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PARASTACOIDEA IN THE NORTHERN HEMISPHERE

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ABSTRACT

Description of a new genus and species of crayfish from the Eocene McAbee beds in southern British Columbia, Canada, marks the first occurrence of Parastacoidea Huxley, 1879, in the Northern Hemisphere. The superfamily is widely distributed in modern aquatic environments in the Southern Hemisphere, except in Africa and Antarctica, as well as in Australia, New Zealand, and South America in the fossil record. The occurrence of a single species in the Eocene of North America suggests a Cretaceous or Paleogene dispersal from the Southern Hemisphere through eastern Asia. Remarkable preservation of the specimens reveals traces of muscles, the endophragmal skeleton, and the intestinal tract.

KEY WORDS: British Columbia, crayfish, Eocene, Parastacoidea, remarkable preservation

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INTRODUCTION

Freshwater crayfish are among the rarest decapod crustacean fossils in North America with only two species known to us (Hobbs, 1974; Feldmann et al., 1981; Schweitzer et al., 2010). Thus, the discovery of 12 nearly complete specimens representing a new taxon from Ypresian, lower Eocene, rocks of British Columbia, Canada, is a significant addition to our understanding of the history of the crayfish. The combination of morphological features observed on the specimens not only suggests that they are unique, it also poses some challenging evolutionary and biogeographic questions. The discovery is even more significant because the specimens exhibit preservation of soft part and delicate internal tissues not commonly seen in the fossil record.

Geological Setting

The general geological setting of the McAbee fossil beds was outlined by Mustoe (2005). The fossil beds consist of about 30 m of rhythmically-bedded, siliceous sediments within a 550 m-thick sequence dominated by volcanoclastic rocks. This lower Eocene unit is a part of the Kamloops Group (Ewing, 1981). The fossiliferous beds are interpreted as being diatomaceous, lacustrine deposits (Mustoe, 2005) within a regional drainage basin with a generally northerly flow direction (Tribe, 2005). The interpretation that these beds are lacustrine, rather than marine, is based upon the fauna. Fish, representing at least five families of freshwater species (Wilson, 1980), along with insects and terrestrial plant remains, support this interpretation.

The geographic extent of the lake in which the McAbee sediments were deposited is not known because of the discontinuous nature of the lacustrine deposits, although similar diatomaceous beds are known from other sites in south-central British Columbia over 50 km north and south from McAbee. The most remarkable aspect of the beds is the presence of a remarkably diverse and well preserved flora and fauna (Leahy, 2006), including deciduous and coniferous remains and a variety of insects. Some of this biota is described in a special number of the Canadian Journal of Earth Sciences [Archibald and Greenwood (eds.), 2005] and elsewhere.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802
Infraorder Astacidea Latreille, 1802

Remarks.—Placement of these fossils in Astacidea is based upon the overall form of the animals with the cephalothorax and pleon of comparable size as other astacids and with the pleon lying in the same plane as the cephalothorax. Although compressed, the carapace appears to have been cylindrical. Compression is a common component of the preservational style of decapods, particularly those with a relatively thin, flexible carapace. There is no evidence that the carapace was fused to the epistome. The first three pereopods are chelate; the first bears a large cheliped. The exopods of the uropods bear a diaeresis. This combination of characters supports placement in Astacidea and excludes the fossils from other infraorders of decapods.

The infraorder at present contains five superfamilies. *Palaeopalaemonoidea* Brooks, 1962, is restricted to a single genus of Late Devonian lobster in which pereopods 2-5 are subchelate, the telson is triangular, and the endopod and exopod of the uropods are triangular (Schram et al., 1978). This combination of characters clearly distinguishes *Palaeopalaemonoidea* from the specimens in question. *Enoplometopoidea* de Saint Laurent, 1988, have subchelate pereopods 2-5, and the telson bears movable spines (de Saint Laurent, 1988). Neither subchelate pereopods nor movable telson spines are present on the specimens from British Columbia, although these features could reasonably be expected to be preserved. *Nephropoidea* Dana, 1952, have complex groove patterns, and epimeres on the pleon with pointed margins (Holthuis, 1974). The rounded epimeres and reduced groove pattern of the McAbee specimens distinguish them from *Nephropoidea*. All the above superfamilies are strictly marine.

The remaining two superfamilies, *Astacoidea* Latreille, 1802, and *Parastacoidea* Huxley, 1879, are restricted to non-marine habitats. They are most similar in gross morphology to *Nephropidae* within *Nephropoidea* and are phylogenetically a sister clade to *Nephropoidea*. They share several features with *Nephropoidea* that are often observed in the fossil record, including the laterally compressed carapace bearing a variable carapace groove pattern, a prominent pleon extending posteriorly and bearing well-developed epimeres, chelate pereopods 1-3, and hypertrophy of the first cheliped; however, the form of the groove patterns and the epimeres are different in nephropids than in the freshwater forms. Nearly all of the astacoids and parastacoids have rounded epimeres (Souty-Grosset et al., 2006) and the groove pattern is reduced to a single transverse groove, whereas nephropids have pointed epimeres and a more complex groove pattern composed of two or more transverse grooves.

Parastacoidea Huxley, 1879

Parastacidae Huxley, 1879

Diagnosis.—Astacideans with keeled anterior region on cephalothorax, bearing hook on inner margin of carpus and having inner margin of propodus longer than dactylus; first pleonite lacking pleopods. Telson without diaeresis, sometimes with hardened anterior portion and membranous termination.

