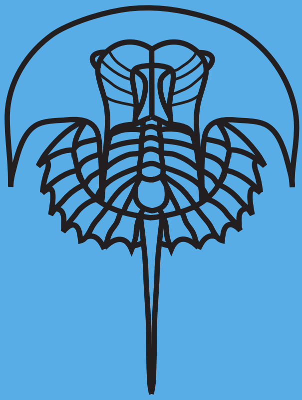

TREATISE ONLINE

Number 178

Part R, Revised, Volume 1: Biotic Interactions

Rodney M. Feldmann and Carrie E. Schweitzer

2024

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas
Lawrence, Kansas, USA

PART R, REVISED, VOLUME 1: TREATISE ONLINE 178:

BIOTIC INTERACTIONS

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Because variation between individuals can be a product of several factors, the analysis of cause and effect can be difficult. A straightforward approach to evaluating causes can be initiated by considering the frequency of occurrence of variation within the population. For example, presence of a single feature or several features different from the typical morphology of the taxon may be the result of symbiotic relationships, disease, or damage. Sexual differences may be reflected in dimorphic morphologies within adult, fully mature individuals. Juvenile males and females may display morphology different from the sexually mature adults. Variation between individuals defines the range of morphology characteristics within the taxon. Causes of variation observable in fossil decapod crustaceans other than individual variations are discussed below.

SYMBIOSIS

Symbiosis embraces a variety of interactions between two dissimilar organisms in close association with one another. Several types of interactions between the host and its symbiont are recognized based upon the cost/benefit value of the host and symbiont (Roughgarden, 1975). Commensal relations do not necessarily provide benefit or detriment to the host and benefit the symbiont. Mutualistic associations benefit both symbionts. Parasitic partnerships benefit the symbiont at the expense of the host (Trilles & Hipeau-Jacquotte, 2012).

Extant decapod crustaceans are subject to a broad spectrum of symbionts, the majority of which are not known to affect the skeletal material of the organisms and are not, therefore, represented in the fossil record. Summaries of symbionts and their effects on extant decapods (Overstreet, 1983; Shields, Williams, & Boyko, 2015; Castro, 2015; Guinot & Wicksten, 2015) document a wide range of organisms, for example bacteria, fungi, barnacles, and isopods, that infect or infest decapods as hosts. However, only a small few result in any evidence that has been recognized in the fossil record. Most symbiotic interactions affect only soft tissue. Results of symbiotic relationships recognizable in the fossil record must have a clear signature on the preserved remains of the organism to document the interaction.

Bopyrids

Bopyrid swellings on the branchial region of decapods are interpreted to be produced by parasitic isopods, most frequently Bopyridae, in the infraorder Epicaridea. First described by Latreille (1802 in 1802–1803), they were subsequently recognized in the caridean shrimp family Palaemonidae in modern-day marine habitats (Bell, 1863). Mc'Coy (1854) was the first to recognize a fossil bopyrid, and Bell was the first to publish an illustration of a supposed fossil bopyrid from the Cambridge Greensand (Bell, 1863, pl. 3,*3*). The specimen, *Notopocorystes stokesii*

Treatise Online is a publication of the Paleontological Institute, The University of Kansas.

Cite: R. M. Feldmann & C. E. Schweitzer. Part R, Revised, Volume 1, Biotic Interactions. Treatise Online 178:1–17, 14 fig. [https://doi.org/10.17161/to.vi.22368].

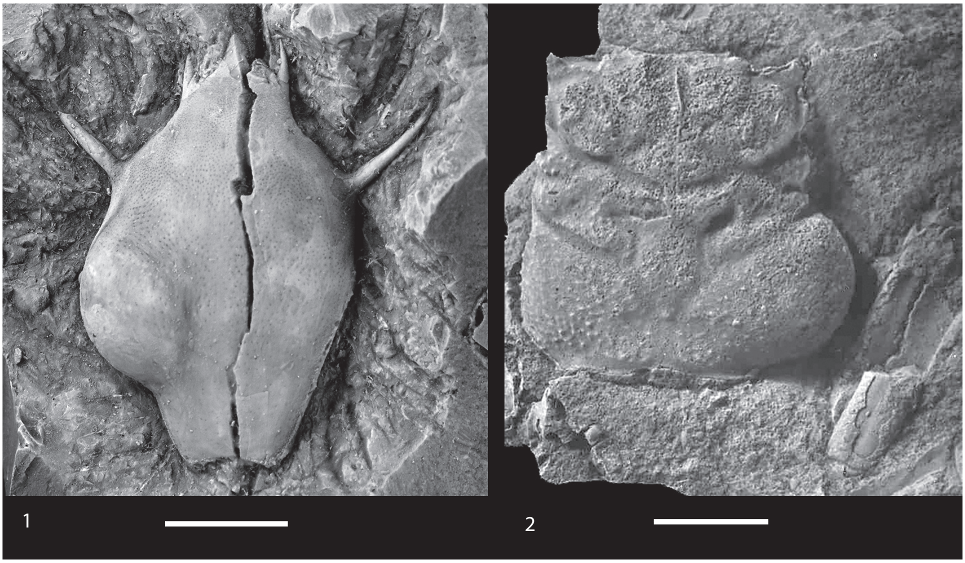

Fig. 1. Branchial swellings attributed to bopyrid isopod parasites. *1*, *Macroacaena rosenkrantzi* (Collins & Rassmussen, 1992), cast KSU D 1813, Maastrichtian, Greenland (new; photo by R. Feldmann); *2*, *Torynomma australis* Feldmann, Tshudy, & Thomson, 1993, holotype, BAS. IN. 2422, Campanian, James Ross Island, Antarctica; scale bars 1 cm (Feldmann, Tshudy, & Thomson, 1993, fig. 27.3).

(Mantell, 1844) (as *Palaeocorystes stokesii*), is a member of the crab group Raninoida which is one of the more heavily infested groups in the Mesozoic. By any measure, bopyrids are the most numerous parasites recorded in the fossil record (Fig. 1).

Klompmaker and others (2018) compiled a list of species with branchial swellings produced presumably by bopyrids and analyzed the frequency of occurrences within genera and within stratigraphic records. Because the isopod responsible for production of the swelling had not been preserved, they erected an ichnotaxon, *Kanthyloma crusta* Klompmaker & others, 2018 for the swelling. Their work followed from similar studies by Markham (1986) and Weinberg Rasmussen, Jakobsen, and Collins (2008). The compilation of Weinberg Rasmussen, Jakobsen, and Collins (2008) revealed that the frequency of occurrence of species with bopyrid swellings within the Mesozoic (Toarcian to Maastrichtian) and that of the Cenozoic (Danian to Pleistocene) is similar. The position of the bopyrids is asymmetrical with more right than left branchial regions infested, and a small number of individuals have swellings on both right and left regions (Weinberg Rasmussen, Jakobsen, & Collins, 2008).

