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Inferences for grooming behavior drawn from epibionts on early to middle Cenozoic crabs of Oregon and Washington state, USA

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Abstract

Among brachyuran decapods, grooming of sensory and respiratory surfaces is common; however, general body grooming is not well developed. The external surfaces of crab carapaces often become colonized by epibionts, and brachyurans exhibit many types of behavior to remove them by grooming. Four species of well-preserved crabs from lower to middle Cenozoic marine sedimentary rocks in a region from northwest Oregon and southwest Washington State have been colonized by epibionts across regions of the dorsal carapace and pereiopods. In order to determine the regions of the carapace that the fossil crabs could have efficiently groomed, the appendages of modern paddle-bearing and non-paddle-bearing crab genera were manipulated to assess the extent of mobility for each limb. Regions of the carapace were distinguished that could be groomed between modern species, differentiating between *in-vivo* and *post-mortem* colonization, as well as grooming potential, between analogous fossil crab taxa. In general, dorsal carapace grooming is more accessible among the paddle-bearing crabs as compared to the non-paddle-bearing brachyurans examined. Variation in carapace size and region location as well as dissimilar appendage lengths and ranges of motion between crab taxa precludes a comprehensive general grooming template of the brachyuran carapace. However, this work could be expanded to analyze further carapace grooming potential of modern brachyurans for comparison with analogous extinct species.

Introduction

It is common for marine organisms that maintain a benthic, sessile lifestyle to colonize the external surfaces of other ocean-dwelling biota. Many decapod crustacean species become infested by these epibionts and must spend time removing them using various types of grooming behavior. Epibionts are a subset of hard substrate-adhering organisms referred to as sclerobionts (Taylor and Wilson, 2002). The most efficient grooming decapods are natant shrimp – these possess streamlined carapace morphologies for swimming and are concerned with body drag, leading to increased pressures to remove colonizing organisms (Bauer, 1981). Less dependent on swimming are the brachyurans that rarely display grooming appendages beyond those necessary to remove colonizing organisms from sensory and respiratory organs (Bauer, 1989; Becker and Wahl, 1996; Waugh *et al*., 2004). General body grooming is not typical among these organisms (Bauer, 1981); in addition, general grooming is less well studied.

The dorsal and ventral carapaces of crabs are divided into bounded subregions (Fig. 1) which may correspond to underlying internal organs, and their locations on a carapace may be distinguished depending on the taxonomic group (Stachowitsch, 1992). Appendages are segmented, providing each with a limited range of mobility. Crabs that have been colonized by epibionts have the potential to manipulate their limbs to groom the carapace as long as epibionts are within range of motion to facilitate grooming, including the 2nd and 3rd maxillipeds; the first pereiopods, which will be referred to as the chelipeds herein; and pereiopods 2 through 5. Some limbs have the potential to

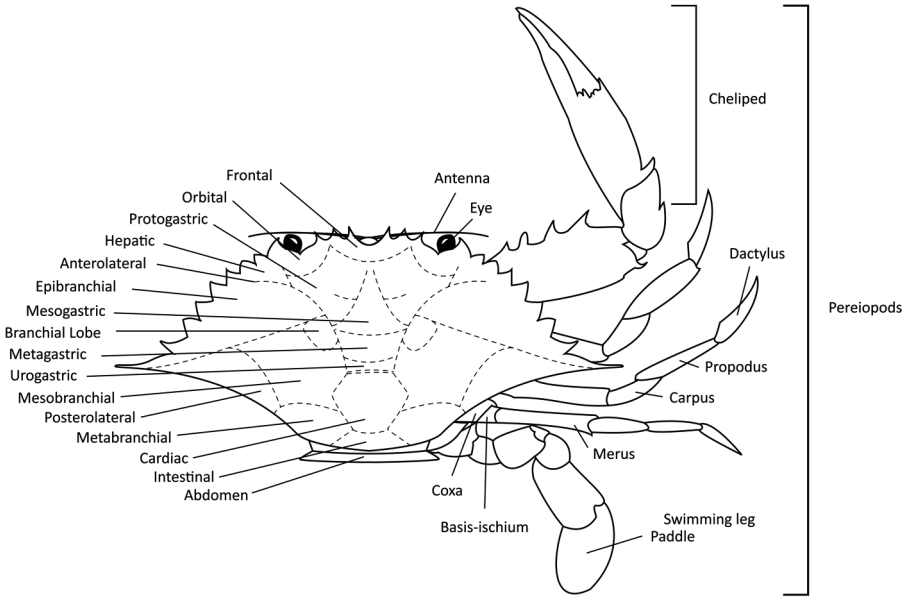


Fig. 1. Diagram of the regions of a portunid crab carapace and appendages. Modified from Glaessner (1969).

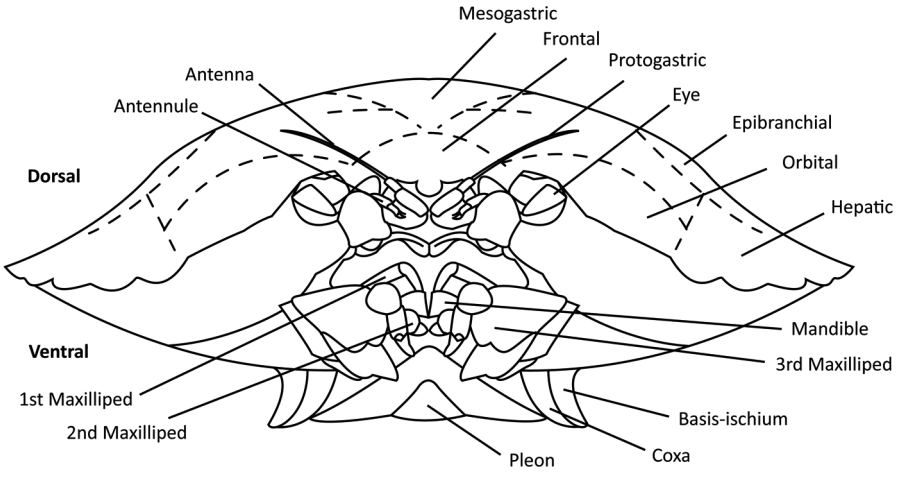


Fig. 2. Diagram of the anterior carapace of a cancrid crab.

groom regions of the dorsal carapace, including the 5th pereiopod in some portunoid crabs that possess paddles on the dactylus of those appendages. Other limbs, such as the 2nd maxillipeds in some groups (Bauer, 1989) and 3rd maxillipeds, can groom the anterior regions of the carapace (Fig. 2), which is where respiratory and sensory organs and appendages are located.

Fossilized brachyurans have been observed with epibionts on external epicuticular or exocuticular surfaces (Waugh *et al*., 2004; Robin *et al*., 2017). Epicuticle is the thin exoskeletal material that lies atop underlying procuticle (Fig. 3). The epicuticle is the surface to which epibionts adhere. Epicuticle can degrade during the life of the host, and after death, which reveals the exocuticle (Waugh, 2004). If the epicuticle is eroded during life, epibionts may adhere to the exocuticle.