Remarks.—The above diagnosis is modified from Glaessner (1969), Hobbs (1974), and Souty-Grosset et al. (2006) and emphasizes only those characters that can be preserved in the fossil record. The presence of a keeled region on the cephalothorax does not distinguish parastacids from either *Cambaridae* or *Astacidae*, the two families in the *Astacoidea*; however, *Astacidae* lack a hook on the inner margin of the carpus and both *Cambaridae* and *Astacidae* have the inner margin of the propodus shorter than the dactylus. The morphology of the telson is diagnostic. Huxley (1879; 1880) noted that only genera within *Parastacoidea* lacked the diaeresis. Glaessner (1969) and Hobbs (1974) reiterated that observation, and the presence

or absence of a diaeresis was used by Rode and Babcock (2003) in their cladistic analysis of crayfish. Thus, the feature seems to be reasonably diagnostic.

Aenigmastacus n. gen.

Type Species.—*Aenigmastacus crandalli* new genus and species, by original designation.

Included Species.—*Aenigmastacus crandalli* new genus and species.

Etymology.—The generic name is derived from the Latin word *aenigma* = inexplicable, and *Astacus*, a common generic name and suffix within *Astacidea*. The gender is masculine.

Diagnosis.—Parastacid with smooth carapace; cervical groove either diminished or absent; smooth chelipeds with inner surface of propodus longer than dactylus; diaeresis on the exopod of uropod; telson without diaeresis.

Discussion.—To our knowledge, only four other named species of *Parastacidae* other than the new one are known from the fossil record. As with extant species of the family, all four previously named species are from the Southern Hemisphere.

Palaeoechinastacus australianus et al., 2008, is the oldest; it is known from the Albian (Early Cretaceous) of Victoria, Australia. The cephalothorax of this species is not known except for a small piece of the branchiostegite, but the pleon exhibits long, slender uropods and the first pereopod has a spiny upper margin on the manus and dactylus. The new species has nearly circular uropods and a smooth upper margin of the manus and dactylus.

Lammastacus longirostris Aguirre-Urreta, 1992, has been described from the Oligocene of Argentina. This species is readily distinguished from the British Columbia fossils because the former has a spinose cephalic region, well-developed cervical and branchiocardiac grooves, a spinose rostrum, very long fingers on strongly heterochelous first pereopods, and a pustulose pleon. The new species apparently has a diminutive rostrum and no spines are evident; the fingers of the first pereopod are not strikingly long and the chelipeds are similar in size. The pleon is keeled, but is not pustulose.

Paranephrops fordycei Feldmann and Pole, 1994, occurs in the Miocene of South Island, New Zealand. This species has a prominent, serrated rostrum, a well-developed cervical groove, and as a relatively narrow, pointed telson. The uropods are ovoid. The telson and uropods are broader and rounded on the British Columbia material and the rostrum is not serrated.

Finally, *Astacopsis franklini* (Gray, 1845) was reported from the Pleistocene of Australia (Wintle, 1886), but he made no reference to the nature of the remains and a comparison with the new species is not possible.

The diagnostic features of *Parastacidae* and *Aenigmastacus* distinguish the new genus from genera within *Astacidae*, *Cambaridae*, and *Cricoidoscelosidae*. Within the *Astacoidea*, *Aenigmastacus* is most like *Procambarus*

superficially, but the pustulose chelipeds, well-developed cervical and branchiocardiac grooves, and denticles on the occlusal surface of *Procambarus* serve to distinguish the two genera.

Aenigmastacus crandalli n. sp.

Figs. 1-4

Procambarus sp., Wehr and Barksdale, 1995, p. 9.

Diagnosis.—As for genus.

Description.—Note: Because of the nature of preservation, descriptive features are not readily observable on all specimens. Therefore, the terminal digits in the catalogue number of the illustrated specimens on which features can be clearly observed are denoted in square brackets. Each specimen is figured and identified by the same number.

Small crayfish, ca. 3-5 cm total length of carapace and pleon. Carapace thin, smooth; pleon smooth. Chelipeds prominent, of similar outline, left slightly longer than right.

Carapace extremely thin, typically preserved as flattened disc with deep, smoothly concave antennal notch [1152]. Rostrum, carapace grooves, and surface ornamentation not known. Posterior border concave dorsally and broadly convex ventrally [1151].

Pleonites generally smooth with slightly thickened rim separating articulating ring from exposed surface [1151, 1158]. Axis of pleon defined by preserved trace of sediment-filled intestinal tract, ca. 0.6 mm wide [1146, 1152]. Tergal length [1151] of somite 1, 2.2 mm; that of 2, 3.5 mm; somites 3-5, 3.3 mm; somite 6, 3.9 mm. Epimeres with rounded terminations [1151], sizes proportional to terga.

Telson quadrate, tapering slightly posteriorly, approximately as wide as long, lacking diaeresis [1145], posterior margin apparently smooth, gently rounded. Uropodal endopod and exopod ovoid in outline; exopod with prominent, serrated diaeresis [1145].

Antennules with flagellae of approximately equal length [1146]. Antennae strong, preserved length of flagellae greater than carapace length [1145]. Antennal scales large; lateral margins thickened, terminating in acute spine; axial margin smoothly convex [1145, 1152]. Eyes not preserved.

First pereopod with prominent, nearly isochelous chelipeds [1152]. Proximal elements not visible, but apparently short. Left cheliped slightly longer than right. Left carpus [1152] with reduced spine on inner surface; propodus [1152] 18.5 mm long with manus 9.0 mm long and 5.4 mm high at midlength. Fixed and movable fingers each 2.3 mm high, edentulous; upper and lower surfaces gently and smoothly convex. Right cheliped [1152] partially exposed; manus 8.5 mm long and 4.8 mm high. Remaining pereopods long, slender. Small chelipeds preserved on pereopods 2 and 3 [1156, 1157]. Remainder of termination not known.

One pair each of long lanceolate pleopods on somites 3-5 (?) with thickened anterior edges [1156].

Etymology.—The trivial name recognizes Prof. Keith Crandall, Brigham Young University, a noted authority on extant crayfish.

