

THE EARLY EOCENE DECAPOD CRUSTACEAN FAUNA OF THE LOOKINGGLASS FORMATION, OREGON

By Eric Paul Gustafson





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ABSTRACT

The Tenmile Member of the Lookingglass Formation (Lower Eocene) of southwest Oregon produces a diverse marine invertebrate fossil fauna including at least eleven genera of decapod crustaceans. This is the earliest Cenozoic crab fauna known from the Pacific Northwest, and is one of the earliest on the west coast of North America. The fossiliferous sediments are generally fine-grained mudstones without much compaction, with evidence suggesting a low-energy environment in relatively shallow water and a mild warm climate. The abundance of complete crabs at some localities is exceptional, and suggests repeated mass mortality caused by environmental conditions. Modern relatives of several of the taxa are burrowers. The fossils are often well-preserved in concretions. Preservation in concretions preferentially involves decaying crab corpses; other taxonomic groups are underrepresented in concretions. The fauna includes an unusual number of raninid crabs, in three genera (Raninoides vaderensis, Rogueus orri, and Doraranina manleyi) of which the latter two genera are only known from this formation. A scyllarid, Llajassus caesius, is one of a very few of this group known as fossils. Dominant in numbers is the euryplacid crab Orbitoplax weaveri, with specimens numbering in the thousands. Other crustaceans include the ghost shrimp *Ctenocheles hokoensis, Panopeus baldwini* (the largest crab in the fauna), Eriosachila orri, Palaeopinnixa rathbunae, and rare examples of Archaeozius occidentalis and Marycarcinus hannae. The abundance of specimens allows examination of several taxa as populations rather than individuals as is frequently the case in fossil crabs.

INTRODUCTION

The decapod crustacean fauna of the Lookingglass Formation was most recently summarized by Feldmann and Schweitzer (2017) and by Gustafson et al. (2019). The present study includes added taxa, illustrates additional specimens and adds population studies, emphasizing variation within populations and between collecting localities (Table 1; Figure 5).

The decapod fauna of the Tenmile Member of the Lookingglass Formation is one of the best documented of its type in Oregon. Early collections were made by Orr and Kooser (1971) and Kooser and Orr (1973). Collecting for this study from localities in the Agness area in Curry County, Oregon began in 1991. Further specimens in the University of Oregon's collections come from Lookingglass Formation outcrops near Glide, Camas Valley and Dora (Fig. 1, 2). All of these localities are late early Eocene (Ypresian) in age, about 50 million years old. Previous descriptions of the decapod fauna are scattered, so this work attempts to present this set of taxa as an integrated group. The total of nine genera and species makes it the second most abundant in Oregon, second only to the decapod fauna of the Eugene Formation, which has fourteen taxa. The total number of concretions collected so far is in the thousands; however only a few of them have been properly prepared out of the matrix. A partial description of the associated invertebrate fauna is included, along with interpretation of the paleoenvironment. The author's collection and specimens collected by several other donors have been curated in the Condon Museum of the University of Oregon, a division of the U.O. Museum of Natural and Cultural History.

METHODS

Collections from the Agness area were made by the author and others primarily by harvesting concretions which naturally weathered out of cliff exposures and were concentrated along the base of the exposures, most commonly along the shoulder of an adjacent road. On occasion, blocks of matrix fell to the base of the exposure; these were examined in detail and identifiable fossils collected. The primary locality producing previously-described fossils, UO 2594, has been picked over by both professional and amateur collectors to the point where I could not be confident in the statistics of that fauna, so it was not considered in analysis. Fossils in the Glide and Dora areas are largely found in stream-bed exposures, also preserved in concretions. Measurements of fossils were made with CE digital calipers, potentially accurate to within 0.01 mm, however, in practice, rarely is a measurement to better than a tenth of a millimeter useful. Variations in preservation, distortion caused by compression or breakage, variations in the shape of spines, and interference by adhering matrix greatly inhibit the achievable precision and accuracy of measurements. However, in several cases, measurements taken from a large sample set fairly accurately portray the variation of certain populations.

Abbreviations: CL= carapace length, CW=carapace width, UO= prefix of University of Oregon localty number, F=prefix of University of Oregon fossil specimen number, CM=Carnegie Museum, Pittsburgh, PA., UOMNCH=University of Oregon Museum of Natural and Cultural History (Condon Collection), USNM=United States National Museum of Natural History, UWBM=University of Washington Burke Museum; Ma=millions of years

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LOOKINGGLASS FORMATION GEOLOGICAL SETTING

The Eocene geology of southwest Oregon was mapped by Diller (1898), who described these Paleogene sedimentary units as the Umpqua Formation. Various workers further established regional age relationships within the Umpqua sediments, particularly Turner (1938), who described several sections and the molluscan paleontology of the area. Much of the more recent geological study of the Eocene sediments in southeastern Oregon (Fig, 1) was done by Ewart Baldwin (Baldwin and Beaulieu, 1973; Baldwin, 1974, 1975). These authors divided Eocene sedimentary rocks in the southern Coast Range area, previously included in the Umpqua Formation, into several smaller formations at significant unconformities. Formations which now comprise the Umpgua Group (Thoms, 1975) include the Roseburg Formation, the Lookingglass Formation, and the Flournoy Formation. Those sediments producing fossils used in this study are assigned to the Eocene Lookingglass Formation.

The Lookingglass Formation unconformably overlies the Roseburg Formation and other older sediments, much of which are composed of accreted terranes on a basaltic basement (Siletzia terrane of Wells et al., 2014) and which show much more deformation. Baldwin (1974) described three members in the Lookingglass Formation; a basal conglomerate called the Bushnell Rock Member, sandstones and siltstones of the Tenmile Member, and the overlying conglomeratic Olalla Creek Member. The type area for the Lookingglass Formation is near Lookingglass, southwest of Roseburg (Fig. 2).

In the area of Agness, at the southern end of the synclinal structure which encompasses the Eocene sediments of the Coast Range, the Eocene sediments are bounded by a major fault on their west side, which divides the Tertiary rocks from pre-Cenozoic sedimentary and metamorphic rocks (Ahmad, 1986). Other faults mapped by Ahmad lie on the east side of the exposures and within the Lookingglass Formation. The Bushnell Rock Member is widely exposed at the base of the section. It forms the majority of the thickness of the Lookingglass sediments here (ca. 730 meters out of ca. 970 m total) by Ahmad's measurements. The Tenmile Member is exposed along the Rogue River and in the valleys of Snout Creek and Shasta Costa Creek, both of which flow into the Rogue River east of Agness, just north of its confluence with the Illinois River. Some exposures



Figure 1. *Left,* Suggested paleogeography of Lookingglass embayment during Tenmile time (from Ahmad, 1986). *Right,* Geological map of Eocene marine sediments (Umpqua Group and Tyee Formation) and sequence of formations in the Oregon Coast Range (from Miles, 1981).

near Illahee and along the road north to Powers (and other areas north and east) show a complex of presumed turbidite sandstones and siltstones (pers. obs.). At the fossil localities east of Agness, the sandstones are absent, and the exposures of the Tenmile Member are essentially all siltstone.

Heavy vegetation and weathering prevents accurate measurement and correlation of the several exposures. Total thickness of the Tenmile Member was estimated to be 240 meters (Ahmad, 1986). The thickest exposed section at a fossil locality (UO 4233, Fig. 3) is about 70 meters. A conglomerate bed at least 3 meters thick, apparently the upper part of the Bushnell Rock Member, defines the base of that section. Along National Forest Road NF-23 north of Shasta Costa Creek are numerous exposures of the Tenmile Member and a few exposures of a coarse conglomerate which apparently overlie the Tenmile, especially prominent in the area where faulting is mapped by Ahmad (1986), and in the slopes overlying the fossiliferous Tenmile Member at the most productive spot (UO 4234). This conglomerate appears to be the basal White Tail Ridge Member of the Flournoy Formation which caps the Lookingglass Formation. The Olallie Creek Member of the Lookingglass is absent in this area. Exposures along Snout and Shasta Costa Creeks dip gently to the west, with a prevailing north-south strike (Ahmad, 1986).

The total thickness of the Lookingglass sediments in the Agness area is only a fraction of the thickness of these deposits in the type area in the Lookingglass Valley, where total thicknesses may exceed 1500 meters (Baldwin, 1974).

AGE OF THE TENMILE MEMBER

The age of the Umpqua Group sediments has been accepted as Eocene since its first formal description by Diller (1898), though Thomas Condon had recognized Eocene fossils from the area by 1885 (McCornack, 1928; Clark, 1989). The part of the section now described as the Tenmile Member of the Lookingglass Formation has been studied most thoroughly in the section near Glide, which Turner (1938) correlated with the Eocene sediments of California based on the molluscan fauna. His evidence suggested approximate equivalence to the Capay or Domenguine stages (early to middle Eocene), with a possible faunal connection to the "upper Llajas stage" (a part of the Llajas Formation). The studies by Orr and Kooser (1971) and by Kooser and Orr (1973) and by Baldwin (1975) did not narrow the temporal uncertainty significantly.

Benthic foraminifera from the Agness area have been assigned to the upper Ulastisian to lower Penutian stages of Mallory (1959). Micropaleontological studies published by Miles (1977, 1981) concluded that sediments of the Roseburg and Lookingglass formations were deposited fairly rapidly, as the foraminiferal zonation in this part of the Umpqua Group could not be subdivided. His foraminiferal samples containing the greatest abundance and diversity suggest "the middle part of the early Eocene Epoch", assigned to Zones P7/8 of a standard planktonic foraminiferal zonation (late lower Eocene; Berggren et al., 1995), and equivalent to the Penutian stage of Mallory (1959) or the Ypresian Stage of international stratigraphic usage.

Working with a detailed paleomagnetic stratigraphic section of the Tenmile member near Glide and an additional sample from the type area near Tenmile, Prothero (2009) summarized the available data, combining paleontological work by Turner (1938) and Miles (1981) with the established paleomagnetic timescale (Berggren et al., 1995). All samples from the Lookingglass Formation showed a reversed polarity orientation. Prothero's conclusion was that "Based on Zone P8 planktonic foraminifera, Penutian benthic foraminifera, Zone NP12-CP10 nannofossils, and a Capay/Domenguine molluscan fauna, the likeliest correlation is with early Chron C22r (49.8-50.8 Ma)."

Wells et al. (2014), in a regional study of early Cenozoic continental and oceanic plate movements, concluded that the Bushnell Rock conglomerates marked the accretion of the Siletzia terrane with the North American continent at about 50.5 Ma. Subduction of the Siletzia terrane under Mesozoic



Figure 2. Map of outcrop areas of Lookingglass Formation, in black. From geologic maps by Baldwin (1973, 1974). Highways 101 and 42 and Interstate 5 shown for orientation.

rocks created the Umpqua basin along the continental margin, which allowed deposition of Umpqua Group sediments at about 50 Ma, followed soon after by continental White Tail Ridge sediments. The latter study used a combination of calcareous nannoplankton zones, paleomagnetic evidence and radiometric dates to produce a result consistent with the previous dating by Prothero (2009).

I conclude from the above evidence that the Lookingglass Formation was deposited during a transgressive-regressive tectonic event on the Oregon coast lasting at most about a million years, about 50 million years ago. The Tenmile Member was deposited during the period at which the transgression was at its peak.

Fossiliferous areas

Several areas of outcrop of the Tenmile Member have produced fossil marine faunas. For this study, which concentrates on the Condon Museum collections, only three areas, near Agness, Dora, and Glide (Fig. 2) have produced substantial samples of decapod crustaceans. Other localities, for example near Camas Valley, have produced a few specimens, and Lookingglass faunas have been reported from near Tenmile and along the Middle Fork of the Coquille River (Turner, 1938; Baldwin, 1974). Neither stratigraphic nor biostratigraphic evidence is available to place these localities in a time sequence.

Ten fossiliferous localities are reported in the area immediately east of Agness; three by Orr and Kooser (1971), one by Ahmad (1986), and the remainder in this report (Table 1). I was unable to relocate Ahmad's locality or collections, but located and collected from all of the others. Maximum distance between any two of these Agness localities is about 5.6 km (3.5 miles). Productivity of the localities varies greatly, from a few specimens to thousands. Most productive are UO 2594 (reported by Orr and Kooser), UO 4233 (Fig. 3, locality known as the Big Road Cut) and UO 4234 (locality called Rusty Rail), reported here.