Several factors prevent epibionts from being commonly fossilized. These include intrinsic factors such as molting, burrowing, and grooming behaviors, and extrinsic factors which include taphonomic processes related to brachyuran cuticle and its tendency to degrade or dissolve after the host has perished (Robin *et al*., 2017). Fossil decapods can be preserved inside concretions which can lead to bias in the sampling of crabs infested with epibionts. Often, when a concretion is split, planes of weakness lie between internal cuticle laminations which can separate the epicuticle and exocuticle from the underlying endocuticle (Fig. 4). This can prevent epibiont recognition on the resulting concretion part and counterpart (Waugh *et al*., 2004). There are rare cases where the part and counterpart of a concretion will split with little degradation of the epicuticle, preserving colonizers and external cuticle layers. Careful fossil preparation can also expose colonized surfaces without destroying exoskeletal material, using methods that include waterblasting techniques (Jakobsen and Feldmann, 2004).

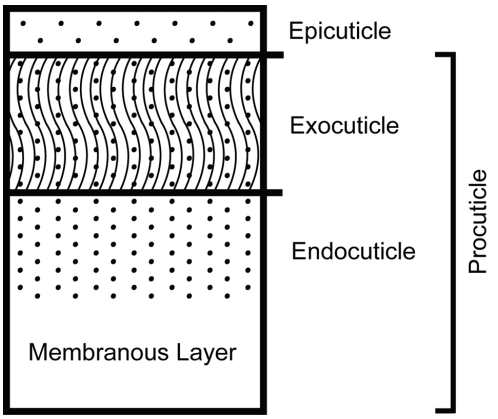


Fig. 3. General cuticle cross-section of crustaceans. Vertical wavy lines = tanned layers; dense circles = heavily mineralized layers; sparse circles = weakly mineralized layers (modified from Plotnick, 1990).

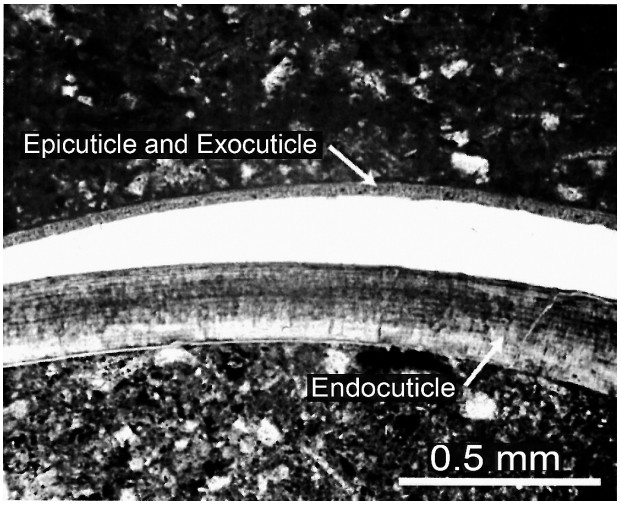


Fig. 4. Thin section of the part (bottom) and counterpart (top) of the Eocene crab *Orbitoplax tuckerae* Schweitzer, 2000, which shows epicuticle and exocuticle together having separated from endocuticle when this concretion split (Waugh *et al*., 2004).

Meticulous preparation uncovered epibionts on the brachyurans preserved in concretions that are the subject of the present study.

The purpose of this study is not to provide a comprehensive coverage of epibiont occurrences on crabs, but to expand upon the current understanding of the effects of grooming on epibiont settling, the variation of grooming potential in various crab taxa, and the different patterns of *in-vivo* and *post-mortem* settlement. The range of motion for several modern paddle-bearing and non-paddle-bearing brachyuran specimens was analyzed to determine the extent to which the appendages of each species could efficiently groom regions of the dorsal and anterior carapace. Modern species were utilized as analogues for eight fossil brachyuran specimens arrayed in four, concretion-preserved species that were collected by one of us (BAT) and his colleagues from marine sedimentary rocks of northwest Oregon and southwest Washington. Careful preparation ensured the conservation of external cuticle layers and polychaete worm tubes or barnacles that had attached to various regions of the carapace. The fossil crabs were then examined in order to determine whether the species in question could have been able to remove epibionts that had colonized regions of the carapace, distinguishing *in-vivo* and *post-mortem* infestation. Additionally, this study permits a better understanding of general body grooming among paddle-bearing and non-paddle bearing brachyurans.

Previous work

Grooming behaviors related to morphological structures of decapod crustaceans were scrutinized by Bauer (1981, 1989). Natant decapods that include shrimp and prawn species were found to exhibit more efficient grooming behaviors relative to brachyurans, for which grooming is generally poorly developed. Bauer (1981) determined that species with less intense grooming pressures may have developed antifouling mechanisms which are not related to appendage morphology. The antifouling abilities of decapod appendages were studied by Bauer (1989), who recognized the limited grooming potential of limbs among brachyurans, in that members of this group possess few structures specialized for removing epibionts. In addition, cleaning of the gills and antennae was recognized among modern crabs. The present analysis expands on studies conducted by Bauer in that the ranges of motion of modern brachyuran appendages are considered for their potential in removing colonizing organisms from the dorsal and ventral carapaces of fossilized specimens.

Geologic setting

Specimens of the four brachyuran crab species under study were collected from marine sedimentary rocks that range from middle Eocene to Miocene in age. From oldest to youngest, the formations are the Cowlitz Formation of Washington County, Oregon; the Keasey Formation of Columbia County, Oregon; the Lincoln Creek Formation of Wahkiakum County, Washington; and the Astoria Formation of Lincoln County, Oregon. All four units occur in stratigraphic succession in northwest Oregon and southwest Washington (Fig. 5). However, the uppermost Keasey Formation of Oregon is a stratigraphic correlative of the lower Lincoln Creek Formation of Washington (Fig. 6) (Armentrout, 1987).

The oldest crab specimen in the present study originates from the middle Eocene Cowlitz Formation of Washington County (Oregon), which unconformably overlies the Yamhill

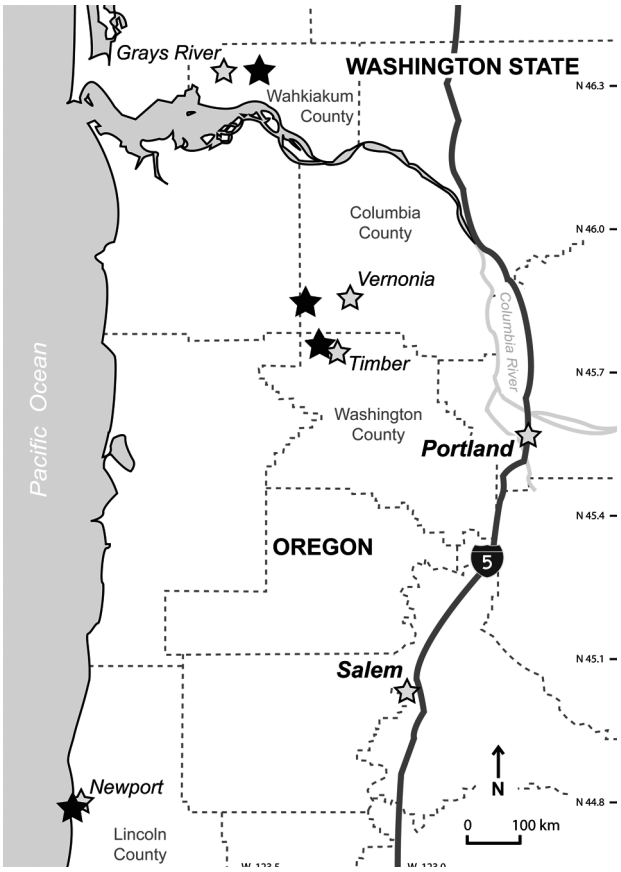


Fig. 5. Map of southwest Washington State and northwest Oregon. Towns are indicated by light stars; specimens were excavated from areas indicated by a black star.