Types.—The holotype, TRUIPR L-018 F-1146 and F-1147 (part and counterpart) and 11 paratypes, TRUIPR L-018 F-1143 and F-1144 (part and counterpart), F-1145, F-1148- F-1151, F-1152 and 1153 (part and counterpart), F-1154, F-1155, F-1156 and F-1157 (part and counterpart) and F-1158 are deposited in the Thompson River University Invertebrate Paleontology Repository, Kamloops, B.C., Canada.

Occurrence.—The specimens were collected from the McAbee beds of the Kamloops Group at the McAbee locality, 50°47.181'N, 121°08.568'W, east from Cache Creek, British Columbia, Canada (Manchester and Dillhoff, 2004).

Age.—Ewing (1981, p. 1471) cited ages of 52 ± 2 , 51 ± 2 , and 49 ± 2 Ma for ash beds in the McAbee beds as determined by Hills and Baadsgaard (1967). The oldest and youngest ages were based upon analysis of plagioclase in ash beds 1 and 2; the intermediate age was based upon analysis of biotite from ash bed 2. These ages place the McAbee beds within the late Ypresian (early Eocene) (Gradstein and Ogg, 2004).

DISCUSSION

Fossil crayfish are extremely uncommon. To our knowledge, only 13 species of Astacidae, Cambaridae, Cricoidoscelosidae, and Parastacidae are known (Schweitzer et al., 2010) (Table 1). Among these, only two species, *Pacifastacus chenoderma* (Cope, 1871), in Astacidae, and *Procambarus primaevus* (Packard, 1880), in Cambaridae, are known from North America. Neither bears a close resemblance to *A. crandalli*. Both previously described species have well-developed cervical grooves, neither has smooth chelipeds, and both exhibit a diaeresis on the telson. In fact, *A. crandalli* bears a combination of characters that set it apart from all known crayfish. The smooth carapace with the cervical groove either diminished or absent, smooth chelipeds, and diaeresis on the exopod of the uropod and none on the telson comprise a combination of characters sufficiently unique to erect a new genus and species.

It is noteworthy that the first published illustration of a specimen from the Cache Creek area and referable to this species was that of Wehr and Barksdale (1995). One of us (RMF) identified the specimen from a photograph by R. Ludwigsen as a species of *Procambarus*. The specimen preserved only the cephalic portion of the cephalothorax and the chelipeds. Other than the conformation of the chelipeds, none of the characters judged to be diagnostic of Parastacidae were preserved so that the specimen was reported to be a member of Cambaridae. *Aenigmastacus crandalli* does resemble *Procambarus primaevus* more than it does *Pacifastacus chenoderma*.

The specimens forming the basis for this new genus and species are compressed on bedding planes so that they exhibit almost no relief. The cuticle was apparently very thin so that the carapaces were splayed out on the surface and preserved as films, making interpretation of surface morphology virtually impossible. The pleomeres and appendages were also flattened. The flattening of the