Parasitic Castration

Castration resulting from introduction of a rhizocephalan barnacle to a decapod host has been documented in a wide range of extant decapods (Shields, Williams, & Boyko, 2015); however, the condition has been recognized in the fossil record only once, in a tumidocarcinid crab from the Miocene of New Zealand (Feldmann, 1998). The condition develops as a larval rhizocephalan invests the mantle cavity and gill chamber of the host, feeding upon the soft tissue including the reproductive organs of the host via the haemocoelic spaces (Walker, 2001) by means of tendrils or rootlets extending from the body of the barnacle into the tissue (Reinhard, 1956). Ultimately the reproductive phase of the parasite is manifested as a sac-like externa carried between the sternum and pleon in a manner much like an egg mass. Neither

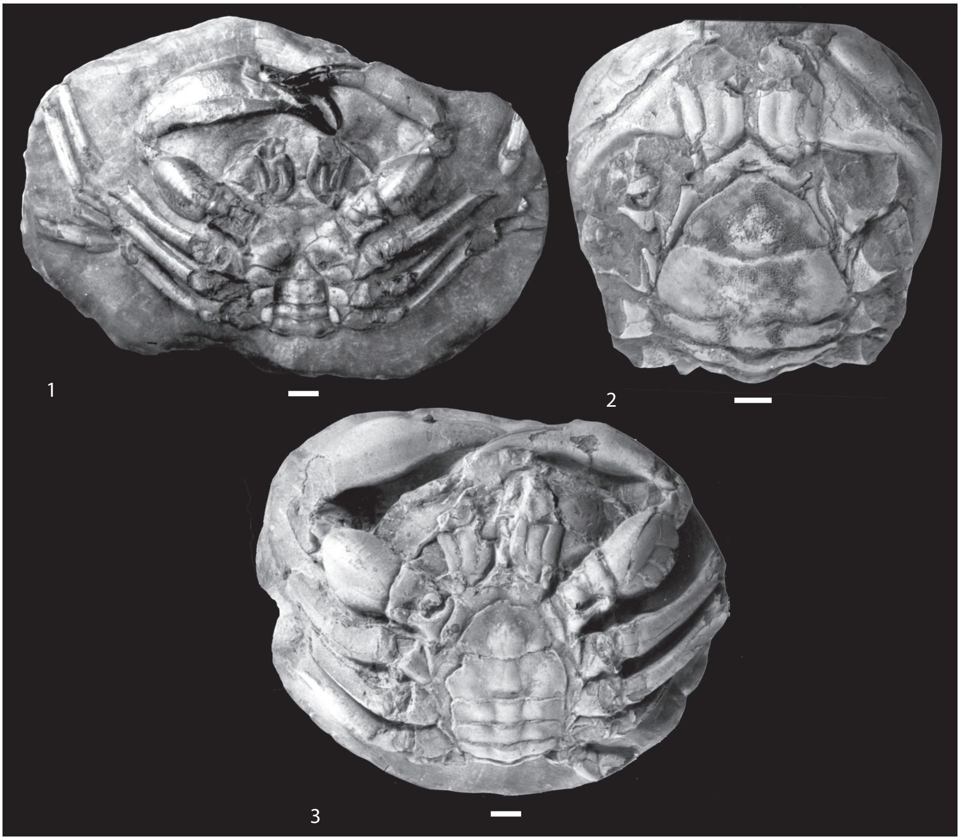

Fig. 2. Feminization of *Tumidocarcinus giganteus* Glaessner, 1960, attributed to a rhizocephalan barnacle; *1*, mature male, private collection of A. Fear, Christchurch, New Zealand; *2*, mature female, A122 from private collection of A. DeBode, Lyttelton, New Zealand; *3*, feminized male, ZFC 274, Canterbury Museum, Christchurch, New Zealand; scale bars 1 cm (Feldmann, 1998, fig. 3.1, 3.2, & 3.4, respectively).

the internal feeding nor the externa of the barnacle directly affect the morphology of the dorsal carapace. The effect of parasitic castration must be interpreted in fossil specimens by changes in features related to secondary sexual characters. In addition to feminization of the male pleon and reduction of cheliped size, the morphology of the cheliped surface is also transformed. Females infected by the isopod do not grow to the same size as unaffected females.

Unlike other forms of parasitism in the fossil record that can be identified in a single individual, parasitic castration can be detected most convincingly by examining a suite of fossil individuals within a population. The condition manifests itself as relatively small females with fully mature pleonal morphology and as males with inhibited male secondary sexual development and female-like pleons. Although these two latter conditions, smaller than anticipated mature females and feminized males, might be evidence of the presence of rhizocephalan parasitism, the most convincing demonstration is when infected individuals can be compared to unaffected individuals within the population (Fig. 2) (Feldmann, 1998).

Although parasitic castration is almost invariably attributed to rhizocephalan barnacles, Inui and others (2021) documented a similar phenomenon in a varunid brachyuran, *Ptychognathus ishii* Sakai, 1939, attributed to an entoniscid isopod, *Entionella* sp.

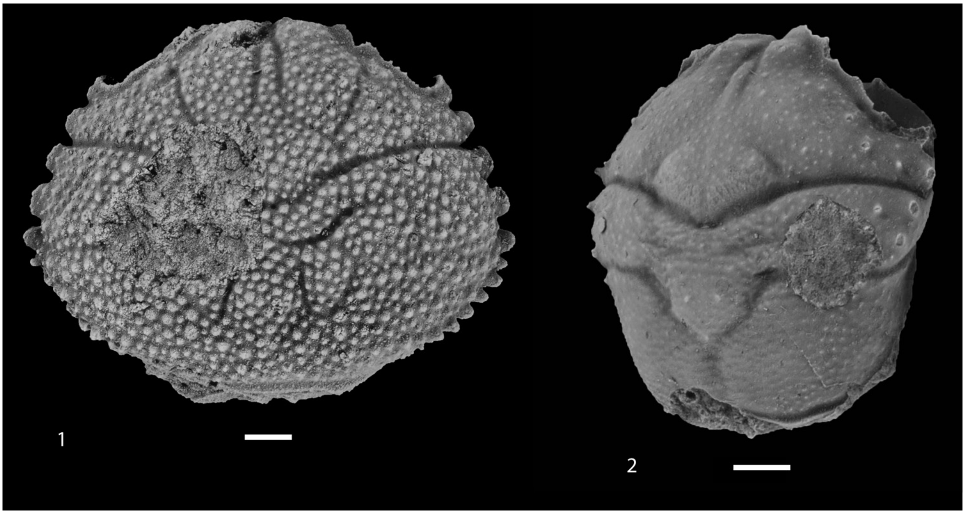

Fig. 3. Shell lesions attributed to chitonoclastic microorganisms. *1*, *Distefania inserta* (Bell, 1863), MAB k2940, Cretaceous of Spain; *2*, *Goniodromites laevis* Van Straelen, 1940, MAB k2499, Cretaceous of Spain; scale bars 1 mm (Klompmaker & others, 2016, fig. 3A, F).