Formation and Tillamook Volcanics. The formation is composed of micaceous to basaltic siltstone and sandstone that are both marine and nonmarine in origin and likely indicate a warm, subtropical environment (Armentrout, 1987). Easterly outcrops more likely represent deltaic environments while open-marine strata crop out to the northwest. Specimen UOMNCH F-66375 was collected in Oregon from the Cowlitz Formation of late Eocene age, about 3 miles northwest of Timber, Washington County (Oregon), in a sequence of interbedded calcareous and volcanic sandstones (Van Atta, 1971).

Overlying the Cowlitz Formation are mudstones and siltstones of the upper Eocene Keasey Formation, from which the majority of crab specimens under investigation were collected. The unit is thick, consisting of approximately 700 meters of fossiliferous, gray, deep-marine, tuffaceous siltstone, sandstone, and massive mudstone, with the uppermost 50 meters comprising calcareous beds and siltstone concretions (Prothero and Hankins, 2000). Specimens UOMNCH F-65952, F-66372, F-66373, F-66374, and T185, were collected as float or were pried from siltstone sediments as concretions from various sites in the Nehalem River drainage area near Rock Creek, within 10 miles of Vernonia, Columbia County (Oregon).

Only one specimen, T246, was collected from lower Oligocene deposits (Prothero and Armentrout, 1985) of the lower part of the Lincoln Creek Formation near Fossil Creek in Wahkiakum County (Washington), about 9 kilometers east of the town Grays River. These rocks are correlative with those of the Keasey Formation from northwest Oregon (Armentrout, 1987).

The youngest unit under consideration is the lower Miocene Astoria Formation, which crops out in Starfish Cove near the city of Newport, Lincoln County (Oregon), from which specimen UOMNCH F-66376 was collected. The Astoria Formation is composed of fossiliferous fine- to medium-grained volcaniclastic and marine siltstone and sandstone, with micaceous and calcareous beds that locally contain calcareous concretions, some containing crabs and other large marine fossils, and sulfide nodules (Rau, 1981; Moore, 1983; Prothero *et al*., 2001).

Material and methods

Brachyuran crabs comprising four species were prepared and made available by Mr. Greg Gentry, Andrew Bland, and one of us (BAT). These were collected from four formations in northwest Oregon and southwest Washington. Measurements were taken using digital metric calipers with an accuracy of 0.01 mm. Each specimen was photographed using a Nikon D70s camera. Microsoft Excel was utilized for morphometric calculations of both crabs and serpulid worms. Photographs were edited using Adobe Photoshop CS3 and diagrams showing the carapace regions that can be efficiently groomed by portunoid and non-portunoid crabs were created using Adobe Illustrator CS2 graphics software. Modern specimens from the KSU Geology Department spirit collection including three portunids, two cancrids, and one geryonid preserved in 70% ethanol were analyzed for degree of movement for each appendage.

Institutional abbreviations - UOMNCH University of Oregon Museum of Natural and Cultural History Condon Collection, Eugene (Oregon, USA).

Results

A total of eight crab specimens were studied from sediments in northwest Oregon and southwest Washington. These crabs comprise four species belonging to four families, including three specimens of the tumidocarcinid *Pulalius vulgaris* (Rathbun, 1926); one mathildellid (*Branchioplax washingtoniana* Rathbun, 1916); one varunid (*Globihexapus paxillus* Schweitzer and Feldmann, 2001); and three specimens of the macropipid *Megokkos macrospinus* (Schweitzer, Feldmann, Tucker, and Berglund, 2000), which is the only portunoid species in the collection. This taxonomic placement is based on the dactylus of the fifth pereiopod that is modified

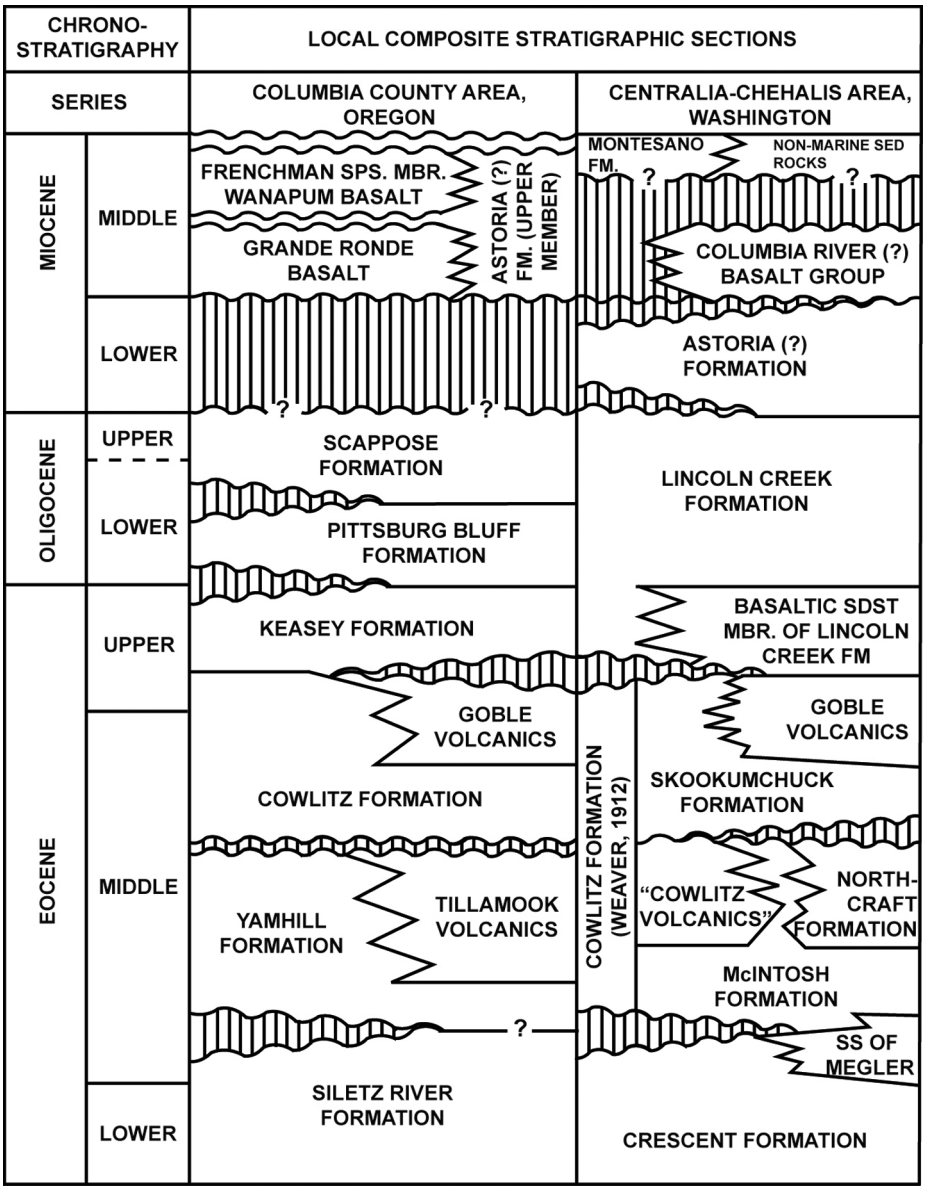


Fig. 6. Stratigraphic sections of the rocks exposed from Columbia County, Oregon, and correlative sections from the Centralia-Chehalis area, Washington (modified from Armentrout, 1987).

into a paddle-like segment used for swimming (Schweitzer and Feldmann, 2000a) or burrowing. One specimen of *P. vulgaris* from the Lincoln Creek Formation of Washington bears an exposed dorsal carapace that had been colonized by epibionts. This specimen also has an exposed ventral carapace (Fig. 7), while *G. paxillus* possesses only an exposed venter; neither specimen shows any indication that the ventral carapaces were colonized by epibionts. All other crabs, excluding *B. washingtoniana*, which lacks epibionts, were colonized by polychaete worms or barnacles on the dorsal carapace; the venters were unavailable for analysis as specimens could not be further prepared by us.