Localties in the Dora area are generally not well exposed. Most specimens have come from fresh roadcuts and the bed of Steele Creek just to the west of Dora. Collections in the Condon collection were made by Vic Favier and Bob Manley.

Localities in the Glide area are in exposures along the North Fork of the Umpqua River. Turner (1938) described and mapped this area. Decapod crustacea are relatively less common here than near Agness, though the molluscan fauna, detailed by Turner, includes 87 identified species. The largest number of these species (28) were held in common with the "Upper Llajas, Rose Canyon shale, or Domenguine" of California. Microfossils from this section were examined by Thoms (1975) and Miles (1981).



Figure 3. Exposure of Tenmile Member of Lookingglass Formation at locality UO 4233. Lithology is a dark finegrained mudstone with obvious layering but no shaly parting, with numerous layers of small concretions and scattered layers with larger concretions. Vic Favier (center) gives scale.

Decapods from this area in the Condon collection were donated by Vic Favier One small roadcut in the Camas Valley area, collected at by Greg Retallack, produced a few decapod fossils.

The faunal list presented here includes taxa listed by Orr and Kooser (1971) and my preliminary identifications of specimens in collections from the Agness area. It must be noted here that, although this study has not compared in detail the non-decapod faunas of the Glide versus the Agness areas, there are some striking differences in the molluscan fauna. For example, Venericardia, common at Glide according to Turner, has not been found near Agness; instead, the large bivalves are *Crassatella*. Among gastropods, *Pseudoperissolax blakei*, a widespread species (Squires, 2015) is relatively common at two Agness localities. Turner reports it from the "Lower Umpqua" Roseburg area fauna and the overlying Tyee Formation, but not from the "Upper Umpqua" Lookingglass Formation at Glide.

Species list, Lookingglass Fm., Tenmile Member, Agness localities

Mollusca

Bivalvia *Acila decisa (Conrad) *Anomia mcgoniglensis Hanna *Crassatella cf. uvasana matthewsoni (Gabb) Crassatella dalli * Glycimeris fresnoensis Dickerson Glycimerus perrini Isocardia sp. Macrocallista sp. Mercimonia bunkeri *Nuculana gabbi (Gabb) *Ostrea sp. *Solena (Eosolen) cf. coosensis Turner * Tellina soledadensis Hanna Teredo? sp. Thracia sp.

Gastropoda

*Fusinus merriami Dickerson
*Homolopoma wattsi (Dickerson)
Latirus roseburgensis
*Mitra cretacea Gabb
*Olivella mathewsoni umpquaensis Turner

Pseudoperissolax blakei Polinices sp. Simum obliquum *Siphonalia cf. bicarinata Dickerson *Turritella buwaldana coosensis Merriam Turritella uvasana hendoni Merriam Turricula cowlitzensis *Volutocorbis oregonensis Turner Scaphopoda *Dentalium sp. Nautiloidea Eutrephoceras or Nautilus sp.

Arthropoda Decapoda

Llajassus caesius Ctenocheles hokoensis Rogueus orri Doraranina manleyi Raninoides vaderensis Marycarcinus hannae Eriosachila orri Archeozius occidentalis Panopeus baldwini Orbitoplax weaveri Palaeopinnixa rathbunae

Echinodermata

Echinoidea Schizaster sp. Annelida ?Spirorbis sp. or Rotularia? sp.

Vertebrata

Chondrichthyes Shark tooth

Osteichthyes

Fish scales

*Listed by Orr and Kooser, 1971

Preservation

The number of specimens of decapod crustaceans in the current collections far outnumbers the number of specimens of all other macrofauna and flora combined (Fig. 4). Decapod remains are scarce in many other fossil faunas. Examination of modern sediments where crabs are present suggests that complex and delicate decapod exoskeletons exposed at the sediment surface have a low probability of preservation, especially when compared to cooccurring molluscs, and a nearly complete loss of crab remains usually occurs prior to burial (Stempien, 2004). Similar rapid degradation has been observed in shrimp (Mutel et al., 2008). Once a crab is buried, however, preservation may be considerably better (Plotnik et al., 1988). The obvious conclusion is that most of the organisms were buried in life or very soon after death.

Formation of concretions

As with many exceptionally-preserved fossil faunas around the world, the formation of concretions in the Lookingglass sediments meant that delicate, complex and usually ephemeral remains could be fossilized. Conditions under which fossiliferous concretions would form were not uniform during deposition of the Lookingglass member. Only a few localities had the right conditions. The origins of such concretions have been much discussed (i.e. McCunn, 1972: Martill, 1988; Coleman, 1993; Wilson and Brett, 2012; and many others). Close examination of the many Lookingglass concretions shows features which may test hypotheses of formation. It is apparent that concretions must have formed quickly, often before normal degradation of soft tissues can have progressed very far, and therefore probably before deep burial can have happened. Modern examples showing rapid formation of concretions have occasionally been reported. Allison and Pye (1994) report concretions forming in carbon-rich marsh and tidal-flat sediments on the coast of England, with siderite and calcium carbonate cements. Wilcox (1981) described formation on concretions around fish in a polluted lake.

A recent study by Yoshida et al. (2018) elucidated the conditions in which many concretions formed. The most significant variables include sediment grain size (preferably silt or clay), presence of decaying organic matter (the result of microbial activity), presence of calcium ions in the interstitial water, and appropriate high pH. Their analysis of carbon isotopes in the concretions they studied suggest that "the



Figure 4. Relative frequency of decapod crustacea (84.6%) as opposed to all other fossil macroorganisms in Agnessarea localities (Mollusca, 8.4%; echinoids, 1.3%; plants, 1.6%; all others, 4.1%).

carbon source of concretions... are consistent with the HCO3- that precipitated as calcite being a byproduct of fatty acid decomposition... that originates in decaying organisms within concretions. Therefore the concretions have been formed by reaction between carbon supplied by the organic source and Ca2+ in the surrounding seawater-derived pore water." As the organic carbon diffuses outward, it forms a reaction front at which calcite crystallization occurs. If uninterrupted, the concretion will have a spherical shape with a sharp outer boundary. Otherwise, the shape may be controlled by the hard parts of the organism. When the supply of organic carbon runs out, the growth stops. Their estimation of formation rates indicate that many smaller concretions must have crystallized in a period of weeks at most, certainly "three to four orders of magnitude faster than previously estimated timescales" according to Yoshida. Although most fossils in small isolated concretions apparently formed around body tissue as the carbon source, accumulations of other organic material (for example, feces) may cause precipitation of CaCO3 in layers or in tubes following the shape of burrows.

The "seed" on which concretion grew was decaying organic matter, so if there is no hard material present, the concretion contains no visible fossil organism, as is the case with about three-fifths of the Lookingglass concretions. In crabs, the majority of organic carbon was inside the carapace and secondarily in the chelipeds. The observed shape of many concretions shows that the carapace was actually a barrier to concretionary growth, hence the dorsal side of the carapace and outside of chelipeds are often exposed (Fig. 7, 1-7). The amount of concretionary cement was dependent on the amount of organic carbon in the fossilized animal, and the calcium content of fluids in the surrounding sediment. Thus the concretionary material may fill a carapace, include the carapace and chelipeds with no surrounding concretion (Fig.7, 1), form a concretion barely concealing the animal, or bury the fossil deep within a thick layer of calcitecemented rock (Fig. 7, 4-7). Multiple centers of crystallization often merged, so one concretion may contain multiple fossils (Fig. 32)

Weathered concretions are common at some localities, apparently derived from the soil zone at the outcrops. These concretions retain enough porosity to allow acidic meteoric water to enter and completely remove cementing crystals, leaving mostly clay, though still retaining a fairly solid form. Weathering produces a regular sequence of color changes in the decapod exoskeleton, from black in the most mineralized specimens, to brown, to white. Fossils in the most weathered concretions are often preserved as molds, retaining excellent surface detail. The open space often accumulates iron oxides, sometimes coloring the whole concretion red. Iron carbonate (siderite) may be part of the concretionary cement. Yoshida et al. (2018) noted a concentration of iron in their sample concretions compared with surrounding sediment. Crystals of pyrite (iron sulfide) are few and very small.

Fossils are common in some layers in the Agness area Lookingglass siltstones and may be distributed throughout the sediments (Fig. 3). The most fossiliferous localities produce numerous small concretions, and are also associated with some thicker concretionary layers up to about 30 cm thickness, seldom of more than a few meters lateral extent. Few concretions contain echinoids, although Schizaster tests are fairly common otherwise. Bivalves and gastropods (and some decapods, as Fig. 7, 3) tend to be peripheral in concretions. Epibionts are absent from the decapods—there are no attached tubeworms, barnacles, or bryozoans. This suggests that carapaces were not exposed for any length of time at the surface. In the Lookingglass localities, some cylindrical concretions formed around elongated accumulations of fish scales. These are interpreted as coprolites produced by piscivorous carnivores

The most common fossiliferous concretions in the Lookingglass Formation contain decapod crustaceans, especially *Orbitoplax*. The second-most-common are raninids. Modern raninids use their elongated shape as part of a burrowing adaptation. The abundance of *Orbitoplax* suggests that they too were infaunal burrowers.

Decapod concretions in this study often are of a distinctive flattened oval shape (Fig. 7, 7), rarely attached to tubular concretions (a "bulb" form). The carapace is usually central especially when the crab is complete and bilaterally symmetrical. Orbitoplax specimens show various stages of disarticulation. 1, oval, bilaterally symmetrical, completely articulated specimens; 2, complete but partly disarticulated (Fig. 8, left), may be just carapace and chelae; 3. Associated carapace and chelae or other parts, not articulated (Fig. 8, right); 4. Isolated carapace, filled with concretionary carbonate in body cavity (Fig. 7, 1 and 2). In typical Orbitoplax concretions, chelae may be exposed or near the surface, the ends of walking legs were exposed and are typically missing. Some concretions have a "pot-belly" shape, flattened



Figure 5. Concretion shapes and cross-sections. 1a-b. F-63028, *Orbitoplax* carapace filled with matrix with concretionary cementation; 1a. dorsal (left anterior shell missing, exposing internal mold) and 1b. ventral views; 2. *Orbitoplax* carapace as center of circular concretion; 3. *Orbitoplax* carapace partially incorporated into surface of concretion grown around separate center; 4-7. Sequence showing incorporation of complete crab (all *Orbitoplax*) into progressively growing concretion; 4. F-60900 (UO 4234), Minimal concretion development, including interior of shell and attached chelae in life position; 5. F-62409 (UO 4233), Increased development of concretion outside of shell; 6. F-63289 (UO 4234), Concretion covering most of crab, only dorsal carapace and anterior surface of chelae exposed; 7. Concretion from UO 4234, complete coverage of shell, only "elbow" of cheliped exposed (arrow); 8. CAT scan sagittal section (same specimen as 7) through carapace and fingers of chela of *Orbitoplax*; 9. F-59399 (UO 4234), Complete small *Orbitoplax* centered in larger concretion; 10. F-59664 (UO 4234), typical *Orbitoplax* nearly filling ovoid concretion, with distal ends of walking legs left outside of concretionary cementation. Scale bars = 1 cm.



Figure 6. *Left*, F-66406 (UO 4233), complete *Orbitoplax* with postmortem separation of left cheliped and left eyestalk. *Right*, F-61035 (UO 4234), *Orbitoplax*, disassociated carapace, sternum and other elements, probably from moulted exoskeleton. Scale bar = 1 cm.

dorsally and rounded ventrally. Confinement of decaying matter has the effect of restricting crystallization, so that the dorsal surface of the carapace, lacking soft tissue, often remains exposed. Most of interiors are filled with sediment; although claws and legs are sometimes not sediment-filled, but crystal (calcite) filled. There is little obvious growth zonation; therefore it appears that concretionary calcite formed about the same time in the zone of decay.

Concretions formed around both exuviae (shed exoskeletons) and whole bodies. Specimens found in non-concretionary matrix may be as complete as those in concretions, are also not compressed, but are harder to collect, and the original shell is not usually preserved. *Orbitoplax* specimens were seldom compressed in concretions, most are completely 3-dimensional. The eyes are usually preserved in *Orbitoplax* but not other decapods. *Raninoides* sometimes shows a longitudinal crack, where the carapace was slightly flattened (Fig. 16, 1 and 2).