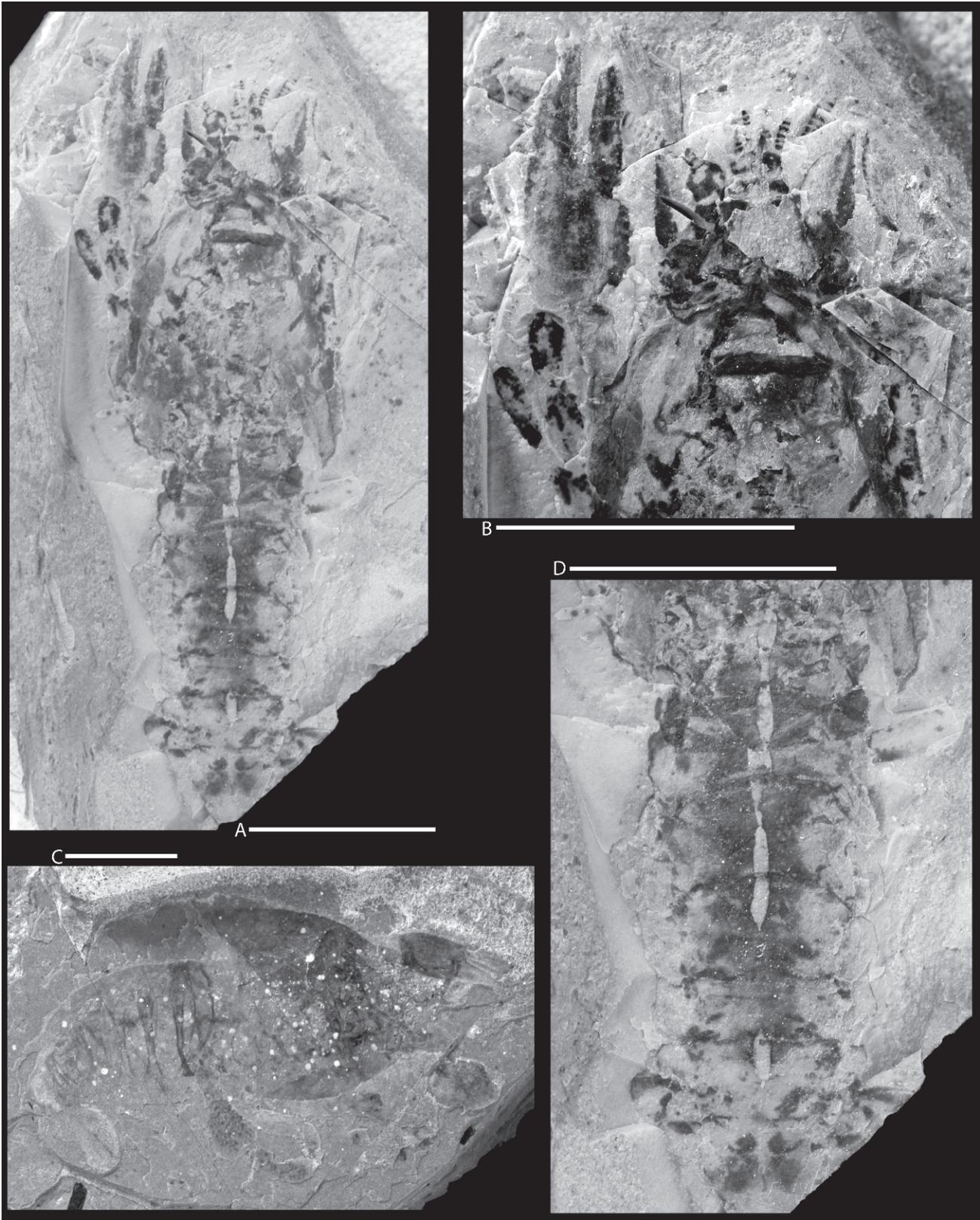


Fig. 1. *Aenigmastacus crandalli* n. gen. n. sp. A, B, D, holotype, TRUIPR L-018 F-1146 A, dorsal view; B, enlarged view of anterior region showing detail of scaphocerite, antennae, and left first pereiopod; D, enlarged view pleon showing detail of preservation of intestinal tract; C, paratype, TRUIPR L-018 F-1146, right lateral view showing diaphanous nature of cuticle. Scale bars = 1 cm.

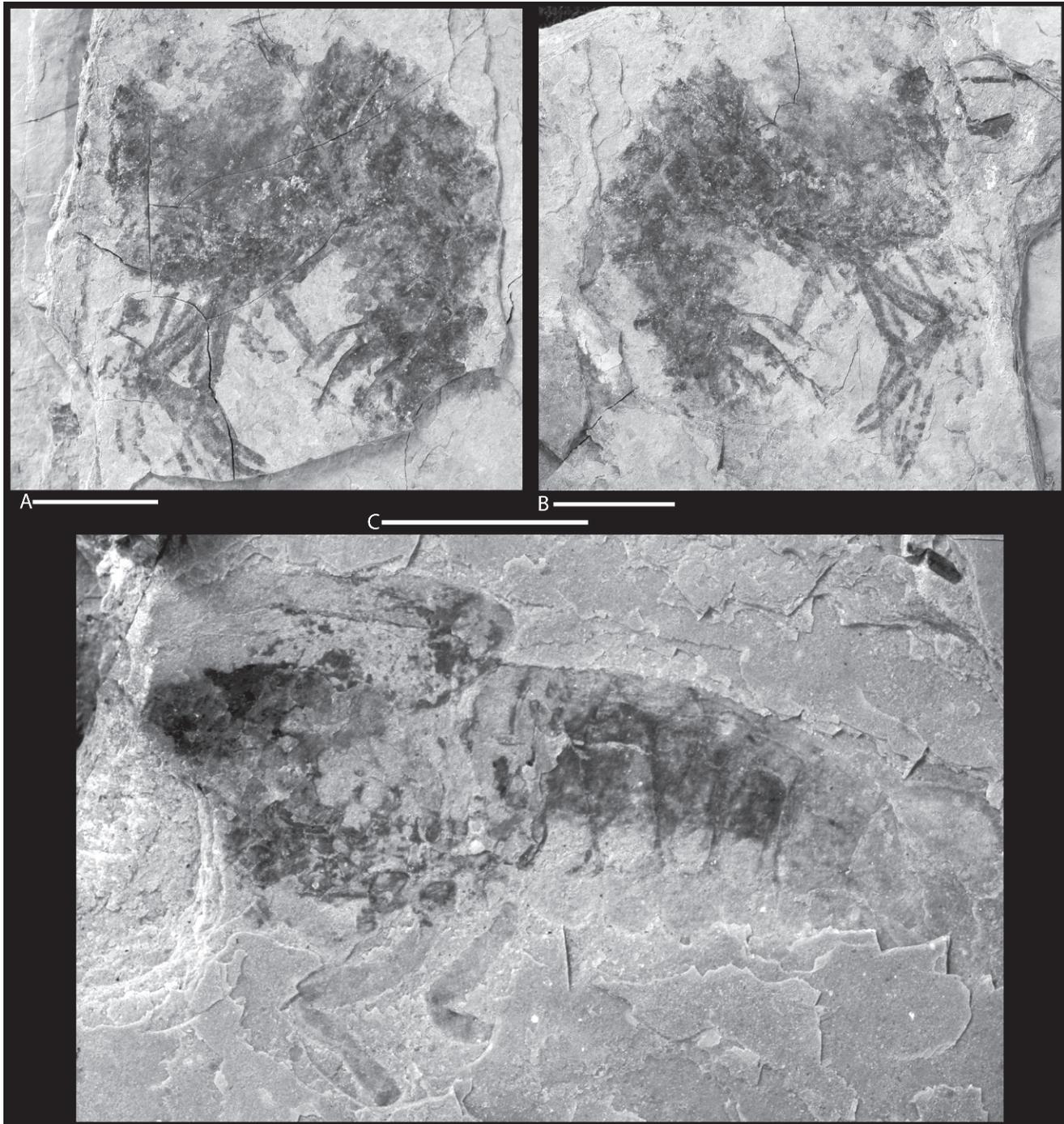


Fig. 2. *Aenigmastacus crandalli* n. gen. n. sp. A, B, part and counterpart of paratype, TRUIPR L-018 F-1156, showing parts of pereopods 2-5 and pleopods on posterior segments of pleon; C, paratype, TRUIPR L-018 F-1151, showing outline of epimeres. Scale bars = 1 cm.

specimens distorts width measurements but does not have an appreciable effect on length dimensions. The specimens also exhibit regions of black film that may represent preservation of soft tissue as will be discussed below. Because none of the specimens is complete, and preservation of different regions may be best seen on just a single specimen, the description is a composite of observations.

