THE DECAPODA (CRUSTACEA) AS PREDATORS ON MOLLUSCA THROUGH GEOLOGIC TIME

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ABSTRACT

The relationship between predator and prey is a persistent theme in marine paleontology. Herein we focus on the decapod Crustacea, the shrimps, lobsters, and crabs, and their role as predators on the Mollusca through geologic time. Five major means by which decapods crush shells or eat shelled prey might be recorded in the body-fossil record, as they require specialization of the appendages. These include use of (1) heterochelous first pereiopods, (2) molariform teeth on the fingers of the chelae, (3) a curved proximal tooth on the movable finger of the chela, (4) calcified mandibles, and (5) flattened pereiopods (walking legs). Decapods have had adaptations for durophagous predation on mollusks since the early Triassic. Durophagous adaptations had appeared among multiple clades by the Late Cretaceous. The myriad means by which decapods prey upon Mollusca, and the multiple uses for which pereiopods and other appendages are adapted, suggests that predation studies should incorporate more decapod types and more types of predation when examining predation as a driver of evolution.

INTRODUCTION

One of the persistent themes in the literature on marine paleontology has been the effect of predation by decapod crustaceans on the evolutionary biology of their prey—commonly, the Mollusca. This type of predation is called durophagy, defined as the consumption of prey with a hard shell or skeleton, most often by crushing or drilling (Aronson, 2001). Pelecypods and gastropods have evolved a variety of strategies to reduce the effects of decapod predation, including the evolution of thicker shells and various elements of ornamentation. This relationship has been considered part of the Mesozoic Marine Revolution (MMR) (Vermeij, 1977a, 1987) and other evolutionary events (Walker and Brett, 2002). Typically, the interpretation of the predator-prey relationship has been viewed heavily from the perspective of the response of the prey species. Less attention has been placed on the multiple strategies used by the predators, their concomitant morphological expression, and the fact that not all predation may be obvious on shell remains in the fossil record.

Nearly all decapods are categorized as generalists based on their dietary preference, although a few have an amazingly limited diet. From the standpoint of the paleontological record, it is possible to infer the manner of food capture and manipulation based on the morphology of the decapod. Thus, various styles of predation may be suggested even under circumstances in which little or no trace of predation is evident on putative prey species. Approaching the predator-prey relationship from this standpoint may reveal potential interactions that cannot be deduced simply by studying effects on prey.

The purposes of this paper are to (1) review the major documented adaptations for durophagy in the Decapoda and (2) document the first appearance of adaptations known to facilitate durophagy in modern decapods and lineages known to have modern congeners that are durophagous.

There are five major means by which decapods crush shells or eat shelled prey that, as they require specialization of the appendages (see Lau, 1987 on extant forms), might be recorded in the body fossil record. There are also several types of feeding that may only chip the shells or simply pry them open, which are often not apparent in the fossil record. All types of feeding on shelled organisms must affect evolution of the shelled organism, based on recent studies that illustrate how predation takes precedence over other aspects of the environment in driving evolution (Stanley, 2008). Studies of predation, evolution, and escalation should, therefore, consider all decapods that have adaptations for durophagy or that have adaptations for durophagy in extant forms, not just those that leave easily recognized marks on shells.

There are some *a priori* assumptions in all studies related to decapod predation. One assumption is that the thickening of molluscan shells and the development of more ornate ornamentation on shells is an evolutionary adaptation to survive increased durophagous predation (Vermeij, 1977a, 1987). A second assumption is that strong chelae armed with stout denticles evolved as a predatory device, rather than for any other function (Lee, 1995; Schenk and Wainwright, 2001). A third assumption is that shell-crushing appendages or other parts were used in a way similar to present-day representatives in the Decapoda. Many adaptations facilitating capture and predation of Mollusca could also facilitate predation on such shelled prey as Bryozoa and Brachiopoda.

Systematic Definitions

Various groups of the Decapoda are defined in the following section. Definitions are arranged alphabetically for ease of use.

Anomura.—A diverse group in which the abdomen may be carried behind or underneath the cephalothorax (body) or in a shell or other structure, such as sea anemones, and in which the last pair of pereiopods is generally reduced and the abdomen may be asymmetrical. This group includes the king crabs, snow crabs, mole crabs, hermit crabs, and squat lobsters.

Brachyura.—The true crabs, an apparently monophyletic lineage of decapod crustaceans holding a symmetrical abdomen entirely or mostly under the cephalothorax and usually with five pairs of pereiopods, the first of which is chelate and the second through fifth are generally achelate, although some have chelate or pseudochelate fifth pereiopods.

Crab.—A general term for a decapod crustacean with an abdomen that is held entirely or mostly under the cephalothorax. This group includes brachyurans and anomurans.

Heterotrematous Crabs.—Brachyurans in which the females possess genital openings on the sternum (ventral surface) and the males possess genital openings on the coxae of the fifth pereiopods. This group may be monophyletic and is considered more derived than many other brachyurans; studies are ongoing (De Grave et al., 2009).

Lobster.—A general term for a decapod crustacean in which the carapace and abdomen are well-calcified and the abdomen extends

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posteriorly from the cephalothorax. There are chelate (Astacidea, some Palinura), achelate (Palinura), and pseudochelate (Glypheoidea) lobsters. Extant achelate lobsters are commonly called spiny lobsters.

Podotrematous Crabs.—Brachyurans in which both males and females possess genital openings on the coxae of the pereiopods (fifth and third, respectively). The group is probably polyphyletic; studies are ongoing (De Grave et al., 2009). This group is considered to embrace the most primitive brachyurans.

Thoracotrematous Crabs.—Brachyurans in which the both the males and females possess genital openings on the sternum (ventral surface). The group may be monophyletic; studies are ongoing (De Grave et al., 2009). This group is considered to contain the most derived brachyurans.

Institutional Abbreviations

Listed below are the institutional abbreviations used in this paper.

BMNH: The Natural History Museum, London, UK.

UKKSU D: Decapoda Collection, Department of Geology, Kent State University, Kent, Ohio, USA.

SDSMT: Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA.

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

UT: University of Texas at Austin, Non-Vertebrate Paleontology Lab, Austin, Texas, USA.

ZRC: Collections of Department of Zoology, National University of Singapore.

DECAPOD MORPHOLOGY AND MODES OF PREDATION

Overview

Predation by decapods has often been considered as a driving force in the evolution of mollusks with strong shells (Vermeij, 1977a) and is facilitated by several morphological traits. Although primary emphasis has been placed on crushing by stout chelipeds, several other morphological adaptations, coupled with specialized predatory behavior, are also used. If the relationship between the evolution and radiation of decapods is to be considered as a force in the MMR (Vermeij, 1977a; Walker and Brett, 2002) and other evolutionary events, it is necessary to evaluate all modes of predation that are exhibited by the living representatives, some of which do not leave evidence of predation on the prey species. Several morphological adaptations can be easily observed in the fossil record, including heterochely, molariform teeth, a curved proximal tooth, and well-calcified mandibles. Less likely to be observed in fossils are flattened dactyls of pereiopods (walking legs) 2–5 or pereiopods 1–5 in achelate lobsters.

Heterochely.—Heterochely refers to the condition in which the chelae of the first pereiopods, usually in lobsters and brachyurans, markedly differ in size and often are used for different purposes. It is generally used as a synonym for handedness, which refers to the condition in which one claw is different from the other. A crusher claw (Figs. 1A–B) in a heterochelous pair is robust, stout, and often bears molariform teeth interpreted to crush shells or other types of prey. A cutter claw (Fig. 1B) is slender, longer, and bears smaller, sharper teeth interpreted to tear the tissue of prey into smaller pieces for mastication. Sometimes heterochely does not involve a crusher and a cutter, but rather claws of differing shape or size. In these instances, the larger is called the major or master claw, and the smaller the minor claw. Heterochely is considered to be an adaptation for predation (Herrick, 1909, p. 273; Lau, 1987; Dietl and Vega, 2008) but can be an adaptation for other uses, including mating rituals. Evidence of heterochely is commonly preserved in the fossil record.

Lobsters that have large, usually heterochelous, chelae are found chiefly in the superfamilies Nephropoidea and Enoplometopoidea within the Astacidea (see Supplementary Data[1]). The Nephropoidea includes several extinct and extant lineages, and their claws tend to be strongly heterochelous. Variation within the Nephropoidea is so great that it is difficult to generalize on the manner in which food is obtained (Wassenberg and Hill, 1989). For example, a few taxa within the Thaumastochelidae have extremely specialized claws, hypothesized to be adapted for raking the seafloor and grasping soft-bodied prey. Most nephropoids, however, have claws similar to those of the American lobster.

In the American lobster, *Homarus americanus* H. Milne Edwards, 1837, a member of the Nephropidae, the first pereiopods are heterochelous. These animals have a cylindrical carapace and carry the claws anterior to the carapace. We have observed that these animals typically move forward and backward rather than sideways so it is probable that they approach prey straight on. Prey is attacked by the crusher claw and the majority of breakage accomplished by the chelipeds. Manipulation by the minor claw and mastication by the mandibles would further comminute the shell material. Shells would be shattered as a result, and we hypothesize that these fragments would be indistinguishable from shell material that had been broken up by abiotic processes.

