figure 2).

Macrocheira jayi new species
Figure 3

Diagnosis. Carapace pyriform, widest at midwidth of branchial region; carapace regions well-defined, ornamented with numerous tubercles and bulbous regions; rostrum bifid, tubular, diverging weakly from carapace midline; ocular eave large, orbit poorly developed, separated by preorbital, intercalated, and postorbital spines; frontal region ornamented with four tubercles; hepatic region highly inflated, acute spine positioned on lateral margin; protogastric region rounded, bulbous; mesogastric region flask-shaped; metagastric region broadly U-shaped, axially highly inflated; urogastric region depressed; cardiac region diamond-shaped in outline, three large tubercles axially; intestinal region flat, broadly trapezoidal in outline; epibranchial region oblong, several rounded and oval tubercles form bulbous inflation; mesobranchial region rounded, distinct sinuous ridge paralleling lateral margin; large liver-shaped tubercle centrally positioned; metabranchial region highly inflated with one large tubercle.

Description. Carapace pyriform, longitudinally vaulted, transversely weakly vaulted; longer than wide, widest at midwidth of branchial region; carapace regions well-defined, inflated, separated by deep, broad grooves or shallow depressions; carapace ornamented with numerous tubercles and bulbous regions of various sizes; lateral margin of branchial region rounded; posterior margin nearly straight. Rostrum bifid, extending approximately 1.1 cm distance forward from tip of preorbital spine; rostral elements tubular, diverging weakly from carapace midline; proximally broad, narrowing to acute spines laterally that are weakly directed anterolaterally; ocular eave large, flared, rimmed, weakly triangular, apex directed anterolaterally, situated on basal portion of rostrum, terminating distally in broadly rounded, triangular preorbital spine, directed anterolaterally, weakly curving forward. Orbits poorly developed; intercalated spine very small, rounded; postorbital spine triangular, acute, directed forward, about one-third larger than preorbital spine. Frontal region weakly triangular, apex directed posteriorly; ornamented with four tubercles, first two east-west oval in shape, positioned at

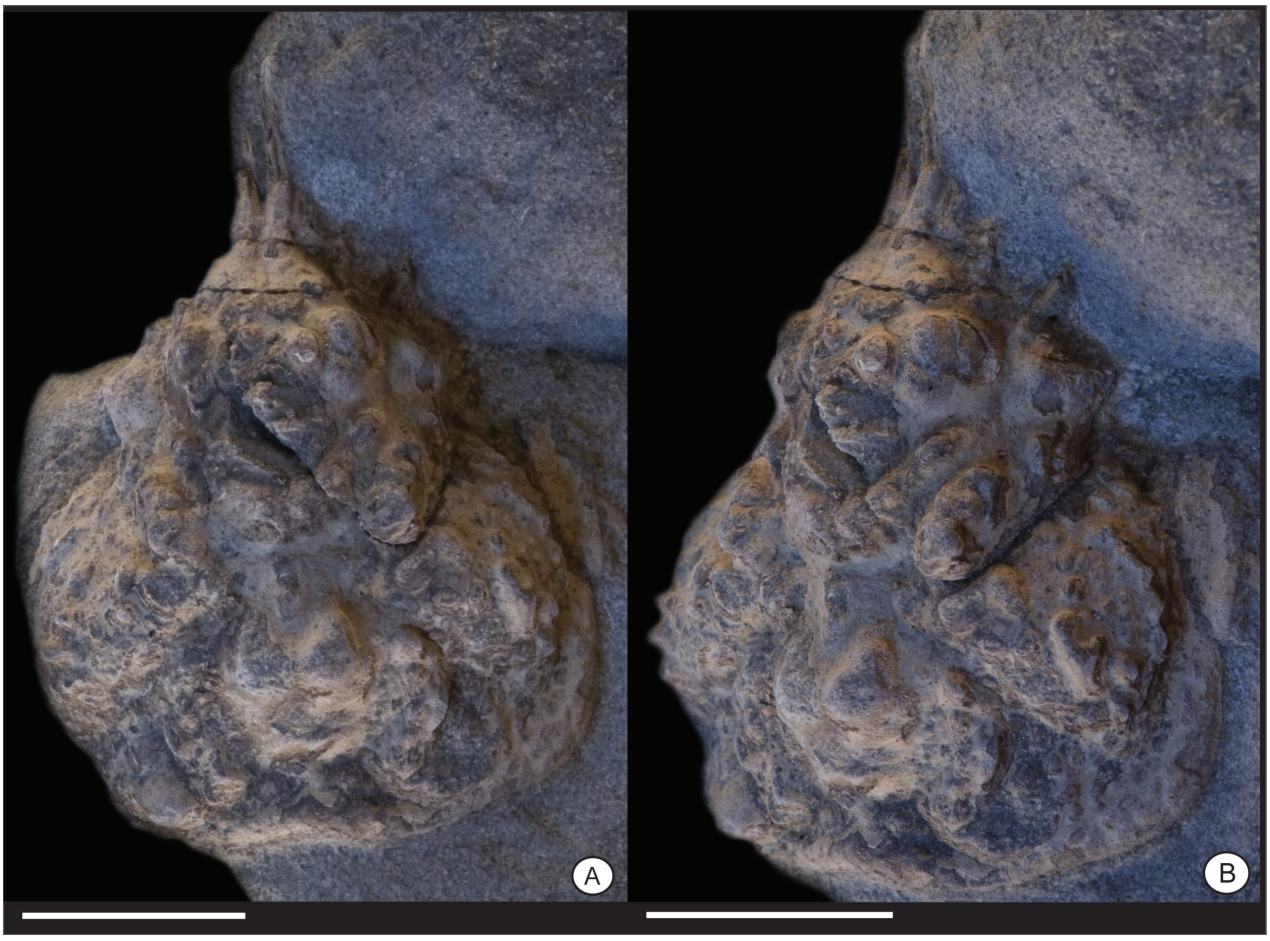

Figure 3. *Macrocheira jayi* n. sp., Holotype, CDM O49. A) dorsal view of carapace. B) oblique view of carapace to emphasize metagastic and mesobrachial regions. Scale bar equals 1 cm.