SHELL DISEASE SYNDROME

Cuticle of decapods can be subjected to attack by a variety of bacteria and occasionally fungi in both marine and freshwater environments (Shields, Williams, & Boyko, 2015). Although first described at the beginning of the twentieth century (Happich, 1900), interest in the condition has become more intense in the late twentieth century. The disease occurs at a low frequency in natural populations and increases markedly in polluted and confined populations; hence, the increase in interest by the fisheries industry (Sindermann, 1989).

Although the disease can be produced by a number of chitinoclastic microorganisms (Sindermann, 1989), they all manifest themselves as lesions penetrating the exocuticle and endocuticle of the host. The lesions can be present on all parts of the carapace as well as the chelipeds (Sindermann, 1989; Noga, Smolowitz, & Khoo, 2000) and can grow from a localized region to a broad area. The disease has been reported in extant shrimp, crayfish, lobsters, anomurans, and true crabs. The sole occurrence of shell disease recognized in the fossil record was that of two species of late Albian dromiacean crabs, *Distefania incerta* (Bell, 1863) and *Goniodromites laevis* Van Straelen, 1940), from Spain (Fig. 3) (Klompmaker, Chistoserdov, & Felder, 2016). The specimens are part of a quite diverse, normal marine assemblage setting (Klompmaker, 2013).

PATHOLOGIES

Abnormal Development of Appendages and Carapaces

Presence of abnormal claws on decapods has been known since the seventeenth century. The first published illustrations of the condition appear to be those of Berniz (1671) in which he illustrated a carapace of *Gammarus leprosus* and two isolated claws of *Astaci marini monstrosa*. The *Gammarus* specimen appears to bear a dual, truncated rostrum, and the *Astaci* exhibit a dual fixed finger and deformed dactyl as well as barnacle, serpulid, and bryozoan epibionts.

Subsequently, Rösel von Rosenhof (1755) rendered more realistic illustrations of deformed chelipeds of the crayfish *Astacus astacus* (Linnaeus, 1758), showing a variety of duplications of dactyls and excrescences

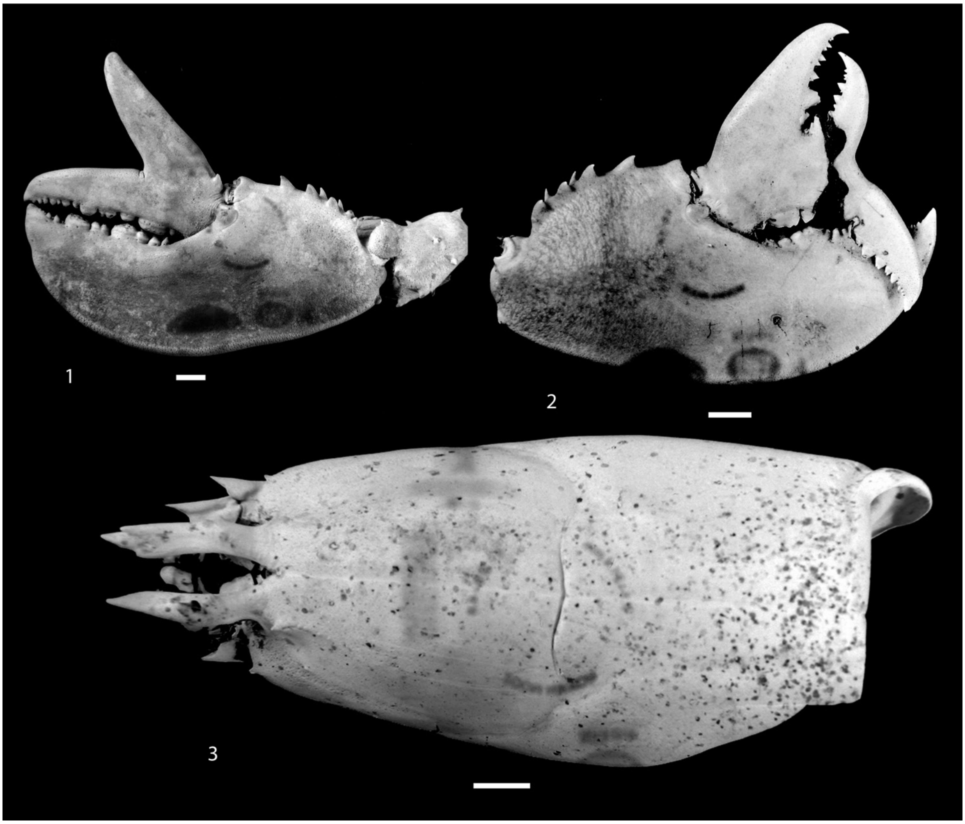

Fig. 4. Regenerational abnormalities on *Homarus americanus* H. Milne Edwards, 1837 in 1834–1840: *1*, partial replication of dactylus, USNM 3314; *2*, replication of occlusal surfaces arising from a deformed dactylus, USNM 13110; *3,* replication of rostral region, USNM unnumbered specimen; scale bars 1 cm (new, photos by R. M. Feldmann).

arising from the propodus. During the nineteenth century, several notes of the condition expanded upon the occurrences but added little to the understanding of the cause of the condition. Emmel (1907) summarized the contributions of his predecessors and provided three possible causes for the deformations: congenital issues, injuries, or products of regenerational abnormalities. These remain the potential causal factors. Emmel (1907, p. 149) concluded that the malformations resulted most likely as a result of damage during the regenerative process of terminal segments of appendages.

More recent records of malformations in extant decapods are on the terminal limbs in shrimp, crayfish, anomurans, and brachyurans (Fig. 4) (Scholtz, 2020 and references therein).Replication of carapace structures including the rostrum (Fig. 4) and telson have also been documented (Aguirre & Hendrickx, 2005, as well as others). Scholtz (2020) provided a review of the literature documenting these occurrences.

Although there are numerous records of teratological individuals in the literature of extant forms, there are only two notices in the geological literature. Schweigert and others (2013) described a pathological left chela of the Jurassic pagurid, *Schobertella simonsenetlangi* Schweigert & others, 2013, from Franconia, Germany (Fig. 5). The specimen bears a partial chela and fixed finger as an outgrowth of the lower surface

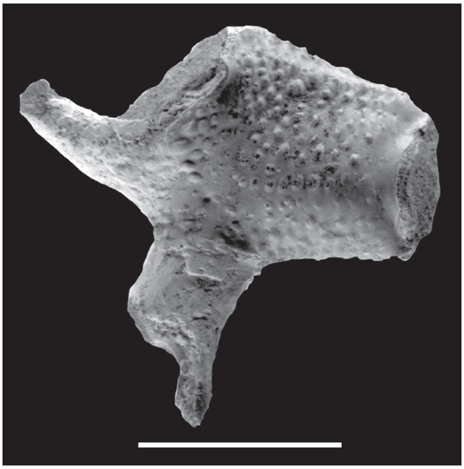

Fig. 5. Regenerational abormality on S*chobertella simonsenetlangi* Schweigert, & others, 2013, BSPG 2011 XI 61, Early Jurassic, Germany, scale bar 5 mm (Schweigert & others, 2013, fig. 6B).

of the manus of the left chela. In a specimen of the polychelid lobster *Knebelia bilobata* (Münster, 1939) from the Upper Jurassic Solnhofen Limestones, a malformed tail fan with abnormally short telson and uropods has been reported (Audo & others, 2013). The scarcity of fossil examples is probably a result of the limited number of individuals documenting most species.