Oji et al. (2003), however, suggested that shells broken as a result of durophagous predation might be recognizable. Studies of foregut contents of *Metanephrops* spp. from Australia indicated a diet of fish, crustaceans, squid, and small amounts of pelecypods and gastropods (Wassenberg and Hill, 1989). The forward-extended claws (Fig. 1C) were interpreted to be useful in attacking and grasping actively mobile prey. In another study, Thomas and Davidson (1962) noted poly-chaetes, crustaceans, and pelecypods as food items in the diet of *Nephrops norvegicus* (Linnaeus, 1758), in the North Sea. Thus, Nephropoidea clearly include Mollusca as part of their diet.

In a study of the feeding habits of 15 species of hermit crabs in the Paguroidea, arrayed within the Paguridae, Pylochelidae, Diogenidae, and Parapaguridae, Schembri (1982) found that the often heterochelous chelipeds may serve purposes of herbivory, scavenging, and closure of the occupied shell rather than for predation. Predatory feeding was used in three species studied, all within the Paguroidea; one species each in the Paguridae, Parapaguridae, and Pylopaguridae used predatory feeding as a secondary feeding habit after suspension feeding or scavenging. The only mollusks recorded as prey were small gastropods that were crushed by the major claw and ingested.

Heterochely in brachyurans (Figs. 1D–E) varies widely between taxa, genders, and age groups. The sum of morphological characters of carapace shape, claw morphology, and claw orientation makes crabs remarkably versatile in their predatory habit. They are able to skillfully manipulate prey, using several different strategies for attacking hard-shelled prey. The cheliped is typically carried transverse to the medial axis of the animal and tends to lie directly in front of the anterior margin. The motion of the pereiopods is quite broad as is the direction of movement of the animal, although the latter is typically sideways as opposed to forward and backward. Complete crushing of the shell to gain access to the soft tissue is often accomplished by a crusher claw.

Shearing is yet another highly specialized manner of breaking mollusk shells. A pelecypod is positioned between the major claw and the teeth along the anterolateral margin of the carapace, and the two valves are opened by a shearing action (Lau, 1987). Williams (1978) observed shearing in the feeding habit of *Scylla serrata* (Forskål, 1775).

Molariform Teeth.—Molariform teeth are stout denticles along the occlusal surface of the fingers of the chelae that aid in crushing (Figs. 1A–B, D–E) (Herrick, 1909; Seed and Hughes, 1995; Dietl and

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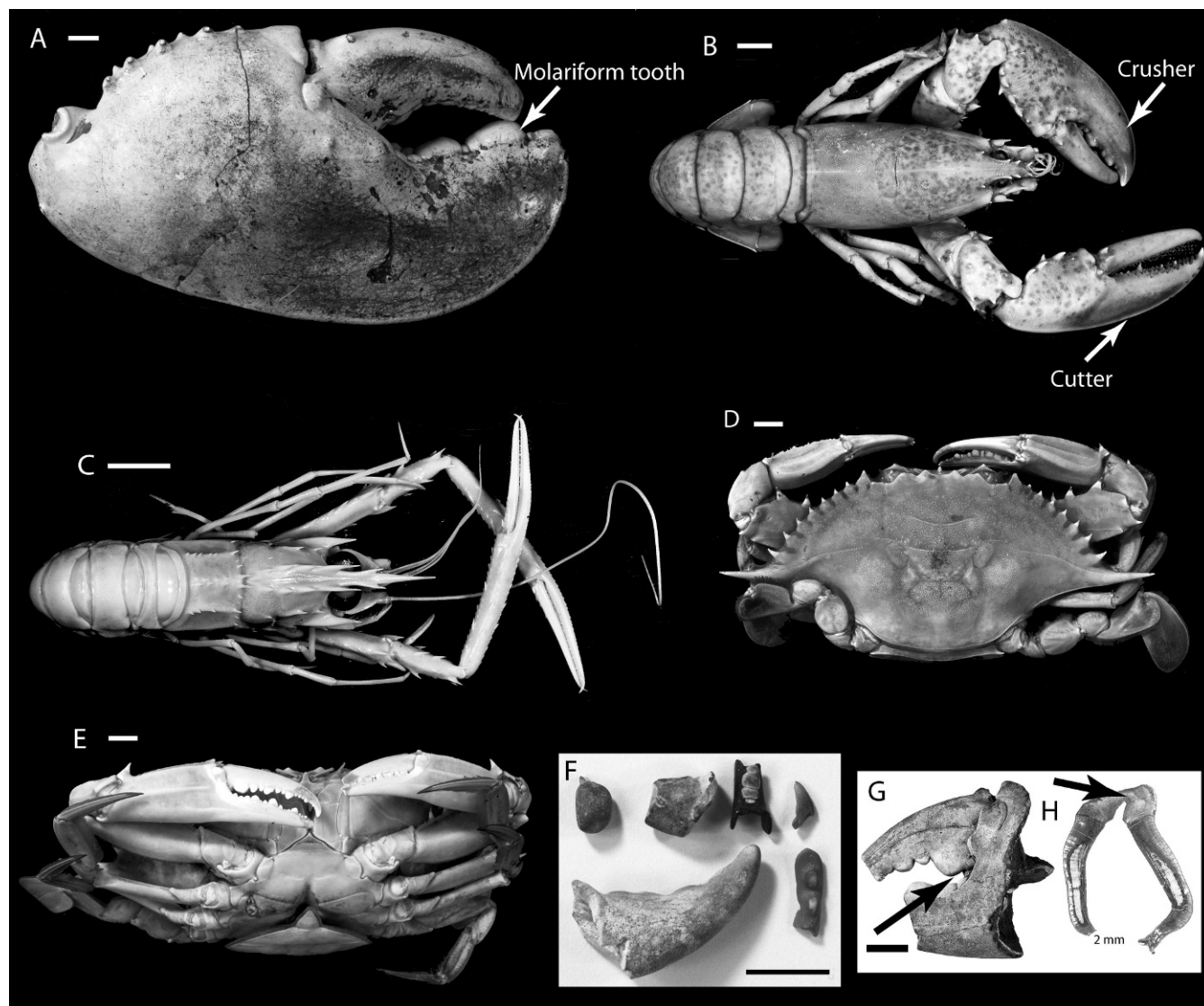[1] www.paleo.ku.edu/palaios

FIGURE 1—A) Extremely large crushing claw of *Homarus americanus* (H. Milne Edwards, 1837), uncatalogued specimen in Kent State University collection. B) *Homarus americanus*, USNM 99746, showing left crushing claw and right cutting claw, dorsal view. C) *Metanephrops binghami* (Boone, 1927), USNM 170698, dorsal view. D–E) *Callinectes sapidus* Rathbun, 1896, KSU D 1079, dorsal view (D) and oblique frontal view (#) showing heterochelous crusher (right) and cutter (left) claws. F) Brachyuran fingers and molariform teeth, sieved from beach sediment at Calvert Cliffs, Maryland. G–H) *Callinectes sapidus*, thin section of a claw of an uncatalogued extant specimen modified from Waugh et al. (2006), showing wear pattern on denticle (arrows). Scale bars 1 cm, except where indicated.

Vega, 2008). These usually occur on the crusher or major chela in a heterochelous pair but can occur on claws that are not noticeably heterochelous, such as in the brachyuran family Cancridae (Latreille, 1802). They are often fortified with extra calcite, high-magnesium calcite, or phosphorus (Waugh et al., 2006). This feature is readily preserved in the fossil record; sieving molluscan fragments in Holocene sediments often yields only the hardened molariform portion of the claws, attesting to their resistance to wear both in life and in sediments (Fig. 1F). Thus, presence of these teeth is taken to indicate that the animal is adapted for durophagous predation, whether or not the claws are heterochelous. Shell crushing can also be accomplished with claws with denticles that are not molariform (Schenk and Wainwright, 2001).

There may be a test for the use of molariform teeth in durophagous predation that has not been exploited to any extent. Waugh et al. (2006) examined the microstructure of occlusal surfaces in Pleistocene and extant *Callinectes sapidus* Rathbun, 1896, and *Scylla serrata* Forskål, 1775, and noted that the teeth and the claw tips were more dense, harder, and contained more phosphorous than the remainder of the fingers. Further, they noted that the cuticular laminations within the

teeth were worn away, indicating that they had been abraded (Figs. 1G–H). The development of increased hardening and the appearance of wear on the teeth is strong evidence that the animals were engaged in durophagous predation. It may be possible to positively correlate such teeth with known durophagous predators in modern oceans and to extend these correlations to fossils in which teeth are not necessarily large and molariform. Examination of teeth in geologically older specimens may make it possible to identify the onset of durophagy and to document that the claws were serving this purpose, in addition to any of their other functions.