Decapod fauna

Usually relatively rare as fossils, the decapod fossil record from this and other crab-rich fossil faunas, now in the Condon Museum and other museum collections, has reached a point where studies based on populations should become more frequent. The large number of well-preserved specimens of several of the taxa should allow for very detailed analysis of anatomy and variation, studies which will require more thorough and extensive preparation of specimens than has been possible for this study. Distribution of species at Lookingglass Formation localities is shown in Table 1; the following discussion should be read in association with the table.

Orbitoplax weaveri (Rathbun, 1926) always constitutes a majority of decapod specimens in the known Lookingglass fossil localities. Specimens show a large range in size and many are relatively complete. This taxon has abundance proportions at the various localities in a range from 58% to 100% of decapods. In the Llajas Formation of California, *O. weaveri* also seems to be relatively abundant (Nyborg et al., 2008). *Orbitoplax* was widely distributed in the Eocene, from Alaska to Mexico.

Among other brachyurans, *Eriosachila orri* Schweitzer and Feldmann (2000) and *Palaeopinnixa rathbunae* Schweitzer, Feldmann, Tucker, and Berglund (2000) are relatively common, although neither accounts for more than 8% of the decapods at



Figure 7. Concretions containing multiple fossils. 1. F-62267 (UO 4233), complete *Orbitoplax* (ventral view) and *Eriosachila* carapace; 2. F-59012 (UO 4234) Concretion with *Palaeopinnixa* on top surface, small *Orbitoplax* internally, with similar orientation; 3. F-62724 (UO 4233), Concretion with two similar-sized *Orbitoplax* carapaces; 4. F-62289 (UO 4233) Concretion with two complete Orbitoplax, stacked and facing opposite directions. Scale bars = 1 cm.

any locality. Neither has been found at Glide, though *Eriosachila* occurs at Dora. *Panopeus baldwini* Kooser and Orr (1973), on the other hand, though scarce overall, is found at Glide but has not been found at Dora.

Two of the three raninids appear to be the most restricted in distribution. *Doraranina manleyi* Gustafson, Nyborg and Van Bakel (2019) has only been found at Dora. *Rogueus orri* Berglund and Feldmann (1989) has only been reported from localities in the Agness area. *Raninoides vaderensis* Rathbun (1926), the most common raninid overall, can account for 10% of decapods at certain localities, and has a range far outside the local region, having been reported from as far away as Alaska, and the genus *Raninoides* (including several species) is relatively common in West Coast Eocene faunas.

Marycarcinus hannae (Rathbun, 1926) and

Locality area:	Agness									Camas Mtn	. Dora	Glide
	Burnt Ridge Road					Bear Creek Road				1 1		
UO locality no.	4236	2592	2593	2594	4233	4243	4239	4244	4234	1592	4577	4332
Llajassus			x	x								
Ctenocheles					X				x		X	
Rogueus	x	x		x	x			x	x			
Doraranina							1				x	
Raninoides	x			x	x				x	x		
Marycarcinus.				x					x		x	
Eriosachila	x	x			x				x		x	
Archaeoziu <u>s</u>									x			
Panopeus				x	x				x			x
Orbitoplax	x	x	x	x	x	x	x	X	x	x	x	X
Palaeopinnixa	x	x			x		x		x			

TABLE 1: DECAPOD DISTRIBUTION by locality

Archaeozius occidentalis (Schweitzer, Feldmann, Tucker, and Berglund, 2000) are both extremely rare. Each is otherwise reported from very restricted localities, *Marycarcinus* from California and *Archaeozius* from Washington.

Ctenocheles hokoensis Scheitzer and Feldmann (2003) occurs at Dora and two Agness area localities, but has not been reported from Glide. It was probably a burrowing animal, but parts of the exoskeleton other than the chelae were not well mineralized. The chelae are not particularly rare, though small and easily overlooked. In most mid-Eocene and later west coast decapod faunas, the common "mud shrimp" are of the genus *Callianassa* or its close relatives. *Callianassa* has not been reported from the Lookingglass Formation.

Llajassus caesius (Squires, 2001) is a rare small slipper lobster, otherwise found only in the Llajas Formation of California.

A census of the taxa found at six localities in the Agness area (Fig. 5), which fall within a very limited geographical area, shows that in a small part of the local embayment, substantial differences in abundance can exist. In all localities, *Orbitoplax* is the most common decapod. Locality UO 4233 had the overall best diversity of taxa. The raninids *Raninoides* and *Rogueus* are found in almost equal numbers at UO 4233, but *Raninoides*, very common at locality UO 4234 and UO 4236, are outnumbered by *Rogueus* or are absent at UO 2592, UO 4239 and UO 4244. *Eriosachila*, although widely distributed, is only relatively common at UO 4233 but rare at the most productive site, UO 4234. *Palaeopinnixa* has been found at the most productive localities in numbers which seem to reflect the overall fossil abundance. *Panopeus*, which is scarce overall, is most common at two Agness localities (UO 2594 and UO 4233), and at Glide.

Correlative decapod faunas

The fauna of the Umpqua Group is older than other Eocene marine faunas of Washington and Oregon (Nesbitt, 2018). Fossiliferous early Eocene sediments are not common along the Pacific Northwest coast of North America (Prothero, 2001). Paleocene and very early Eocene decapod faunas have not been reported. The known early Eocene decapod faunas on the West Coast of North America all show considerable similarities, as the warrn-temperate to subtropical environment was extraordinarily widespread at this time (Nesbitt, 2018).

Far to the north, a small decapod fauna is reported from the Orca Group of Prince William Sound in Alaska (Tucker and Feldmann, 1990). It includes *Orbitoplax pflakeri* Tucker and Feldmann, *Branchioplax washingtoniana* Rathbun, and *Raninoides vaderensis* Rathbun. The Orca Group has been dated radiometrically as 50.5-53.5 + 1.6 Ma, placing it at about the end of the early Eocene, perhaps slightly older than the Lookingglass (Tenmile) sediments.

In Washington, the Crescent Formation on the Olympic peninsula provides the earliest available Eocene decapod fauna from that State, the decapods reported being *Orbitoplax tuckeri*, *Archaeozius occidentalis*, and *Branchioplax washingtoniana* (Squires et al., 1992, Schweitzer, 2000). The Crescent



Figure 8. CRAB TAXA; variation in abundances by locality, six Agness area localities. N=total number of specimens of all taxa (including non-decapods) from that locality. Black rectangles indicate relative abundance of each taxon (actual total numbers are indicated), except that for the two most prolific localities, the relative size of the *Orbitoplax* rectangle had to be reduced to fit the diagram.

Formation is dated as 50.5 + 1.6 Ma by Babcock et al. (1994). The Pulali Point decapod fauna (Schweitzer et al., 2000) is reported to be in a slightly younger ?Aldwell Formation directly overlying the Crescent Formation on the east side of the Olympic Peninsula. This fauna includes *Portunites macrospinus*, *Archaeozius occidentalis*, *Pulalis dunhamorum*, *Branchioplax washingtoniana*, *Palaeopinnixa rathbunae*, and four raninids, *Raninoides vaderensis*, *R. goedertorum*, *R. fulgidus* and *Macroacaena alseanus*.

The type localities of *Raninoides vaderensis* and *Palaeopinnixa rathbunae* are about a mile apart just west of Vader, Washington, in sediments mapped as the Cowlitz Formation (Weaver 1912, 1937; Nesbitt, 2018). The Cowlitz sediments are considered middle Eocene, similar in age to the Coaledo Formation of Coos County, Oregon. The Coaledo also produces *Raninoides vaderensis*, although the *Palaeopinnixa rotunda* found there differs from the species found in the Lookingglass Member.

In California, the Llajas Fm.is an onlap-offlap deposit similar to the Lookingglass, producing *Orbitoplax weaveri, Portunites insculpta, Llajassus caesius, Palaeopinnixa aff. P. rathbunae, Raninoides slaki* (Squires, 1984, 2001) and *Eonomus californianus* Nyborg, Garassino and Slak (2017).. Bottjer et al. (2012) date the Llajas Formation at 52.5 to 49.5 Ma by paleomagnetic correlation. The type specimen of *Orbitoplax weaveri,* also from California, came from Eocene sediments in Fresno County, about 180 km north of the Llajas localities.

A decapod fauna from the El Bosque Formation in Chiapas Mexico (Vega et al., 2008), is dated to the lower Eocene (about 52 Ma by strontium isotope dating). Of the fourteen genera reported, four genera also occur in the Lookingglass Formation. These are *Raninoides, Eriosachila, Panopeus* and *Orbitoplax,* though all are identified as other species than in the Lookingglass Formation.

PALEOENVIRONMENT

Decapod diversity in estuaries and bays (such as the hypothesized Umpqua embayment described below) has been investigated in a few modern geographical areas. For example, on the west coast of India, the Gulf of Khamba and mudflats of the estuary of the Mahi River were examined by Pandya and Vachhrajani (2013). Their census turned up ten brachyuran species, four of which were abundant, four solitary or occasional, and two which were rare. These numbers are roughly comparable to the abundance numbers from the Tenmile Member sediments, for a warm-climate estuary.

Comparisons with most modern bays of similar size to the Umpqua embayment are difficult for a number of reasons. Controlling factors, such as temperature, depth, and salinity, are highly variable. Accurate census data for decapod faunal lists are not common. Most taxonomic studies are heavy on anatomy and light on other aspects of biology. Modern studies tend to emphasize commercially valuable species, and recent introductions of invasive species have distorted the ecology of decapod faunas, especially in areas such as San Francisco Bay. Details of the life cycles, food and shelter, and migratory behavior are not common except with some near-shore or intertidal species.

Crabs and other decapods thrive in a huge variety of environments. In the Tenmile Member sediments, effective ecological partitioning of this local habitat (a muddy bottom) into multiple niches is indicated by the variation in size, morphology, and variations in abundance and distribution of the overall decapod fauna (Table 1, Fig. 8). Figure 9 illustrates this variation in size and shape among populations of six brachyuran taxa from the Agness area localities, indicating differentiation in adaptations. Variation in size and shape would have been accompanied by variations in behavior. Carapace proportions among burrowing raninoids, which are relatively elongate (mean CL/CW = 1.7/1 in *Raninoides*, 1.5/1 in *Rogueus*), clearly separate this group from the wider but more equidimensional carapaces of most other crabs (0.69/1 in Palaeopinnixa; 0.75/1 in Orbitoplax; 0.8/1 in Panopeus; 0.97/1 in Eriosachila). The non-raninoids show clear differentiation in size ranges, from tiny *Palaeopinnixa* to much larger Panopeus. Among raninids, all presumed to be burrowers, Rogueus averages substantially larger than Raninoides. Doraranina is similar in size to Rogueus but the two have not been found together. Presence of specialized burrowers does not mean other crabs were not burrowers (as this is one of the best ways for small, edible animals to escape predation), but that their style of hiding in the relatively featureless mud could differ. Modern raninoids frequently burrow into substrate just enough to cover their carapace and keep their eyestalks above the surface, while modern hexapods, (relatives of Palaeopinnixa) frequently. occupy the burrows or shells of other organisms. Others (e.g. Orbitoplax) have periods in which they were active on the surface, alternating with periods





in which they buried themselves in the substrate. Likewise, modern *Panopeus*, often known as mud crabs, may bury themselves (Plotnik et al., 1988).

Baldwin (1974) and Orr and Orr (2010) describe the Lookingglass Formation as deposited near the south end of an early Eocene basin (Umpqua embayment, or Tyee Basin of Orr and Orr). The source of sediment was from the uplifted subaerially-exposed rocks of a series of accreted terranes, and the distal end of the depositional area was presumably at a subduction zone in the depths of the basin (Orr and Orr, 2012; Wells et al., 2014).

Baldwin (1974) suggested this early Eocene embayment may have been as much as 150 km (about 90 miles) from north to south and 120 km west to east (Fig. 1), somewhat larger than modern San Francisco Bay (which is about 94 km or 60 miles north to south and much narrower) or Puget Sound.

The fossiliferous Agness-area sediments, mostly fine-grained, apparently were farther from the river sources of the Tenmile Member sediments than exposures to the north, which have large beds of sand interspersed with the siltstones. Overall the evidence suggests nearshore upper continental shelf environments with a relatively smooth muddy bottom. Intertidal mudflat conditions seem unlikely because of a lack of cut-and-fill sedimentary structures which would form in tidal channels. Concretions are common; Yoshida et al. (2018) suggest that such concretions should preferentially form in water of a depth of a few tens of meters.