Intersex Specimens

Placement of genital openings in decapods follows a set pattern. All decapods except some brachyurans are characterized by male and female genital opening, the gonopores, situated on the coxa of pereiopod 5 in males and pereiopod 3 in females. Within Brachyura, the term podotreme refers to a polyphyletic group in which the plesiomorphic coxal position of gonopores in males and females is retained. A second polyphyletic group, the heterotremes, is characterized by the female gonopod situated on the sternum whereas the male structure is retained on the coxa. The most derived brachyurans, the thoracotremes, have both male and female gonopores positioned on the sternum.

Within the podotrematous Dakoticancroidea, a sexually aberrant crab was first described in the Late Cretaceous *Dakoticancer overanus* Rathbun, 1917, in South Dakota, USA, by Bishop (1974). Subsequently, he discovered another specimen in 1983, and Jones, Schweitzer, and Feldmann (2022), documented several others in which multiple gonopores were noted in a single specimen (Fig. 6) and the positions of the gonopores was abnormal. Jones, Schweitzer, and Feldmann (2022, p, 12) attributed the condition to either early abnormal development affecting sex chromosomes, or, less likely, an environmental pollution. To date, the phenomenon has not been observed in any other species of brachyuran.

DECAPODS AS SUBSTRATES

Many decapods serve as substrates for epibionts. In general, those decapods that are epifaunal and benthic are more likely to serve as hosts than those that are infaunal or pelagic. Active living animals as well as molts and corpses may serve as a surface for attachment. In the event that fouling by epibionts interferes with the functioning of the host, grooming behavior may be employed to remove the pest (Bauer, 1981). Evidence of epibionts on fossil epifaunal benthic hosts can provide evidence of the condition of the organism at the time of the infestation. Many, if not all, decapods possess some kinds of grooming structures that remove epibionts and annoying particulate material from sensitive areas such as sensory structures (Bauer, 1981). If organisms attempt to attach to those surfaces of an active, living animal, grooming activity will clear the sensitive area (Tashman & others, 2018). Thus, the pattern of placement of fouling organisms will suggest that the animal was living if the sensitive structures or areas that can be groomed are clean or that it was dead when those regions are infested (Fig. 7). Robin and others, 2016, described the association of Early Cretaceous anomiid

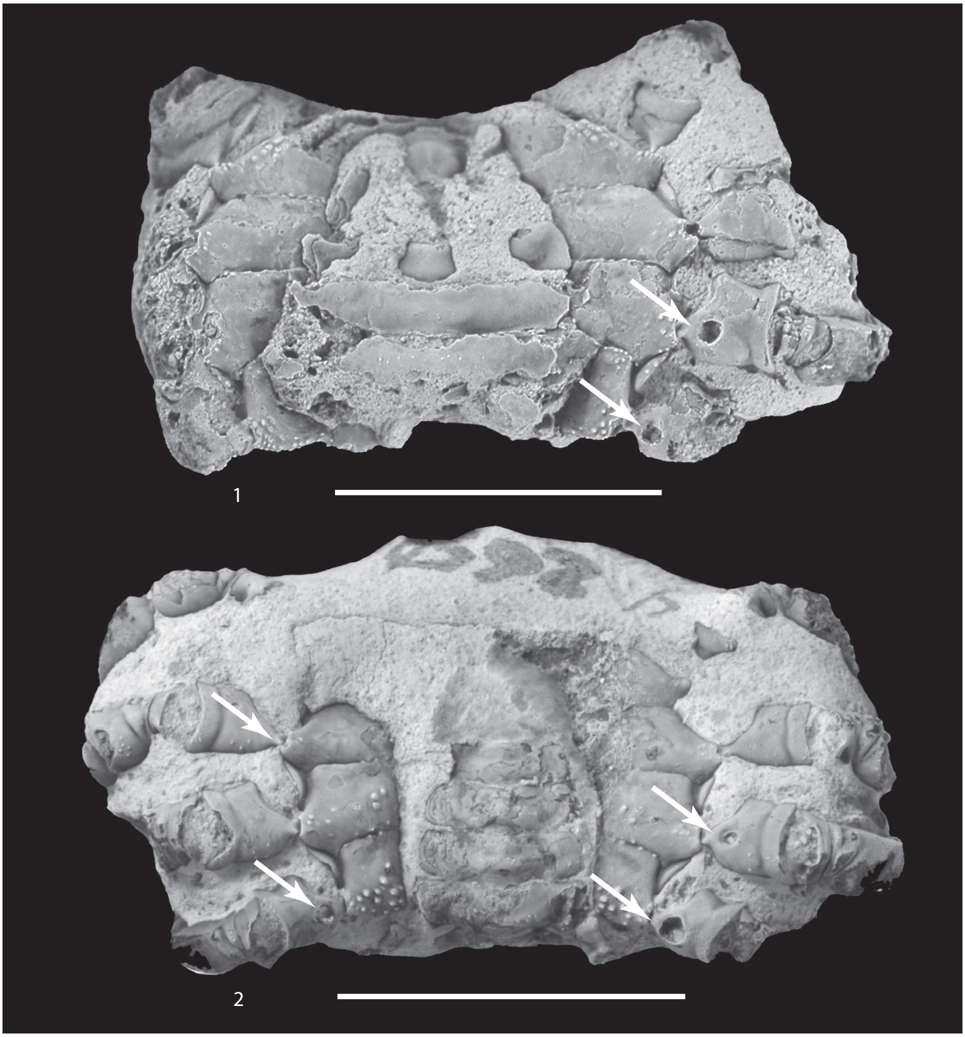

Fig. 6. Intersex individuals in *Dakoticancer overanus* Rathbun, 1917, Maastrichtian, South Dakota, USA: *1*, female, SDSM 4006, with gonopores on coxae 3 and 4 (arrows); *2*, male, SDSM 4005, with gonopores on left coxae 3 and 4 and right coxa 4 (arrows) (and possibly coxa 2); scale bars 1 cm (Jones, Schweitzer, & Feldmann, 2022, fig. 5A and 4J).

bivalves and mecochirid lobsters and noted that the distribution of the bivalves was consistent with attachment of the molluscs on living hosts.