Freshwater crayfish are assigned to two superfamilies, Astacoidea Latreille, 1802, and Parastacoidea Huxley, 1879

(Schweitzer et al., 2010) (Table 1). The bases for distinguishing the two superfamilies as reported by Hobbs (1974) are primarily reproductive structures (Keith Crandall, personal communication to RMF, 5/2010) not likely to be preserved in fossils, and certainly not preserved on the specimens at hand. One criterion that has been used to distinguish the groups is presence or absence of a diaeresis on the telson. Huxley (1879, 1880), Glaessner (1969), and Hobbs (1974) noted this as one of the distinguishing

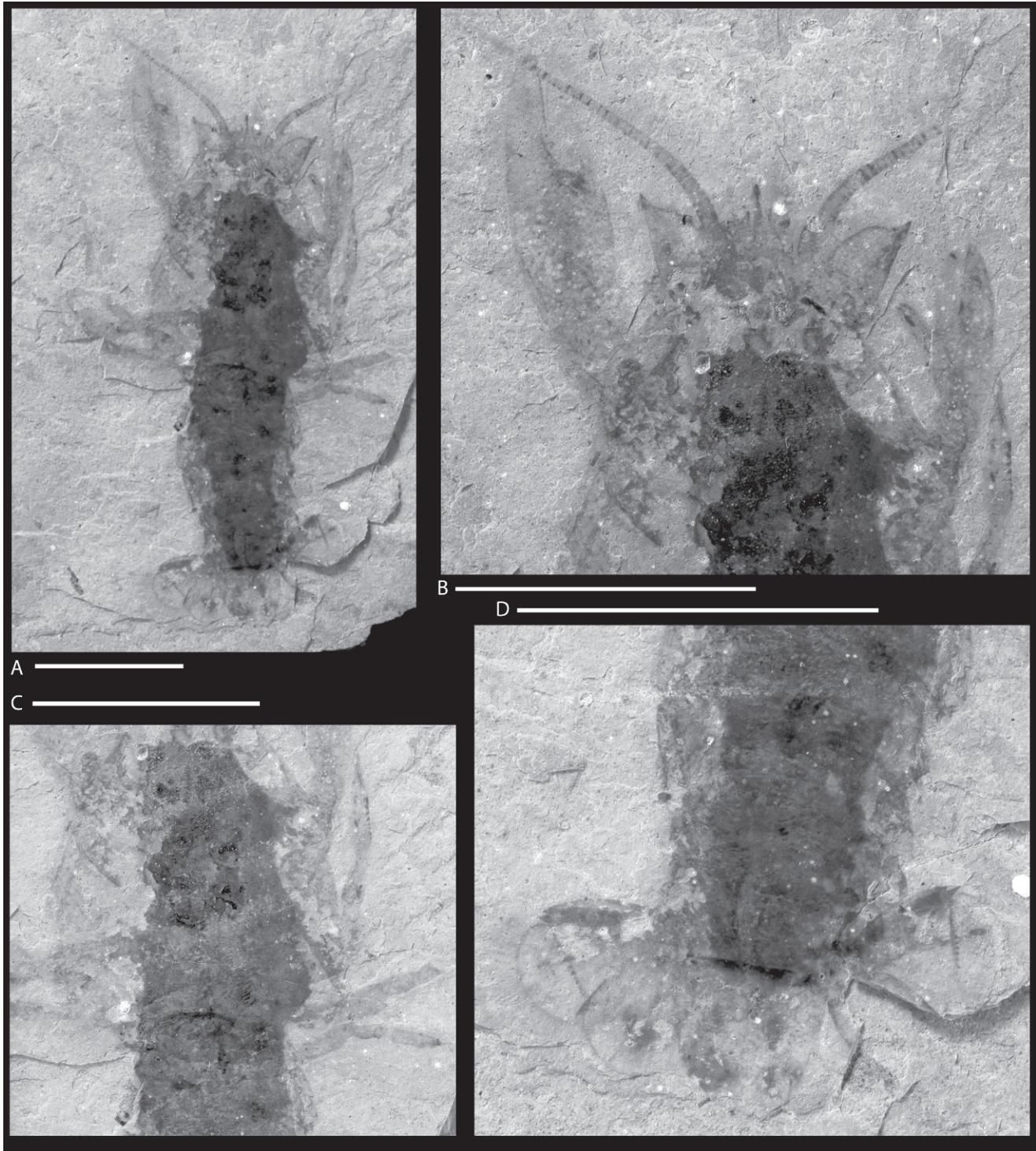


Fig. 3. *Aenigmastacus crandalli* n. gen. n. sp. A-D, paratype, TRUIPR L-018 F-1145, A, dorsal view; B, enlargement of anterior regions showing detail of antennae, scaphocerite, and left cheliped; C, detail of dorsal view of cephalothorax showing poorly preserved endophragmal skeleton; D, enlarged view of posterior part of pleon showing diaeresis on the uropods and complete, broad telson. Scale bars = 1 cm.

features between Astacoidea and Parastacoidea. Astacoidea exhibit a diaeresis on the telson as well as the exopods of the uropods, whereas Parastacoidea have a diaeresis only on the exopods of the uropods. This same distinction was noted by Rode and Babcock (2003) in which they scored all parastacids as lacking a diaeresis, except *Euastacus*

armatus (von Martens, 1866) which bears a “partial diaeresis.” All of Astacoidea have diaereses. *Aenigmastacus crandalli* is represented by three specimens (1145, 1146, and 1151) on which some or all of the telson is preserved, and there is no evidence of a diaeresis. This is particularly striking on 1145, which preserves the diaeresis