Curved Proximal Tooth.—One of the best known methods of durophagous predation is that of tubercular peeling, in which gastropod shells are opened by crabs with very specialized chelipeds (Shoup, 1968). The process involves chipping away the aperture in successive breaks to produce an arcuate reentrant around the aperture of the gastropod until the animal is released and extracted. The results of this process are readily recognized in the fossil record, and an extensive literature has resulted (Vermeij, 1987). The cheliped form responsible for this manner of attack is exemplified by that of the
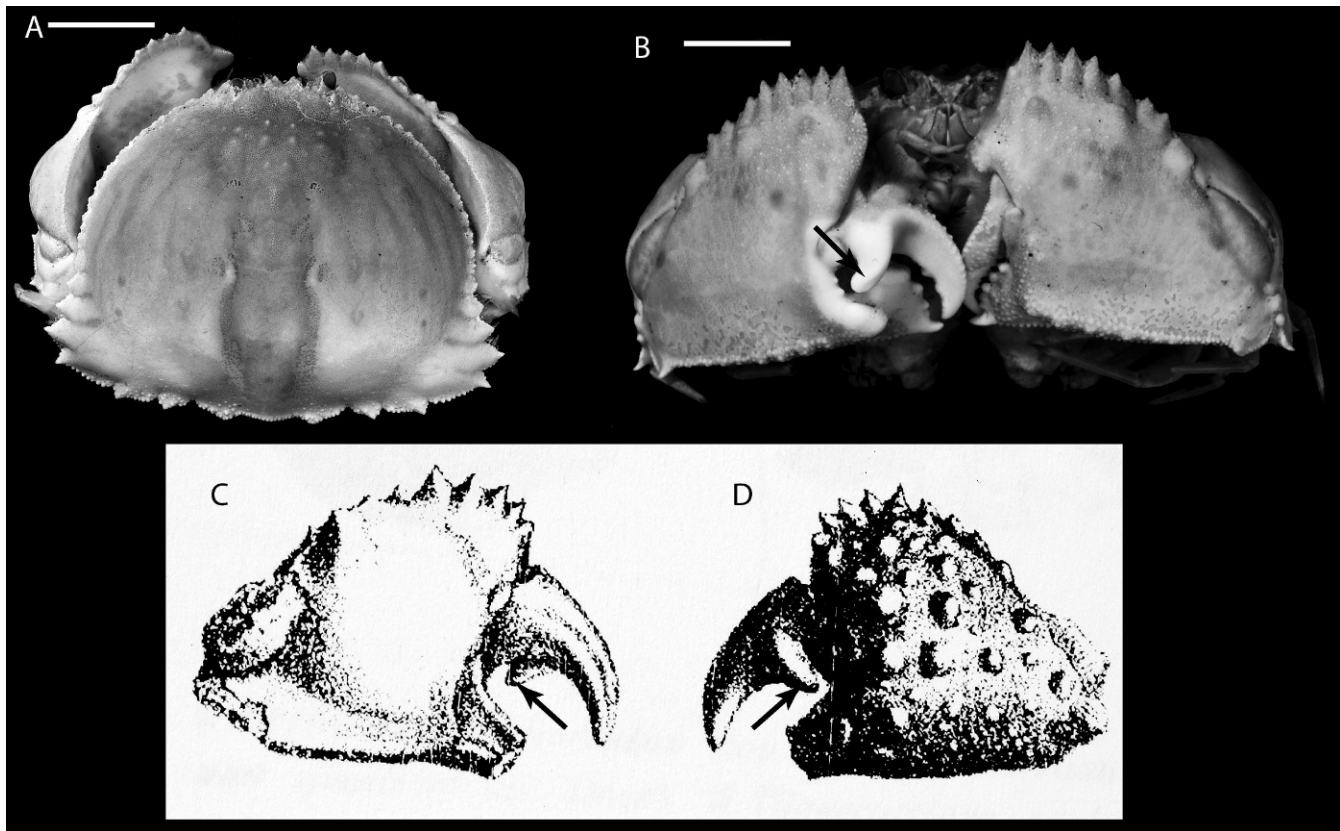
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FIGURE 2—A–B) *Calappa lophos* (Herbst, 1785), KSU D 335, dorsal view (B) and frontal view, showing modified tooth on right cheliped for chipping shell margins; scale bars 1 cm. C–D) *Calappa* sp., Eocene, digital images from Bittner (1875, pl. I, figs. 7a–b); arrows indicate curved proximal tooth on movable finger.

brachyuran family Calappidae (Shoup, 1968) (Figs. 2A–B). The propodus markedly broadens distally and the fixed finger tends to be relatively short. The dactylus bears a stout, protuberant denticle oblique to the occlusal surface near its proximal end. When the tooth is positioned so that the aperture lies between the tooth and the axis of the cheliped, the crab can rotate the claw slightly and nip off a piece of the margin (Lau, 1987). This process is continued until the prey is released. The curved proximal tooth can be preserved in the fossil record, as long as the proximal portion of the movable finger is present (Figs. 2C–D).

Mandibles.—The mandibles of decapods (Fig. 3), the first pair of feeding appendages, can be well-calcified and used for durophagy (Figs. 3A–B). Mandibles are sometimes preserved in fossils, although this region of the animal is often covered by such appendages as the maxillipeds, so even if they are preserved, they are often not visible unless destructive techniques are used. The Infraorder Palinura, the spiny lobsters including the Palinuroidea and Eryonoidea, includes various forms that may lack chelae but include mollusks as a regular part of their diet (Wassenberg and Hill, 1989; Robles et al., 1990). Within the Palinuroidea, observations on the feeding habits of *Panulirus interruptus* (Randall, 1840) document manipulation of the prey using the pereiopods and chipping and breaking of shells using the mandibles (Robles et al., 1990). The Palinuridae have a carapace that is quadrate in transverse cross section; pereiopods of approximately similar size that are carried in an anterolateral position; extremely strong mandibles; and large, stout antennae that have a wide range of motion (Figs. 3A–D). The animals generally move forward and backward, and they typically approach prey from the front. Studies on the foregut content of species of *Linuparus* White, 1847 confirm that mollusks, both pelecypods and gastropods, form a substantial part of their diet (Wassenberg and Hill, 1989).

Another group of spiny lobsters, the Eryonoidea, have broad, flattened carapaces, and four to five pairs of chelate appendages

(Glaessner, 1969). With the exception of the abyssal genus, *Polycheles* Heller, 1862, all are extinct, and information about dietary habits is not known. The chelae are extremely long, slender, and delicate, which suggests that they would be poorly adapted for crushing hard-shelled organisms (Fig. 3E). Their flattened shape suggests that they may have ingested mollusks in a manner similar to the achelate palinuran forms using their mandibles.

Lobsters within the Glypheoidea lack true chelae but have dactyli that extend either parallel or more or less at right angles to the axis of the propodus; in the latter case, they occlude against the distal portion of the propodus (Fig. 3F). Typically, they are only weakly hetero-chelous. The propodus in the Glypheidae typically bears a distal spine that may permit the animals to grasp prey. The superfamily had an extensive geologic history, but extant forms are limited to two genera from the Indo-Pacific (Forest, 2006). To our knowledge, their dietary habits are not known. Glypheoids have an elongate, cylindrical carapace and carry the first pereiopod in front of the carapace in a manner similar to the nephropids. Thus, they probably move forward and backward, rather than sideways, approaching prey from the front. If, indeed, they attack molluscan prey, we hypothesize that they probably manipulate the animals toward the mouth with the pereiopods and crush the shell using the mandibles. All decapods have mandibles, but because glypheids are typically preserved in lateral aspect, the mandibles have not been exposed in fossils to our knowledge.

Brachyurans, for example, the spider crab *Notomithrax* Griffin, 1963 (Woods, 1993), use the mandibles in chipping and biting, a process that involves nipping at the margin of a shell until access to the soft tissue is obtained. The result of the attack would be a shell damaged along part of its margin.

Flattened Pereiopods.—Many decapods use flattened pereiopods other than the chelipeds to facilitate taking of shelled prey. Usually, the
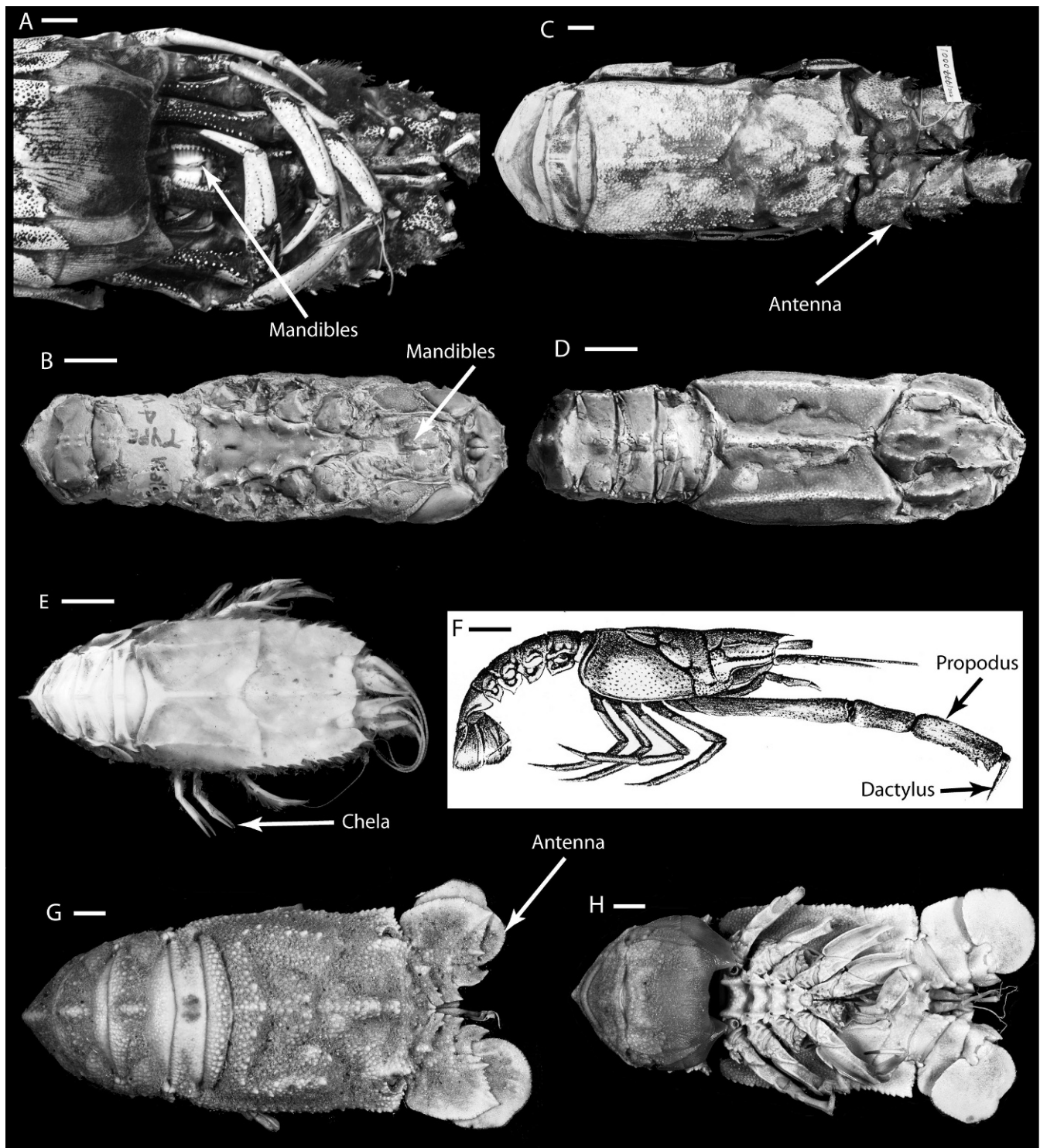
FIGURE 3—A–B) *Linuparus somniosus* (Berry and George, 1972), ZRC 1999-0001, deposited in the Department of Zoology, National University of Singapore, ventral view (A), showing achelate pereiopods and large, strong mandibles, and dorsal view (B). C–D) *Linuparus grimmeri* (Stenzel, 1945), syntype UT 21067, ventral (C) and dorsal (D) surface. E) *Polycheles typhos* (Heller, 1862), KSU D311, dorsal view. F) Drawing of *Glyphea regleyana* (Desmarest, 1822; illustrated in Étallon,1859, pl. 3, fig. 11). G–H) *Scyllarides nodifer* (Stimpson, 1866), USNM 274950, dorsal view (H) and ventral view, showing flattened pereiopods and smaller, more delicate mandibles. Scale bars 1 cm.