Armentrout (1975) considered California, Oregon, and Washington one biogeographic province in the Eocene, and faunal similarities continue farther north in British Columbia and Alaska. Eocene climates in western North America were relatively warm, and Eocene temperatures reached a maximum at about 55 Ma ago, about 4-5 Ma earlier than deposition of the Tenmile member (Sluijs et al., 2006). Squires (1984) analysed environmental ranges of a fauna from the Llajas Formation, of similar age to that described here. Many of the genera in the California Eocene fauna are still extant. Of this extant fauna, 10 genera are shared with the Lookingglass, and of those, eight were primarily found in tropical environments and two are primarily from warm temperate environments. Only one genus (the bivalve *Acila*) was most common in boreal and warm temperate environments

Presence of burrowing organisms (echinoids, raninoids, burrowing shrimp, bivalves, gastropods, probably *Orbitoplax*) suggests bioturbation should have been prevalent; however it was not extreme, as indicated by preservation of layering and articulated bivalves, echinoids and decapods. Fossils (other than terrestrially-sourced wood) show no evidence of postmortem transportation, so the faunal composition probably reflects the local ecology.

The reasons for the mass mortality of crabs of all size ranges is uncertain. In one previously documented case, a crab fauna seems to have been smothered by an eruption of volcanic ash (Crawford et al. 2008). There is no evidence of such ash accumulation in the Tenmile Member sediments. Neither is there evidence for sudden deposition of a thick layer of sediments by landslide or sediment flow which might have smothered the fauna. A large percentage of the well-preserved fauna was infauna, probably already living buried in the sediment where they died, so no sudden burial event is necessary to explain their preservation. Richards (1974) studied a group of 83 nearly complete specimens of Longusorbis in concretions in the Cretaceous Spray Formation of British Columbia, and concluded that most of his specimens were exuviae, and that the animals resorted to burrows for protection during shedding of the exoskeleton (ecdysis) and the period after moulting before the new shell hardened, while the animals were most vulnerable to predators. The exuviae, fully articulated, would remain in the burrows, where they were easily preserved. His evidence included the presence of open pleural sutures, which would only occur after ecdysis. I see no such prevalence of open pleural sutures in the Orbitoplax specimens. Although exuviae are certainly present, many are disassociated and no longer in life positions.

Another explanation for mass mortality would be the occurrence of "red tides", influx of high concentrations of microorganisms such as algae which either were toxic in themselves or which produced anoxic conditions during decay. Anoxia would help explain the presence of many growth stages in some taxa, lack of scavenging of complete corpses, and formation of carbonate concretions, which form preferentially under low-oxygen conditions (Wilcox, 1981; Mozley and Burns, 1993). Retallack (2011) discussed the occurrence of exceptionally-preserved faunas, or Lagerstatten, and their appearance at distinct periods in the geologic past. He suggests that the current warming of ocean waters, coinciding with Pacific coastal anoxic zones in recent years (which are observed to kill crabs and other near-shore marine organisms), are analogous to periods in the past when a relatively large number of well-preserved fossils were formed. The Tenmile decapod fauna may be a record of this type of event.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802 Infraorder Achelata Schultz and Richter, 1995 Superfamily Palinuroidea Latreille, 1802 Family Scyllaridae Latreille, 1825 Genus *Llajassus* Nyborg and Garrasino, 2017

Llajassus caesius Squires, 2001

Figure 10

Parribacus caesius Squires, 2001

Scyllarus manleyi Feldmann and Schweitzer, 2017

Llajassus caesius Squires, 2001; Nyborg and Garassino, 2017

Specimens: F-69399, Locality UO 2593, and UWBM 105851, Ross Berglund Burke Museum collection, probably from UO 2594.

Description: Small achelate "slipper lobster", CW range from 1.8 to ca. 2.4 mm.

Discussion: Scyllarids ("slipper lobsters") differ from other decapods in having no chelae on the first periopod and having enlarged, flattened antennae. Living scyllarids are widespread, mostly inhabiting warm shallow water and many depend on burial in sediment for protection from predators (Lavalli et al. 2019).

Squires (2001) described the first fossil scyllarid decapod from the west coast of North America, from Eocene sediments in the Simi Valley of Southern California. Two new specimens were found from roadcuts in Lookingglass outcrops near Agness (localities UO 2593 and UO 2594, sources of specimens for Orr and Kooser, 1971). Both were independently studied in 2016, one by Feldmann and Schweitzer (2017 and the other by Nyborg and Garassino (2017).

Squires (2001) gave his specimen the new species name *Parribacus caesius*. Feldmann and Schweitzer (2017) referred their specimen to the genus *Scyllarella* (largely on the basis of characters of the sternum) and gave it the new name *S. manleyi*. They mentioned but did no detailed comparison to Squires' specimen from California. Nyborg and Garassino (2017) compared their specimen to *Parribacus caesius*, deciding largely on the basis of dorsal carapace morphology that it was the same species but qualified as a new genus, renaming it *Llajassus caesius*. Examination of figures and specimens has convinced me that the latter name is correct, and that the Lookingglass specimens are conspecific with the California specimens (therefore *S. manleyi* is a junior synonym), and that a new genus name was justified.

As was noted by Feldmann and Schweitzer (2017), modern scyllarids commonly inhabit sandy or muddy bottoms in relatively warm shallow water, usually less than 150 meters deep. This is consistent with other evidence for the depositional depth of the Tenmile Member.

Presence of the genus *Llajassus* in the Tenmile fauna, though rare, is a significant connection to the Llajas Formation.

Infraorder Thallasinidae Latreille, 1831 Superfamily Callianassoidea Dana, 1852 Family Ctenochelidae Manning and Felder, 1991 Genus *Ctenocheles* Kishinouye, 1926

Ctenocheles hokoensis Schweitzer and Feldmann, 2001

Figure 11

Specimens: 21 specimens from Agness Localities UO 4233; UO 4234; Dora (USNM 512167, from Berglund locality RB57).

Diagnostic features: Heterochelous ghost shrimp, pectinate (comblike) teeth on the fingers of chelae, i.e. long fingers and acicular teeth. Most specimens preserve primarily the well-calcified chelae, and then frequently only the palm and a small portion of the fixed finger. The body of species of *Ctenocheles* is poorly calcified. The long, slightly curved fixed finger with many sharp teeth is distinctive. The teeth, or denticles, occur as several well-separated longer teeth with multiple shorter teeth between each pair of



Figure 10. *Llajassus caesius* (Squires, 2001), 1-3, F-69399 from Feldmann and Schweitzer 2017; 1. Dorsal view of carapace; 2. Anterior; 3. Ventral. 4. Reconstruction of body, including abdomen and lateral spines, dorsal view, based on three available specimens, by Torrey and Garassino (2017).

longer teeth. Chelipeds are asymmetrical; a major and minor chela are present. Palms are generally rounded or bulbous. The fixed finger is deflexed from the axis of the palm, more so on some of the major chelae, but also in at least some of the minor chelae. In the type material, the fixed finger is relatively parallel to the axis of the palm in the minor chela; at least one specimen in the Agness collection is the same (Fig. 11, 2). Characters of Agness specimens closely match those of the type specimens, one of which (a paratype, USNM 512167, illustrated by Schweitzer and Feldmann, 2001, Fig. 10, 3) came from the Lookingglass Formation at Dora.

A unique specimen preserves the chelae and a poorly-preserved abdomen (F-63597, Fig. 11, 3). The latter preserves the major chela only as a mold on the edge of the concretion; little can be said of it except that it was larger and more rounded than the minor chela. The minor chela is well-preserved. The palm of the minor chela is more than twice as long

as wide, with relatively straight dorsal and ventral margins. The fixed finger is slightly longer than the palm, deflected about 30^o downward. Denticles are not preserved. This specimen is considerably different from other specimens identified as minor chelae, such as F-61026 (Fig. 11, 2), but the extent of chela variation in *Ctenocheles* is virtually unknown so it is difficult to assess the significance of the differences. The abdomen is somewhat crushed and distorted. Visible surfaces are smooth. Margins of abdominal segments are not clear, though apparently no portion of the carapace is preserved. There appear to be two relatively large anterior abdominal segments, of similar size. Behind these appear to be four much smaller posterior segments and elements of the tail fan, though the shape of individual elements is obscure. What can be seen is consistent with the abdomen of modern Ctenocheles (e.g. Matsuzawa and Hayashi, 1997).

The earliest occurrence of *Ctenocheles* is in the



Figure 11. *Ctenocheles hokoensis chelae.* 1, F-62865 (UO 4233) major chela; 2, F-61026 (UO 4234), minor chela; 3. *Ctenocheles* with abdomen and chelae in concretion, F-63597 (UO 4234), A=abdomen, Mi=minor chela, Ma=impression of palm of major chela. Scale bars = 1 cm.

Late Cretaceous of Madagascar (Middle Coniacian) or Bohemia (Hyzny, Veselka and Dvorak, 2014), and the genus is widespread in modern oceans. Extant species are largely Asian and Indo-Pacific in distribution, in deeper water, though Feldmann (1995) hypothesized a shallower-water origin. Modern species appear to occupy burrows in soft sediments.

This callianassid is poorly known, either in living species or as fossils (Matsuzawa and Hayashi, 1997). All specimens from the Tenmile collections but two so far are chelae. The fingers are delicate and difficult to prepare, and fixed fingers are often broken off. Even extant species are known from few and often incomplete specimens (often in trawl nets). Several specimens have been identified, from Rusty Rail locality (UO 4234), from Big Road Cut (UO 4233) and from near Dora (Schweitzer and Feldmann, 2001), all showing the characteristic features of *C. hokoensis*. The species is otherwise known in Oregon from the early Eocene Elkton Formation at Basket Point, Douglas County, and from Washington from the late Eocene Hoko River Formation at Neah Bay. A second, Middle Eocene species of *Ctenocheles* (*C. secretanae*) distinctive for its short, essentially equidimensional palm, is known from the Santiago Formation, San Diego County, California (Schweitzer and Feldmann, 2002).

> Infraorder Brachyura Linnaeus, 1758 Superfamily Raninoidea, DeHaan, 1839 Family *Raninidae* De Haan, 1839

The raninid crabs, with their elongate carapaces and pipe-wrench-shaped claws are relatively common in the Eocene and Oligocene of the Oregon faunas. Three genera of raninids (*Doraranina, Rogueus,* and *Raninoides*) occur in the Lookingglass sediments. They can be most easily determined by the pattern of spines on the anterior margins (Fig. 12). Both *Doraranina* and *Rogueus* have carapaces covered with small pits, while carapaces of *Raninoides* are relatively smooth. The three raninid genera known from the Lookingglass Formation are not commonly found together.

Subfamily Rogueinae Karasawa, Schweitzer, Feldmann and Luque, 2014

Genus Rogueus Berglund and Feldmann, 1989

Rogueus orri Berglund and Feldmann, 1989

Figures 13, 14

Raninoides washburni of Orr and Kooser, 1971, Fig.4 D, E.

Specimens: Locality UO 2592, 20 specimens; UO 2594, 2 specimens in earlier Orr and Kooser collection, 19 specimens reported by Berglund and Feldmann, 1989; UO 4233; 25 specimens; UO 4234, 2 specimens; UO 4236, 2 specimens; UO 4244, 1 specimen.

Diagnostic features: CL greater than CW, CL/CW ratio= 1.6/1. CL size range = 25 mm to 50.4 mm. Carapace strongly arched side-to-side, less convex than *Raninoides* but similar to *Doraranina*, slightly convex front to rear, widest at or just ahead of center of length, posterior margin straight and about half of maximum width. Front margin width about ³/₄ of maximum carapace width, with prominent rostrum whose tip is divided into two small rounded points by a small longitudinal groove. Inner-orbital spine small, not pronounced, marked laterally by closed notch. Intra-orbital spine wide, short, rounded, with sinuous anterior margin, not divided from outer-orbital spine by notch. Outer-orbital spine short, medial margin



Figure 12. Differentiating the three raninoid genera found in the Lookingglass Formation; anterior margins and lateral spine configurations.



Figure 13. *Rogueus orri.* 1-3, F-59095 (UO 2592); 1. Right chela; 2. Carapace, dorsal view, with well-preserved anterior margin; 3. Cross-section, just anterior to widest part of carapace, CAT scan; 4. F-44155 (UO 2594), carapace of large individual, dorsal view. Scale bar = 1 cm.