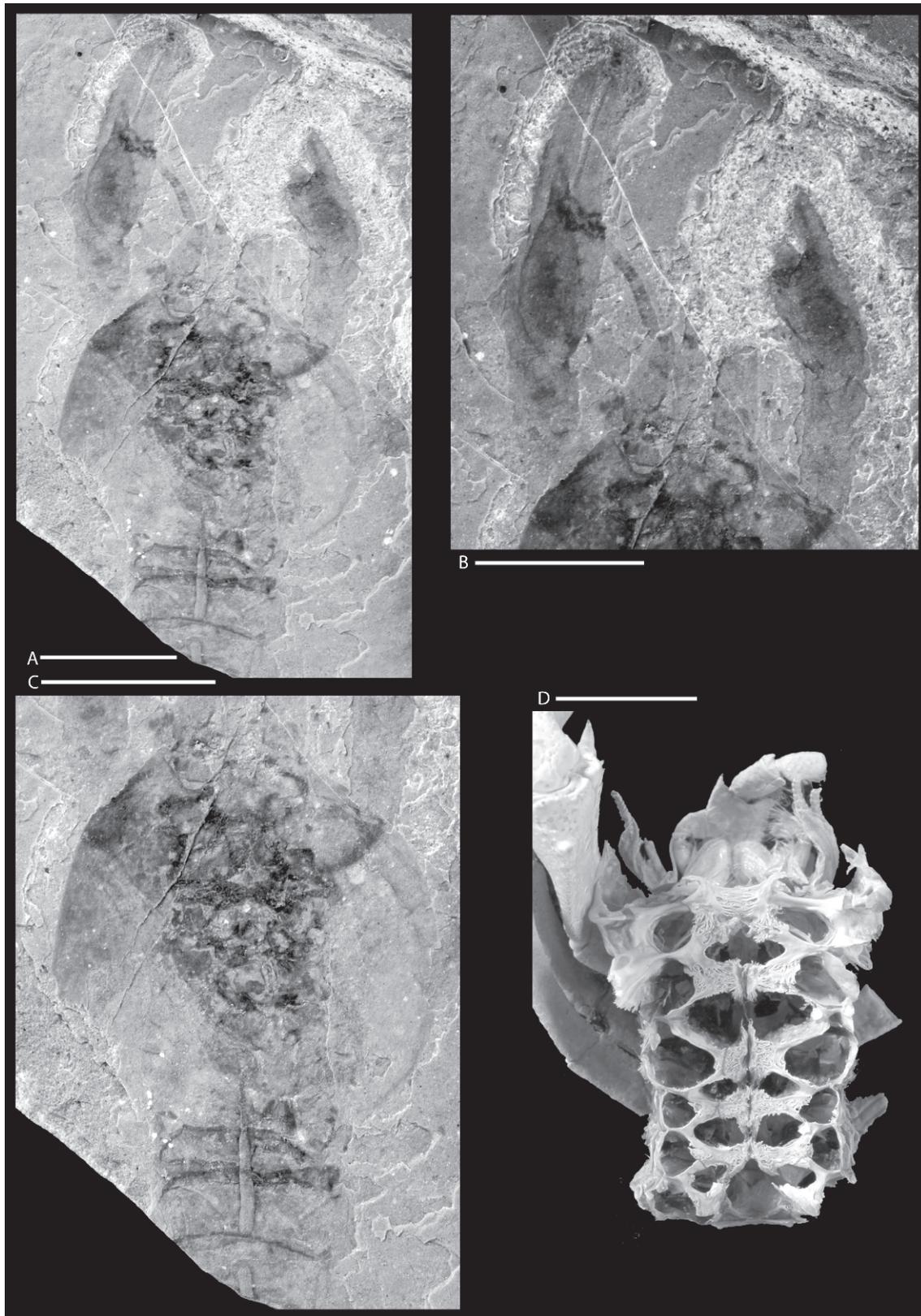


Fig. 4. A-D, *Aenigmastacus crandalli* n. gen. n. sp., paratype, TRUIPR L-018 F-1152. A, dorsal view; B, enlarged view of anterior of specimen showing preserved flexor muscle in the propodi of the first pereiopods; C, enlarged view of cephalothorax and pleonites 1-3, showing flattened, diaphanous nature of the cephalothorax, preservation of the endophragmal skeleton, and intestinal trace in the pleon; D, endophragmal skeleton of *Procamburus* sp. For comparison with that seen in 3. Scale bars = 1 cm.

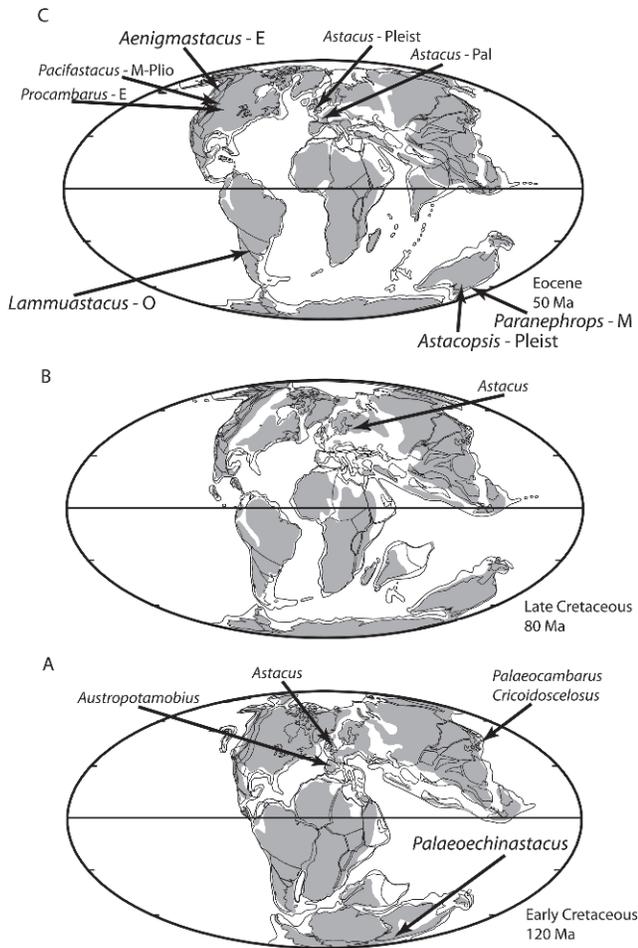


Fig. 5. A-C, Paleogeographic maps depicting the distribution of genera of crayfish. A, Early Cretaceous; B, Late Cretaceous; C, Eocene. Genera within the Parastacoidea are indicated in large, bold print. Taxa of varying ages are depicted on the Eocene map. E = Eocene, M = Miocene, O = Oligocene, Pal = Paleocene, Pleist = Pleistocene, Plio = Pliocene. Maps from Scotese (2006).

on both uropodal exopods quite clearly, but the structure is not to be seen on the telson.