Morphologically, *Branchioplax washingtoniana* and *Pulalius vulgaris* possess similar form and carapace regions. Pereiopods in both species are walking appendages, and none has been modified for swimming as in portunoids. *Globihexapus paxillus* is likewise not a swimming crab, as it possesses only walking pereiopods.

Modern portunid, cancrid, and geryonid crabs were grouped as "paddle-bearing crabs" or "non-paddle-bearing crabs" and were utilized as modern proxies for the four extinct species represented in the present study. The modern portunids studied bear paddle-like appendages much like *Megokkos macrospinus*, while modern non-paddle-bearing crabs were used as analogues for the extinct walking crabs *Pulalius vulgaris*, *Globihexapus paxillus*, and *Branchioplax washingtoniana*. Each modern crab specimen was manipulated to determine the extent of their appendage mobility and whether or not the dorsal or anterior carapace could be efficiently groomed in each group. The limb mobility described herein involves that of the 3rd maxillipeds, chelipeds, and four additional pereiopods,

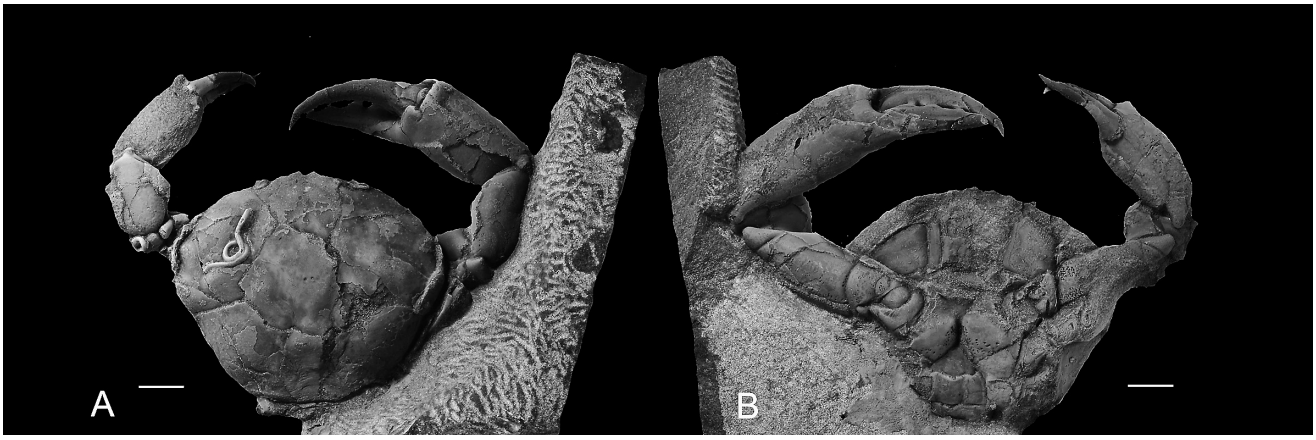


Fig. 7. *Pulalius vulgaris*, specimen T246, in dorsal (A) and ventral (B) view, in the collection of Bruce Thiel. Scale bar = 1 cm.

which are appendages whose functions may include grooming. Although the branchial chambers are common substrates for epibionts, they were omitted from the present study because they are unlikely to be exposed in fossils (Waugh *et al*., 2004).

Three modern portunoid specimens belonging to the following species were analyzed: the portunids *Charybdis japonica* (A. Milne-Edwards, 1861), and *Callinectes sapidus* Rathbun, 1896, and the carcinid *Ovalipes catharus* (White, 1843), all of which bear paddles. Not all portunoids exhibit paddles on the fifth pereiopods, but those examined in the present study do.

In *Charybdis japonica*, the 3rd maxillipeds bear grooming setae on the carpus, propodus, and dactylus, and they can be manipulated to reach the eye using the propodus and dactylus, and can extend distally from the medial line to just below the eye, and proximally across the structure containing the mouthparts, also referred to as the buccal frame. The antennules, which bear olfactory setae (Bauer, 1989) can be lowered to reach the 3rd maxillipeds. The cheliped can be manipulated to the venter on the opposite side, where it can reach up to the 5th thoracic sternite. However, the cheliped cannot extend dorsally, except just above and between the eyes in the frontal region. The 2nd pereiopod can slide against the cheliped merus, but it cannot reach the dorsal carapace. It can also flex toward the pleonites and across the ventral carapace, but as the pereiopods are achelate and do not possess setae, they likely do not function well as antifouling appendages. The 3rd pereiopod can only effectively reach the anterior sternites on the side to which that walking leg is attached, while the 4th pereiopod cannot reach the ventral carapace at all. The 5th pereiopod bears a paddle on the dactylus, and functions as a swimming or burrowing appendage. It is the only limb that can effectively lie across the dorsal branchial regions and reach the hepatic and orbital regions above the eye. The propodus and dactylus of each paddling leg exhibit setae that can be used as a brush for antifouling measures on the dorsal carapace.

Ovalipes catharus is similar to *Charybdis japonica* in many ways, except that the 3rd maxillipeds can extend slightly laterally beyond the orbital region along the anterolateral margin, and they bear setae that are larger and more dense than those exhibited by the 3rd maxillipeds of *C. japonica*. They are long enough to groom the eyes and antennules effectively. Additionally, the 5th pereiopod paddles of *O. catharus* are the only appendages that can effectively lie across the dorsal branchial regions and reach the hepatic regions. However, they may be less effective than the paddle of *C. japonica* in terms of grooming the hepatic region due to possessing smaller setae.

Callinectes sapidus is another portunid whose 3rd maxillipeds can brush across the eyes, antennules, the overlying orbital region, and the buccal frame, as well as extend to the second anterolateral marginal spine from the orbital region using the dactylus and propodus on those appendages. The cheliped of *C. sapidus* can reach between the orbital regions to the rostrum, but can be manipulated only to the buccal frame and above it, and not below the buccal frame or to the dorsal carapace (Fig. 9B). Pereiopods 2 through 4 can curl inward toward the ventral carapace but they cannot easily reach the venter. These can only extend laterally and distally from the body of the crab, and are not capable of reaching the dorsal carapace. The 5th pereiopod of *C. sapidus* bears a paddle on the dactylus and is the sole appendage that can effectively lie across the dorsal carapace; however, unlike *Charybdis japonica* or *Ovalipes catharus*, it cannot reach the hepatic region, or the proximal regions beyond the branchial lobe and epibranchial margins. The merus, carpus, propodus, and dactylus of the 5th pereiopod bear setae that likely act as an effective grooming mechanism in regions posterior to the hepatic that include the branchial lobe, epibranchial, mesobranchial, posterolateral, and metabranchial regions (Fig. 8).