Grooming behavior and degree of sensitivity varies markedly within different decapod groups. In general, swimming organisms, such as many shrimp, are most affected by fouling (Bauer, 1981) because it impedes their mobility. Epifaunal bottom dwellers typically have less extensive grooming strategies. Animals that burrow or bury themselves are less likely to require antifouling measures. Within shrimp, the first to third pereiopod or the third maxilliped clean the antennae and antennules and the overall body. The carapace of macrurans may be cleaned by setal brushes on pereiopods, setal brushes on pereiopod 5 or on 4 and 5 in anomurans, and pereiopods 4 and 5 in some brachyurans

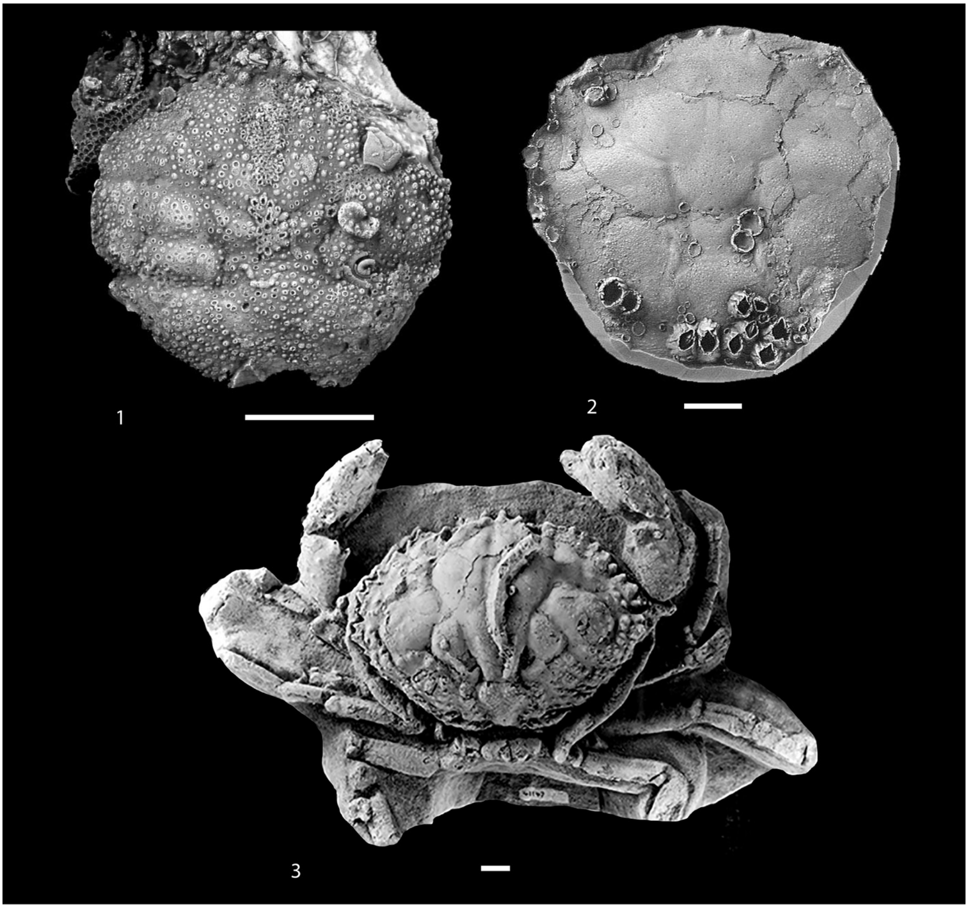

Fig. 7. Epibionts on brachyurans: *1*, serpulids and bryozoans on *Dromiopsis rugosa* (Schlotheim, 1820 in 1820-1823), MGUH unnumbered specimen, Danian, Denmark (photo by S. Jakobsen); *2*, barnacles on *Coeloma* sp., KSU D 128, cast of MGUH 26727, Danian, Denmark (photo by R. Feldmann); *3,* serpulid annelids on *Lobocarcinus pustulosus* Feldmann & Fordyce, 1996, OU 41147, Miocene, New Zealand; scale bars 1 cm (Feldmann & Fordyce, 1996, fig. 2).

(Bauer, 1981; Tashman & others, 2018). Depending on the pereiopods involved and their range of motion, different areas on the carapace will be groomed. Molted and dead remains can potentially be the site of epibiont emplacement on any exposed surface.

Epibionts may include any organism requiring a firm substrate. The groups that most frequently are encountered in fossils are balanid barnacles, bryozoans, and serpulids (Jakobsen & Feldmann, 2004) (Fig. 7). Oyster spats may attach to the surface of corpses or molts (Bishop, 1981; Tshudy & Feldmann, 1988). A Jurassic specimen of *Cycloprosopon dobrogea* Feldmann, Lazăr, and Schweitzer, 2006, associated with a sponge bioherm documents the use of decapods as a substrate for attachment by foraminiferans. These organisms firmly attach to the carapace or pereiopod surfaces. Some epibionts appear to orient in such a way as to take advantage of currents around the host to maximize feeding strategies (Fig. 7) (Feldmann & Fordyce, 1996) as well as to be positioned beyond the reach of grooming structures. Others, such as sponge gemmules (Petit & Charbonnier, 2012), attach but leave no lasting scar (Fig. 8). Their

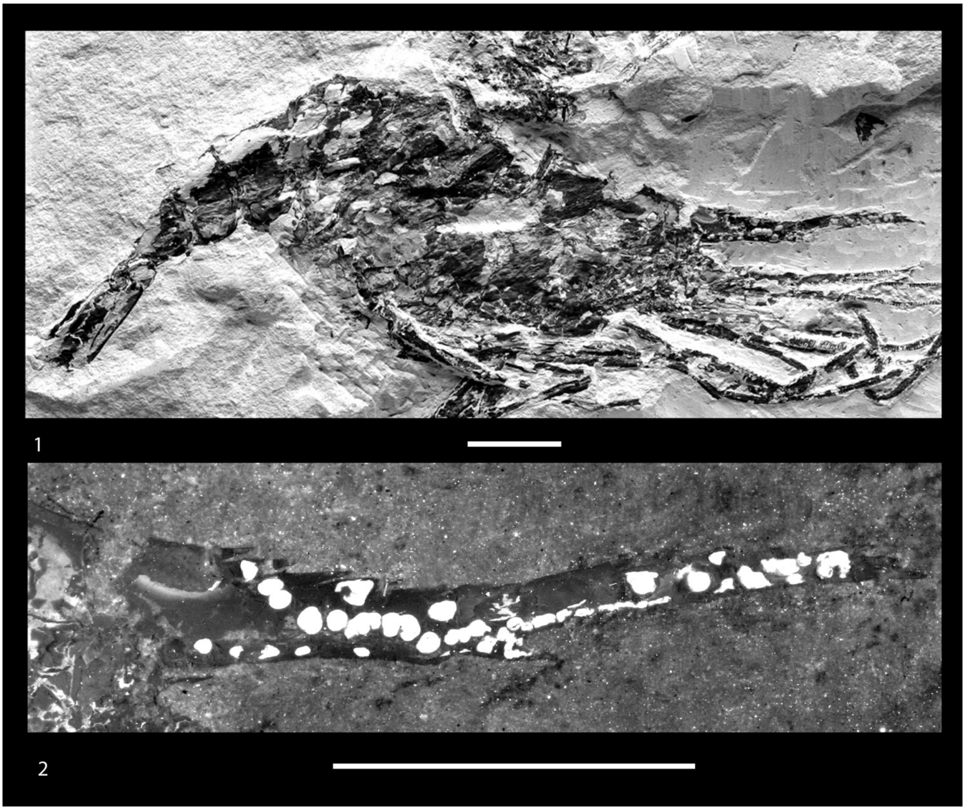

Fig. 8. Sponge gemmules on *Carpopenaeus garassinoi* Petit & Charbonnier, 2012: *1,* holotype, MNHN.F.A.33532, Late Cretaceous, Lebanon; *2,* enlargement of rostrum under UV light, showing sponge gemmules; scale bars 1 cm (photos by Philippe Lowbry & Christian Lemzaouda).