basal lateral edge of rostrum; second two two east-west oval in shape, about half the size of the first, positioned just posterior and slightly axially from first. Hepatic region highly inflated; lateral margin triangular in outline; small, acute spine positioned on lateral margin, directed anterolaterally, weakly curving forward.

Protogastric region rounded, bulbous, consisting of several rounded and oval tubercles separated by shallow grooves. Mesogastric region flask-shaped; anteriorly narrow, ornamented with tubercles of various sizes; posteriorly rounded, highly inflated, bulbous; consisting of several rounded and oval tubercles separated by shallow grooves. Shallow grooves separate frontal, hepatic, protogastric, and mesobastric regions. Metagastric region broadly U-shaped, narrowest at termination near the protogastric-hepatic constriction; axially widest, rounded, separated by a narrow groove anteriorly and a wide groove posteriorly; axially highly inflated, bulbous, consisting of numerous rounded and oval tubercles separated by shallow grooves; laterally forming small depression. Urogastric region depressed; ornamented with several small tubercles. Cardiac region diamond-shaped in outline; ornamented with numerous tubercles of various sizes; three large tubercles axially; first north-south oval shaped; second and third slightly larger than first, positioned slightly posteriorly and laterally from first, weakly triangular with rounded edges, apex directed toward metagastric region; posterior base with east-west oval shaped tubercles forming ridge; region separated by broad grooves. Intestinal region flat, broadly trapezoidal in outline, apex directed anteriorly; ornamented with numerous small tubercles of various sizes; posteriorly ridged forming sinuous posterior margin. Epibranchial region oblong, paralleling metagastric region; narrow grooves separate region; highly inflated, several rounded and oval tubercles form bulbous inflation. Mesobranchial region large, rounded, weakly broadly triangular, apex directed axially; separated from metabranchial region by narrow groove; distinct sinuous ridge paralleling lateral margin; large liver-shaped tubercle centrally positioned; remainder of region ornamented with numerous rounded and oval tubercles of various sizes. Metabranchial region highly inflated with one large rounded tubercle paralleling posterior margin; inflated, bulbous, concave ridge parallels lateral groove of cardiac region; narrow groove lateral of ridge. Sternum and appendages unknown.

Etymology. The species name honors Jay Hawley of Courtenay, Vancouver Island, British Columbia, Canada who found and kindly donated the sole specimen for research.

Material. One specimen in dorsal view with carapace just preserved, holotype CDM O49.

Type locality. Hesquiat Formation near Escalante Point, along the Hesquiat Peninsula, Vancouver Island, British Colombia, Canada (49°31'35"N, 126°33'59"W).

Geological age. Late Eocene to Oligocene.

Measurements. Holotype, CDM O49 – lcxp: 28 mm; wcxp: 20.3 mm.

Discussion. *Macrocheira jayi* n. sp. is based upon one specimen preserved within a concretion. *Macrocheira jayi* n. sp. is confidentially placed within *Macrocheira* in having a pyriform carapace that is longer than wide, a bifid rostrum, a rudimentary orbital eave, an orbit that is poorly developed and is separated by pre-orbital, intercalated, and postorbital spines, a carapace surface that is ornamented with numerous tubercles of various sizes, inflated epi-, mesobranchial, and protogastric regions, a flask-shaped mesogastric region, a U-shaped metagastric region, a depressed urogastric region, a long, narrow cardiac region, and a flattened metabranchial region.

Macrocheira jayi n. sp. differs from the other fossil and extant species of *Macrocheira* in having the entire dorsal carapace ornamented with distinct inflated and bulbous regions, including a cardiac region with three large tubercles, two of which are triangular in shape; a large turbercle and ridge on the metagastic region; and a ridge and large liver shaped tubercle on the mesobrachial region. In addition, the rostral elements are different in size and shape between *M. jayi* n. sp. and the other fossils and extant species of *Macrocheira* (Figure 2).

Macrocheira sullivani new species
Figure 4

Diagnosis. Carapace pyriform, widest at midwidth of branchial region; carapace regions well-defined, ornamented with numerous tubercles and bulbous regions; rostrum bifid, tubular, diverging weakly from carapace midline; ocular eave large, orbit poorly developed, separated by preorbital, intercalated, and postorbital spines; frontal region ornamented with four tubercles; hepatic region inflated; long, acute spine positioned on the lateral margin; protogastric region bulbous, consisting of several rounded and oval tubercles separated by shallow grooves; mesogastric region flask-shaped, several rounded and oval tubercles separated by shallow grooves; metagastric region broadly U-shaped, separated by a very deep groove anteriorly and a narrow groove posteriorly; laterally inflated, large tubercle axially; cardiac region diamond-shaped, three large tubercles axially; Urogastric region with two large tubercles axially; intestinal region flat, broadly trapezoidal in outline; epibranchial region oblong; mesobranchial region large, rounded, separated from metabranchial region by shallow groove; metabranchial region inflated, one large rounded tubercle paralleling posterior margin.