dactyl, the distalmost segment, is used. Dactyls are usually less well calcified than other segments of the decapod; articles of the walking legs (pereiopods 2–5) are not as well preserved in fossils as the dorsal carapace or the chelipeds (pereiopod 1).

The Scyllaridae, within the Palinura, bear a dorsoventrally compressed carapace; delicate mandibles; isochelous first pereiopods, carried laterally or anterolaterally; and short, often foliaceous antennae

(Figs. 3G–H). The direction of motion of the animals may be forward, backward, and sideways. *Scyllarides squammosus* (H. Milne Edwards, 1837) has been observed attacking mollusks by mounting a pelecypod, grasping the commissure by some of the pereiopods, prying the shell open, and detaching the adductor muscles using another pereiopod, a process referred to as direct wedging by Lau (1987). The dactyls used in this process are flattened, bladelike elements, not circular in cross
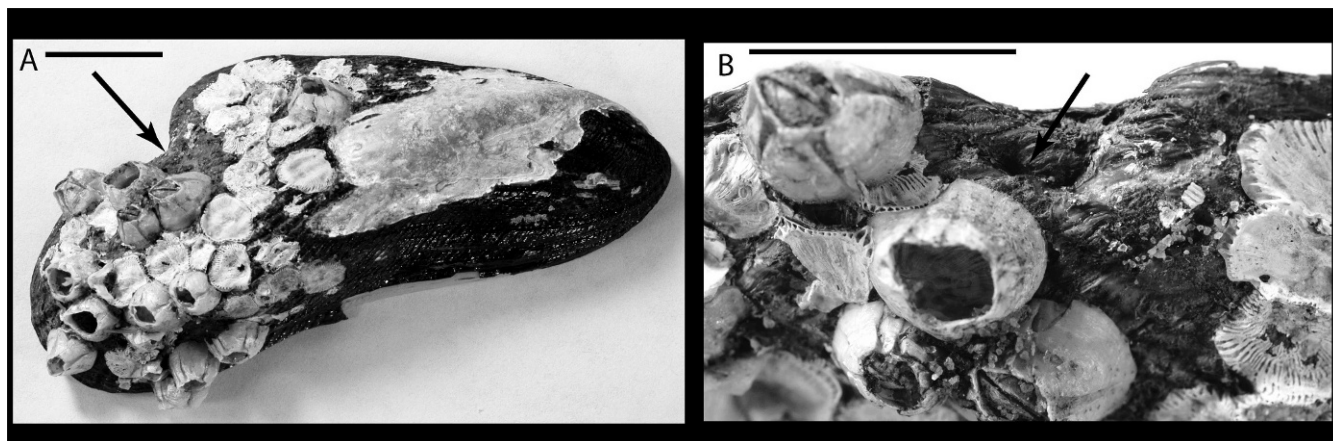
FIGURE 4—A) Uncatalogued specimen of *Lithophaga* sp. showing bored and repaired region (arrow) in position of posterior adductor muscle. B) Enlargement of damaged region on same specimen (arrow). Scale bars 1 cm.

section, as is more usual. Durophagous predation by scyllarids can be very sophisticated. In some cases, the lobster simply grabs and pries the shells open, whereas in other cases, it may hover over the pelecypod until the animal opens the valve to resume respiration and feeding. At that time, the lobster quickly inserts the dactyli into the open margin and attacks the muscles; this approach was referred to as patience attack by Lau (1987). Whichever approach is applied, the prey may exhibit a slightly chipped margin or lack any evidence of attack. The Scyllaridae must be considered significant predators, the role of which would not be recognized by simply examining prey species, because they range from the Early Cretaceous to the Holocene.

Brachyurans including spider crabs (Woods, 1993) apply pelecypod wedging and prying as techniques to enter the shell without necessarily damaging the shell itself or leaving evidence of the attack. Clam shells can be wedged open as dactyls are inserted along the commissure, and the shell is forced open to an extent sufficient for another dactyl to be inserted into the shell to scrape loose the adductor muscles. Alternatively, the dactyls can be inserted along the commissure and the shell directly pried open. Thus, presence of spider crabs in the fossil record indicates that this type of predation pressure must have been present.

Gastropods may be preyed upon by the predator grasping the animal by soft tissue in order to prevent the operculum from closing. Using dactyls, the crab then removes some of the soft tissue until the animal can be released from the shell. Woods (1993) described *Notomithrax* using its cheliped to block closure of the gastropod opening with the operculum and then grabbing the soft tissue to pull it out. No obvious evidence of this style of attack would result.

Use of Unspecialized Chelae.—Often durophagy is accomplished using unspecialized chelae. Chipping and peeling of the shell margin of gastropods and pelecypods can be accomplished by predators that may or may not have specialized crushing claws. In the event that the prey is too robust or too large to crush, the predator may nip at the margin of the shell with the cheliped until access to the interior is achieved. This type of attack is evident on the shell of the prey and may provide some evidence of the relative size of the predator and prey (Lau, 1987; Seed, 1993).

A particularly sophisticated method of predation is that of boring, whereby the predator enters the shell by using the tip of the dactyl to drill a hole into the hinge, expanding the hole by nipping around the margins of the hole, and separating the adductor muscle from the shell (Figs. 4A–B). This process has been observed (Elner, 1978) as *Carcinus maenus* (Linnaeus, 1758) bored into the mussel *Mytilus edulis* (Linnaeus, 1758). Although this process is probably not widespread, the scar should clearly indicate the style of predation. The scar is distinguishable from gastropod drilling scars by its lack of a circular or oval shape and beveled edge, as well as its position in the hinge of the pelecypod shell.

Rochette et al. (2007), in addition to the techniques described by Lau (1987), described predation on gastropods by winkling. This method involves grasping the soft tissue of the snail. Using the major claw, the crab rotates the soft body of the snail around the inner lip, while the minor claw rotates the shell in the opposite direction. The shell is left undamaged; therefore, this method would go undetected in the fossil record.

Decapoda Known from Gut Content to Consume Mollusks.—Many types of decapods, not just those that crush, bore, or chip their prey, and undoubtedly more than are reported here, eat mollusks as a minor component of their diet. Studies from which these data are taken analyzed decapod gut contents; thus, it is not known how the animal took the prey. Many of the lineages have a lengthy fossil record; thus, we infer that animals in these lineages would have exerted selective pressure on Mollusca. The first appearance of each of the families is summarized in Supplementary Data[1], so that the families can be considered in future studies of predation by Decapoda.

The king crabs, Lithodidae, are generalized feeders and, not, to our knowledge, active predators. The stomach contents of *Paralithodes brevipes* (H. Milne Edwards and Lucas, 1841) yielded a broad variety of plant and animal material, the majority vegetal (Sasaki and Kuwahara, 1999). Mollusk remains, limited to pelecypods, were incidental. Although king crabs bear large claws, they are apparently used for purposes other than durophagous predation.

Within the squat lobsters, Galatheoidea Samouelle, 1819, predatory behavior has been observed in *Munida sarsi* (Huus, 1935), but the observed prey were krill (Hudson and Wigham, 2003). Similarly, examination of stomach contents of *M. subrugosa* (White, 1847) indicated that mollusk remains comprised a minor part of the diet (Romero et al., 2004). Galatheids apparently do not engage regularly in durophagous predation on mollusks. In the Aeglidae, a freshwater family within the Galatheoidea, examination of stomach contents indicated a small percentage of mollusk shell fragments, but the manner of food gathering was not noted (Santos et al., 2008). Aeglids possess stout chelipeds that might serve as shell crushing devices (Fig. 5). They are mentioned here because this aquatic group had marine origins in the Late Cretaceous (Feldmann, 1984).