Two modern species belonging to the family Cancridae were examined: *Metacarcinus novaezelandiae* (Hombron

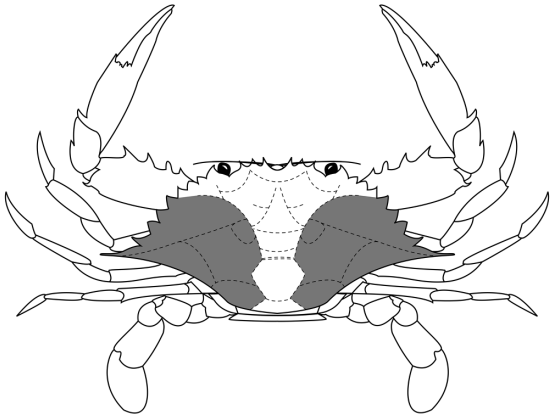


Fig. 8. Diagram of the dorsal carapace of *Callinectes*. Areas in dark gray can be groomed by the setae along the merus, carpus, propodus, and dactylus of the 5th pereiopod appendages.

and Jacquinot, 1846), and *Cancer irroratus* Say, 1817. Neither of these bears paddling appendages.

The 3rd maxillipeds of *Metacarcinus novaezelandiae* do bear setae, but they are short and sparse. The carpus, propodus, and dactylus, of the 3rd maxillipeds have difficulty extending to the eye, but the antennules can be lowered for grooming. The chelipeds can reach the eyes, but are unable to extend above or between them. All other pereiopods (2 through 5) can only slide against the ventral carapace, but are achelate and lack setae for grooming. None can make contact with the dorsal carapace at all. All are walking legs, including the 5th pereiopod.

The specimen of *Cancer irroratus* examined was inhabited by algae and 2–3-mm-large bivalves, particularly between the joints of the cheliped and along the length of the first pereiopod ventral surface of the merus. Many of the other pereiopods, as well as the ventral, and particularly dorsal carapace have been colonized by bryozoans. The area around the buccal frame that includes the left and right anterior carapace up to the second anterolateral spine is unfouled. This groomed area is within reach of the left and right 3rd maxillipeds, and the uncolonized portions also mimic the shapes of these appendages (Fig. 9). The 3rd maxillipeds can sweep sideways about 5 mm to the left and right, and may have prevented the growth of algae on either side of each appendage; however, the antennae and antennules are missing from the specimen. Also unfouled are the eyes and the area between them that includes the rostrum; the 3rd maxillipeds are not long enough to extend to the eyes. The propodus and dactylus of the 3rd maxillipeds do bear short setae and could thus be used for grooming. The chelipeds can reach the eyes, but not above or between them. Pereiopods 2 through 5 have a very limited range of motion ventrally and cannot be manipulated to make contact with the ventral carapace at all. Most come within 10–12 mm of reaching the venter, and none can be manipulated dorsally. The 5th pereiopod is a walking limb and does not bear a paddle.

One modern geryonid species, *Chaceon quinquedens* (Smith, 1879), was examined. This taxon, like the cancrid crabs, exhibits only walking limbs and does not possess paddles. Unfortunately the specimens described lacked the 3rd maxillipeds and therefore the extent to which they can groom could not be determined. The chelipeds can easily make contact with the buccal frame and associated mouth parts, as well as the eyes, but strain to reach between the eyes. Additionally, they cannot be manipulated dorsally, or posterior to the eyes along the anterolateral margins. Pereiopods 2 through 5 cannot be manipulated dorsally or ventrally, and can only extend posterolaterally and away from the carapace.

While the goal is to distinguish areas on a crab that can be groomed, it is evident that different taxa possess varying carapace and appendage morphologies as well as diverse ranges of motion (see also Bauer, 1989). Therefore, the

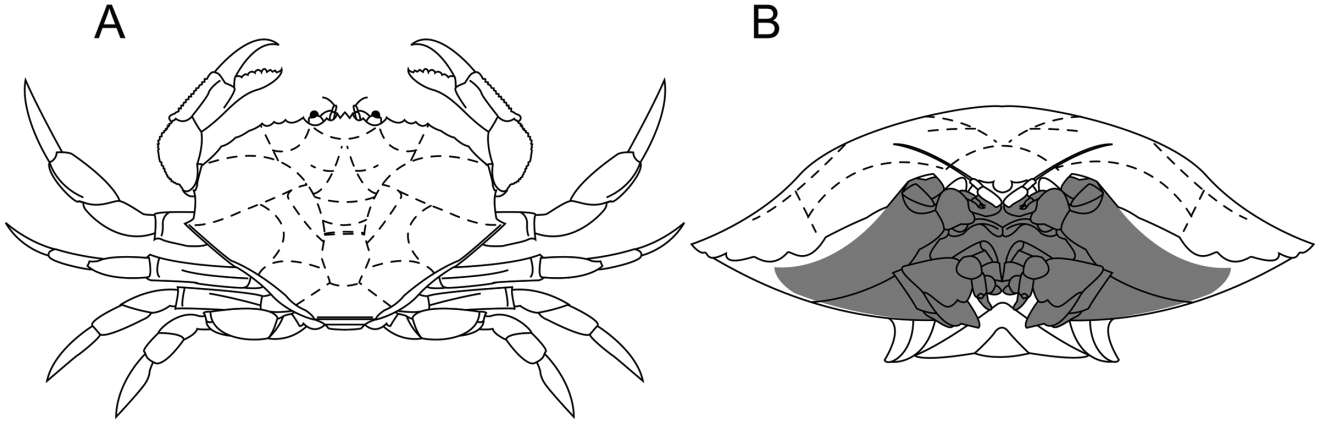


Fig. 9. Diagrams of the dorsal (A) and anterior (B) carapace of *Cancer*. Areas in gray are within range of appendages for grooming, and areas in white are not within reach of appendages for grooming. B) similarly reflects the ranges of the 3rd maxillipeds and chelipeds as antifouling mechanisms on the anterior carapace for the portunid crab *Callinectes*.

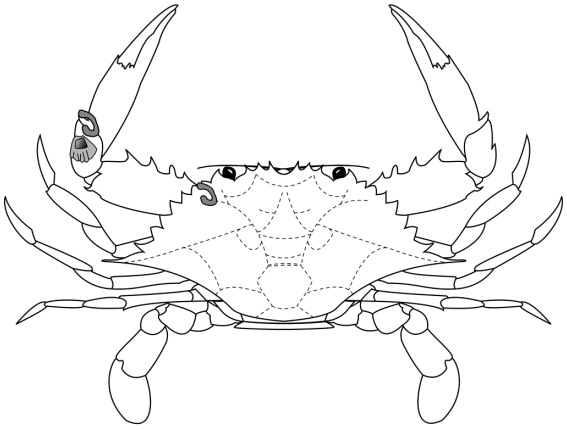


Fig. 10. A diagram using the carapace structure of *Callinectes* as a proxy for fossilized portunoids, showing the total number and type of epibionts found on dorsal regions of all specimens of *Megokkos macrospinus*.

