LYREIDUS ALSEANUS RATHBUN FROM THE PALEOGENE OF WASHINGTON AND OREGON, U.S.A.

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ABSTRACT

Forty-four specimens of Lyreidus alseanus Rathbun, collected from deep water, offshore, Eocene to Oligocene rocks at ten localities in western Washington and Oregon, provide the first corroboration of the validity of this species. The species can be referred to the L. channeri group extending the geographic range of this, the most broadly distributed, species group within the genus. The occurrence of Lyreidus in deep water settings in the Eocene tends to suggest that the genus, which first evolved in shallow water habitats, rapidly radiated into deep water environments.

INTRODUCTION

Lyreidus is an extant genus of raninid crab that has recently been the subject of a comprehensive study (Griffin, 1970). However, no attempt was made by Griffin to investigate the fossil record of the group. As a result of extensive collecting of Eocene decapods from Antarctica, Feldmann and Zinsmeister (1984) described a new species, Lyreidus antarcticus, and summarized information available on fossil representatives of the genus. One pattern that seemed to be well documented was that the genus evolved in high southern latitudes, probably in a high energy, shallow water habitat and, subsequently, radiated into the deeper water, offshore environments typical of the living species. The earliest occurrences of the genus are from Eocene rocks of Antarctica (Feldmann and Zinsmeister, 1984; Feldmann and Wilson, 1988) and New Zealand (Glaessner, 1960, 1980). Living species occupy a variety of sites in the Indo-Pacific region and one species, Lyreidus nitidus (A. Milne-Edwards) (=L. bairdii) is known from the North Atlantic and Caribbean (Griffin, 1970; Goeke, 1985).

Fossil representatives of the genus have been collected at only a few sites in the northern hemisphere. The only two European species, Lyreidus hungaricus Beurlen and L. parona Crema, from Oligocene and Miocene rocks, respectively, are documented by few, moderately well-preserved specimens. Two species, L. fastigatus Rathbun (1919) and L. alseanus Rathbun (1932), have been described from Oligocene rocks in North America. The former, from the West Indies, is represented by a poorly preserved claw and the latter, from Oregon, was based upon a badly distorted, partial cephalothorax (Fig. 1). Feldmann and Zinsmeister (1984) concluded that this material was inadequate to confirm the generic assignment. Thus, until now there have been no well documented occurrences of Lyreidus from North America.

The purposes of this paper are to establish clearly that Lyreidus alseanus is, in fact, referable to that genus and to expand upon the description of the species. Because L. alseanus has now been collected at ten localities, it is also possible to

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Fig. 1.—*Lyreidus alseanus* Rathbun, holotype, USNM 371901. Part and counterpart of sole specimen upon which the original description was based. Scale bar equals 1 cm.

Fig. 2.—Map showing sites in Washington and Oregon, northwestern U.S.A., from which *Lyreidus alseanus* has been collected. The numbered sites are described within the text. The site labelled “T” is the type locality, as described in Rathbun (1932).
describe the range of stratigraphical and paleoecological settings in which it lived and to confirm its systematic assignment.

Miss Rathbun originally based the species upon a crushed, distorted, part and counterpart of the anterior portion of the cephalothorax of one individual. Her assignment of the specimen to *Lyreidus* must have been based on the relatively narrow front, and possession of anterolateral spines, which she described (1932: 240) as, “broad, curving forward.” Having carefully examined this specimen several times, I remain convinced that, given only this specimen, it would be nearly impossible to assign this specimen to *Lyreidus* or even to the Raninidae. Within the past several years, additional collecting in the type area, as well as in other fossiliferous localities in Oregon and Washington (Fig. 2), has resulted in the acquisition of 44 specimens which are assignable to *Lyreidus alseanus*. The style of preservation and the manner of fragmentation of some of the specimens is so similar to that of the type specimen that there is little doubt of the association of them with the type specimen.