occurrence is documented by the fortuitous preservation of the sponges on the rostrum of a shrimp.

The frequency of occurrence of fossil epibionts is reduced as result of taphonomic processes. If the surface of attachment is the epicuticle, the thin, waxy, uncalcified layer, there will be no permanent evidence retained on the exocuticle. In other cases, particularly specimens preserved within concretions, exposure of the fossil occurs along a plane of weakness between the endocuticle and exocuticle. Evidence of epibionts will be hidden on the outer surface of the exocuticle within the counterpart (Waugh & others, 2004). Preservation of the bryozoan *Berenicea* Lamouroux, 1821, on both the exocuticle and the inner surface of the carapace of the homolodromioid *Tanidromites raboeufi* Robin & others, 2015, support attachment during life of the crab and postmortem attachment.

Not all epibionts are detrimental and not all leave evidence of their presence in the fossil record. Several brachyurans actively recruit epibionts to serve as camouflage. Dromiidae, the sponge crabs, selectively carry a piece of living sponge or tunicate over the carapace as a means of concealment (McLay, 1983). In a similar fashion, many other primitive crabs including Homolidae, Homolodromiidae, and Latreillidae, secure living material as camouflage (Guinot & Wicksten, 2015). The means of acquiring and holding the material employs either pereiopod 5 or pereiopods 4 and 5. The terminal articles of these legs are modified as small cheliform structures or are equipped

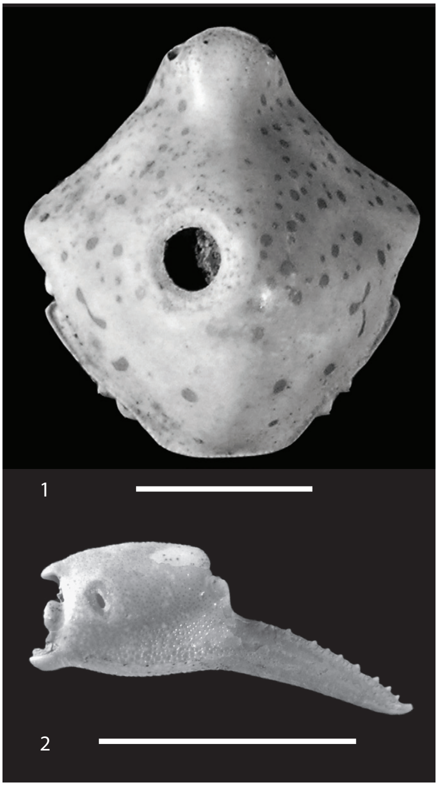

Fig. 9. Drill holes by predators: *1*, gastropod drill hole on *Urnalana haematosticta* (Adams,1847), MFM 142511, holocene, Japan; *2*, octopus drill hole on *Philyra syndactyla* Ortmann, 1892, MFM 142515, Holocene, China Sea; scale bars 5 mm (Klompmaker & others, 2013, fig. 4d and 3F).

with setal bristles that permit grasping and holding. Majoid crabs possess hooked setal hairs, much like Velcro, that entrap plant material or debris to cover the carapace (Guinot & Wicksten, 2015).

PREDATION AND SCAVENGING

Drill Holes

Presence of drill holes in fossil decapods is relatively rare (Klompmaker & others, 2013). As with these structures recognized in fossil and extant molluscs, penetration of the cuticle is either achieved through a circular hole tapering inward or by an ovoid opening elongate on the surface terminating inward as an ovoid opening. The former is attributable to gastropod boring (Fig. 9) (Carriker, 1961) whereas the latter is attributed to octopods. Positioning of the drill holes is variously set on the dorsal carapace or on the terminal segments of the first pereiopods. Drilling activity on decapods attributed to gastropods and octopods has largely been recognized in the Cenozoic (Harper, 2006), perhaps as one evidence of the escalation of predator-prey relationships with the expansion of the heterotreme crabs (Schweitzer & Feldmann, 2015). However, drilling activity on decapods has been documented as early as the Early Cretaceous (Albian) in Egypt (El-Shazly, 2015). El-Shazly described unsuccessful boreholes and one complete penetration of the cuticle on the branchial region of the lobster *Hoploparia longimana* (Sowerby, 1826) produced by an unknown predator.

Drill holes in decapod crustaceans may indicate scavenging rather than predatory activity. Unlike bivalves and gastropods, decapods tend to be active and most exhibit aggressive defense behavior. Given their active lifestyle, it seems unlikely that boring behavior would be brought to successful conclusion. Boring of shell material is time consuming; in molluscs a successful borehole may require several hours or days to complete (Chung, Kim, & Back, 2011). The boring process employs both chemical and mechanical activity (Carriker, 1961) in which fluids are secreted from the accessory boring organ (ABO) to initiate solution along with radular abrasion to physically erode the tissue. It seems far more likely that boring of decapod prey would be more successful as a scavenging tactic than it would be a predatory tactic. However, as with nearly all trace fossils, the precise activity of the tracemaker is conjectural.

Evidence of attack by more aggressive predators is even more rare. Bishop (1972) described bite holes in a Cretaceous raninid crab presumably made by a small fish. He concluded that attack was unsuccessful because the remains were preserved.

Successful attacks would have resulted in ingestion of the prey.

Partial Remains

Partial remains of decapods are most commonly limited to the most durable parts of the exoskeleton. The selective preservation of these elements is facilitated by hydrodynamic processes and durability. Wave and current activity coupled with solution of more delicate articles results in disarticulation of elements and selective preservation of the more heavily calcified parts. In some cases, however, decapod remains yield evidence of predation. Disproportionately large numbers of cephalothorax remains relative to pleons in the lobster *Hoploparia stokesi* (Weller, 1903) in the Cretaceous of Antarctica (Tshudy, Feldmann, & Ward, 1989) was interpreted to result from selective scavenging of the posterior parts of the lobster by cephalopods. Laboratory experiments documented this scavenging pattern employed by extant *Nautilus macromphalous* Sowerby, 1849 (Fig. 10). Scavenging by birds was invoked to explain an unusual breakage pattern on freshwater crayfish (Fig. 11) (Feldmann & May, 1991). Specimens of the Upper Jurassic prawn *Antrimpos undenarius* Schweigert, 2001 often show indication of predation by scavengers, possibly nautilids, and their cuticle remains frequently occur within vertebrate coprolites (Schweigert, 2017).