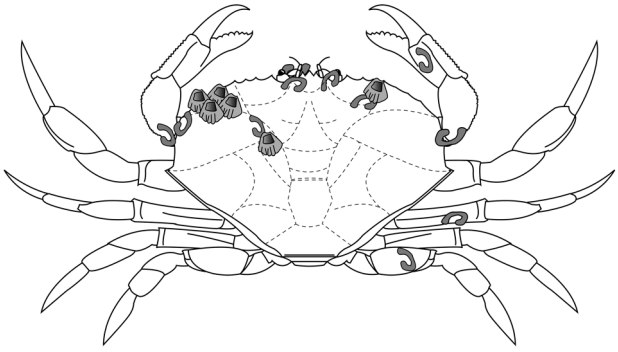


Fig. 11. A diagram using the carapace structure of *Cancer* as a proxy for fossilized non-paddle-bearing crabs, showing the total number and type of epibionts found on dorsal regions of the carapace for all three non-paddle-bearing species studied.

areas of a crab that can be effectively groomed are not constant across extant or extinct taxa belonging to the same families or superfamilies. Consequently, it is not appropriate to use one species or genus of crab to represent different genera for a clear understanding of antifouling mechanisms used across regions of a carapace. However, in general, paddle-bearing portunoids are capable of maneuvering the 5th pereiopods anteriorly and across the dorsal carapace up to the epibranchial and sometimes hepatic regions, though they cannot always be directed toward the medial carapace including the protogastric and mesogastric regions. Additionally, the 3rd maxillipeds, and sometimes the 2nd maxillipeds of some decapods have the ability to grasp and groom the distal segments of the pereiopods (Bauer, 1989), but none of the pereiopods (other than the chelipeds) of modern brachyurans could be manipulated anteriorly to this extent. Bauer (1981, 1989) reported that cheliped grooming is rarely described in brachyurans; they are poorly adapted for grooming, which is consistent with our findings.

Megokkos macrospinus is the only fossil portunoid examined herein, and epibionts were noted on three specimens (Fig. 10). The carapace of specimen UOMNCH F-66374 was infested with one polychaete worm tube. However, the fossil is poorly preserved and it is difficult to determine the regional orientation of the epibiont, and thus, whether or not the crab might have been fouled on a carapace region that could have been groomed by its 5th pereiopod paddle. One epibiont that is too poorly preserved to determine its taxonomic assignment was attached to the carpus of the left lateral cheliped of specimen UOMNCH F-66372. It is unlikely that this epibiont could have been removed from this location on the cheliped, as the grooming limbs of examined portunoids do not reach anteriorly to that extent. Finally, specimen UOMNCH F-66373 is infested by two polychaete worm tubes; one fouled the left cheliped lateral joint between the propodus and carpus. The second worm tube is on the left hepatic region of the dorsal carapace. It was determined by us that some paddle-bearing portunoids have the ability to groom the hepatic regions using their 5th pereiopod, while others possess shorter 5th pereiopods and cannot extend beyond the epibranchial region.

Fossil crabs that do not possess paddle-like appendages were also examined and described based on the locations of epibionts on the carapace (Fig. 11). Three specimens of *Pulalius vulgaris* exhibit epibionts on the dorsal carapace, and one of these three, T246, had an exposed venter; however, epibionts were not found on the ventral surface of this specimen. Four polychaete worm tubes was observed, one on the left cheliped distal joint between the merus and carpus. One broken worm tube was on the anterolateral margin of the left epibranchial region, while another is found on the proximal margin of the left epibranchial region. The fourth worm tube extends along the merus of the right 3rd pereiopod. Specimen T185 has seven polychaete worm tubes scattered across its carapace. Three of these colonized the anterior carapace, including the right orbital, the left frontal that crosses into the side of the left orbital, and the left eye and suborbital region. Another worm tube extends across the posterior right orbital. One is found broken on the right cheliped propodus, and another is curled on the posterolateral merus and oriented toward the 4th pereiopod. The last worm tube inhabited the 5th pereiopod merus. The potential to remove worm tubes that colonize the limbs is low as no appendages have the mobility or morphology to groom these areas. The last specimen of *P. vulgaris*, UOMNCH F-65952, bore six epibionts that are all balanid barnacles. Four are found covering the left hepatic, one is on the anterior left branchial, and one is on the right hepatic region. There are no epibionts on the limbs. The last two non-paddle-bearing crab fossils are *Branchioplax*

Table 1. Morphological parameters of crab specimens and observed macro-epibionts.

SPECIMENS	UOMNCH F-65952	Bruce Thiel T246	Bruce Thiel T185	UOMNCH F-66375	UOMNCH F-66376	UOMNCH F-66372	UOMNCH F-66373	UOMNCH F-66374
Locality and Formation	**Near the Nehalem River, Columbia County, Oregon USA; Keasey Formation**	**Wahkiakum Co. Washington State, USA; Lincoln Creek Formation**	**Columbia County, Oregon, USA; Keasey Formation**	**Washington Co., Oregon, USA UO 4670 Robinson Creek; Cowlitz Formation**	**Lincoln County, Oregon USA UO 4671 Starfish Cove, Newport; Astoria Formation**	**Columbia County, Oregon, USA UO 4669 Rock Creek; Keasey Formation**	**Columbia County, Oregon, USA UO 4669 Rock Creek; Keasey Formation**	**Columbia County, Oregon, USA UO 4669 Rock Creek; Keasey Formation**
Age	Late Eocene	Oligocene	Late Eocene	Late Eocene	Miocene	Late Eocene	Late Eocene	Late Eocene
Species	***Pulalius vulgaris***	***Pulalius vulgaris***	***Pulalius vulgaris***	***Branchioplax washingtoniana***	***Globihexapus paxillus***	***Megokkos macrospinus***	***Megokkos macrospinus***	***Megokkos macrospinus* (?)**
Orientation	Dorsal	Dorsal and ventral	Dorsal	Dorsal	Ventral	Dorsal	Dorsal	?
Carapace Length (mm)	69.78	59.96	64.26	28.24	11.56	25.20	26.24	-
Carapace Width (mm)	82.84	64.65	72.46	31.37	13.92	38.46	36.17	-
Left Claw Length (mm)	-	32.03	22.18	11.80	4.90	8.84	11.57	-
Left Claw Width (mm)	-	14.39	12.85	8.13	3.29	4.27	7.67	-
Right Claw Length (mm)	41.52	31.63	34.07	7.72	4.99	11.05	-	-
Right Claw Width (mm)	31.13	20.56	19.28	4.32	2.90	11.37	-	-
Epibiont Type	**Barnacles**	**Polychaete worm tubes**	**Polychaete worm tubes**	**None**	**None**	**Barnacle?**	**Polychaete worm tubes**	**Polychaete worm tube**
Epibiont Number	6.00	4.00	7.00		-	1.00	2.00	1.00
Epibiont avg diameter (mm)	11.66	1.59	2.16		-	6.18	2.25	2.96
Epibiont avg height (if barnacle) (mm)	6.56	-	-		-	3.03	-	-
Epibiont length (if worm tube) (mm)	-	37.67	31.36	-	-	-	10.77	16.61

washingtoniana, exhibiting an unfouled dorsal carapace, and *Globihexapus paxillus*, the smallest crab studied herein (carapace length 11.56 mm, see Table 1) which exposed only an unfouled venter.

Discussion

In marine environments, the rigid carapaces of decapods and other arthropods are commonly colonized by the larvae of sessile organisms such as tube-building worms (serpulids) and thoracican crustaceans (McGaw, 2006). The abundance and prevalence of infesting organisms relate to several factors associated with the host itself, including the ontogenetic stage; general physiology; behavioral patterns (including burrowing, molting, and grooming); and sex (Becker, 1996).