Figure 14. *Rogueus orri*, scatter diagram, carapace width vs. length, Agness area localities. Holotype specimen indicated by X.

concave, point directed very slightly laterally, only about half of the length of the rostrum. Anterolateral (shoulder) spine robust, bifurcated, with anterior fork smaller than lateral fork. Carapace prominently ornamented with small pits.

The ventral anatomy is observable on very few specimens. The sternum is illustrated in Fig. 18, 5, there compared with sterna of *Raninoides* and *Doraranina*. A right cheliped is illustrated in Fig. 13, 1.

Discussion: *Rogueus orri* is known from seven localities, all in the Agness-area Lookingglass Formation . It is very common and the only raninid found at one locality (UO 2592), common but about equal in numbers to *Raninoides* in another (UO 4233) but somewhat less common at most localities (Fig. 8). In the most productive locality (UO 4234) it is far less common than *Raninoides*. In poorly-preserved specimens these can be hard to separate, especially when, as is common, the anterior margin and spines are not well preserved. *Rogueus* averages larger, with a slightly wider, more flattened carapace which is covered with small pits. The anterior margin over the orbits is sinuous, unlike those of *Raninoides* and *Doraranina*.

Genus *Doraranina* Gustafson, Nyborg and Van Bakel, 2019

Doraranina manleyi Gustafson, Nyborg and Van Bakel, 2019

Figure 15

Specimens: Dora, Steele Creek (UO 4577); F-62673 (Holotype), F-65910 (Paratype).

Diagnostic features: Carapace length 29.5 to about 40 mm. Carapace longer than wide (CL/CW = 1.6/1), widest about one-third of length behind anterior



Figure 15. *Doraranina manleyi.* 1. Holotype, F-62673 (UO 4377), dorsal view; 2. Paratype, F-65910 (UO 4377), dorsal view; 3. F-62673, lateral view of carapace showing surface texture (specimen coated with ammonium chloride); 4. *Doraranina* outline drawing. Scale bar = 1 cm.

margin, flattened posterior border. Rostrum triangular with single point, orbits large, with two closed supraorbital grooves, inner-orbital spine small, triangular, intra-orbital spine longer, extended point to lateral side, outer-orbital spine longer, directed distinctly outward, not bifurcate but with distinct angle on inner side, lateral side concave. Anterolateral margin short, with one long bifurcate spine strongly outwards directed, with inner (anterior) branch shorter than outer one. Posterolateral margin long, converging backwards, rimmed. Dorsal regions undefined, branchiocardiac grooves indistinct, dorsal carapace finely covered in small shallow pits.

The sternum is preserved on the type specimen. It is generally more similar to that of *Rogueus* than that of *Raninoides* (see Fig. 18, 4), as the sternite 4 is relatively large, there is no central groove and there is a deep indentation at the posterior end of sternite 5. Sternites 6-8 have not been observed. Only the bases of the pereiopods 2-5 are present, but much of the left cheliped and part of the right chela are preserved.

Discussion. *Doraranina* is only known from the Lookingglass Fm in the vicinity of Dora, Oregon. It possesses forked lateral spines, a pitted dorsal surface and a sternum similar to those of *Rogueus* but the anterior margin is more similar to *Raninoides*.

Subfamily Raninoidinae Lorenthey, 1929 Genus *Raninoides* Milne Edwards, 1837 *Raninoides vaderensis* Rathbun, 1926

Figures 16, 17, 18, 19

Specimens: Agness area: UO 2594, 6 specimens; UO 4233, 28 specimens; UO 4234, 190 specimens; UO 4236, 10 specimens. Camas Mountain area, UO 1592,



Figure 16. Raninoides vaderensis. 1. Carapace, F-59243 (UO 4234); 2. F-59278 (UO 4234), Carapace; 3. F-59283 (UO 4234); 4, 5. F-59233 (UO 4234); dorsal view of carapace and legs, and closer view of posterior legs and abdomen; 6. Juvenile carapace, F-59201 (UO 4234). Scale bar on 4 = 1 cm. Scale bar on 6 = 0.5 cm



Figure 17. Some variations in *Raninoides vaderensis* carapace shape, all from UO 4234, all adjusted to same length. 1. F-59243 (sides straight, parallel, wide anterior, outer-orbital spine prominent, short rostrum); 2. F-59283, (sides parallel, narrower anterior, anterolateral spines farther back, more prominent rostrum); 3. F-60769, (carapace wider at center, anterolateral spines thicker); 4. F-59274, (mostly an internal mold, widest in center of carapace, posterior more rounded, spines do not show original length, very prominent rostrum); 5. F-59233 (widest in mid-carapace, narrow anterior, very prominent rostrum.

1 specimen.

Diagnostic features: CL greater than CW, CL/CW ratio = 1.7/1, CL size range= 6mm to 37 mm. Carapace strongly arched side-to-side, more so than *Rogueus* or Doraranina., gently arched front-to-rear. Carapace shape behind anterolateral spines somewhat variable, lateral margins may be nearly parallel in central area (Fig. 17, 1, and 2), or distinctly convex (Fig. 17, 4 and 5). Posterior third of carapace tapers to a posterior margin which is straight to slightly convex and less than half maximum carapace width. Frontal margin width averages just under three-fourths maximum carapace width. Prominent triangular rostrum which frequently extends forward well beyond other anterior spines (but see Fig. 17, 1). Two fissures on dorsal margin of orbit, not tightly closed. Inner-orbital spine triangular, tip oriented outward; Intra-orbital spine narrower but of similar length, point oriented forward; outer-orbital spine longer, sometimes extended as far as the tip of the rostrum though usually shorter, inner margin L-shaped to sometimes truly bifurcate but with a minor point oriented inward, lateral margin straight. Anterolateral spines prominent, sharp, extending laterally and forward at about a 35° angle from the midline (range 29° to 41°)

Dorsal regions are not marked by grooves, the dorsal surface is smooth, sometimes glossy, Dorsal surface of carapace covered with microscopic pores or tiny pits. Branchiocardiac grooves often visible but not prominent.

The sternum (Fig. 18, 1, 3) is similar to that of

Raninoides slaki Squires 2001 (his Fig. 50B). The small anterior lobe is fused sternites 1-3 (Guinot, 1993), followed by a moderate-sized sternite 4 which forms the anterior support for the basal segment (coxa) of the cheliped or first pereiopod. Sternite 5 with an alate process forms the posterior support for pereiopod 1. The posterolateral margin of sternite 5 and anterolateral margin of sternite 6 form a concave curve which supports the base of pereiopod 2, while the posterolateral margin of sternite 6 helps support pereiopod 3. A sharp groove extends along the midline from the posterior part of sternite 4 through sternite 6. Sternites 7 and 8 have not been observed.

The legs have not been prepared from the matrix on most of the Condon collection specimens. What can be seen (Fig. 16) shows that the cheliped (pereiopod 1) is very similar to that illustrated by Squires (2001, Fig. 50C) for *R. slaki*. An exception is specimen F-59233, which preserves part (the anterior two segments) of the abdomen, which extends posterior of the carapace, unlike most non-raninid brachyurans. Also preserved are the posterior walking legs, pereiopods 3-5. Pereiopod 4 is larger than P5, and the last three segments (carpus, propodus, and dactylus) are flattened in a specialization for swimming or burrowing. The last leg (P5) has its base dorsal to that of P4, and it is more slender, extending in front of P4.

Discussion: *Raninoides vaderensis* is the secondmost-common crab in the Lookingglass fauna at some localities, ranging in size from about a centimeter to about 4 cm in length. The carapace is generally



Figure 18. 1, *Raninoides vaderensis*, sternum, F-63315; 2. F-59502 (both from UO 4234), scale bar for both is 1 cm; 3. Reconstruction of complete sternum (A, sternite 1-3; B, sternite 4; C, sternite 5; D, sternite 6), compared to: 4. *Doraranina manleyi*, and 5. *Rogueus orri*, (from Berglund and Feldmann, 1989), not to scale.

narrower and smoother than that of *Rogueus*, lacking the obvious pitted dorsal surface, the lateral spines are short and not forked, and the anterior margin is spikier. The abundance of this taxon at locality UO 4234, presumed to be from a short time span and a large local population allows for some evaluation of variation in characters which have been considered of value in determining species, from carapace size (Fig. 19) to shape of carapace and prominence of anterior spines. As several species of *Raninoides* have been described from the West Coast Eocene, it seems wise to justify this species designation.

The taxonomic history of Raninoides on the west coast of North America is complex, and the following summary is necessarily oversimplified. Raninoides is extant, with several living species. Rathbun (1926) described seven fossil species of Raninoides from the west coast, including four from Oregon, in the Eugene Formation (near the Eocene-Oligocene boundary, Retallack et al., 2004), including *R.washburnei*, *R.* eugenensis, R. fulgidus, and R. asper. She described Raninoides lewisanus and R. vaderensis from the "Tejon" (now the Cowlitz Formation) near Vader, Washington, including one specimen of *R. vaderensis* from Basket Point ("Umpqua Fm."), Oregon. Rathbun (1932) described *R. oregonensis* from the middle Eocene Rickreall Limestone near Dallas, Oregon. Tucker (1998) described R. goedertorum (as Laeviranina), from the upper Eocene Hoko River Formation of Washington. The first actual mention of Raninoides vaderensis (as Raninoides cf. R. vaderensis) in the Lookingglass fauna was in Berglund and Feldmann (1989).

Glaesner & Withers (1931) divided *Raninoides*, placing some species in another genus, *Laeviranina*, a somewhat controversial decision, not followed by some later workers. *R. vaderensis* was included in *Laeviranina*. Orr & Kooser (1971) working in the Agness area, described several specimens as *R. washburni*, which in the original descriptions was said to have a relatively wide, shallow carapace with a pitted surface. The specimens in their figure 4 D and E are *Rogueus orri*, missing the distinctive anterior margin. Their Fig. 4 G (a specimen not found in the collections) is *Raninoides vaderensis*, (the anterior margin is partly preserved), as is the pictured sternum.

Feldmann (1991), Tucker (1998), and Schweitzer et al. (2000) reviewed raninid crabs, redescribed *Laeviranina vaderensis*, and cast doubt on the usefulness of several characters which were being used to distinguish between *Raninoides* and *Laeviranina*, particularly the presence or absence of a postfrontal ridge. This postfrontal ridge is subtle, highly variable, and has been found on species attributed to both genera.

Schweitzer et al, (2006) finally synonymized Laeviranina with Raninoides. In a summary of the currently accepted species of the genus, she lists 36 species of Raninoides worldwide, living and fossil. The list included nine species of Raninoides from the west coast Eocene and Oligocene. Oregon and Washington species considered valid by Schweitzer



Figure 19. *Raninoides vaderensis*, size distribution, scatter diagram. Specimens from UO 4234. X=Holotype specimen from Vader, Washington, CL=33mm, CW=18.3mm, measurement from Rathbun, 1926.

include *R. eugenensis* Rathbun, 1926, *R. fulgidus* Rathbun, 1926; *R. oregonensis* Rathbun 1932; and *R. vaderensis* Rathbun 1926.

Raninoides vaderensis Rathbun, 1926, the species to which the Lookingglass specimens are assigned, was originally described from a locality in the middle Eocene Cowlitz Formation just west of Vader, Washington. Rathbun described a second species from a nearby locality as *R. lewisana*, but it was later synonymized with R. vaderensis (Schweitzer et al., 2000). The type specimen of *R. vaderensis* showed a dorsal carapace and two fragments of appendages. As it was the first Pacific Coast fossil Raninoides species described, this name has established priority. Specimens assigned to R. vaderensis have been reported from Alaska (Tucker and Feldmann, 1990), the Hoko River (Tucker, 1998) and Cowlitz Formations of Washington, Basket Point (Umpqua group), the Lookingglass Formation and middle Coaledo Formation of Oregon, and the Llajas Formation of California (Cushman and McMasters, 1936).

Raninoides eugenensis Rathbun, 1926 was described from a nearly complete carapace (the holotype, in the University of Oregon collections). Rathbun mentions "an impression and portions of two other carapaces, one of which may be considered a paratype" but these specimens have not been found. The specimens came from the Eugene Formation, which straddles the Eocene-Oligocene boundary (Retallack et al., 2004). The species was described as relatively flat, with a coarsely punctate dorsal surface, relatively straight posterolateral margins, narrower than *R. washburni* and tapering more rapidly to the rear. No further specimens have been described.