Description. Carapace pyriform, longitudinally vaulted, transversely weakly vaulted; longer than wide, widest at midwidth of branchial region; carapace regions well-defined, inflated, separated by deep, broad grooves or shallow depressions; carapace ornamented with numerous tubercles and bulbous regions of various sizes; lateral

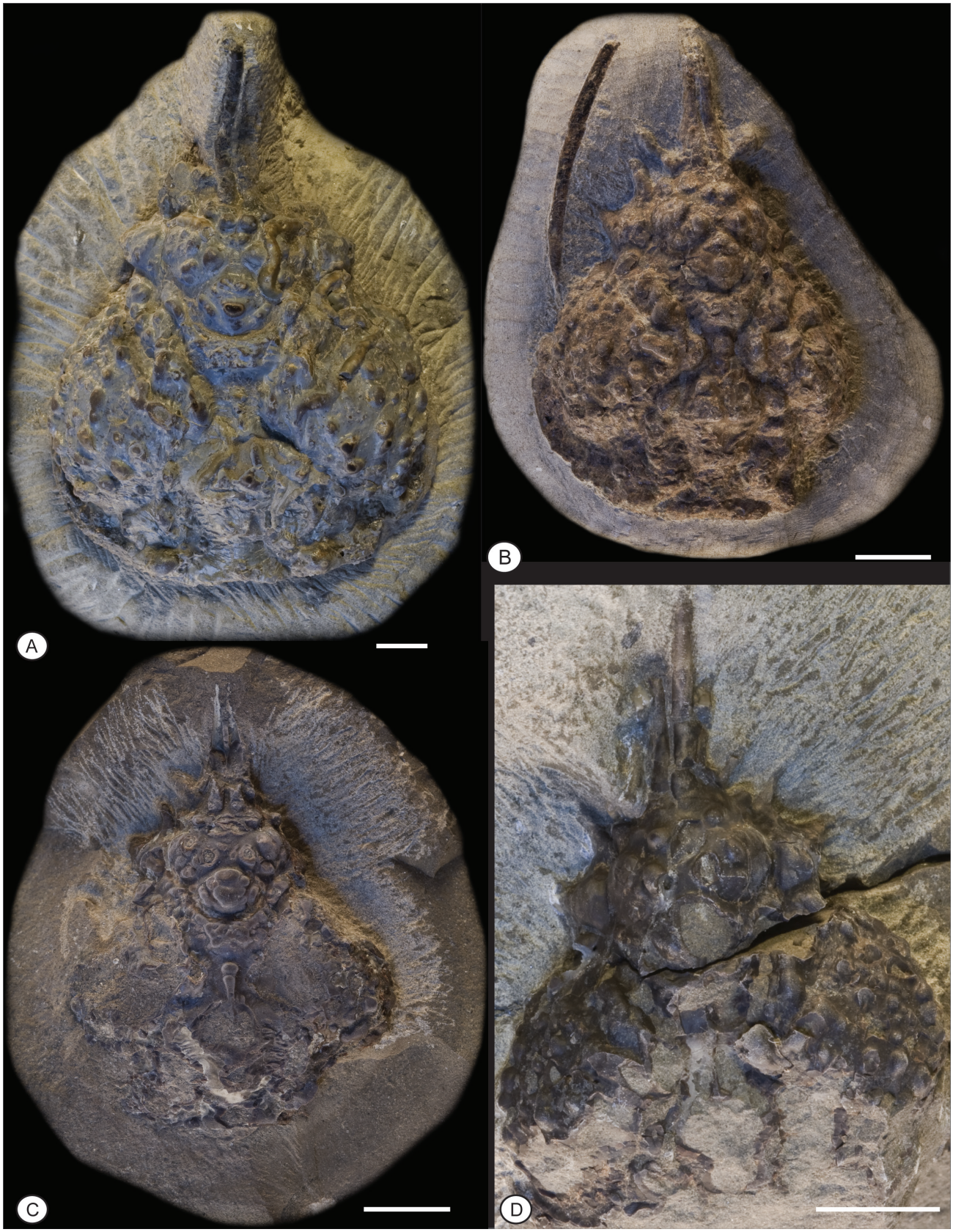

Figure 4. *Macrocheira sullivani* n. sp. A) dorsal view of carapace, holotype, CMNH F-64319. B) dorsal view of carapace, paratype UWBM 105251. C) dorsal view of carapace, paratype, CMNH F-35655. D) dorsal view of carapace, paratype, LACMIP 14645. Scale bar equals 1 cm.

margin of branchial region rounded; posterior margin nearly straight. Rostrum bifid, extending approximately 1.7 cm distance forward from tip of postorbital spine; rostral elements tubular, diverging weakly from carapace midline; proximally broad, narrowing to acute spines laterally; ocular eave small, narrow, rimmed, situated on basal portion of rostrum, terminating distally in broadly rounded preorbital spine, directed anterolaterally. Orbits poorly developed, with broadly rounded intercalated spine positioned at base of orbit; postorbital spine long, acute, proximally broad, triangular, directed anterolaterally, weakly curving forward. Frontal region weakly triangular, apex directed posteriorly; ornamented with four tubercles, first two east-west oval in shape, positioned at basal lateral edge of rostrum; second two two east-west oval in shape, about half the size of the first, positioned just posterior and slightly axially of first. Hepatic region inflated; long, acute spine slightly larger than post orbital spine, proximally triangular, positioned on the lateral margin, directed anterolaterally, weakly curving forward.