Other features diagnostic of Parastacoidea include presence of a prominent hook on the carpus of the first pereopod coupled with the inner surface of the propodus being longer than the dactylus (Souty-Grosset et al., 2006). Although the presence of a hook is subtle, the dimensions of the cheliped on the new taxon are clear. As with other characters, the dimensions of the chelipeds within Parastacoidea are not without exception. Whereas the inner surface of the propodus is longer than the dactylus in *Cherax* Erichson, 1846 (Souty-Grosset et al., 2006) and in *Paranephrops* White, 1842 (Feldmann and Pole, 1994), the relationship is variable in species of *Euastacus* Clark, 1936 (Morgan, 1997). Based upon a variety of observations, it may be more precise to say that the inner margin of the propodus is always less than the length of the dactylus in Astacoidea. Coupled with the absence of the diaeresis, the attributes of the cheliped morphology strongly support placement within Parastacoidea.

The lack of the diaeresis on *Aenigmastacus crandalli* is even more perplexing when considering the geographic

distribution of the two superfamilies. All other Parastacoidea, lacking a diaeresis, are exclusively Southern Hemisphere forms (Fig. 5). Thus, *A. crandalli* is the sole crayfish from the Northern Hemisphere to exhibit this morphology. As a result, this new occurrence in British Columbia poses a unique paleobiogeographic challenge. It is possible that the absence of a diaeresis on the telson of *A. crandalli* represents a homoplastic character representing loss of the diaeresis on the telson in the astacoid lineage. This possibility would solve the paleobiogeographic dilemma. However, the absence of the diaeresis coupled with the morphology of the chelipeds provides convincing evidence that the specimen is a parastacoid.

The interpretation that the specimens are parastacooids would most likely require a chance dispersal from the Southern Hemisphere to the Northern Hemisphere. This is conceivable when one considers a route through eastern Asia. Several elements in the McAbee biota have Asian affinities, including *Ginkgo* Linnaeus, 1771 (Mustoe, 2002), other floral elements (Greenwood et al., 2005), and insects (Archibald, 2005). A dispersal pathway from the Southern Hemisphere through eastern Asia is, therefore, a possibility, perhaps in the Late Cretaceous or the Paleogene. One potential problem in postulating this dispersal pattern is that extant crayfish are limited in their distribution to temperate climates; they do not live in low altitude, low latitude sites (Keith Crandall, personal communication to RMF, 8/2010). This limitation would render this interpretation somewhat tenuous.

Schram (2001) noted that the disjunct distributions reflected by extant crayfish could be partially resolved by considering an interpretation of their historical biogeography. Based upon evidence from the trace fossil record (Kowalewski et al., 1998; Hasiotis, 1999), he postulated an origin for crayfish perhaps as early as late Paleozoic. He plotted the current distributions of the group on a Triassic paleogeographic map and suggested that the origin of Cambaridae was in the tropical and subtropical Northern Hemisphere and that of Astacidae was in the subtropical and temperate region of that hemisphere. Parastacoidea remained Gondwanan. This interpretation demands that the early history of crayfish was in low latitude regions and suggests that subsequent development of Astacidae and Cambaridae resulted in adaptation to temperate regimes and excluded them from the tropics. His reconstruction does not fully resolve the disjunct distributions observed today, nor does it provide any resolution to the introduction of a single parastacoid into the Northern Hemisphere.

Because the interpretation of trace makers is problematic, we have confined our interpretation of crayfish history and biogeography to confirmed body fossils. The oldest records of crayfish are either Late Jurassic or Early Cretaceous. *Cricoidoscelosus* was originally described as Late Jurassic (Taylor et al., 1999), but recent work on the Jehol Formation in China has confirmed an early Cretaceous age (Chang et al., 2009). Vía (1971) described *Astacus llopsi* from Spain. The unit from which it was collected has an unresolved Late Jurassic or Early Cretaceous age. Plotting the distribution of known fossils on paleogeographic maps of appropriate age (Fig. 5)

Table 1. Families, genera, and species of Astacoidea and Parastacoidea, indicating their stratigraphic ranges and geographic locations.