The Anomura often bear large claws of various forms, many of which could function as shell crushers, but none of the literature known to us documents durophagous predation on mollusks. Most seem to prefer plant material and probably are best characterized as herbivores and scavengers rather than aggressive predators.

Within the Brachyura, members of the Plagusiidae eat mollusks as a minor component of their diet, although they are primarily algae eaters
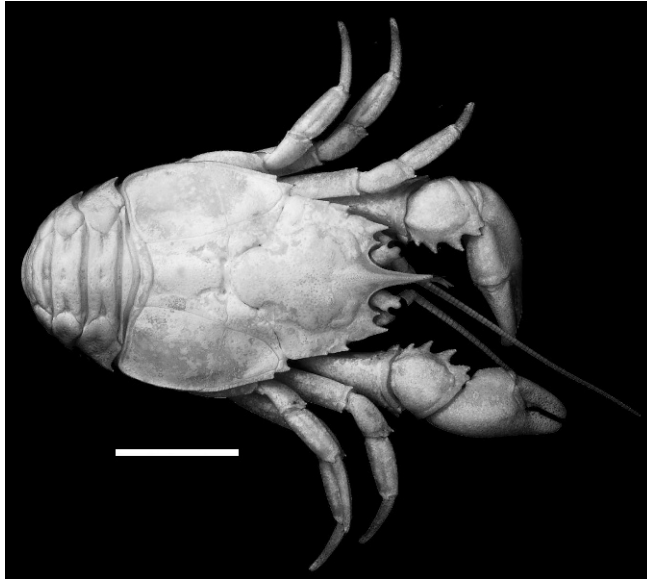
FIGURE 5—*Aegla* sp., KSU D1077, dorsal view. Scale bar 1 cm.

(Samson et al., 2007). Species of *Hepatus* Latreille, 1802, of the family Aethridae, eat a broad diet that includes mollusks (Mantelatto and Petracco, 1997). *Paromola* Wood-Mason in Wood-Mason and Alcock, 1891, of the very long-ranging family Homolidae, eats small mollusks as a small but significant component of its diet (Mori, 1986; Cartes, 1993). Individuals have been observed using their first pereiopods to extend into the bottom sediment, perhaps to grab buried prey (Cartes, 1993). *Geryon* Krøyer, 1837, in the Geryonidae, generally inhabiting deep-water environments in oceans today, eats mollusks as a small part of its diet (Cartes, 1993; Domingos et al., 2007). Members of the Superfamily Majoidea Samouelle, 1819, the spider crabs are most commonly reported as herbivores (Rorandelli et al., 2007), but some consume mollusks; this is hypothesized to be due largely to their small and delicate chelipeds (Woods, 1993). *Notomithrax*, described earlier, applies wedging and chipping to ingest mollusks, and the snow crab *Chionoecetes* Krøyer, 1838, is a benthic majid that eats clams and snails

as a minor part of its diet (Lovrich and Sainte-Marie, 1997; Squires and Dawe, 2003).

TIMING OF APPEARANCE OF DUROPHAGOUS SPECIALIZATIONS IN DECAPODA

Studies of predation and paleoecology have often included the Decapoda because they are known predators on various groups of animals in modern ecosystems. Thus, Decapoda were thought to be capable of driving evolution and escalation as far back as the mid-Paleozoic (Brett and Walker, 2002; Walker and Brett, 2002, p. 135), although major innovations for shell crushing generally were thought to appear, at least in the Brachyura, in the Cenozoic (Vermeij, 1977a, 2002; Walker and Brett, 2002). Recent work on the fossil record and the extant groups of Decapoda has greatly altered interpretations of the timing of appearance of the major lineages within the group and, thus, the timing of appearance of many of these major innovations (Table 1).

Dietl and Vega (2008) reported that shell-crushing specializations in brachyuran crabs appeared during the Late Cretaceous. Specializations such as those seen in the Calappidae appeared as early as the Eocene, based upon breakage patterns of shells (Vermeij, 1987). This timing of appearance of shell-crushing specializations in the Brachyura largely seems to be the case, although similar specializations had been present for some time in lobsters.

An important caveat in working with fossil decapod crustaceans is that their record can be extremely sparse. A species may be known from one or only a few specimens. For example, in *Palaeopalaemon newberryi* (Whitfield, 1880), the chela is known from one specimen. The data presented in Supplementary Data[1] represents the sum of all of the known data on fossil decapod crustaceans, based upon a list of all known fossil decapod crustacean species (Schweitzer et al., 2010). We have examined type specimens, voucher specimens, or original literature for every record.

The confirmed fossil record for the Decapoda is extremely limited before the Triassic Period, despite the assumption that decapods with shell-crushing claws first occurred in the Devonian and radiated in the late Paleozoic (Brett and Walker, 2002). We consider the only confirmed mid-Paleozoic decapod, *Palaeopalaemon* Whitfield, 1880, from the Devonian of Ohio, Kentucky, and Iowa, to be a lobster with questionable affinities. Its appendages are poorly known; the propodus

TABLE 1—Major groups of decapods and timing of appearance of major adaptations to durophagy. Adaptation plotted during time interval of first confirmed appearance in fossil record. X = earliest record of group if different from earliest appearance of major adaptation; E = early; M = middle; L = late; H = Heterochelous first pereiopods; MT = molariform teeth on occlusal surface of fingers; CT = curved tooth on proximal end of movable finger; Ma = well-calcified, large mandibles. Numbers in parenthesis indicate number of families in which adaptation(s) appeared.

Taxon	Paleozoic	E. Triassic	L. Triassic	E. Jurassic	M. Jurassic	L. Jurassic	E. Cretaceous	L. Cretaceous	Paleocene	Eocene	Post-Eocene
Chelate (clawed) lobsters	X	H		MT							
Spiny lobsters			X					Ma (1)			
Hermit crabs (Anomura)				X	MT					H	
Brachyura											
Podotrematous Crabs (most primitive crabs)											
Dakoticancroidea							MT (1)				
Raninoidea							MT (1)				
Heterotremata (derived crabs)											
Aethridae (includes modern *Hepatus*)							H, MT, CT?				
Calappidae (includes *Calappa*)										MT, CT	
Parthenopoidea											H, MT (1)
Cancridae										MT	
Carpilioidea								X		H, MT (2)	
Xanthoidea *sensu lato*							H, MT, CT (1)				
Xanthoidea *sensu stricto*										H, MT (1)	
Eriphioidea										H, MT (1)	
Goneplacoidea							H, MT (1)				
Portunoidea (swimming crabs)							H, MT (3)				

of the first pereiopod looks rather like a mitten, and the dactylus is unknown (Schram et al., 1978, text-fig. 4). Thus, it is not appropriate at this time to consider this a decapod with a shell-crushing appendage, due to insufficient evidence.

Other Paleozoic and Triassic taxa originally referred to the Decapoda have been previously or are herein removed from the group. Examination of the holotype (SDSNH 25139) of the Mississippian *Imocaris tuberculata* Schram and Mapes, 1984, suggests that it is not a brachyuran decapod; it lacks key rostral, orbital, and dorsal carapace features, such as a cardiac region, that are diagnostic of the group. It is represented only by a carapace; no appendages or ventral surface are preserved. The recently described *Imocaris colombiensis* Racheboeuf and Villarroel, 2003, has no appendages preserved. The Permian *Palaeopemphix* Gemmellaro, 1890, has been referred to the Phyllocarida (Feldmann et al., 2004). The Triassic occurrence of the Eubrachyura (Rinehart et al., 2003) has already been reinterpreted as an arthropod of unknown affinities (Schweitzer and Feldmann, 2005). *Protoclytiopsis* Birshtein, 1958, a member of the Erymidae, was confirmed as occurring in latest Permian deposits (Schram, 1980), but no appendages were preserved. It is the only other confirmed Paleozoic occurrence of Decapoda. Thus, at this time, there is no reason to attribute a considerable, driving role for decapods in the escalation of molluscan shell thickness, ornamentation, and other antipredator adaptations before the Triassic.

Vermeij (2008) suggested that during the MMR, evolutionary innovations mostly occurred during two periods, the Late Triassic to Early Jurassic and the Late Cretaceous. Our examination of the Decapoda suggests that innovations for durophagy were more broadly distributed in time and among groups (Table 1). We have identified the decapod infraorders, superfamilies, and families in which evolutionary innovations for durophagy have evolved or in which durophagous behavior is well documented in extant forms, as well as the first known appearance of those groups in the fossil record. We have also included extinct groups with known adaptations to durophagy or in which we have inferred them based upon relationships and morphological similarity to extant forms. Table 1 contains summary data; see Supplementary Data[1] for detailed data used throughout the following discussion.

During the Early Triassic, chelate lobsters exhibited heterochely. Well-developed molariform teeth appeared in the early Jurassic. Anomuran hermit crabs exhibiting heterochely first occurred during the Late Jurassic. During the Late Triassic to Early Jurassic, spiny lobsters appeared, which have congeners that are known to be durophagous in modern oceans. Fossil spiny lobsters have the same general body form as extant Palinuridae and are inferred to have eaten shelled prey using mandibles as do extant forms. Recovery of fossils with preserved, robust mandibles would permit testing of this hypothesis. During the Middle Jurassic, confirmed members of the Brachyura appeared, but no lineages with known specializations for durophagy. Shrimp taxa were abundant at this time as well, but did not then, and do not now, have large chelae. Most do not exhibit chelae adapted for durophagy, and extant shrimps generally do not exhibit durophagous behavior.