Protogastric region rounded, bulbous, consisting of several rounded and oval tubercles separated by shallow grooves. Mesogastric region flask-shaped; anteriorly narrow; posteriorly rounded, highly inflated, bulbous; consisting of several rounded and oval tubercles separated by shallow grooves. Shallow grooves separate frontal, hepatic, protogastric, and mesogastric regions. Metagastric region broadly U-shaped, narrowest at termination near the protogastric-hepatic constriction; axially widest, weakly triangular, apex directed posteriorly; separated by a very deep groove anteriorly and a narrow groove posteriorly; laterally inflated, bulbous, consisting of numerous rounded and oval tubercles separated by shallow grooves; large east-west oval shaped tubercle axially. Urogastric region weakly diamond-shaped in outline; ornamented with two large tubercles axially; first east-west oval shaped; second north-south elongated oval shaped, twice as large as first, situated just posterior of first, tapers slightly posteriorly. Cardiac region diamond-shaped in outline; ornamented with several small tubercles and one large axial east-west oval shaped tubercle. Intestinal region flat, broadly trapezoidal in outline, apex directed anteriorly; ornamented with numerous small tubercles of various sizes. Epibranchial region oblong, paralleling metagastric region; shallow groove posterior of metagastric-hepatic constriction; numerous rounded and oval tubercles within groove; remainder of region ornamented with rounded and oval tubercles; posteriorly becomes part of the mesobranchial region. Mesobranchial region large, rounded, weakly broadly triangular, apex directed axially; separated from metabranchial region by shallow groove; ornamented with numerous rounded and oval tubercles. Metabranchial region inflated, ornamented with numerous small tubercles, one large rounded tubercle paralleling posterior margin. Sternum and appendages unknown.

Etymology. The species name honors Bill Sullivan of Vernonia, Oregon, who was a mentor and friend of the authors. Bill helped organize the North America Research Group in 2004, (NARG), an organization of local fossil enthusiasts to help develop collecting policies and preserve local area fossils. Bill served as president and board member for a number of years and left an extensive fossil collection to the organization for display and for the University of Oregon Condon Collection.

Material. The new species is based upon the holotype and three paratypes which are all contained within concretions. Holotype, CMNH F-64319 preserves the entire dorsal carapace. Specimen was collected along the Nehalem River near the town of Mist, Oregon. Paratype, UWBM 105251 preserves the entire dorsal carapace. Specimen was collected from the Smithwick-Haydite abandoned rock quarry by Ross Berglund. Paratype, CMNH F-35655 preserves most of the dorsal carapace. Specimen was collected along the Nehalem River near the town of Mist, Oregon. Paratype LACMIP 14645 preserves the anterior portions of the dorsal carapace. Specimen was collected from the Smithwick-Haydite abandoned rock quarry.

Type locality. The holotype was collected within the Nehalem River near the town of Mist. The Nehalem River cuts through rock deposits of the Keasey Formation. The two paratypes were collected from the Smithwick-Haydite abandoned rock quarry, now a part of the Banks-Vernonia Linear Trail Oregon State Park in the NE1/4, Section 8, T3N, R4W of the Vernonia Quadrangle, Oregon; 7.5 minute series topographic map.

Geological age. Late Eocene to early Oligocene.

Measurements. Holotype, CMNH F-64319 – lcxp: ~ 84 mm; wcxp: 59.7 mm. Paratype, UWBM 105251 – lcxp: ~ 58 mm; wcxp: ~ 37 mm. Paratype, CMNH F-35655 – lcxp: ~ 50 mm; wcxp: ~ 33 mm. Paratype, LACMIP 14645 – wcxp: ~ 29 mm.

Discussion. *Macrocheira sullivani* n. sp. is based upon four well-preserved specimens. All were collected within concretions typical of the Keasey Formation. All four only preserve the dorsal carapace.

Macrocheira sullivani n. sp. is confidentially placed within *Macrocheira* in having a pyriform carapace that is longer than wide, a bifid rostrum, a rudimentary orbital eave, an orbit that is poorly developed and is separated by preorbital, intercalated, and postorbital spines, a carapace surface that is ornamented with numerous tubercles of various sizes, inflated epi-, mesobranchial, and protogastric regions, a flask-shaped mesogastric region, a U-shaped metagastric region, a depressed urogastric region, a long, narrow cardiac region, and a flattened metabranchial region.

Macrocheira sullivani n. sp. differs from *M. jayi* n. sp. in having less inflated and bulbous regions. The epibranchial, mesobrancial and metabrachial regions in *M. jayi* n. sp. have distinct groupings of tubercles not seen in *M. sullivani* n. sp. The postorbital spine in *M. sullivani* n. sp. is larger

and directed anterolaterally whereas in *M. jayi* n. sp. the postorbital spine is smaller and directed forward. The rostral elements are also different in size and shape between these two species (Figure 2).

Macrocheira sullivani n. sp. differs from *M. teglandi* (Rathbun, 1926) and *M. columbiaensis* n. sp. in having more bulbous and inflated frontal, protogastric, mesogastric, and metagastric regions. In addition the position and sizes of the orbital and lateral hepatic spines are distinctly different (Figure 2).

Macrocheira sullivani n. sp. is most similar to *M. longirostra* Schweitzer and Feldmann, 1999 in placement of dorsal carapace tubercles and inflated regions. However *M. longirostra* has distinct rostral elements that are very long and diverge anteriorly; a unique feature that sets this species apart from the other *Macrocheira* species. In addition, the preorbital spine in *M. longirostra* is long and triangular, whereas in *M. sullivani* n. sp. the preorbital spine is small and rounded. Lastly, the postorbital and lateral anterolateral spines are positioned differently between the two species (Figure 2).