**Systematic Paleontology**

*Order Decapoda Latreille, 1803*
*Infraorder Brachyura Latreille, 1803*
*Section Podotremata Guinot, 1978*
*Subsection Archeobrachyura Guinot, 1978*
*Superfamily Raninoidea de Haan, 1839*
*Family Raninidae de Haan, 1839*
*Genus Lyreidus de Haan, 1830*

*Lyreidus alseanus* Rathbun, 1932

Figs. 1.1, 1.2, 3.1-3.8, 4.1, 4.2

**Diagnosis.**—Raninid with tridentate frontoorbital margin; fusiform carapace outline; hypertrophied, straight, slender, lateral spines; and sinuous anterolateral margin with small spine.

**Description.**—Moderate sized raninid, largest individual with carapace length exceeding 40 mm, greatest width about 60 percent carapace length, narrow front, two pairs anterolateral spines, posteriormost pair hypertrophied and elongate, hexagonal, longitudinally and transversely vaulted carapace. Front narrow, attenuated, about 45 percent maximum carapace width in smaller individuals to about 40 percent maximum width in larger ones, tridentate. Rostrum triangular, about 1½ times as long as wide, subtly sulcate axially, with narrow, well defined rim; postorbital spines parallel or slightly divergent anteriorly, narrow, as long as rostrum; orbits smooth concave arcs interrupted by two fissures abaxial to deepest part of orbits, outermost fissure subtle, at base of postorbital spine, innermost fissure deeper, with depressed margin on some specimens. Anterolateral margin sinuous with protuberant area, developed as small spine or as broadly swollen area, located posterior to midlength, and hypertrophied straight or slightly curved spine at posterior end of anterolateral margin forming about 50° angle with midline of carapace. Lateral margins comprised of two nearly straight elements, anteriormost portion shorter, straight, slightly convergent posteriorly with maximum carapace width developed at anterolateral corner just posterior to spine base; posteriormost portion slightly concave, convergent toward well defined posterolateral corner. Posterior margin narrower than or about equal in width to frontal width, slightly concave. Posterior and posterolateral margins with narrow, well defined, beaded rim. Dorsal surface of carapace generally smooth, axial regions elevated above carapace level, widest in cardiac region, becoming narrower in intestinal region. Branchiocardiac grooves arcuate, well defined, broadest and deepest anteriorly, converging toward axis at midlength and diverging posteriorly. Metabranchial region slightly less elevated than remainder of branchial area. Surface of carapace with setal pits, coarsest laterally and axially.

Buccal frame longer than wide, widest at midlength, poorly preserved. Sternum (Figs. 3.8, 4.2) poorly exposed, documented by partial mold of interior, conforming to form of sterna of other species within genus, anterolateral corners appear to be acute.
Abdomen unknown.

Chelipeds robust, compressed, carpus elongate, widest at carpus-propodus joint, with single prominent spine on upper surface near distal end; propodus widening distally, with three spines on inner surface, distal two about equal in size, prominent, about 33 percent length of fixed finger, proximal spine smaller; fixed finger deflected from axis of propodus with occlusal surface forming angle of about 82° with axis of hand. Dactylus elongate with arcuate upper surface, compressed, bordered by setal pits. Denticles varying in size, but generally triangular, forming serrated occlusal edges; tip of dactylus closing inside tip of fixed fingers. Pereiopods known only from slender, long fragments with nearly circular cross sections.

Measurements.—Measurements, in millimeters, are given in Table 1. Orientation of measurements is illustrated in Fig. 4.1.

Studied specimens.—Fifteen specimens, USNM 431289–431303, are deposited in the U.S. National Museum of Natural History. Twenty-six additional speci-
mens, CM 35530-35555, are curated in the collection of The Carnegie Museum of Natural History.

Localities and stratigraphic positions.—Specimens of *Lyreidus alseanus* were collected from localities listed below. At the end of each locality description, initials and numbers denote the collectors: RB = Ross Berglund, JLG = James Goedert, GP = Guy Pierson. Finally, catalogue numbers are given for specimens collected from each of the localities.