Dick *et al*. (1998) observed an increase in frequency of occurrence and average number of epibionts linked to greater age of crabs, as determined by carapace size. Colonization can be related to general host size and age, as crabs in late ontogenetic stages usually are larger than younger individuals of the same species and are more frequently fouled than those that are smaller. For example, balanid (acorn) barnacles have been known to settle more frequently on large crustaceans than their smaller counterparts (Becker, 1996). The smallest fossil specimen studied is the species *Globihexapus paxillus* which is a non-paddle-bearing crab and shows only a preserved venter not colonized by epibionts. Representatives of *G. paxillus* have been described exhibiting diminutive overall carapace size as adults (Schweitzer and Feldmann, 2001). Specimens of *Megokkos macrospinus* in the present study might also be mature, because carapace lengths were between 22.9 and 28% larger on average than carapace lengths of 4 described *M. macrospinus* specimens in the literature (Schweitzer *et al*., 2000). The two largest specimens studied belong to *Pulalius vulgaris* and yield the most epibionts (6 barnacles and 7 serpulid worm tubes, respectively), which is consistent with increased size being positively correlated with increased number of epibionts in crustaceans (Table 1). It can be argued that the specimens of *Pulalius vulgaris* are likely mature crabs whose carapaces are prone to fouling due to infrequent molting behaviors. Indeed, they are between 41.8 and 65% larger than a sizeable specimen described by Schweitzer (2000), indicating late stages of ontogeny. The only other species in the genus, *Pulalius dunhamorum* Schweitzer, Feldmann, Tucker & Berglund, 2000, differs from *P. vulgaris* in several ways, including possessing a rounder, more ovate, and less vaulted carapace. Average measurements of the length and width of nine specimens of *P. dunhamorum* are less than half the size of the fossils of *P. vulagris* in question (Schweitzer *et al*., 2000), which may provide further evidence that those studied herein are adults. Finally, specimen UOMNCH F-66375 of *Branchioplax washingtoniana* is more than twice the size of a juvenile described by Schweitzer (2001), and is within the parameters of the average length (30.2 mm) and width (35.7 mm) of 70 specimens of *B. washingtoniana* (Schweitzer, 2000), indicating the specimen herein was also either an older juvenile or mature. All the crabs in the present study are in late stages of ontogeny based on the presence of two groups of epibionts on the carapaces as well as the abundance of infesting organisms on each crab, in addition to general carapace size. Furthermore, the fossil record tends to be biased toward adult specimens as juveniles are more delicate and less likely to be preserved.

Throughout ontogeny, crabs undergo ecdysis, which temporarily removes colonizers with molted cuticle from the carapace until the epicuticular carapace surface becomes settled again. The intermolt stage of crabs larger than 4.5 cm in width has been observed to last at least 30 days; some epibionts have even synchronized fouling behaviors with molting of arthropod hosts (Becker, 1996). Polychaete larvae tend to prefer settling upon surfaces with a bacterial film, which may take several months to form on crabs, indicating extended intermolt stages or hosts that have reached maturity (McGaw, 2006). Because molting is a frequent process in juveniles but becomes less common until just after a crab has reached puberty, mature crabs must rely on alternative antifouling mechanisms. These include chemical defense mechanisms, as in some decapods that contain poisonous antifouling substances in the exoskeleton which may also prevent predation, as observed in catechol repellants produced by crayfish (Becker, 1996).

Some crabs exhibit frequent burrowing behavior, in which case epibionts are less likely to colonize buried surfaces as they are less favorable for epizoic growth (Bauer, 1981; Dick *et al*., 1998). Host burrowing behaviors likely have many consequences for colonizing organisms, including reduced time for settling upon exposed carapaces, sediment abrasion on epibiont surfaces (Key, Jr. *et al*., 1997), and oxygen depletion due to exposure to fine sediments (Becker and Wahl, 1996). Although many portunoid species are recognized for having paddling appendages that are used for swimming, many paddle-bearing crabs, including the portunoids *Callinectes sapidus* (Frey *et al*., 1984; Key, Jr. *et al*., 1997) and *Ovalipes catharus*, are known to utilize their streamlined and smooth carapaces and flattened pereiopods for rapid burial in order to seek temporary refuge or concealment from predators (Frey *et al*., 1984). The 5th pereiopod, which is paddle-shaped, assists with a backward burrowing motion into the substrate (McLay and Osborne, 1985). The fossil portunoid *Megokkos macrospinus* may have used its 5th pereiopod paddles as burrowing

appendages, which would also have reduced the chance that a carapace would become infested. However, each of the studied *M. macrospinus* fossils was colonized by epibionts. In specimen UOMNCH F-66373, infestation of the hepatic region and of the joints between pereiopod segments could indicate the individual had perished before it was colonized due to no longer exhibiting burrowing behaviors that would otherwise have prevented fouling. Although there is little evidence to suggest that the non-paddle-bearing fossil species *Globihexapus paxillus* and *Pulalius vulgaris* were burrowing crabs, the tumidocarcinid *P. vulgaris* bears morphological features similar to the mathildellid *Branchioplax washingtoniana* (Schweitzer *et al*., 2000), which may have exhibited burrowing behavior in females (Conkle and Schweitzer, 2005). It could be argued that *P. vulgaris* was likewise fossorial. One argument against such behavior in *Pulalius vulgaris* is that the carapace may have been too highly vaulted for burrowing, as crabs that burrow tend to possess streamlined, smooth, and flattened bodies (McLay and Osborne, 1985). However, calappid crabs are well-known burrowers with highly vaulted carapaces (Bellwood, 1996), and therefore burrowing behaviors are not dependent on possessing a flattened carapace.

Morphological features commonly used to determine sex among brachyurans include relative pleonal proportions and cheliped size. The pleon is narrow in males compared to females, which possess wide pleons that cover a majority of sternal surfaces. The major cheliped claws in males generally are larger than females of the same carapace size, and the presence of large claws is indicative of sexual maturity in males (Feldmann, 1998). Modern male specimens of *Cancer* have been described with greater epibiont species richness and diversity than females, which are smaller than their male counterparts (McGaw, 2006). Only two fossil specimens studied exposed ventral surfaces, i.e., *Globihexapus paxillus*, which is considered to be mature, and *Pulalius vulgaris* specimen T246, which is also considered to be in a late stage of ontogeny based on an increased right claw size and large carapace (Table 1). The relatively narrow pleon in both specimens indicates these are males. The prevalence and abundance of epibionts on these specimens is more likely related to carapace size, and therefore ontogenetic stage, rather than displaying male morphology. This is because *G. paxillus* lacks epibionts completely and is the smallest brachyuran studied while *P. vulgaris* (specimen T246), possesses the greatest abundance of epibionts on its carapace and is the second largest fossil studied.