Finally, the extant *M. kaempferi* (Temminck, 1836) differs from *M. sullivani* n. sp. as stated above.

Macrocheira columbiaensis new species
Figure 5

Diagnosis. Carapace pyriform, widest at midwidth of branchial region; carapace regions well-defined, ornamented with numerous tubercles and bulbous regions; rostrum bifid, tubular, diverging weakly from carapace midline; ocular eave large, orbit poorly developed, separated by preorbital, intercalated, and postorbital spines; frontal region weakly triangular, two large tubercles, transversely placed; hepatic region highly inflated, one large centered tubercle, small, sharp spine, situated on the lateral margin; protogastric region rounded, two large tubercles axially centered; mesogastric region flask-shaped, two large, axially centered, rounded tubercles; metagastric region inflated, broadly U-shaped; intestinal region ornamented with two acute tubercles proximal to the posterior margin; epibranchial region oblong, distally subdivided by two deep depressions, two large, acute tubercles, axially centered; mesobranchial region large, rounded; metabranchial region weakly depressed, triangular.

Description. Carapace pyriform, longitudinally vaulted, transversely weakly vaulted; wider than long excluding rostrum, widest at midwidth of branchial region; carapace regions well-defined, inflated, separated by deep, broad grooves or shallow depressions; carapace ornamented with numerous rounded and sharp tubercles of various sizes; lateral margin of branchial region rounded; posterior margin nearly straight, weakly sinuous. Rostrum bifid, extending approximately 1.4 cm forward from tip of postorbital spine; rostral elements tubular, horn-like, diverging weakly from carapace midline; proximally broad, triangular; ornamented with various tubercles of various sizes; ocular eave small, narrow, broadly rimmed, situated on basal portion of rostrum, terminating distally in broadly triangular, preorbital spine, directed forward, weakly curving laterally. Orbits poorly developed, equally divided in two by small, triangular intercalated spine, directed forward, weakly curving laterally; postorbital spine long, acute, about twice the size of preorbital spine and two-thirds the size of intercalated spine, directed laterally, weakly curving forward. Frontal region weakly triangular, apex directed posteriorly; ornamented with numerous tubercles of various sizes and two large, rounded tubercles, transversely placed, paralleling shallow depression, demarcating frontal and protogastric regions. Hepatic region highly inflated, bulbous; ornamented with numerous tubercles of various sizes and one large, acute, centered tubercle, proximal to deep, narrow depression, demarcating hepatic and protogastric regions; small, sharp spine, situated on the lateral margin, directed laterally, weakly curving forward. Protogastric region rounded, weakly triangular, apex directed between intercalated spine and postorbital spine; ornamented with two large tubercles and numerous other tubercles of various sizes; first tubercle rounded, axially centered, proximal to protogastric region; second tubercle oblong, centered, situated slightly anterior from first. Mesogastric region flask-shaped, anteriorly narrow; posteriorly rounded, highly inflated; ornamented with various tubercles of numerous sizes and two large, axially centered, rounded tubercles; first tubercle long directed forward; second tubercle posterior and half as long as first tubercle. Metagastric region inflated, broadly U-shaped, narrowest at termination near the protogastric-hepatic constriction; axially widest, weakly triangular, apex directed posteriorly; separated by a very deep groove anteriorly and a narrow groove posteriorly; ornamented with numerous tubercles of various sizes, several of which appear oblong. Urogastric region depressed, not well known. Cardiac region not preserved, appears to be diamond-shaped in outline. Intestinal region partially preserved; ornamented with numerous tubercles of various sizes and two very acute tubercles proximal to the posterior margin. Epibranchial region oblong, paralleling metagastric region; distally subdivided by two deep depressions; first depression just posterior of metagastric-hepatic constriction; second depression proximal to lateral margin; inflation between two depressions, separated anteriorly by shallow depression; posteriorly becomes part of the mesobranchial region; ornamented with many tubercles of various sizes and two large, acute tubercles, axially centered. Mesobranchial region large, rounded, weakly broadly triangular, apex directed axially; separated from metabranchial region by shallow branchiocardiac groove; ornamented with numerous sharp tubercles, especially along lateral margin.

Figure 5. *Macrocheira columbiaensis* n. sp., holotype, UWBM 97194 A) dorsal view of carapace. B) cast of exterior mold of dorsal carapace. C) close-up view of frontal region from cast of exterior mold of dorsal carapace. Scale bar equals 1 cm.

Metabranchial region weakly depressed, triangular, apex directed axially and forward; ornamented with numerous acute tubercles.

Etymology. The species name refers to the town near the locality where the specimen was collected.

Material. The holotype, UWBM 97194, is deposited at the Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, U.S.A.

Type locality. The holotype and sole specimen was collected from the SE1/4, SW1/4, Section 9, T9N, R8W of the Roseburg Quadrangle, Washington-Oregon; 7.5 minute series topographic map. The concretion was collected from a sandy-siltstone exposure within the Pigeon Bluff intertidal zone, along the north shore of the Columbia River, near the town of Altoona, Washington. This locality has been mapped as part of the early to middle Miocene Astoria Formation (Wolfe and McKee, 1972).

Geological age. Early to middle Miocene.

Measurements. The sole specimen of *Macrocheira columbiaensis* n. sp. does not preserve enough of the dorsal carapace to make dorsal carapace measurements. A reconstruction drawing of this species is given in Figure 2.

Discussion. *Macrocheira columbiaensis* n. sp. is based upon one well-preserved specimen in a very sandy concretion preserving most of the dorsal carapace, part of the sternum, and the merus of one of the pereiopods.