Raninoides fulgidus Rathbun, 1926 was described from fourteen specimens, all from the Eugene Formation. Rathbun states that "This species can always be distinguished by the ornamentation of the carapace, consisting of punctae and fine granules in combination." Among other features she notes the very convex carapace, and the short rostrum, shorter than the adjacent (intra-orbital and extra-orbital) spines. The intra-orbital spine is distinctively long, and the outer-orbital spine is strongly bifid, the whole frontal region appearing to taper slightly forward.. This species has also been reported from the Pulali Point fauna of Washington (Schweitzer et al., 2000).

Raninoides goedertorum Tucker, 1998 was described from a sample of 22 specimens from the Hoko River Formation of Washington. It is distinctive in having a more ovate (egg-shaped) carapace, wide posterior margin, and very small, forward-directed anterolateral spines. This species has also been reported from the Pulali Point fauna. Size range of the known specimens falls within the upper half of the range of *R. vaderensis* (Fig. 19).

Raninoides oregonensis Rathbun, 1932 is only known from the middle Eocene Rickreall limestone, and is a larger species, easily distinguished from *R. vaderensis* by the wider, flatter carapace and relatively small anterolateral spines.

Another 4 species are listed from California and Mexico: *R. slaki* Squires, 2001 (Llajas Fm.); *R. proracanthus* Schweitzer et al., 2006 (Mexico); *R. acanthocolus* Schweitzer et al., 2006 (Mexico); *R. dickersoni* Rathbun, 1926 (California)

Raninoides slaki Squires, 2001 was described from a group of about 90 specimens from one small area in the Llajas Formation. The size range of his population falls within the lower two-thirds of my sample from UO 4234. Squires mentions that "Cushman and McMasters (1936) reported several specimens of *Raninoides vaderensis* in a drill core in the Llajas Formation", said to have been sent to the USNM but now lost. Squires (2001) differentiated his new species from *R. vaderensis* by several features, including "a wider carapace, rostrum much less projected, outer orbital tooth wider posteriorly but more projected anteriorly, outer orbital tooth directed more outward, medial tooth much shorter, and the alate process on sternite 4 more produced." His reconstruction of a generalized outline of *R*. *slaki* bears a strong resemblance to some of the Tenmile specimens assigned to *R. vaderensis*, particularly F-59243 (Fig. 16, 1, Fig. 17, 1) in having a less projected rostrum than in most of the Agness samples. The anterolateral spines are also projected more forward (22° from midline) than in most *R*. *vaderensis*. A consistent difference between the Oregon and California samples may exist, but will have to be demonstrated by further study.

Raninoides proracanthus Schweitzer et al., 2006, was described from a single specimen from a locality in central Baja California, Mexico; *R. acanthocolus* Schweitzer et al., 2006, was described from two specimens from the same locality in the middle Eocene Bateque Formation. The specimen of *R. proracanthus* is large, falling into the upper range of *R. vaderensis* at UO 4234 (Fig. 19) but the specimens of *R. acanthocolus* are small for *Raninoides*, falling into the lowest part of the *R. vaderensis* range. Both have small to very small anterolateral spines. The incomplete nature of the specimens makes it difficult to evaluate the distinctive features listed for the two species, but the extremely short frontal and anterolateral spines of *R. acanthocolus* and even shorter anterolateral spines of *R. proracanthus* clearly distinguish both from *R. vaderensis*.

Raninoides dickersoni Rathbun, 1926, was described from a single specimen from "near base of Tejon group", middle Eocene. Only the ventral side was illustrated (Rathbun 1926, Fig. 20, 5). Another specimen, missing most of the anterior margin, was questionably referred to this species by Schweitzer and Feldmann (2002). No detailed comparison is currently possible.

Superfamily Dorrippoidea MacLeay, 1838

Family Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003

Genus *Marycarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003

Marycarcinus hannae Rathbun, 1926

Figure 20

Necrocarcinus hannae Rathbun, 1926, p. 84, pl. 18, figs. 1-2.

Necrocarcinus hannae Rathbun, 1926. Schweitzer, C.E., and R.M. Feldmann, 2000, p. 242, Figs. 11-12. *Marycarcinus hannae* (Rathbun, 1926), Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003, p. 40, Fig.13, 2-3.

Specimens: Agness, F-59206 (UO 4234); CM 45974 (UO 2594); Dora (Steele Creek), F-65910 (UO 4577).

Diagnostic features: Holotype (at California Academy of Science, from Rathbun); CW= 21mm, CL=19.3mm. F-59206; CW= 17+ mm , CL=19.9mm . CM45974, CW= 25.2mm, CL= 25.2mm . F-65910; CW= 22.2mm, CL = 21.7mm.

The carapace of *Marycarcinus hannae* has been described in detail by Rathbun (1926), by Schweitzer and Feldmann (2000) and by Schweitzer et al. (2003). Of the four known specimens, only the Dora specimen (F-65910) preserves the anterior and lateral spines nearly intact, and adds substantially to known morphology (Fig. 20. 1-3, 5). All specimens (which vary little in size) have a deep carapace about as long as wide, a similar pattern of swellings, grooves, and tubercle on the dorsal surface, and a relatively angular outline. There are 15 dorsal tubercles, three on the center line and six on either side. The rostrum projects forward and apparently was tipped by four small spines. The orbits are not well preserved, but their dorsal margin had inner-orbital, intraorbital,



Figure 20. *Marycarcinus hannae.* 1-3. Dora specimen (UO 4577), F-65910, dorsal, anterior and left lateral views; 4. Revised drawing of dorsal view of *M. hannae*, based on Dora specimen; 5. Agness specimen (UO 4234), F-59206, dorsal view of internal mold, lacking much of anterior and anterolateral margins. Scale bar = 1 cm.

and outer-orbital spines, the latter being largest and bifurcated, projecting forward about as far as the rostrum does. There are two sets of anterolateral spines. The anterior of these is smaller, triangular, and placed halfway between the outer-orbital spine and the larger posterior spine. The posterior anterolateral spine was only suggested on earlier specimens; it is by far the largest spine and curves forward near the tip. The presence and shape of this spine drastically changes the overall restored appearance of the carapace of *M. hannae*.

The ventral morphology and appendages are not preserved on the known specimens.

Disccussion: *Marycarcinus hannae* is an extremely rare member of the Lookingglass fauna, with only two specimens known from the Agness area and one from Dora. The only example from the Agness area, is a partial carapace, not well-preserved (Fig. 20, 5). The other Agness specimen was collected by Ross Berglund and is at the Carnegie Museum (illustrated

by Schweitzer and Feldmann, 2000, Fig. 11). The third specimen (Fig. 20, 1-3), collected by Bob Manly from Dora, is in a concretion which also contains a carapace each of *Doraranina* and *Eriosachila*.

The type specimen of *Necrocarcinus hannae* was collected by G. Dallas Hanna from a location one mile southwest of Oil City, Fresno County, California, from sediments identified as the "Tejon" of Arnold (1909, "a part of the middle Eocene") according to Rathbun. The word Tejon has been used variably to refer to a formation, group or series, and as a time-stratigraphic unit (Clark and Vokes, 1936), and has been applied to strata in southwest Washington (now the Cowlitz Formation), far from its California correlative deposits (Dickerson, 1915). In a stratigraphic sense it was later restricted to the type area of the Tejon Formation in the southern San Joaquin Valley (Weaver, 1937). Critelli and Nilsen (2000) point out that the type Tejon Fm. includes, in its lower beds, some faunas from earlier stages (Capay and Domengine). Revisions of these stages (i.e. Squires, 1988) indicate that the type



Figure 21. *Eriosachila orri*, 1-4; Type F- 28871, (UO 2594), original drawings from Kooser and Orr, 1973; 5-6, same photos, dorsal and anterior views; 7 and 8. Agness specimen F-59080, internal mold, dorsal and anterior views; 9. Dora specimen, F-65910, dorsal view. Scale bar = 1 cm.

of *M. hannae* may be early middle Eocene, whereas the Lookingglass specimens are late early Eocene. Notably, Rathbun (1926) records several occurrences of *Orbitoplax weaveri* from localities near the type locality of *Marycarcinus* in California.

Superfamily Calappoidea De Haan, 1833

Family Aethridae Dana, 1851

Genus Eriosachila Blow and Manning, 1996

Eriosachila orri Schweitzer and Feldmann, 2000

Figures 21, 22

Plagiolophus weaveri Rathbun, Orr and Kooser, 1971, Fig. 5A.

Zanthopsis rathbunae Kooser and Orr, 1973, Fig. 1-4.

Specimens: Locality UO 2592, 3 specimens; UO 2594, 8 specimens (including holotype, F-28871); UO 4233, 41 specimens; UO 4234, 2 specimens; UO 4236, 4 specimens; UO 4239, 3 specimens; UO 4244, 1 specimen; Dora (Steele Creek), UO 4577, 1 specimen.

Diagnostic features: Detailed descriptions are given in Kooser and Orr (1973) and in Schweitzer and Feldmann (2000). Size: CW = 4.3-17.0 mm. Carapace shape is an irregular circle or rounded octagon, CL/ CW ratio averages 0.97/1, but some specimens are slightly longer than wide. Carapace relatively tall. Orbits round, directed forward and slightly outward, with narrow raised rim. Frontal margin between orbits with central notch flanked by small tubercles; another small tubercle just medial to the orbit. A pair of tiny tubercles straddles the dorsal midline just behind the frontal area. Anterolateral margin strongly convex, forming a rim between the dorsal and lateral surfaces of the carapace, with two or three small projections. Another small projection just behind widest part of carapace, and another just anterior to posterolateral-posterior angle. Dorsal surface just inside lateral margins slightly concave. Posterior margin straight, narrower than interorbital width. Dorsal surface with eight large swellings; low, paired protogastric swellings, a central mesogastric swelling and a smaller but higher cardiac swelling, and paired epibranchial and narrower but higher mesobranchial swellings. The top surfaces of the swellings are ornamented with a pattern of tiny bumps.

Ventral anatomy is not exposed in the available specimens. Kooser and Orr (1973) illustrated a chela of this species (Fig. 20, 1).

Discussion: *Eriosachila* is a small, knobby crab, very distinctive but not extremely rare. Orr and Kooser (1971, Fig. 5A) illustrated a specimen then thought to be a juvenile *Orbitoplax*, and later (Kooser and Orr, 1973) included that specimen (F-28228) as a paratype of *Zanthopsis rathbunae*. Unknown to them the name *Zanthopsis rathbunae* was preoccupied,



Figure 22. Eriosachila orri, all localities, size variation scatter diagram. X=Holotype specimen.

used for a taxon from Venezuela by Maury (1930) in a Brazilian publication. Blow and Manning (1996) erected the genus *Eriosachila* for specimens from the middle Eocene of South Carolina, including Maury's *Z. rathbunae* in *Eriosachila*. When Schweitzer and Feldmann (2000) revised Kooser and Orr's species into *Eriosachila*, they found that this name was a junior homonym of *Eriosachila rathbunae* (Maury, 1930), therefore preoccupied. They then proposed a new replacement name, *Eriosachila orri*.

Eriosachila is now known from both east and west coasts of North America and from northern South America. *Eriosachila* is known also from the Hoko River fauna of Washington, though the two known specimens are assigned to a different species (*E. rossi* Schweitzer and Feldmann, 2000). Schweitzer and Feldmann (2000) include *Eriosachila* in the Family Hepatidae, and comment that members of the Hepatidae inhabit primarily shallow water areas, typically in the tropics, although they may have had a broader ecological tolerance in the past.

Size distribution in the available population of *E. orri* (Fig. 21) is notable for the preponderance of mature animals and paucity of smaller, juvenile individuals. This distribution contrasts with the size distributions of the two most common crabs in the fauna, *Orbitoplax* (Fig. 28) and *Raninoides* (Fig. 18), in which the populations are not notably skewed toward mature individuals. This skewed size distribution suggests potential seasonal variation in

reproduction, or alternatively, migration occurring after maturation of the animals.

Superfamily Eriphioidea MacLeay ,1838

Family Pseudoziidae Alcock, 1898

Genus Archaeozius Schweitzer, 2003

Archaeozius occidentalis Schweitzer, Feldmann, Tucker, and Berglund, 2000

Figure 23

Carpilius occidentalis Schweitzer, Feldmann, Tucker, and Berglund, 2000, Fig. 12 A-C.