As noted by Vermeij (2008) for other lineages, the Late Cretaceous appears to have been a time of innovation within the Decapoda in terms of durophagous adaptations (Figs. 3C–D; 6A–C). Durophagous characteristics are well known from Cretaceous brachyurans (Table 1). Notably, durophagous adaptations appeared in a broad range of taxa, including lobsters and podotrematous and several superfamilies of heterotrematous brachyurans. The appearance of durophagy in numerous lineages suggests that although there may indeed by a phylogenetic component to durophagous adaptations, they also have arisen more than once. Clearly, the polyphyly of these adaptations is shown in their appearance within the lobsters, anomurans, and brachyurans as well as in a variety of brachyuran lineages.

Major shell-crushing adaptations appeared in the Heterotremata, a group of more derived crabs, and the brachyuran lineage that embraces almost all shell-crushing crabs in modern oceans, during the Cretaceous, including the Calappoidea, Portunoidea, and Carpilioidea. Interestingly, much of the literature on extant brachyurans with specializations for shell crushing is concentrated on these three superfamilies or their close relatives. In addition to the Brachyura, well-formed, large mandibles are known from palinurid lobsters of Late Cretaceous age (Woods, 1925–1931; Figs. 3C–D).

The first documented appearance of an adaptation to the chelae or other part of the body for durophagy can occur after the first occurrence of the family in the fossil record (Table 1). Fossil decapod crustaceans are, however, often preserved solely as dorsal carapaces; this is especially true in carbonate rocks of the Jurassic, Eocene, and Miocene (see, for example, Schweitzer and Feldmann, 2009; De Angeli and Garassino, 2006; and Müller, 1984, respectively). Thus, claw morphology for the first occurrence of the family may be unknown, as it is for all those groups in our dataset in which the appearance of durophagous adaptations is later than the first occurrence. The actual appearance of durophagous adaptations could have been earlier; recovery of relevant appendages will be required to test this hypothesis.

After the Cretaceous, durophagous adaptations appeared within other groups of Brachyura. Confirmed first records of adaptations to durophagy occurred in Paleocene occurrences of one superfamily, and several other families appeared within superfamilies that were already known to have adaptations to durophagy (see Supplementary Data[1]). The Eocene, like the Cretaceous, was a time of major radiation, as has long been known (Glaessner, 1969; Schram, 1986; Schweitzer, 2001b; Schweitzer et al., 2002; Fraaije, 2003; Feldmann, 2003; Schweitzer and Feldmann, 2005). In the Eocene, several families first occurred in the record, within superfamilies that have either confirmed adaptations to shell-crushing in modern congeners (Fig. 6D) or reports of durophagy in modern congeners. Several families with durophagous adapatations made first appearances also, the Calappidae, Carcinidae, Portunidae, and Xanthidae *sensu stricto*, all of which had been preceded by appearances of other members of their respective superfamilies.

Synthesis

The role of the Decapoda in the MMR and their pre- and post-Mesozoic influence on molluscan prey must be considered in light of the timing of appearance of the various decapod lineages. Prior to the Mesozoic, there is little record of Decapoda and virtually no record of their appendages (one confirmed genus and species). The primary decapod predators during the Triassic and Jurassic would have been chelate lobsters and probably achelate lobsters that pried open shells or used their mandibles, based upon the fossil record of recognized adaptations to heterochely. In order to fully appreciate the role of decapods in the MMR, these types of predators must be considered and integrated into analyses of predatory behavior and relationships. It may be possible to determine if indeed shell priers do leave scars on mollusk shells, for example. A radiation of decapods with specializations for crushing shells is documented in the fossil record from the Early Jurassic in lobsters and the Late Cretaceous in the Brachyura. Other methods of molluscan predation were undoubtedly present prior to the Cretaceous; those types leave less obvious scars, and they must be taken into consideration as well.

It is also important to recognize that decapods have quite broad diets. Most will eat a broad variety of food items, with only a few groups that are very specialized. Many decapods considered to be mollusk specialists (e.g., see Vannini et al., 1989) will eat a wide variety of food, including a small amount of mollusks. Claws may be used for multiple functions, some of which may be at odds with specializations for crushing prey. Non-claw-bearing decapods in fact eat mollusks now
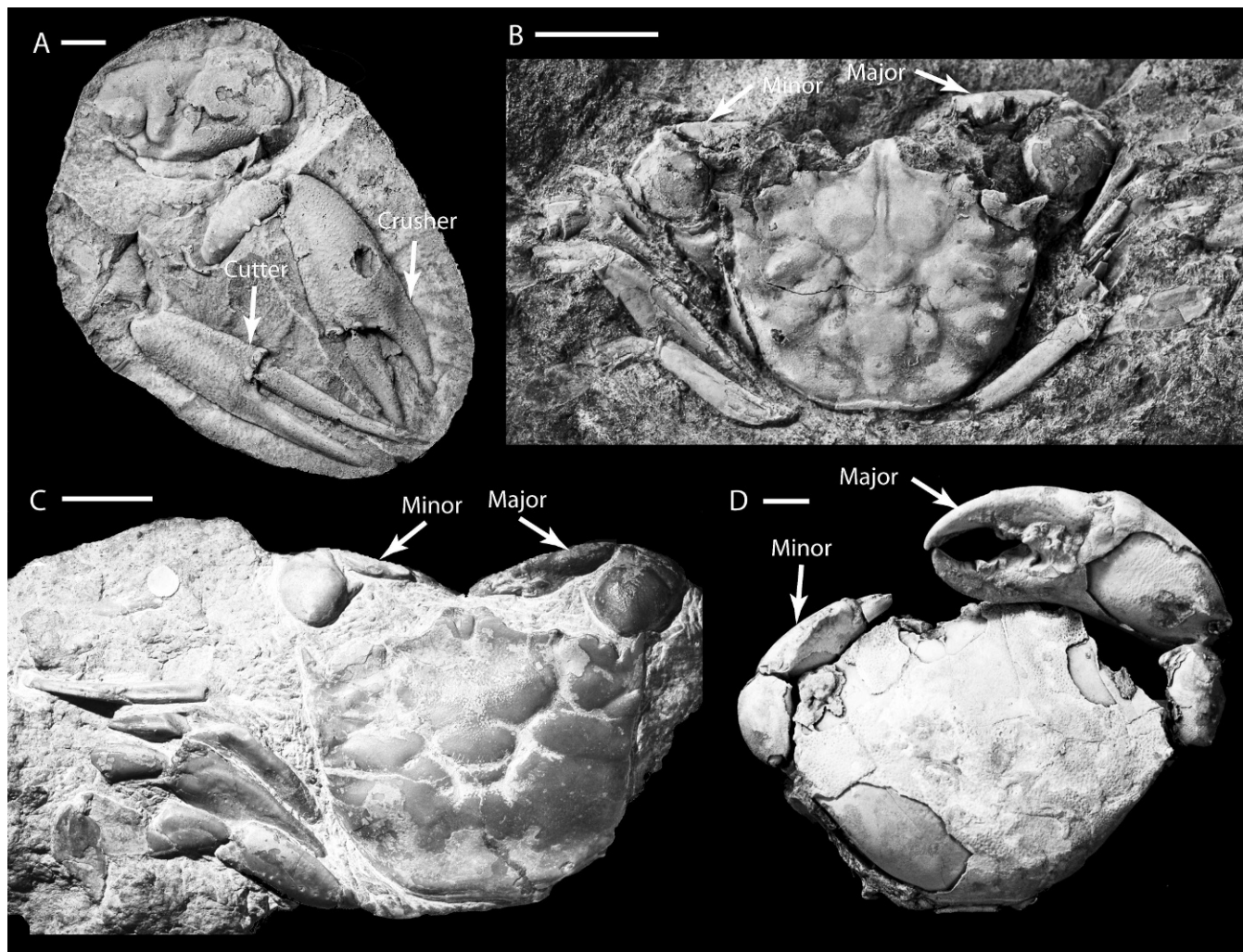
FIGURE 6—A) *Hoploparia stokesi* (Weller, 1903), Late Cretaceous, Antarctica, showing well-developed heterochely. B) *Longusorbis cuniculosus* (Richards, 1975), Campanian, British Columbia, showing heterochely. C) *Carcineretes woolacotti* (Withers, 1922), holotype BMNH In. 20780, Late Cretaceous, Jamaica, showing heterochely. D) *Harpactocarcinus* sp., KSU D25, showing marked heterochely. Scale bars 1 cm.

and undoubtedly did so in the past. Thus, all of these factors must be integrated into understanding the role of Decapoda in the MMR and an understanding of predator-prey relationships through time.

CAVEATS TO ESCALATION STUDIES

Examination of the biological literature on durophagy, chelipeds, and diet preferences within the Decapoda indicates decapod chelae are remarkably plastic in their morphology and are used for multiple activities (Seed and Hughes, 1995). Large pereiopods may not be used for eating, and other appendages may be used for durophagous feeding. Bilateral asymmetry seems to be widespread among active, mobile organisms (Babcock, 1993, 2005); thus, the observation that probably all decapods are heterochelous to some extent, even though the difference in claws may only be a few millimeters in one or more dimensions (Vermeij, 1977b). Heterochely serves a variety of functions other than food gathering, including display, defense, mate selection, and clasping during reproduction (Lee, 1995; Schenk and Wainwright, 2001). Many morphological features and behavioral habits other than crusher claws and strong heterochely provide evidence of predatory behavior, and further, other selective pressures have been at work besides escalation to produce a larger and stronger claw. Studies of predation must account for a full suite of features to determine the

method of predation, the extent of predation, and the impact of the predator on prey and vice versa.