DECAPODS AS SYMBIONTS

Galls

Crabs within the Cryptochiridae are dwellers of cavities, called galls, within corals (Castro, 2015; Klompmaker & Boxshall, 2015). The food preferences of gall crabs remains contentious. Potential feeding mechanisms include scavenging, feeding on mucous on the coral tissue surface, or preying on coral tissue. Various researchers

Fig. 12. Cryptochirid domiciles in the coral *Manicina areolata* (Linnaeus, 1758), UF257523, Pleistocene, Florida, USA, scale bar 1 cm (photo by Sean Roberts, FLMNH).

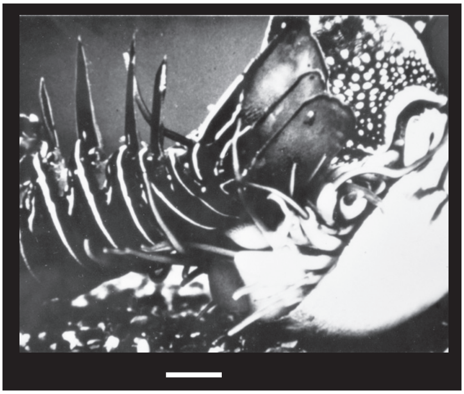

Fig. 10. Scavenging of a spiny lobster by *Nautilus macromphalous* Sowerby, 1849. Aquarium experiment in Burke Museum of Natual History, Seattle,Washington, scale bar 1 cm (Tshudy, Feldmann, & Ward, 1989, fig. 1).

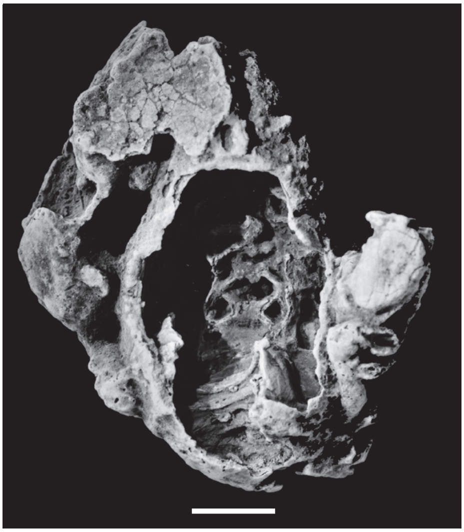

Fig. 11. Predation by a bird on a cambarine crayfish, USNM 451375, Pleistocene, Oklahoma, USA, scale bar 1 cm (photo by R. Feldmann).

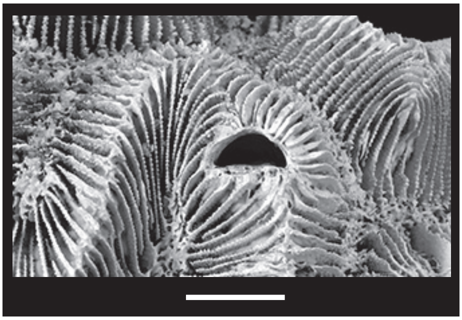

Fig. 12. See explanation at left.

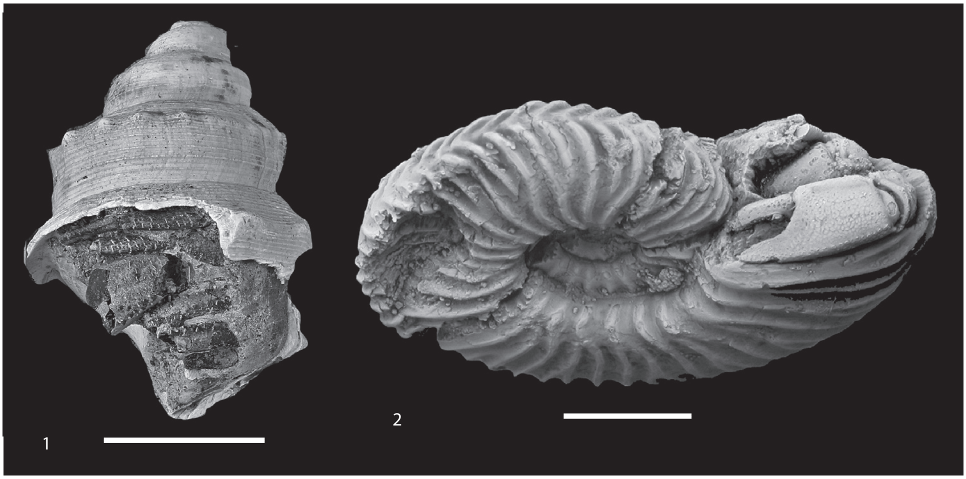

FIG. 13. Hermit crabs preserved in their domiciles. *1, Pagurus clifdenensis* HAYDEN & FOREST, 1980, within *Struthiolaria subspinosa* MARWICK, 1924. OU 11797. Miocene, New Zealand; *2, Palaeopagurus vandenengeli* FRAAIJE, 2003, within *Simbirskites gottschei* (KOENEN, 1902), MAB k.0012, Early Cretaceous, UK (England); scale bars 1 cm (photos by R. Fraaije).

have supported different food preferences, and CASTRO (2015) prefers the more general term symbiosis as a behavioral life-style. The crabs are tiny and delicate, so that the possibility of preservation in the fossil record is low. The chambers in which the crabs live are small, and because there may be other reentrants in most coral colonies, the galls may be overlooked.

The fossil record documents galls within the Pleistocene Bermont Formation in Florida (Fig. 12) (KLOMPMAKER, PORTELL, & VAN DER MEIJ, 2016). Prior to this record in the Pleistocene, the Cryptochiridae had been know only from the Holocene. Although the tracemaker is not in evidence, the small size and shape of the opening is consistent with that of extant galls. It is semicircular with a flattened truncation.

RARE AND PUTATIVE ASSOCIATIONS

Decapods are known to employ numerous types of organisms as living sites and refuges in the modern environment (ROSS, 1983). These relationships do not often result in firm evidence of their association so that most are inferred by close associations within the rock record. Pinnotherid clams preserved within bivalves have been documented in the late Pleistocene of Oregon, USA. (ZULLO & CHIVERS, 1969) as the only intimate association of pinnotherids and hosts. In most cases, pinnotherids and hosts are inferred by association with extant members in molluscs, echinoderms, and brachiopods (FELDMANN & others, 1996). BISHOP & PORTELL (1989) reported the association of porcellanid anomurans with sea stars in Pliocene rocks from Florida. Close association of pinnotherids and potential hosts in the fossil record suggest that similar ancient relationships existed but has left no tangible proof. RADWAŃSKA (2018) examined alpheid shrimp claws and otoliths of gobiid fish that co-occur at several localities in the Miocene of southern Poland. She interpreted the association as the remains of organisms sharing a common burrow.