Macrocheira columbiaensis n. sp. is confidentially placed within *Macrocheira* in having a pyriform carapace that is longer than wide, a bifid rostrum, a rudimentary orbital eave, an orbit that is poorly developed and is separated by preorbital, intercalated, and postorbital spines, a carapace surface that is ornamented with numerous tubercles of various sizes, inflated epi-, mesobranchial, and protogastric regions, a flask-shaped mesogastric region, a U-shaped metagastric region, a depressed urogastric region, a long, narrow cardiac region, and a flattened metabranchial region.

Macrocheira columbiaensis n. sp. differs from the other fossil species in having a larger amount of sharp tubercles on the dorsal carapace, including on the rostral elements, and two sharp tubercles on the mesogastric region. It also differs in the placement and sizes of rostrum and orbital spines (Figure 2).

Macrocheira jayi n. sp., *M. longirostra* Schweitzer and Feldmann, 1999, and *M. sullivani* n. sp. have more inflated, bulbous regions then *M. columbiaensis* n. sp. *Macrocheira teglandi* (Rathbun, 1926), in placement and sizes of the dorsal carapace tubercles is most similar to *M. columbiaensis* n. sp.; however, *M. teglandi* has fewer tubercles on the dorsal carapace, and they are more rounded, whereas *M. columbiaensis* n. sp. has about three times as many tubercles including several very sharp tubercles not seen on *M. teglandi*. The rostral elements on *M. columbiaensis* n. sp. are shorter and have tubercles, whereas in *M. teglandi* the rostral elements are longer and have no tubercles (Figure 2).

Finally, the extant *Macrocheira kaempferi* (Temminck, 1836) differs from *M. columbiaensis* n. sp. as stated above.

4. Conclusions

The *Macrocheira* species from the North Eastern Pacific are considerably smaller than the extant species *M. kaempferi* (Temminck, 1836), reportedly the largest crab in the world, which may attain a carapace width of 305 mm and a maximum length of 335 mm, with a leg span of up to 2.5 meters from tip to tip (Sakai, 1976; Carpenter and Niem, 1998). From the known fossil occurrences of *Macrocheira*, the genus appears to have evolved in the the North Eastern Pacific, having been collected from Eocene, Oligocene, and Miocene rocks of this area, dispersing sometime during the Miocene in Japan and Taiwan, where it is endemic today (Figure 1).

Based upon larvae development, *Macrocheira* was previously considered the most primitive form of the subfamily Inachinae (Rice, 1980). Phylogenetic relationships of the subfamilies of the family Majidae have shown that *Macrocheira* is allied more with the basal taxon within the family Majidae, and is more closely related to the subfamily Oregoniinae (Clark and Weber, 1991; Marques and Pohle, 1998; Pohle and Marques, 2000; Ng *et al*., 2008).

Acknowledgements

We wish to thank Elizabeth Nesbitt and Ron Eng of the Burke Museum; Austin Hendy of the Natural History Museum of Los Angeles County; and Edward Davis and Eric Gustafson of the Condon Museum of Natural History for loaning specimens used in this paper. Steve Hetrick helped in fossil preparation of several of the specimens. Bruce Thiel wrote the etymology section for *Macrocheira sullivani*. We also thank the two reviewers Gale Bishop and Alex Ossó for their comments and suggestions in making this manuscript ready for publication.

References

Arakawa, K., 1964, On the mating behavior of the giant Japanese crab, *Macrocheira kaempferi*: Researches on Crustacea, 1, 41–46.

Banks, H.P., Ortiz-Sotomayor, A., Hartman, C.M., 1981, *Pinus escalantensis*, sp. nov., a new permineralized cone from the Oligocene of British Columbia: Botanical Gazette, 142(2), 286–293.

Burns, C., Campbell, K.A., Mooi, R., 2005, Exceptional crinoid occurrences and associated carbonates of the Keasey Formation (Early Oligocene) at Mist, Oregon, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, 227, 210–231.

Cameron, B.E.B., 1971, Tertiary stratigraphy and microfaunas from the Hesquiat–Nootka area, west coast, Vancouver Island (92E): In Report of Activities, Part B, Geological Survey of Canada, Paper, 71-1, 91–94.

Cameron, B.E.B., 1975, Geology of the Tertiary rocks north of Latitude 49°, west coast of Vancouver Island: Report of Activities, Part A, Geological Survey of Canada, Paper 75-1A, 17–19.

Cameron, B.E.B., 1980, Biostratigraphy and depositional environment of the Escalante and Hesquiat formations (early Tertiary) of the Nootka Sound area, Vancouver Island, British Columbia: Geological Survey of Canada, Paper, 78–9, 28 pp.

Carpenter, K.E., Niem, V.H., 1998 – 1999, FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific, Rome: FAO, vols. II.

Clark, P.F., Weber W.R., 1991, A redescription of *Macrocheira kaempferi* (Temmink, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura): Journal of Natural History, 25, 1259–1279.

Cushman, J.A., Schenck, H.G., 1928, Two foraminiferal faunules from the Oregon Tertiary: University of California Publications in Geologic Sciences, 27, 305–324.

Dall, W.H., 1909, Contributions to the Tertiary paleontology of the Pacific Coast I. The Miocene of Astoria and Coos Bay: U.S. Geological Survey Professional Paper, 59, 1–278.

Durham, J.W., 1942, Eocene and Oligocene coral faunas of Washington: Journal of Paleontology, 16, 84–104.

Etherington, T.J., 1931, Stratigraphy and fauna of the Astoria Miocene of Southwest Washington: University of California Publications in Geological Sciences, 20(5), 31–142.