Heterochely

Heterochely undoubtedly is not an adaptation solely for predation; thus, interpretation of a heterochelous fossil decapod taxon as a durophagous predator could be erroneous or overly simplistic. Possession of heterochelous appendages, while common and well documented within certain decapod lineages, is more variable than is generally acknowledged in the paleontological literature. Smith and Palmer (1994) demonstrated that claw size can change under artificial circumstances. If a crab is forced to use one claw over another, that claw will become stronger to compensate for the loss of use of the other claw; this also happens in nature. If a claw of a brachyuran is lost due to autotomy, the crab will reverse handedness following the next molt cycle (Simonson, 1985). Thus, heterochely is advantageous but is also plastic and can change with relative ease, the selective advantages of which are manifold.

There is an extensive literature documenting reversal of handedness in crabs and the age and molt number at which it occurs (Hamilton et al., 1976; Simonson, 1985, and references therein). If the crab was initially right handed, it will become left handed after molting, thus

eliminating any advantage that may have been served by handedness. Although handedness is initially fixed in many brachyurans, they are able to survive if handedness changes, as switching handedness after autotomy demonstrates. Thus, the evolutionary advantage of being right handed and the ability to subdue dextrally coiled snails, for example (Ng and Tan, 1984), can be lost during growth and molting. Other selective pressures besides those driving preference for handedness must be at work.

Also interesting is that many crabs regrow claws after autotomy and will often exhibit two cutter claws instead of a crusher and a cutter claw. Two ideas have been advanced for this response; one is that once the cutter is regrown, it is relatively easy for it to change into a crusher claw (Przibram, 1931), and the other is that possessing two cutter claws must be more advantageous than having two crusher claws (Hamilton et al., 1976). Having two cutter claws is not disadvantageous because the crabs survive, which has interesting implications for shell-crushing predation. Crabs can survive without the adaptation and, thus, must be broadly adapted to eating a varied diet. Handedness and heterochely are beneficial to the shell-crushing decapod but are not factors critical to their survival.

Handedness in decapods apparently can have a genetic basis within some lineages but may not in others. Herrick (1909) noted that the number of right handed (handedness is defined as bearing the crusher on the right side) and left handed individuals of the American lobster, *Homarus americanus*, was about equal (differing by about 100 in a sample of over 2000 individuals). He concluded as had others before him that lobsters do not appear to exhibit a strong preference for handedness. Some brachyurans, on the other hand, seem to be strongly right handed. Numerous studies have indicated that brachyurans, at least among certain superfamilies, begin life right handed (Przibram, 1931; Abby-Kalio and Warner, 1989), although this can change later as the crab either molts or loses its first pereiopod due to autotomy.

A genetic component of handedness is suggested by several other factors. Muscles in crushers and cutters are different. Crushers often have slower, stronger muscle fibers and cutters have faster muscles (Warner and Jones, 1976; Warner, 1977). The muscle types are reconfigured when claws are removed to accommodate the reversal of handedness (Govind and Pearce, 1994), indicating some level of genetic control over the process. Exposure of alpheid shrimps to ecdysal hormones can similarly accelerate molting and the reorganization of muscle tissue in response to reversal of handedness, thus indicating at least some molecular control over the process (Mellon and Greer, 1987). There must also be some inherent nerve differences that accompany handedness and switching from right to left, as claws are used for different purposes (Hamilton et al., 1976).

Evolution from the reptant form to the brachyuran form may have facilitated the selection for handedness, which could explain why the lobsters do not display it and crabs do. Such an event as mutation may have facilitated handedness occurred later in the brachyuran lineage, possibly more than once, as the crusher and cutter phenomena are seen in the heterotrematous crabs, and only in certain superfamilies (Calappoidea, Carpilioidea, Xanthoidea, Eriphioidea, Portunoidea). Interestingly, members of the genus *Uca* Leach, 1814, a thoracotrematous crab, do not exhibit preferred handedness (Abby-Kalio and Warner, 1989). The podotrematous crabs do not exhibit strong tendencies for handedness either. Thus, investigations of possible decapod predation in which handedness seems to be a dominant feature might focus on the heterotreme lineages.

Plasticity in handedness, the ability to switch the crusher from right to left or for one claw to grow stronger if the other is lost, was suggested by Smith and Palmer (1994) to be a possible origin of heterochely in evolutionary history. A simple need, or the simple advantage, of being able to break a molluscan shell could very rapidly result in specialized, heterochelous first pereiopods. Thus, it should not be surprising that heterochely and other specializations in pereiopod morphology for shell

crushing arose numerous times and in numerous lineages in decapod history (Jurassic–Paleogene) (Table 1), based on the fossil record. Plasticity is undoubtedly a large part of what makes crustaceans, and arthropods in general, so successful. Plasticity is also what makes it difficult to assign a direct cause-and-effect relationship to the development of specialized appendages in crustaceans. The decapod appendage is used for many functions and has demonstrated considerable plasticity within the lifetime of one individual, not to mention over generations. The many selection pressures on the decapod appendage and the entire morphology of the decapod must be considered, therefore, when integrating it into predator-prey studies.

Claws are multiuse appendages, and the uses for predation must be balanced by uses for scavenging, mating, display, and defense (Lee, 1995). Marked heterochely in decapods is sometimes used for sexual display (Labadie and Palmer, 1996; Góes and Fransozo, 1997), and heterochely may have originated for this purpose, not for feeding. Males generally have larger claws than females and exhibit more marked dimorphism in the chelae than do females. Some degree of sexual selection has operated on appendages within the Decapoda, and this is likely to be balanced with selection pressures for predation advantage in these same appendages.

Some studies have indicated that males seem to ingest larger quantities of mollusks than do females, based upon the larger size of the chelipeds in males of some species (e.g., Sukumaran and Neelakantan, 1997). Larger, heavier male claws appear to be better able to crush hard-shelled prey, permitting feeding on stronger, more robust prey and reducing intraspecific competition. This results in partitioning of resources so that males and females do not compete for the same food items. The study by Hamilton (1976) demonstrated a similar partitioning of resources. Primarily immature females or small adult male blue crabs (*Callinectes sapidus* Rathbun, 1896) preyed upon snails of the genus *Littorina* Ferussac, 1822, apparently due to their small size. Larger crabs of either sex are presumed to have preferred larger prey and were able to crush it with their generally larger and more dimorphic claws, resulting in resource partitioning. In the Cancridae, numerous studies indicate that larger crabs are more successful at crushing shells, perhaps due to the overall larger size of their claws (Creswell and Marsden, 1990). Thus, smaller crabs must resort to other means by which to obtain meals, and specialized chelae may only be advantageous once a certain size is reached.

Niche partitioning of resources may have been a secondary benefit of sexual selection resulting in sexual dimorphism and development of sexual display in males. The more markedly dimorphic, larger claws in males permit or force them to eat different prey. Such patterns are even noted in such crabs with isochelous claws as the cancrids and some xanthids (Figs. 7A–B), in which males or larger crabs simply have larger claws overall. Biological literature is apparently somewhat split on the issue of niche partitioning as a result of sexual selection in Decapoda (Lee, 1995, and references therein), but this issue seems to be a fruitful avenue of research.

Predation studies should also investigate chelae that are not heterochelous and not overemphasize heterochelous claws. Members of the Cancridae Latreille, 1802, have been well documented as durophagous, and they exhibit heterochely only on the order of a few millimeters between the two chelae (Vermeij, 1977b). Thus, heterochely is not a prerequisite for durophagy, which suggests that many more groups in the fossil record may have been durophagous and currently are not recognized as such.