1. Hoko River Formation, Eocene, N.W. tip of the Olympic Peninsula, on a ridge-top exposure of “muddy-matrix” breccia adjoining the Neah Bay village sanitary disposal site, several hundred meters inland from the south shore of the Strait of Juan de Fuca, SW½, NW¼, Sec. 4, T33N, R15W, Cape Flattery 15’ Quadrangle, Clallam County, Washington. RB-32. USNM 431289.


3. Hoko River Formation?, Eocene, thin-bedded siltstones exposed in high bluffs along the Burnt Mountain road north of Beaver Lake, NW¼, SW¼, Sec. 35, T31N, R12W, Pysht 15’ Quadrangle, Clallam County, Washington. Gower (1960) mapped these rocks as part of the lower member of the Twin River Formation. RB-45. USNM 431291.
Table 1. —Measurements, in cm, taken on specimens of Lyreidus alseanus. The position and orientation of measurements is illustrated in Figure 4.1.

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1 Width determined by doubling measurement made from midline.

4. “Unit B.” Eocene, tuffaceous siltstone in a westercly-facing cut on an extension of the Fish-Hatchery road ca. 400 m east and 530 m south of NW Cor., Sec. 33, in SW¼, NW¼, Sec. 33, T11N, R7W, Grays River 15’ Quadrangle, S. E. Pacific County, Washington. Wolfe and McKee (1968) considered these rocks to be “Unit B” and assigned a late Eocene, lower Refugian age. RB-48. USNM 431292.

5. Makah Formation. Oligocene (Refugian), northern side of the Olympic Peninsula, along the Strait of Juan de Fuca, siltstones exposed along bluffs and intertidal zone, between the mouth of the Lyre River and Whiskey Creek, in loose beach rubble, NW¼, NE¼ Sec. 26, T31N, R9W, Disque 7.5’ Quadrangle, Clallam County, Washington. Brown, et al. (1960) and Tabor and Cady (1978) mapped the rocks as part of the Makah Formation. RB-67. USNM 431293 and CM 35530-35541.

6. “Unit B.” Eocene, stream-cut exposure of tuffaceous siltstone in west bank of Grays River, 1275 m north of SW Cor., Sec. 33 and in NW¼ Sec. 33, T11N, R7W, Grays River 15’ Quadrangle, S. E. Pacific County, Washington. Wolfe and McKee (1968) assigned the “Unit B” designation. RB-72. USNM 431294 and 431295 and CM 35542-35545.

7. “Unit B.” Eocene, well-indurated marine tuffaceous siltstone in a small quarry in Grays River Valley, approximately 50 m east and 600 m north of SW Cor., Sec. 3, in NW¼, SW¼, Sec. 3, T10N, R7W, Grays River 15’ Quadrangle, Wahkiakum County, Washington. Designated “Unit B” and assigned late Eocene, lower Refugian age by Wolfe and McKee (1968). RB-79. USNM 431296 and CM 35546-35548.

8. Nestucca Formation, roadcut exposure of badly weathered shales and siltstones, ca. 530 m south and 100 m east of NW Cor., Sec. 9, T13S, R11W, Waldport 15’ Quadrangle, Lincoln County, Oregon. Mapped as Alsea Formation (Snively et al., 1975). JLG-223, RB-84, GP. USNM 431297-431300 and CM 35549-35555.

9. Nestucca Formation, badly weathered shale, in badly slumped and poorly exposed roadcut ca. 300 m south and 280 m east of NW Cor., Sec. 9, T13S, R11W, Waldport 15’ Quadrangle, Lincoln Co, Oregon. See comment on 8. JLG-224. USNM 431301.

10. Nestucca Formation, shale exposed at low tide on northeast side of mouth of Salmon River and ca. 100 m north of mouth of Teal Creek, SW¼, Sec. 14, T6S, R11W. Hebo 15’ Quadrangle, Tillamook County, Oregon. JLG-226 and JLG-227 (float from beach in vicinity of JLG-226), GP. USNM 431302 and 431303 and two specimens at KSU.