Carpilius occidentalis Schweitzer, 2000. Fig. 1.

Specimens: UO 4234; F-59006, F-59007, F-59008.

Measurements: F-59006, CL=21.5 mm, CW=29.8 mm; F-59007, CL=22.8 mm, CW=36.7 mm; F-59008, CL=20.2 mm, CW=27.2 mm.

Diagnostic features: Medium size, CW from 27.2 to 36.7 mm. Wide pointed-ovoid carapace; carapace smooth, regions not marked by grooves. Frontal margin slightly sinuous with small central notch. Orbits circular with raised rim. Anterolateral margin strongly convex, ending laterally at anterior of two short spines. Posterolateral margin straight or slightly convex, ending laterally in posterior of two lateral teeth or short spines. Posterior margin short, straight, about 25% of carapace width.

The ventral morphology and appendages are not



Figure 23. Archaeozius occidentalis, dorsal and anterior views. 1 and 2, F-59006; 3 and 4, F-59007, both from UO 4234; 5. Outline restoration of carapace, dorsal view, based on F-59006. Scale = 1 cm.

preserved on the known specimens.

Discussion: Archaeozius occidentalis has been previously reported only from the Pulali Point fauna (Aldwell (?) Formation, just above the top of the Crescent Formation; Schweitzer et al., 2000) and the Blue Mountain Unit of the Crescent Formation, both of Washington State (Schweitzer, 2000). It is rare in the known faunas. In the Agness area it has only been found at UO 4234, the Rusty Rail locality.

All three specimens are preserved in oval concretions. All consist of only the carapace, so are probably molts.

Schweitzer et al. (2000) originally referred this species to *Carpilius*, an extant genus of widespread occurrence in shallow warm waters, and named a new species. Subsequent study led to moving this species from the Carpiliidae to the Family Pseudoziidae and naming the new genus *Archaeozius* (Schweitzer, 2003).

Superfamily Xanthoidea MacLeay, 1838

Family Panopeidae Ortmann, 1893

Subfamily Panopeinae Ortmann, 1893

Genus Panopeus Milne-Edwards, 1834

Panopeus baldwini Kooser and Orr, 1973

Figures 24, 25, 26

Cancer sp., Orr and Kooser 1971, Fig. 4H,I

Lophopanopeus baldwini Kooser and Orr, 1973, Plate 1, 5-7.

Panopeus baldwini (Kooser and Orr); Schweitzer, 2000

Specimens: Locality UO 2592; 1 specimen. Locality UO 2594 (Type locality): F-28227 (Holotype), F-28868-F-28870 (Paratypes). Locality UO 4233; 11 specimens; Locality UO 4234, 2 specimens; Locality UO 4332 (Glide); 3 specimens.

Diagnostic features: CL less than CW, CL/CW ratio = 0.8/1, CL size range =16 to 37 mm (Fig. 26). Carapace roughly hexagonal. Orbits circular, directed forward and slightly outward with distinct raised rim and dorsal fissure just lateral to center of orbit, a second smaller orbital fissure at lateral corner of orbit. Interorbital margin with strong central notch, anterior margin on each side of notch sinuous. Lateral corner of orbit forms a short sharp point. Anterolateral margin strongly convex with obtuse projection just lateral to the orbit, followed by three short teeth, each curved forward to a point, posterior tooth smaller



Figure 24. *Panopeus baldwini.* 1-3, Holotype specimen, F-29227 (UO 2594); drawing from Kooser and Orr 1973, anterior, dorsal and ventral views; 4-6, Holotype specimen photos, anterior, dorsal and ventral views; 7-9, Paratype specimen F-28868 (UO-2594), anterior, dorsal and right lateral views; 10-11, Paratype F-28870, anterior and dorsal views. Scale bars = 1 cm.

than first two. Posterolateral margins longer than anterolateral, slightly convex, tapering to a broad convex posterior margin with a central indentation. Dorsal surface relatively flat, almost planar but with distinct differentiation of regions. Low transverse ridges present on protogastric and hepatic regions (variably prominent on the type and paratype specimens), a significant factor in Schweitzer's (2000) referral of this species to *Panopeus*. Mesogastric region with distinct diamond-shaped central area and long narrow anterior projection reaching to the frontal region. Urogastric region a small depressed lateral bar. Cardiac region broad, relatively flat, with shallow lateral concavity dividing it from the intestinal region. Mesobranchial region only slightly swollen, smaller than epibranchial region. Surface ornamented by very small bumps, usually not well preserved.

The original description of this species included drawings of the anterior, dorsal and ventral aspects of the type specimen (Fig. 24, 1-3), which can be compared to photos of the original (Fig. 24, 4-6). The anterior view shows that the specimen is flatter dorsally than in the drawing and the eyes are larger and more circular. The dorsal view photo shows more



Figure 25. *Panopeus baldwini*, dorsal views, anterior margin and chelae. 1-3, F-44162, (UO 4332, Glide), dorsal and anterior, and detail of anterior margin, left (minor) chela preserved; 4. F-66146 (UO 4234, Agness), anterior view of right chela, probably a minor chela. 5 and 6, F-62230, (UO 4233, Agness); dorsal and ventral views, with major chela; 7. F-44172, (UO 4332, Glide), anterior view of chelae, right (minor) chela much smaller than left (major) chela.

differentiation of the regions. The original description said little about the ventral anatomy (other than it was interpreted as a male, with a narrow abdomen). The ischium of the third maxilliped is well exposed; it is large and rectangular. The sternum varies considerably from the drawing, being much larger than shown. Its anterior segment, the large shieldshaped sternite 4, is broad and the posterolateral corner forms a posteriorly-directed hook around the lateral edge of sternite 5. It has a lateral notch into which a projection of the coxa of the first pereiopod (the cheliped) articulates. Sternite 5, in turn, forms a hook around the lateral edge of sternite 6. The suture between sternites 6 and 7 is indistinct.

The pereiopods (walking legs and chelipeds) were not preserved in the original sample except for the bases of the first three pereiopods on the right side of the type. Several examples in this collection exist of the limbs (Fig. 25). The walking legs (presumably pereiopods 4 and 5) preserve a long proximal segment, or merus, which attached at the rear of the carapace. The two limbs are similar in length and width, robust, with a row of raised papillae on the dorsal side. The species is significantly heterochelate, with a major claw and a minor claw. The major claw is on the right in one specimen and the left on another, the preserved minor claws include two left and two right. The dactylus, or movable finger on the major claw has at least two large, blunt teeth (the end is broken off), suggesting considerable crushing strength, aided by a large muscle mass in the rounded palm of the manus. The dactylus of the minor claw is

more slender, has two longitudinal dorsal ridges and four or five small blunt teeth. The fixed finger of the minor claw also has four or five small blunt teeth.

Discussion: Species of *Panopeus* living today are often known as "mud crabs" (Ryan, 1956), and are known to inhabit muddy substrates, although some species prefer sandy bottoms, oyster beds (where they may occupy the shells of dead oysters), or mangrove swamps (Benedict and Rathbun, 1891; Williams, 1983). Widespread in the Atlantic coasts, their modern habitats include embayments and estuaries, relatively shallow water, but not low salinity areas. *P. herbstii* is known to feed on young oysters and mussels in Chesapeake Bay.

Specimens of *Panopeus* include the largest crabs in the Lookingglass fauna, with maximum carapace width of about 5 centimeters. Some examples show one greatly enlarged chela. This is a feature (heterochelate) often seen in crabs today which have specialized feeding habits or which are sexually dimorphic. The chelae, particularly the major chela, are armed with large blunt teeth suitable for crushing hard-shelled prey.

This crab resembles *Branchioplax washingtoniana* Rathbun 1926, particularly in the shape of the anterolateral carapace dentition which is very similar in the two species. The dorsal surface of *P. baldwini* in much flatter, and that of *B. washingtoniana* is more inflated and rounded, particularly in the branchial regions. The cardiac region on *Panopeus* is much broader, and the anterior margin in *Panopeus* has a strong central notch.

Superfamily Goneplacoidea MacLeay, 1838

Family Euryplacidae Stimpson, 1871

Orbitoplax weaveri Rathbun, 1926

Figures 5, 6, 7, 27, 28, 29, 30, 31

Plagiolophus weaveri Rathbun, 1926, Plate 9, 5 and 6.

Glyphithyreus weaveri Glaessner, 1969.

Plagiolophus weaveri Rathbun, Orr and Kooser 1971, Fig. 4-5.

Orbitoplax weaveri (Rathbun); Schweitzer, 2000.

Referred specimens: Agness area:UO 2592, 65 specimens; UO 2593, 15 specimens; UO 2594, ca. 100 specimens; UO 4233, 1066 specimens; UO 4234, 1556 specimens; UO 4236, 69 specimens. Camas Mountain area, UO 1592, 2 specimens. Glide area, 20 specimens. Dora area, 12 specimens.

Diagnostic features: CL less than CW, CL/CW ratio = ca. 0.75/1, size very small to medium, size range is substantial, CW from 7 to 27mm. at Agness localities, 12 to 33 mm at Dora. A detailed description including comparisons to other species of *Orbitoplax*



Figure 26. *Panopeus baldwini* scatter diagram, CLxCW, from all Lookingglass localities. Holotype specimen indicated by X.

is available in Schweitzer (2000). The frontal margin is almost straight, with a small central notch. The particularly well-calcified eyestalks articulate within the inner curve of the medial orbit; they are of a length to fit neatly within the elongated orbit like a jackknife blade. The distal eyestalk has a concavity on the posterior side of the distal end, though it is not clear how this morphology relates to the position of the optical lenses. The orbits dominate the anterior margin, as each is longer than the frontal margin, with a slightly raised rim. The dorsal edges of the orbits are sinuous, with a distinct central convexity. The anteromedial corner of the orbits turn laterally, and the lateral corners extend forward into a short spine. The anterolateral margin of the carapace bears two spines, which are variable in prominence. The



Figure 27. *Orbitoplax weaveri.* 1. Restoration of appearance in life; 2. F-65717 (UO 4234) dorsal view; 3, F-59666, carapace with eyestalks, shell preserving ornamentation but with most of calcite leached out; 4. Carapace with well-calcified shell showing exceptionally preserved ornamentation; 5. F-60625 (UO 4234), anterior view of chelae; 6-8. F-71028 (UO 4307, Dora), mostly complete large specimen, dorsal, front angle, and anterior views. Scale bars = 1 cm; 3 and 4 not to scale.



Figure 28. *Orbitoplax weaveri*, sternum, ventral view. 1. F-61035 (UO 4234), isolated sternum showing female gonopores on medial half of sternite 6; 2. F-62383 (UO 4233), sternum with triangular sternites 1-2 in place; 3. F-62267 (UO 4233), ventral view of complete crab, female, with abdomen.

posterior spine is at the widest part of the carapace, usually forming a sharp point, though sometimes quite small. The anterior of the two, halfway between the orbit and posterior spine, varies from a blunt bump to a distinct sharp point, and may occasionally be larger than the posterior spine. These spines are a significant distinction from the other species of *Orbitoplax*, which generally bear a single anterolateral spine. The posterolateral border is significantly convex, curving into the posterior border, which has a slight central concavity.

The dorsal surface is covered in fine granulations, mostly present on the inflated areas and not in the furrows (Fig. 27, 3 and 4). The regions are very distinct, divided by well-defined furrows and grooves. The cervical grooves are prominent, flowing posteriorly into deeper, narrow branchiocardiac grooves, which wrap around and meet at the back of the cardiac region. The frontal region is divided by a shallow anteroposterior furrow, with a slight oval swelling on each side. Behind this is the protogastric region, which seems to bear smaller granulations than posterior regions. The mesogastric region is large, with a relatively short narrow extension medially forward into the frontal furrow. The metagastric region is small, narrowing rapidly back into a lateral depression, posterior to which is a hexagonal cardiac region. The intestinal region is somewhat depressed. Lateral to the orbit, the hepatic region is distinctly swollen. Behind it the epibranchial region is divided from the lateral margin by a shallow furrow. A short but distinct lateral furrow divides the epibranchial from the mesobranchial region. A small metabranchial region is divided from the cardiac and intestinal regions by pinched narrow grooves.