Haan, W.De., 1833–50, Crustacea, *in* Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava Imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus, illustravit, ix–xvi, I–xxxi, vii–xvii,1243 p., pl. A-Q, 1–55, circ. 2, A. Arnz, Lugdunum Batavorum.

Hickman, C.J.S., 1969, Oligocene marine molluscan fauna of the Eugene Formation in Oregon: University of Oregon Museum of Natural History Bulletin, 16, 112 pp.

Hickman, C.S., 1976, Bathyal gastropods of the family Turridae in the Early Oligocene Keasey Formation in Oregon, with a review of some deep-water genera in the Paleogene of the Eastern Pacific: Bulletins of American Paleontology, 70(292), 1–119.

Hickman, C.S., 2014, Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, part IV: The anomalodesmatans: PaleoBios, 1–21.

Huang, J.F., Yu, H.P., Takeda, M., 1990, Occurrence of the Giant Spider Crab, *Macrocheira kaempferi* (Temminck, 1836) (Crustacea: Decapoda: Majidae) in Taiwan: Bulletin of the Institute of Zoology, Academia Sinica, 29, 207–212.

Imaizumi, R., 1957, A Miocene fossil crab, *Paratymolus yabei* n. sp. from Nagano Prefecture: Transactions and Proceedings of the Palaeontological Society of Japan, new series, 25, 26–30.

Imaizumi, R., 1965, Miocene *Macrocheira* from Japan: Researches on Crustacea, 2, 27–36.

Jeletzky, J.A., 1954, Tertiary Rocks of the Hesquiat–Nootka area, west coast of Vancouver Island, British Columbia: Canada Department of Mines and Technical Surveys, Geological Survey of Canada, Paper 53–17, 65 pp.

Jeletzky, J.A., 1975, Hesquiat Formation (new): a neritic channel and interchannel deposit of Oligocene age, western Vancouver Island, British Columbia: Geological Survey of Canada paper 75–32, 55 pp.

Johns, M.J., Barnes, C.R., Narayan, Y.R., 2006, Cenozoic ichthyolith biostratigraphy: Tofino Basin, British Columbia: Canadian Journal of Earth Sciences, 43(2), 177–204.

Johns, M.J., Trotter, J.A., Barnes, C.R., Narayan, Y.R., 2012, Biostratigraphic, strontium isotopic, and geologic constraints on the landward movement and fragmentation of terranes within the Tofino Basin, British Columbia: Canadian Journal of Earth Sciences, 49(7), 819–856.

Kaiser, G., Watanabe, J., Johns, M., 2015, A new member of the family Plotopteridae (Aves) from the late Oligocene of British Columbia, Canada: Palaeontologia Eletronica, 18.3.52A, 1–18.

Karasawa, H., Ohara, M., 2012., Decapoda from the Miocene Kumano Group, Wakayama Prefecture, Japan: Bulletin of the Mizunami Fossil Museum, 38, 53–57.

MacLeay, W.S., 1838, On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith, *in* Smith, A., Illustrations of the Annulosa of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa. . .": 53–71, 2 pls. (Smith, Elder and Company, London).

Marques, F., Pohle., G., 1998, The use of structural reduction in phylogenetic reconstruction of decapods and a phylogenetic hypothesis for fifteen genera of Majidae: testing previous hypothesis and assumptions: Invertebrate Reproduction and Development, 33(2–3), 241–262.

McDougall, K., 1975, The microfauna of the type section of the Keasey Formation in Oregon, in Future Energy Horizons of the Pacific Coast. Paleogene Symposium and Technical Papers, *in* Weaver, D.W. et al., (eds.), American Association of Petroleum Geologists, 343–359 pp.

Moore, E. J., Addicott, W.O., 1987, The Miocene Pillarian and Newportian (molluscan) stages of Washington and Oregon and their usefulness in correlations from Alaska to California: U.S. Geological Survey Bulletin, 1664, 13 pp.

Moore, R.C., Vokes, H.E., 1953, Lower Tertiary crinoids from northwestern Oregon: U.S. Geological Survey Professional Paper 233-E, 113–148.

Muller, J.E., 1977, Evolution of the Pacific Margin, Vancouver Island and adjacent regions: Canadian Journal of Earth Sciences, 14(9), 2062–2085.

Muller, J.E., Cameron, B.E.B., Northcote, K.E., 1981, Geology and mineral deposits of Nootka Sound map-area, Vancouver Island, British Columbia: Geological Survey of Canada, Paper 80–16, 53 pp.

Narayan, Y.R., Barnes, C.R., Johns, M.J., 2005, Taxonomy and biostratigraphy of Cenozoic foraminifers from Shell Canada wells, Tofino Basin, offshore Vancouver Island, British Columbia, Canada: Micropaleontology, 51(2), 101–168.

Ng, P.K.L., Guinot, D., Davie, P., 2008, Systema Brachyuorum: Part I. An annotated checklist of extant Brachyuran crabs of the world: Raffles Bulletin of Zoology Supplement, 17, 1–286.

Niem, A.R., McNight, H.J., Meyer, H.H., Campbell, K.A., 1994, Sedimentary, volcanic and tectonic framework of forearc basins and the Mist Gas Field, northwest Oregon, *in* Geologic Field Trips in the Pacific Northwest: Geological Society of America, Boulder, Colorado, 1F1–1F42.

Niem, A.R., Van Atta, R.O., 1973, Cenozoic stratigraphy of northwestern Oregon and adjacent southwestern Washington: Bulletin Oregon Department of Geology and Mineral Industries, 77, 75–89.