Remarks.—Fossil raninids frequently can be assigned to extant genera even though the latter have been defined on the basis of a combination of characters with highly variable preservation potential. In fact, the outline of the frontoorbital margin, the general conformation of the carapace, and the morphology of the sternum are extremely useful characters in making generic assignments. These
morphological characters are frequently available for study in fossil forms. *Lyreidus* is characterized by a narrow fronto-orbital margin which typically is attenuated and defined laterally by postorbital spines of approximately the same length as the triangular rostrum. Supraorbital fissures tend to be weakly incised and narrow. The carapace surface is generally smooth and vaulted and the overall fusiform outline of the carapace tends to be more slender than species in most other genera. This elongation is also reflected in the long, generally slender outline of the sternum. In all these regards, *Lyreidus alseanus* conforms closely to the generic descriptors.

The only named genus with which confusion might arise is *Lysirude* Goeke, 1985. This taxon was named to embrace two species previously assigned to *Lyreidus*, *Lyreidus nitidus* (A. Milne-Edwards, 1880) (=Raninoides nitidus = *Lyreidus bairdii*) and *Lyreidus channeri* Wood-Mason (1895), and a species named by Goeke, *Lysirude griffini*. The distinguishing characters selected by Goeke (1985:214) to characterize the new genus include the presence of a granular anterolateral margin with a weakly developed spine and possession of a strongly lobate propodus and dactylus on pereiopod 4. However, these characters commonly would be used to make distinctions between taxa at the species, not the genus, level. Therefore, it appears prudent to consider *Lysirude* a junior, subjective synonym of *Lyreidus* until such time as biological material of all relevant species can be examined.

*Lyreidus* has been subdivided into three species groups based upon the relative development of spines in the anterolateral region (Glaessner, 1960; Griffin, 1970). The *L. tridentatus* group, including that species and *L. brevifrons*, comprise species...
with a single spine at the anterolateral corner. The *L. stenops* group, comprising only that species, lacks lateral spines altogether. The third group, *L. channeri* group, includes that species, *L. nitidus*, and *L. griffini* and is distinguished by having a strong lateral spine and a sinuous anterolateral margin with a medial protuberance sometimes developed into a spine. Only the *L. stenops* group lacks a fossil record (Feldmann and Zinsmeister, 1984).

*Lyreidus alseanus* must be placed within the *L. channeri* group. The anterolateral margin of *L. alseanus* is sinuous, possesses a hypertrophied lateral spine, and has a weakly developed spine at midlength along the anterolateral margin. Indeed, *Lyreidus alseanus* is morphologically closely related to *L. channeri* (Fig. 5). The outlines of the carapaces of the two species illustrate only subtle differences. The postorbital spines of *L. alseanus* are about as long as the elongate rostrum. Those spines on *L. channeri* tend to be somewhat longer than the rostrum (Griffin, 1970) but the rostrum of this species is perhaps not as attenuated. The lateral spines of the former tend to be longer, more delicate, and straighter than those of the latter and the posterior margin of *L. alseanus* is, perhaps, somewhat broader. The chelipeds of the two species do differ substantially, however. *Lyreidus alseanus* has claws with three spines along the lower (inner) surface, of which the distal two are long, slender, and nearly equal in size. The proximal spine is reduced. The spines on the lower margin of the propodus of *L. channeri* also number three, but the distal one is stout and substantially larger than the other two (Griffin, 1970). No spines are found on the upper (outer) margin of either species. Distinctions in claw morphology have been used successfully as one point of distinction between species within this genus. Thus, *L. alseanus* is similar to, but can be distinguished from, *L. channeri*.