Thalassinid and annelid burrows are also known to be sites occupied by extant decapods (ROSS, 1983), and KARASAWA & TANAKA (2005) suggested that the same association is documented by the varunid brachurian *Acmaeopluera hichiro* KARASAWA & TANAKA, 2005 found within the burrow filling of a burrow produced by the upogebiid *Upogebia tanegashimensis* KARASAWA & INOUI, 1992.

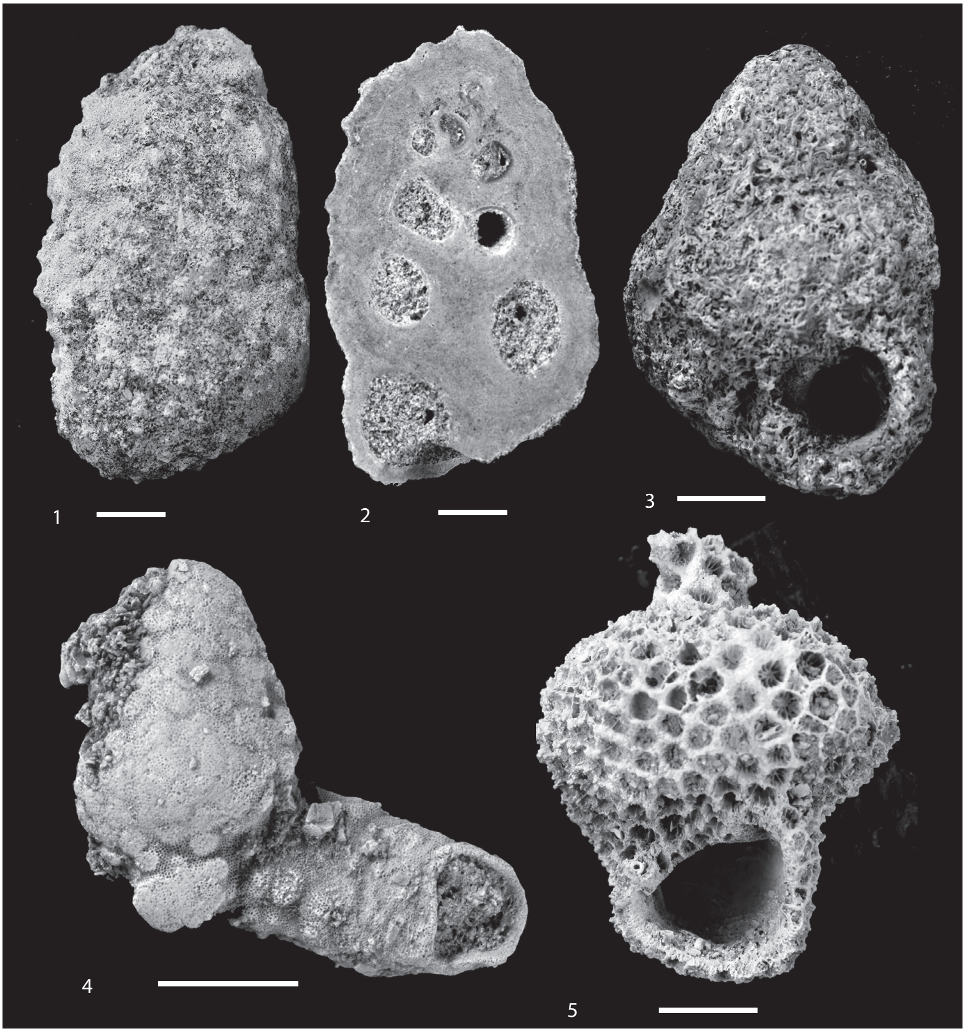

Fig. 14. Epibionts incrusting gastropod shell occupied by hermit crabs. Exterior (*1*) and cross-section (*2*) of hydrozoan encrusted shell, KSU D 3218. Miocene, Argentina; *3,* serpulid encrusted shell, KSU D 3219. Miocene, Argentina; *4,* bryozoan encrusted shell with extended aperture, MMNS IP9936; *5, Septastrea marylandica* (Conrad, 1841), on shell, BM(NH) 53021, Pliocene, Florida, USA; scale bars 1 cm (*1–3* and *5,* new, photos by R. Feldmann; *4,* Feldmann & others, 2019, fig. 3.1).

HERMIT CRAB ASSOCIATIONS

The record of hermit crabs extends from the Jurassic to the Holocene although their remains are frequently only the dorsal shield or chelipeds. Less commonly, the crab is preserved within its host shell (Hyden & Forest, 1980). Gastropod shells provide the most common domicile for hermit crabs in modern times and through most of their geological history (Fig. 13), but cephalopod conchs have occasionally served that purpose during their early history (Fraaije, 2003).

As with other firm substrates, gastropod shells serving as the domicile of a hermit crab can be the attachment site of epibionts. Most commonly, bryozoan colonies may result in multi-layered structures covering the entire shell (Taylor, 1994). The colonial growth may extend beyond the shell to produce a coiled extension mimicking the form of the gastropod. Similar patterns of growth may result from scleractinian corals (Darrell & Taylor, 1989). Walker (1992) summarized gastropod shells occupied by hermit crabs and recorded other epibionts including serpulid worms, barnacles, and clionid sponges (Fig. 14).

ACKNOWLEDGEMENTS

H. Karasawa (MFM), G. Schweigert (SMNS) and D. Thompson (KSU) reviewed an earlier draft of the manuscript. Their constructive comments are appreciated.

ABBREVIATIONS FOR MUSEUM REPOSITORIES

BAS.IN: British Antarctic Survey. Invertebrate paleontology, Cambridge, UK

BM(NH): British Museum of Natural History, London, UK

BSPG: Bayerische Staatsammlung für Paläontologie und historische Geologie München, Munich, Germany

FLMNH: Florida Museum of Natural History, Gainesville, Florida, USA

KSU D: Decapod Comparative Collection, Department of Earth Sciences, Kent State University, Kent, Ohio, USA

MAB k: Oertijdmuseum, Boxtel, The Netherlands

MFM: Mizunami Fossil Museum, Mizunami, Gifu, Japan

MGUH: Geologisk Museum, University of Copenhaven, Copenhagen, Denmark

MMNS: Mississippi Museum of Hatural History, Jackson, Mississippi, USA

MNHN: Muséum National d'Histoire Naturelle, Crustacean Collection, Paris, France

OU: Department of Geology, Otago University, Dunedin, New Zealand

SDSMT: South Dakota School of Manes and Technology, Rapid City, South Dakota, USA

UF: Florida Museum, University of Florida, Gainesville, Florida, USA

USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

ZFC: Canterbury Museum, Christchurch, New Zealand

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