In crabs that do not possess efficient grooming behaviors, defense mechanisms against fouling organisms should be expected if a crab is negatively affected, as in cases where disadvantages outweigh benefits (Becker, 1996). Attachment of colonizing organisms can benefit their hosts; for instance, majoid ("decorator") crabs choose epibionts to attach to the carapace for camouflage (Becker, 1996; Becker and Wahl, 1996; McGaw, 2006), as do dromioid ("sponge") crabs, which possess shortened fifth pereiopods that have been modified for carrying sponges or mollusks above the dorsal carapace (Robin *et al*., 2017). The presence of fouling organisms can cause negative impacts on the host as well. Colonization of epibionts may increase the weight an animal must carry, causing the host to expend more energy than is normal, and resulting in a sluggish lifestyle; additionally, fouling organisms may become competitive with the host for food (Becker, 1996). If a host cannot remove epibionts that have established themselves on the joints between pereiopod segments, or across the orbital or frontal carapace subregions, limited mobility or vision may result, respectively. Alternatively, one could argue a crab had died prior to being colonized across such critical carapace locations (Fig. 12). Growth of a polychaete worm tube on the cheliped lateral joint between the propodus and carpus of *Megokkos macrospinus* specimen UOMNCH F-66373 would have prohibited the ability to flex the claw when feeding. Likewise, the cheliped joint between the merus and carpus in *Pulalius vulgaris* specimen T246 was inhabited by a polychaete worm tube that could have impaired the mobility of that appendage. The growth of the other three worm tubes on T246 may have introduced competition with the crab for food or weighed the carapace down, but likely did not otherwise disturb the crab. It is unknown whether the crab was colonized before or after it perished. In cases like specimen UOMNCH F-66372 of *Megokkos macrospinus* where a barnacle attached to the lateral carpus, the location of the barnacle may not have had detrimental effects on the host as it had not colonized a joint. Likewise, the colonization of *Pulalius vulgaris* specimen T185 by polychaete worm tubes across the posterior orbital region and various segments of the 4th and 5th pereiopods likely did not prevent the crab from carrying out vital functions. However, they may have added weight to the carapace or competed for resources. The presence of three worm tubes on T185 might have been detrimental to vision, having colonized areas affecting the left eye. Because two sets of limbs, the chelipeds and the 3rd maxillipeds, are the only appendages that could potentially groom the eyes, it is likely this crab was colonized *post-mortem*; otherwise, its visual abilities would have been severely impaired. In addition to limited mobility and vision, epibionts can increase drag and decrease the swimming ability of portunoid crabs. The fifth pereiopod dactylus of some portunoids exhibits setae that act as effective brushing or antifouling tools, coupled with the ability of these appendages to sweep anteriorly and across the carapace (Bauer, 1981, 1989). The sizeable serpulid that colonized the hepatic region of specimen UOMNCH



Fig. 12. *Pulalius vulgaris*, specimen T185, with serpulid worm tubes that have fouled the suborbital, frontal, and left orbital regions, in the collection of Bruce Thiel. Scale bar = 1 cm.

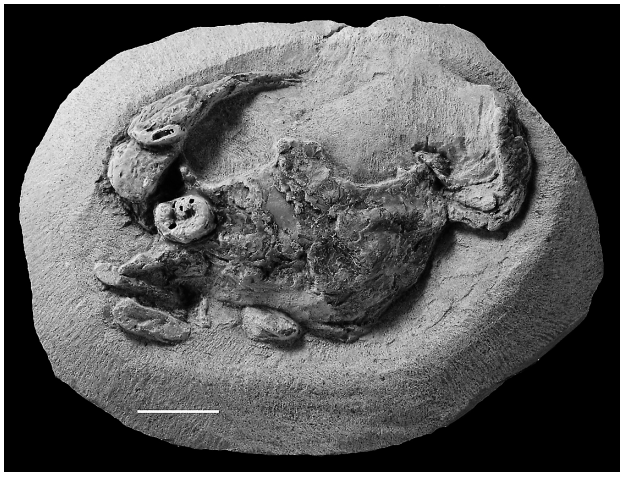


Fig. 13. *Megokkos macrospinus*, specimen UOMNCH F-66373, with serpulid worms. Scale bar = 1 cm.

F-66373, *Megokkos macrospinus*, may have negatively affected the swimming ability of this crab. It is possible that either this individual was fouled after it had perished, or else the presence of this epibiont and the one on the cheliped joint helps to define the range of grooming motion. It can be argued that the presence of these worms would interfere with the mobility of a principal feeding appendage of the animal as well as decrease the streamlined function of its carapace for swimming or burrowing (Fig. 13).

It is also important to consider how quickly epibionts grow after settling upon a living carapace or carcass. Aquarium studies have indicated rapid serpulid worm growth rates of 2.5 mm per day within the first three days of colonization, and 1.3 mm per day for four weeks subsequently, indicating an exoskeleton could be covered by worm tubes or traces within days or weeks post-molt or *post-mortem* (Feldmann *et al*., 2011). In addition, setal brushes along the tips of pereiopods and mouth appendages are used to remove colonizers from around the respiratory and sensory surfaces (Becker and Wahl, 1996), which can develop microbial fouling within days or weeks (Bauer, 1989).

The types of infesting organisms and carapace subregions upon which they colonize can vary as well. The epibionts that have infested the crabs studied here are barnacles and polychaete worms. Key, Jr. *et al*. (1997) observed that barnacles foul females of the modern portunid *Callinectes* more frequently than males, due to barnacle larvae preferring deeper waters with higher salinity, where females are more prevalent. Barnacles were also found by Key, Jr. *et al*. (1997) to prefer the lateral carapace of *Callinectes* instead of medial regions due to the dorsal surface topography. Likewise *Pulalius vulgaris* (specimen UOMNCH F-65952), exhibits several barnacles fouling primarily the left hepatic subregion in addition to one barnacle on the right hepatic. Barnacles are bulkier than worm tubes, and the weight of four barnacles having colonized the left hepatic alone could have been cumbersome to the host. No appendages of *P. vulgaris* could have efficiently groomed these regions of the dorsal carapace. It remains unclear whether the host died before or after it was colonized by barnacles, but the weight of these fouling organisms could have led to a sluggish lifestyle. However, McGaw (2006) found that the presence of epibionts on the external carapace of some cancrid crabs does not seem to impart physiological disadvantages to the hosts due to carrying an increased load. In general, the hepatic region is the most prone to colonization among examined portunoid and non-portunoid crabs; the left hepatic is more prone to epibionts than the right side, perhaps indicating handedness, or in the case of burrowing crabs, preferential burial orientation. McGaw (2006) described barnacle infestations on specimens of the modern cancrid crab genus *Cancer* and found that they were most abundant on the dorsal surfaces of the carapace and the chelae, and less so on the ventral carapace. Calcareous, tube-dwelling polychaete worms were less abundant on the dorsal carapace and tended to prefer ventral surfaces. The ventral carapace of crabs can be host to epibionts, with some groups even preferentially infesting those surfaces (Gili *et al*., 1993; McGaw, 2006), including some polychaete larvae that are photonegative and prefer surfaces that are less frequently subjected to light (McGaw, 2006). While the venter is not available for study in our crabs except for the unfouled *Globihexapus paxillus* and unfouled venter of *P. vulgaris* (specimen T246), polychaete worms are observed across the frontal and orbital regions of the dorsal carapace and on both chelipeds of the colonized crabs. Interestingly, barnacles and serpulid worm tubes were not observed colonizing the same crabs of the eight specimens studied; however, it is not unusual for crabs to host diverse groups of colonizing organisms (McGaw, 2006). Therefore it is difficult to determine epibiont preference for species because too few specimens of each species were available for study.

Conclusions

Crabs that possess paddles on the fifth pereiopod are more capable of grooming the dorsal carapace than are those without paddles. Fossil specimens with epibionts across the anterior carapace and the eyes were likely colonized *post-mortem*. Paddle-bearing species that were infested on the dorsal carapace could have been colonized *post-mortem*, otherwise epibionts would have reduced the streamlined condition of the carapace used for swimming or burrowing. Crabs without paddles that were colonized on the dorsal carapace may have been encumbered, but it is unknown whether these were fouled *in-vivo* or *post-mortem*. Understanding the extent to which limbs of modern crabs can groom regions of the carapace can generate analogues for fossil species. However, variation within crab species related to different appendage lengths and locations of carapace regions prevents the development of a carapace template for grooming that could be applied to all brachyurans.

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