Okamoto, K., 2001, Limb loss in the giant spider crab *Macrocheira kaempferi*: Bulletin of the Shizuoka Prefectural Fisheries Experiment Station, 36, 25–27.

Pohle, G., Marques, F., 2000, Larval stages of *Paradasygyius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae: Proceedings of the Biological Society of Washington, 113(3), 739–760.

Prothero, D.R., Hankins, K.G., 2000, Magnetic stratigraphy and tectonic rotation of the Eocene–Oligocene Keasey Formation, northwest Oregon: Journal of Geophysical Research, 105, 473–480.

Prothero, D.R., 2001, Chronostratigraphic calibration of the Pacific Coast Cenozoic: a summary, *in* Magnetic Stratigraphy of the Pacific Coast Ceonozoic: Pacific Section: Society for Sedimentary Geology, Book 91, 377–394.

Prothero, D.R., Bitboul, C.Z., Moore, G.W., Moore, E.J., 2001, Magnetic stratigraphy of the early and middle Miocene Astoria Formation, Newport Embayment, Oregon, *in* Magnetic Stratigraphy of the Pacific Coast Ceonozoic: Pacific Section: Society for Sedimentary Geology, Book, 91, 272–283.

Rathbun, M.J., 1926, The Fossil Stalk-eyed Crustacea of the Pacific Slope of North America: United States National Museum Bulletin, 138, 155 pp.

Rau, W.W., 1948, Foraminifera from the Miocene Astoria Formation in southwestern Washington: Journal of Paleontology, 22(6), 774–782.

Rau, W.W., 1967, Geology of the Wynoochee Valley Quadrangle, Grays Harbor County, Washington: Washington Division of Mines and Geology Bulletin, 56, 1–51.

Rice, A.L., 1980, Crab zoeal morphology and its bearing on the classification of the Brachyura: Transactions of the Zoological Society of London, 35, 271–424.

Sakai, T., 1976, Crabs of Japan and the Adjacent Seas: Kodansha Ltd., Tokyo. 773 pp.

Samoulle, G., 1819, The Entomologist's Useful Compendium, or An Introduction to the Knowledge of British Insects, London, 496 pp.

Schenck H.G., 1928, Marine Oligocene of Oregon: University of California Publications in Geologic Sciences, 16, 449–460.

Schweitzer, C.E., 2001, Additions to the Tertiary decapod fauna of the Pacific Northwest of North America: Journal of Crustacean Biology, 21, 521–537.

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

Smyth, W.R., 1997, Chapter 2. Bedrock Geology of Brooks Peninsula, in Hebda, R.J., Haggarty, J.C. (eds.), Brooks Peninsula: An Ice Age Refugium on Vancouver Island. BC Parks, Ministry of Environment, Lands, and Parks, Occasional Paper No. 5, 2.1–2.8.

Snavely, P.D. Jr., Brown, D.R. Jr., Hoover, L. Jr., Pease, H.M., Rau, W.W., Roberts, E.A. Schopf, J.M., 1958, Geology and coal resources of the Centralia-Chehalis District, Washington: U.S. Geological Survey Bulletin, 1053, 159 pp.

Steere, M.L., 1957, Fossil localities of the Sunset Highway area, Oregon: The Ore Bin, 19, 37–44.

Temminck, C.J., 1836, Coup-d'oeil sur la faune des Iles de la Sonde et de l'Empire du Japon. Discours préliminaire destiné à la Fauna du Japon: Musée du Pays-Bas, Leiden, The Netherlands.

Van Atta, R.O., 1971a, Sedimentary petrology of some Tertiary formations upper Nehalem River Basin, northwest Oregon. Doctoral dissertation, Oregon State University Corvallis, Oregon, U.S.A., 229 pp.

Van Atta, R.O., 1971b, Stratigraphic relationships of the Cowlitz Formation upper Nehalem River Basin, northwest Oregon: The Ore Bin, 33, 165–181.

Walsh, T.J., Korosec, M.A., Phillips, W.M., Logan, R.L., Schasse, H.W., 1987, Geologic map of Washington – southwest quadrant: Washington Division of Geology and Earth Resources Geologic Map GM-34, scale 1:250000.

Warren, W.C., Norbisrath, H., Grivetti, R.M., 1945, Geology of northwestern Oregon west of the Willamette River and north of latitude 45º51': U.S. Geological Survey Oil and Gas Investigations Preliminary Map 42 (map and text).

Warren, W.C., Norbisrath, H., 1946, Stratigraphy of upper Nehalem River Basin, northwestern Oregon: American Association of Petroleum Geologists Bulletin, 30(2), 213–237.

Weaver, C.E., 1912, A preliminary report on the Tertiary paleontology of western Washington: Washington Geological Survey Bulletin, 15, 80 pp.

Welton, B.J., 1972, Fossil sharks in Oregon: The Ore Bin, 34, 161–170.

Welton, B.J., 1973, Oligocene selachians from the Keasey Formation at Mist, Oregon: Geological Society of America Abstracts with Programs, 5, 121 pp.

Wolfe, E.W., McKee, E.H., 1972, Sedimentary and igneous rocks of the Grays River quadrangle, Washington: U.S. Geological Survey Bulletin, 1335, 70 pp.

Zullo, A., Kaar, R.F., Durham, J.W., Allison, E.C., 1964, The echinoid genus *Salenia* in the eastern Pacific: Palaeontology, 7, 331– 349.

Manuscript received: September 5, 2016.
Corrected manuscript received: November 17, 2016.
Manuscript accepted: November 23, 2016.