The sternum has been described in detail by Schweitzer (2000). Figure 28 illustrates three examples. The specimen in Fig. 28, 2 (F-62383) has a medial anterior triangular structure which is not present on Schweitzer's example, which is probably fused sternites 1 and 2, similar to that seen in some other goneplacoids (Guinot et al., 2013, Fig. 4B,C). I think this is a male, though only small parts of the abdomen are present. Sternite 3 appears to have fused with sternite 4. Sternite 5 appears as two separated triangular structures, centrally pinched between sternites 4 and 6. In Fig. 28, 1, an oval structure is visible on the medial half of each side of sternite 6. This is here interpreted as a female gonopore, or vulva, the sexual opening from which eggs are produced (Guinot et al., 2013). These openings

would normally be covered by the abdomen, which is missing in this specimen. The specimen illustrated by Schweitzer (2000, Fig. 5B) which was identified as male and also is missing the abdomen, has an oval of similar size and shape on sternite 6, suggesting that it also is a female. The first two segments of the abdomen may be visible behind the carapace in dorsal view.

The ventral positioning of the pereiopods is shown in the specimens in Fig. 28, 2 and 3. Pereiopods 1, the chelipeds, attach to the anterolateral side of sternite 4; periopods 2-5 (or walking legs 1-4) attach to the lateral margins of sternites 5-8 respectively. The chelipeds have a relatively short merus (arm). The carpus (wrist) segment is large and bulbous, almost spherical from some angles, but flattened on the mediodistal side, where the manus folds against it. The manus is much longer than wide and generally

smooth, tapering wider distally. The posterior dorsomedial corner of the manus is produced into a broad point, almost a spine, which rests against the side of the carpus when folded in. The dactylus (movable finger) is about a third of the length of the entire carpus, with several small blunt teeth. The fixed finger is slightly deflected down from the palm, and also bears several small teeth. One cheliped generally is slightly larger than the other though the heterochely is not always obvious, especially in smaller individuals. The first walking legs are very often not visible on complete crabs, as seen in dorsal view, and they tend to sit under the chelipeds and concretions tend to break along the dorsal surfaces. In a few specimens they are seen to be long and slender (Fig. 27, 1). The second and third walking legs are almost equal in size and proportions. Frequently only the merus and carpus are preserved (several examples



Figure 29. *Orbitoplax weaveri*, Agness (UO 4234, Rusty Rail), scatter diagram, CLxCW. Size of holotype indicated by X (measurements from Rathbun, 1926).



Figure 30. Scatter diagram, size range of *Orbitoplax weaveri* at Dora (circles); comparison with population from Agness (polygon, from Fig. 29); Size of holotype indicated by X (measurements from Rathbun, 1926).

shown, Fig. 5, 6, 7, 27, 31). The fourth walking leg has a merus a bit shorter and broader than the second and third. The meri of all walking legs are a flattened oval in cross-section and have a row of fine granules on the anterior dorsal surface.

Discussion: Of every ten fossils of any type in this part of the Lookingglass Formation, about six will be specimens of *Orbitoplax weaveri*. Not only does it dominate the fauna, the specimens are frequently nearly complete with eyestalks, chelae and legs

This species has a complex taxonomic history. It was first described as *Plagiolophus weaveri* by Rathbun, 1926, from middle Eocene localities in the Tejon Formation of California. *Plagiolophus* was considered a junior synonym of *Glyphithyreus* in the Treatise on Invertebrate Paleontology (Part R, Arthropoda 4, Vol. 2, Decapoda, Glaessner, 1969). Orr and Kooser, 1971, referencing Rathbun, report *Plagiolophus weaveri* from the Lookingglass Fm. east of Agness, Oregon. Squires (1984), recognizing the Treatise reference and noting Orr and Kooser's paper, reports *Glyphithyreus weaveri* from the Llajas Formation, California. Squires et al. (1992), then reports *Glyphithyreus weaveri* from the Crescent Formation, late Early Eocene of Washington. Meanwhile, Berglund and Feldmann (1989), also report *P. weaveri* from Agness, retaining the earlier generic references to *Plagiolophus*.

Tucker and Feldmann (1990), described a new genus and species *Orbitoplax pflakeri* from Alaska. Schweitzer (2000), transferred *P. weaveri* into *Orbitoplax*, describing specimens from the Agness area, and also described a new species, *O. tuckerae* from the Crescent Formation of Washington, not from the Pulali Point section. She does not mention the previous specimen mentioned by Squires et al. from those strata at Pulali Point in this paper, although she did acknowledge that specimen as *G. weaveri* in another paper (Schweitzer et al., 2000).

More recently, Schweitzer and Feldmann (2002), describe *O. weaveri* from the Mission Valley Formation and Ardath Shale, San Diego County, California. Nyborg, Davis and Nisani (2008), report abundant *O. weaveri* from Llajas Formation of California in a study of growth stages. Also in 2008, Vega et al. refer *Stoaplax nandachare* from Chiapas in southern Mexico, a small species with a single anterolateral spine, to *Orbitoplax*.

Sample numbers of *Orbitoplax* from localities in the Agness area are uniquely very large, numbering in the thousands, and specimens are fairly consistent in size range at all the Agness localities. The scatter diagram (Fig. 27), although based entirely on specimens from UO 4234, encompasses the size range seen in these localities. The increase in size with age appears to be essentially linear, with little of the change in CL/CW ratio with increase in size as suggested by Orr and Kooser (1971). Nyborg et al. (2008) studied a group of 27 individuals of *O. weaveri* from the Llajas Formation of California, in an attempt to find moult increments in the size distribution; they found "a relatively continuous growth series with possible

groupings corresponding to molt stages". With a much larger sample, I find a fairly continuous series with no obvious separation of moult stages. It is likely that individual variation among animals at each moult instar is sufficient to obscure any size grouping by instar. A sample of specimens covering the size range (from small, immature individuals to large mature ones) is shown in Fig. 30.

The sample from Dora (20 individuals, Fig. 29) includes 10 specimens which are larger than those in the Agness localities, although the total size range at Dora widely overlaps that at Agness and includes the size of the Holotype specimen from California The reason for the size difference at Dora is not clear. The two areas are separated by 64 km (40 miles), and though most species are shared between them, the Dora area produces *Doraranina* and the Agness area is



Figure 31. Examples of *Orbitoplax weaveri*, growth series. 1. F-61190 (CW=8.8mm); 2. F-62267 (9.5mm); 3. F-59473 (13.4mm); 4. F-66426 (16.0mm); 5. F-59471 (17.5mm); 6. F-59666 (18.8mm); 7. F-59663 (21.8mm); 8. F-71029 (34.6mm). 1-7 are from UO 4234 (Agness), 8 is from UO 4377 (Dora).

the only known source of *Rogueus*, a similar raninid. Possible ecological differences could include depth and salinity of the water in the bay.

In smaller individuals the chelae are similar in size. Some larger individuals are more heterochelate; for example, the large individuals in Fig. 27, 5-7 and 31, 8, both of which have a right chela somewhat larger than the left. It is not clear if heterochely is correlated to gender.

Cases in which a single crab species dominates a habitat are not uncommon today; an example would include the great abundance of *Neohelice granulata* in parts of the La Plata estuary in Argentina and Uruguay (Ieno and Bastida, 1998).

Superfamily Hexapodoidea Miers, 1886

Family Hexapodidae Miers, 1886

Genus Palaeopinnixa Via, 1966

Paleopinnixa rathbunae Schweitzer, Feldmann, Tucker and Berglund, 2000

Figures 9. 2, 32, 33

Pinnixa eocenica Rathbun, 1926

Pinnixa (Palaeopinnixa) eocenica Via, 1966

Palaeopinnixa rathbunae Schweitzer, Feldmann, Tucker and Berglund, 2000

Specimens: Locality UO 2592, 3 specimens; Locality UO 4233, 11 specimens; Locality UO 4234, 25 specimens; Locality UO 4236, 6 specimens; Locality UO 4239, 2 specimens.

Size: Very small crab, CW range from 3.8 to 10.5 mm. CL/CW ratio = 0.69/1.

Diagnostic features: This species has been described in great detail from excellent specimens from Pulali Point, Washington by Schweitzer et al. (2000). The Agness specimens closely match those described from Vader, Washington and Pulali Point in anatomical details.

Very small crab, CW range from 3.8 to 10.5 mm. CL/ CW ratio = 0.69/1. Carapace shape is a flattened oval wider than long (mean CL/CW ratio is 0.69/1), widest near posterior, lateral margins rounded, tapering slightly to anterior. Rostrum small, indented in center, slightly widened anteriorly. Orbits wider than high, upper and lower borders sinuous. Lateral to orbits, a low ridge divides the lateral surface of the carapace from the dorsal surface; the ridge is most prominent anteriorly and supports a row of fine granules. Dorsal regions of carapace fairly well demarcated, cervical grooves and groove between cardiac and gastric regions prominent. Branchial regions inflated, cardiac region distinct, triangular. Gastric regions prominent but not well demarcated. Posterior margin of carapace is straight when viewed from above, concave upward when viewed from posterior. Posterolateral corner margins of carapace occupied by rimmed semicircular indentations. Dorsal surface of carapace is covered in highly variable fine granules, most prominently in lateral areas, least prominently in the central regions.

No specimens show a complete ventral surface. One concretion which preserves three carapaces also exhibits an isolated sternum (Fig. 32, 10).

Most specimens consist of only the carapace, or a carapace and some legs. Most are probably molts. One specimen preserves a mold of the carapace with indications of the chelae and some walking legs (Fig. 32, 7), but none is nearly complete. Two specimens include multiple individuals in a single concretion (Fig. 32, 8 and 9).

Rathbun (1926) described *Pinnixa eocenica* from a type specimen (UWBM IP 15618) from Eocene sediments near Vader, Washington with dorsal and posterior illustrations of the carapace, deposited at the University of Washington but then without a specimen number. The species was referred to the Family Pinnotheridae, a group of small crabs with the usual five pairs of pereiopods, including four sets of walking legs. New specimens described by Schweitzer et al. (2000) show that only three sets of walking legs were present, and this plus other anatomical details forced a transfer to the Hexapodidae, in which this is the normal configuration.

The name *Palaeopinnixa rathbunae* is now used for specimens which would earlier have been *Pinnixa eocenica* Rathbun (1926). In raising the subgenus *Palaeopinnixa* Via 1966 to genus status and revising several hexapodid species into the genus (Schweitzer et al., 2000), *Pinnixa eocenica* Rathbun, 1926, became a junior homonym to *P. eocenica* Woods, 1922, therefore the trivial name needed to be replaced. Nevertheless, *Palaeopinnixa rathbunae* remains the type species of the genus.

Palaeopinnixa rathbunae includes the smallest crabs in this fauna. Like *Eriosachila*, these crabs are not rare, but they are so small that they are easily overlooked. Specimens from the Agness area are generally smaller than *Palaeopinnixa rotunda* from the Coaledo Formation near Coos Bay which are from somewhat later in the Eocene

Specimens from the Agness localities cluster in



Figure 32. *Palaeopinnixa rathbunae.* 1-6. Carapaces, showing variation in preservation; 1. F-62899 (UO 4233), dorsal view; 2. F-59585 (UO 4234), dorsal view; 3 and 4. F-60865 (UO4233), dorsal and posterior views; 5 and 6. F-61592 (UO 4234), dorsal and anterior views; 7. F-59013 (UO 4234), dorsal natural mold of complete crab on surface of a concretion; 8. F-59378 (UO 4234), concretion with three individual *Palaeopinnixa* (A, B, and C), which were associated with a small *Orbitoplax* in the same concretion; 9. F-62223 (UO 4233) concretion with two small and one larger *Palaeopinnixa*, with disassociated legs and sternum impression; 10. Detail of F-62223, sternum impression, probably from a male. 1-6 to same scale, scale bar = 0.5cm. Other scale bars also 0.5 cm.

size (Fig. 32) close to that of the holotype specimen from the type locality near Vader, Washington (Rathbun, 1926). This population averages smaller in dimensions overall than that from Pulali Point and other localities in Washington, which have produced the best specimens of the species (Schweitzer et al, 2000); the latter populations have a CW range from 5.4 to 16.8 mm. The largest Agness specimens are CW=10.5 mm. Only five of the 28 specimens listed by Schweitzer at al. are less than 10.5 mm.

Modern hexapodids often are commensal with other organisms, for example in burrows of polychaete worms, in burrows of other decapods, both shrimp and brachyurans, and in the mantle cavities of molluscs.



Figure 33. *Palaeopinnixa*, size variation, scatter diagram. Specimens from Agness area localities. Type specimen indicated by X, from Rathbun, 1926.

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