Family	Genus	Species	Range	Locality
Astacidae	<i>Astacus</i> Fabricius, 1775	<i>A. edwardsi</i> van Straelen, 1928 <i>A. laevis</i> Fritsch and Kafka, 1887 <i>A. multicaevatus</i> Bell, 1863 <i>A. pallipes</i> Lereboullet, 1858 <i>A. lavellopsi</i> Vía, 1971 <i>P. chenerma</i> (Cope, 1871)	Late Jurassic – Holocene Early Cretaceous – Holocene Paleocene Late Cretaceous (Cenomanian) Early Cretaceous (Berriasian – Hauterivian) Pleistocene – Holocene Late Jurassic (Kimmeridgian – Tithonian) Late Jurassic (Kimmeridgian – Tithonian)	France Czech Republic England England Spain United States (Idaho)
Cambaridae Hobbs, 1942	<i>Pacifastacus</i> Bott, 1950 <i>Palaecambarus</i> Taylor, Schram, and Yan-Bin, 1999 <i>Procambarus</i> Ortmann, 1905	<i>P. licenti</i> (Van Straelen, 1928) <i>P. primaeus</i> (Packard, 1880)	Miocene – Pliocene Early Cretaceous– Holocene Early Cretaceous Early Cretaceous Eocene– Holocene Eocene Early Cretaceous	China China United States (Wyoming) United States (Wyoming) China
Cricoidoscelosidae Taylor, Schram, and Shen, 1999	<i>Cricoidoscelosus</i> Taylor, Schram, and Shen, 1999	<i>C. aethus</i> Taylor, Schram, and Shen, 1999	Early Cretaceous Early Cretaceous	China China
Parastacidae Huxley, 1879	<i>Aenigmastacus</i> Feldmann, Schweitzer, and Leahy, herein <i>Astacopsis</i> Huxley, 1879 <i>Lammustacus</i> Aguirre-Urreta, 1992 <i>Palaecoehchinastacus</i> Martin et al., 2008 <i>Paranephrops</i> White, 1842	Parastacoidea Huxley, 1879 <i>A. crandalli</i> Feldmann, Schweitzer, and Leahy, herein <i>A. franklini</i> Gray, 1845 <i>L. longirostris</i> Aguirre-Urreta, 1992 <i>P. australianus</i> Martin et al., 2008 <i>P. fordycei</i> Feldmann and Pole, 1994	Early Cretaceous – Holocene Eocene Eocene Pleistocene – Holocene Pleistocene – Holocene Oligocene Oligocene Early Cretaceous (Albian) Early Cretaceous (Albian) Miocene – Holocene Miocene	Canada (British Columbia) Canada (British Columbia) Australia Australia Argentina Argentina Australia Australia Australia New Zealand New Zealand

indicates that, at least as far back as the Early Cretaceous, the groups are confined to temperate zones, much as they are today. Examination of the Eocene paleogeography suggests two possible dispersal routes that might be considered. A pathway from South America along the western margin of the Americas is possible; however, the only fossil record on that continent is Oligocene. A route through eastern Asia in the Late Cretaceous or early Paleogene is more likely. As discussed above, several other elements of the McAbee biota have Asian affinities as do plants in the Eocene Florissant Formation in Colorado (Leopold et al., 2008) and land mammals (Rose, 2006). Neither of these routes resolves the transition across the tropics, however.

An additional factor that makes interpretation of the paleobiogeographic distribution enigmatic is the paucity of the fossil record of crayfish in general. Attempting to outline global distribution patterns in the fossil record will remain highly speculative until and unless more discoveries are forthcoming.

Taphonomy

Examination of one of the specimens (1147) using scanning electron microscopy and energy dispersive X-ray indicates that the matrix is largely siliceous with some associated clay minerals. The traces of carapace have the same composition as the surrounding matrix and are interpreted to be impressions. The dark material within the fossils is fluorapatite. The composition of this material is perhaps not surprising because apatite in one form or another has been observed in decapod fossils from other sites (Bishop, 1986 for example). Two areas of this dark material are of particular note. The claws on two specimens, 1146 and 1152, have dark areas within the manus of the propodus. The form of this "shadow" is particularly striking in the left claw of specimen 1152 in which it assumes the form of the large flexor muscle used to close the dactylus onto the fixed finger. Thus, it appears that some of the soft tissue of the animal was preserved. Similarly, dark regions within the area of the cephalothorax are arrayed in a crossed pattern that is reminiscent of the dorsal surface of the internal (endophragmal) skeleton. Comparison of that pattern of darkened material with the endophragmal skeleton of an extant crayfish (*Procambarus* sp.) confirms the similarity. Using the shadow of muscles in the proximal elements of the first pereopod it is possible to identify the precise thoracic segments present (Figs. 4A, B). Dark shadows in the pleon of 1146 and 1151 may also represent muscle bundles responsible for flexing and extending the pleon.

Another unusual preservational aspect of these specimens is the presence of a sediment-filled trace of the intestinal tract through the length of the pleon in 1143, 1144, 1146, 1149, and 1152. The structure is visible because the cuticle is extremely thin and the intestine is filled with sediment.

Paleoecology

The environment in which the crayfish lived was rich in silica, given that the primary original constituent was

diatoms (Mustoe, 2005) and the EDS analysis of the sediment yielded almost all silica with a small component of a clay mineral, possibly smectite. Mustoe (2005) pointed out that for a fresh water diatomite to accumulate, it is necessary that terrigenous sediments are absent and that water conditions are calm. These conditions are confirmed herein based upon the EDS analyses and the observed fine, uniform laminations of the sediment. This suggests that the body of water was sufficiently devoid of a terrigenous source to permit this type of sediment accumulation. Mustoe (personal communication to RMF 5/2010) pointed out that, although the absence of terrigenous sediment and accumulation of diatomaceous sediments is often taken to indicate deep water, offshore conditions, that need not be the case. He noted that the essential conditions for formation of diatomaceous sediment were an abundance of silica and an absence of terrigenous sediment. These conditions exist, for example, in the shallow lakes within Yellowstone National Park (Mustoe personal communication to RMF 5/2010). Water temperature has not been determined by isotopic analysis; however, the presence of thin dark and light colored rhythmites may suggest seasonal fluctuation and possibly a frozen surface layer. Alternatively, the light layers may represent periodic settling of diatomaceous mats.

Preservational style of the fish in the same sediments that contain the crayfish led Mustoe (2005) to conclude that the bottom conditions were anoxic, a conclusion that would be consistent with the preservational style of the crayfish. Soft-tissue preservation in both fish and crayfish would be highly unlikely in a highly oxygenated environment. Whether the water column was anoxic or whether the sediment and a thin layer of water above it was anoxic is not currently known. However, the crayfish could not tolerate anoxic conditions, yet they were probably not transported a great distance from where they lived to where they were buried. Nearly all the specimens are fully articulated and, because the cuticle is so thin and fragile, it is unlikely that they could have tolerated significant transport. Thus, the presence of the crayfish suggests that anoxia was limited to the sediment-water interface. The environment was likely depleted in CaO so that precipitation of CaCO₃ within the cuticle would be limited.

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