Two other fossil species are referable to the *Lyreidus channeri* group. *Lyreidus waitakiensis* Glaessner (1980), occurs in Eocene rocks of South Island, New Zealand, and *L. hungaricus* occurs in Oligocene rocks of Hungary. Although both of these species are characterized by the sinuous anterolateral margin, neither has the hypertrophied anterolateral spine of *L. alseanus*. Additionally, Fujiyama and Takeda (1980) described *Ranidina teshimai* from the Poronai Formation, Hokkaido, Japan. The age of the unit has been considered to be Eocene to early Miocene, but a late Oligocene age appears to be most probable (Fujiyama and Takeda, 1980:340). This species lacks the longitudinal keels that characterize the type species of *Ranidina, R. rosaliae* Bittner. However, it does bear some resemblance to *Lyreidus alseanus*. The anterolateral spines of *R. teshimai* are extremely long, the anterolateral margins are sinuous and convergent, and the front appears to be narrow and attenuated. The illustration of the sternum (Fujiyama and Takeda, 1980: Plate 40, fig. 2) is difficult to interpret but it also appears to have the general outline of sterna of *Lyreidus* spp. Thus, although it would be inappropriate to suggest that this species is synonymous with *L. alseanus* without examination of the specimens, it is possible to suggest that *R. teshimai* should probably be referred to *Lyreidus*.

The only raninids that have been described from the west coast of the United States that might be confused with *Lyreidus alseanus* are *Ranidina willapensis* Rathbun (1926) and *Eumorphocorystes naseleensis* Rathbun (1926). Both of these raninids were based upon incomplete material so that complete comparison is not possible. *Lyreidus alseanus* tends to have a more finely punctate surface than either of these species. In addition the posterolateral and posterior margin is beaded and the posterolateral spine is longer and more slender on *L. alseanus*.
than on either *E. naselensis* or *R. willapensis*. Finally, the frontal margin of *Lyreidus* spp. is consistently more delicate, with more subtle supraorbital fissures, than in other raninids. The front is not well known on *R. willapensis* and that on *E. naselensis* bears broad, deep supraorbital fissures and less prominent, curved postorbital spines. Unfortunately, the ventral surface is not visible on specimens from either of these species so that it is not possible to classify them unequivocally.

*Lyreidus channeri* has been collected from a variety of Indo-Pacific sites at depths ranging from 410 to 1030 m (Goeke, 1985). *Lyreidus nitidus*, likewise, is known from moderately deep water. This species has been collected at depths ranging from 119 to 475 m (Griffin, 1970). *Lyreidus alseanus* may, also, have been an inhabitant of bathyal depths. The estimates of depth in which the Hoko River and Makah formations, within the Twin River Group, were deposited (Snively et al., 1980). Wolfe and McKee (1972) suggested similar depositional conditions for their unit B. These same rock units have yielded other deep water organisms including foraminiferans (Wolfe and McKee, 1972; Snively et al., 1980) and isopod crustaceans (Wieder and Feldmann, 1989). This occurrence suggests that the limited record of the genus *Lyreidus* in mid-latitude settings may simply reflect lack of available rocks deposited in bathyal habitats.

The discovery of these specimens and the resulting confirmation that *Lyreidus alseanus* inhabited the Pacific coast of North America has several important biogeographic implications. It remains probable that the genus arose in the high latitude habitats of the southern hemisphere (Feldmann and Zinsmeister, 1984). This conclusion is based on the observation that the Eocene occurrences in that region are from inshore, high energy, shallow water habitats which are settings no longer exploited by *Lyreidus*. The pattern of radiation into deeper water, offshore habitats is consistent with the generalization presented by Jablonski et al. (1983). However, previously there has not been any evidence to suggest that the radiation into deep water habitats occurred as early as the Eocene. Thus, available evidence now suggests that the genus arose in shallow water habitats and rapidly expanded its habitat preference into deeper water. Subsequently, the inshore habitats were abandoned.

Finally, it is significant to note that, of the three groups of *Lyreidus* that have been defined, only representatives of the *L. channeri* group have been identified outside the Indo-Pacific region. In fact, this group spans virtually the entire range of the genus; the *L. tridentatus* and *L. stenops* groups are confined to the Indo-Pacific region. It is noteworthy that the extant members of the *L. channeri* group are the species that Goeke (1985) placed in his genus *Lysirude*.

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**Literature Cited**


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