An example of problems for feeding arising from extreme heterochely can be found in *Pseudocarcinus gigas* Lamarck, 1818, a huge crab that may weigh up to 14 kg (Heeren and Mitchell, 1997) and that has the largest chelipeds among the decapods (Hale, 1927; Heeren and Mitchell, 1997). These crabs possess robust, dimorphic claws with crushing molariform teeth that do not really fit into the categories of crusher and cutter (Heeren and Mitchell, 1997, fig. 1). Heeren and
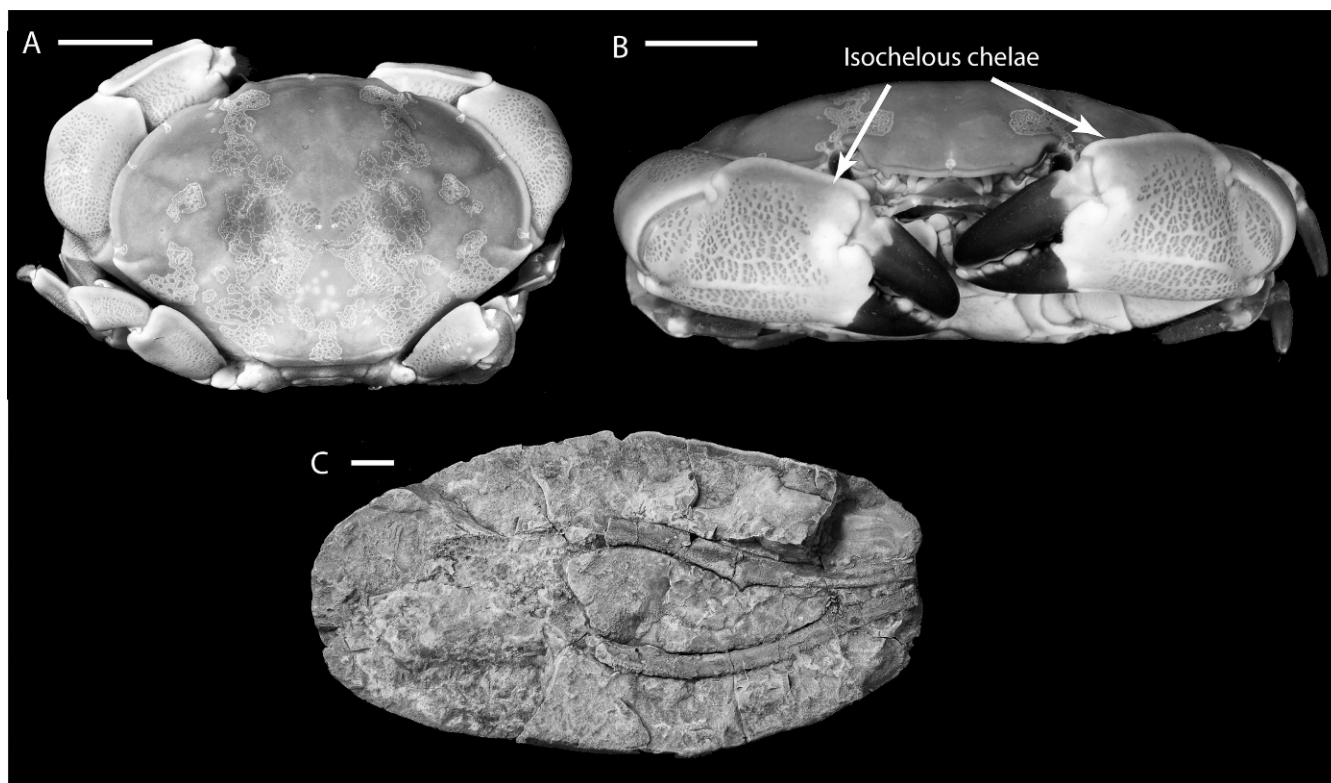
FIGURE 7—A–B) *Atergatis floridus* (Linnaeus, 1767), KSU D341, dorsal view (A) and frontal view , showing nearly equal sized crushing chelipeds. C) *Palaeonephrops browni* (Whitfield, 1907), KSU D1113, Late Cretaceous of Montana, showing extremely large claw for the species; note that the fingers would not occlude. Scale bars 1 cm.

Mitchell (1997) reported that males had a difficult time using their enormous, usually right, claw to manipulate food, using mainly the left claw, whereas females were able to manipulate food much more easily as they do not exhibit such marked dimorphism. In this case, it seems that the marked dimorphism hinders food gathering, and may instead be an adaptation to mating display (Heeren and Mitchell, 1997; Taylor, 2001). Thus, it is important to keep such multiple uses of chelipeds in mind when evaluating the fossil record. Interpretation of some fossil taxa with huge, markedly heterochelous claws as efficient shell-crushers may be erroneous (*Megaxantho* Vega et al., 2001; *Tumidocarcinus* Glaessner, 1960; some species of *Harpactocarcinus* A. Milne-Edwards, 1862; and some species of *Trichopeltarion* A. Milne-Edwards, 1880). Marked gape between fingers or the relationship between carapace width and claw size may suggest that the claw is used more for sexual display and less for shell crushing, despite marked heterochely (Fig. 7C).

Durophagy without Robust Claws

Many studies of predator-prey relationships focus on shell ornamentation, thickness, spines, and other easily measured criteria in prey, because they are readily observed. Predators would drive escalation toward these features which make it more difficult to break shells. Numerous studies have demonstrated this trend (Vermeij, 1977a). A clawed organism, no matter how weak the claw, however, can break at least a thin shell (Dietl and Vega, 2008). Decapods have been documented to possess claws since at least the Triassic, and probably as early as the Devonian, so they may have been breaking shells as at least an incidental part of their diet since that time. A broad range of extant decapods ingest at least small numbers of pelecypods and gastropods, mostly thin shelled, as part of their diet, probably eating them whole or crushing them with their mandibles or other mouthparts. This must have exerted selection pressure on the Mollusca, as representatives of many of these extant decapods have been present

since at least the Jurassic. In what ways have many of these thin-shelled mollusks responded? Are they simply not eaten often enough to respond by developing thick shells or spines? Have they responded by going deeper in overall water depth? Do they dig deeper into the sediment than they once did? Are they smaller and faster (i.e., harder to catch)? Are they larger and, therefore, harder to manage? Has their survival strategy emphasized fecundity over strength of individuals? These are questions that need to be addressed and, in fact, can be, because we do know the fossil record of the decapod families exhibiting such dietary preferences.

Multiple Feeding Strategies

Most decapods which possess claws that are considered to be specialized for crushing hard-shelled prey, in fact, consume a broad and varied diet (Vannini et al., 1989; Mori et al., 1995). Vannini et al. (1989) reported that some species of *Eriphia* Latreille, 1817, do very little crushing to obtain nutrition when living in a rocky, intertidal environment. In addition, they noted that those species that did ingest snail shells seemed to do so especially when hermit crabs inhabited those shells. This suggests a much more complex relationship between predator, prey, and the intermediate form—the gastropod that produced the shell that is used by the hermit crab—than is usually considered in paleontological studies. *Monodaeus couchii* (Couch, 1851), a member of the Xanthidae *sensu stricto*, is a known predator of mollusks, but it actually feeds on a wide variety of organisms and is also a deposit feeder and a scavenger (Mori et al., 1995). Even those decapods exhibiting durophagous specializations are broadly adapted to a variety of feeding strategies, perhaps in part as a response to evolutionary processes within the Mollusca. *Carcinus* Leach, 1814 can crush shells with molariform teeth, but also uses the winkling process described earlier (Rochette et al., 2007). Thus, the specialized crushing teeth are not always used to catch and crush prey. Cartes (1993) described both *Paromola* Wood-Mason in Wood-Mason and Alcock,

1891, and *Geryon* Krøyer, 1837, as opportunists, taking advantage of available prey and scavenging depending on the season.

Generalizations about the use of first pereiopods are very difficult to make because the Decapoda are so varied and the first pereiopod is so plastic and multifunctional. Predators often evolve multiple mechanisms to subdue prey, an example of classic escalation. A crushing chela is useful but not the only means by which to subdue molluscan prey. As gastropods and pelecypods adapted to survive crushing specializations, decapods similarly evolved other mechanisms to subdue prey, some of which leave few to no traces on the shells of prey. This type of escalation is, thus, difficult to directly measure but can be inferred by the presence in the fossil record of members of the same families that exhibit such behavior today. Escalation must be balanced by selective pressures operating on these same appendages for other functions. Thus, decapods must have reasonably broad adaptations to permit them to eat a broad variety of prey. The broad range of behaviors and preferences within the Decapoda must be accounted for in predation studies, and perhaps, signs of predation other than direct shell damage might be sought.

SUMMARY AND CONCLUSIONS

Paleontological literature has primarily focused on three adaptations of decapods to durophagous predation on mollusks: heterochely, molariform teeth, and a curved tooth for shell peeling, because they have a high preservation potential in the fossil record. Other such adaptative morphologies as stout mandibles and flattened dactyls of the walking legs are occasionally preserved. Examination of shape of the cephalothorax, such as the transversely flattened shape typical of mandible crushers, is also important and may bear on timing of appearance and style of predation preserved in the fossil record. Access to the soft tissue of molluscan prey can be achieved by numerous methods involving the chelipeds, the dactyli of the pereiopods, the mandibles, or some combination of these parts. Examination of the fossil record of decapod crustaceans with preserved evidence of these adaptations, or inferred presence of these adaptations due to morphological similarity to or relationship with extant taxa, shows that durophagous adaptations arose in the Mesozoic, and especially in the Late Cretaceous, in most major groups.

Many taxa within the decapod crustaceans, particularly the lobsters and true crabs, use subtle durophagous predation as a significant part of their feeding behavior. Animals so adapted are distributed among several different superfamilies, and each taxon possesses a unique set of morphological features that facilitate predation. It appears that there is some genetic control on the morphology of predation that is expressed at the level of superfamily or family.

Emphasis on heterochely and development of very large, crusher claws as predatory tools might imply that the appendages coevolved as their shelled prey became larger, stouter, and more ornamented. Recognition that the major claw serves a multitude of functions other than predation, however, suggests that it is just as likely that one of these other functions was the selective force for its development. Indeed, in at least one case, the major claw has grown so large that it cannot function as a predatory device.

Although numerous groups within the reptant Decapoda have been documented to be durophagous predators, others prey upon soft-bodied organisms, and some ingest shelled organisms as incidental parts of their diet probably while grazing, scavenging, or sifting sediment. In order to carefully assess the role of decapods as predators through time, therefore, it is important to view the process from the standpoint of the predator as well as the prey. This must involve examination of food resources exploited by taxa; recognition that the possession of heterochelous, large claws may have nothing to do with durophagous predation; and observation that animals superficially lacking in predatory tools may, in fact, be active predators. The geologic range of the taxa that have been documented to engage in all styles of durophagous food gathering must be considered at the level of family or superfamily in order to obtain reliable results in the determination of the role of decapods in driving the evolution of prey species in the MMR and at other times.

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