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Specialized shell-breaking crab claws in Cretaceous seas

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Here we report on a large brachyuran crab species from the Late Cretaceous of Mexico that has claws indicative of highly specialized shell-breaking behaviour. This crab possessed dimorphic claws (the right larger than the left), armed with several broad teeth, including a curved tooth structure found at the base of the movable finger of the right claw. The curved tooth is similar to the one observed on claws of many living durophagous crabs that use it as a weapon to peel, crush or chip the edges of hard-shelled prey, particularly molluscs. These morphological traits suggest that specialized shell-breaking crab predators had evolved during the Cretaceous, which contradicts previous findings supporting an Early Cenozoic origin for specialized shell crushers within the brachyuran clade.

Keywords: Mesozoic marine revolution; brachyuran crabs; predation; durophagy; *Megaxantho*

1. INTRODUCTION

A marked restructuring of shallow marine benthic communities occurred during the Middle and Late Mesozoic, a phenomenon that has been termed the Mesozoic marine revolution (Vermeij 1977*a*). Among these changes, there was an increase in durophagous (shell-breaking) predation evidenced by the diversification of predators, such as teleost fishes and decapod crustaceans (Vermeij 1977*a*, 1987), an increase in breakage-resistant shell armour of gastropods (Vermeij 1977*a*, 1987) and an increase in frequency of breakage-induced shell damage and repair (Vermeij 1987).

While almost every clawed crustacean should be viewed as a potential shell crusher of small thin-shelled prey, among living crabs specialized elements of claw morphology underlie predation on more resistant prey forms. Crabs that feed on well-defended molluscs usually possess dimorphic claws, with one larger, more powerful, claw on the right hand side of the body that functions to crush prey, and one smaller, less robust, cutter claw on the left hand side of the body. Typically, the claws are also armed with several broad molariform teeth (Seed & Hughes 1995). Despite being among the most abundant and powerful shell-breaking predators in modern seas, brachyuran crabs of the Cretaceous are thought to have lacked these specialized shell-breaking traits (Vermeij 1987). The first crabs with these durophagous innovations are thought to have originated during the Cenozoic (Vermeij 1987; Walker & Brett 2002; see also Oji *et al.* (2003) for a similar inference based on patterns of shell fragmentation).

Here, contrary to this general understanding, we report on a crab species from the Late Cretaceous of Mexico that possessed claw morphology indicative of a highly specialized shell-breaking mode of life. We also discuss the environmental circumstances favouring the origin and spread of durophagous innovations in brachyuran crabs.

2. MATERIALS AND STRATIGRAPHIC CONTEXT

Crustacean decapods have been reported from diverse outcrops of the Ocozocoautla Formation (Vega *et al.* 2001). Two specimens of a new species of xanthid crab, *Megaxantho zoque* (Vega *et al.* 2001), were found near the town of Ocozocoautla (locality 1003 of the Instituto de Historia Natural del Estado de Chiapas, IHNCH). The Ocozocoautla Formation is a Late Cretaceous stratigraphic unit in the central portion of Chiapas, southeastern Mexico, and includes 630 m of prodeltaic sediments, including lagoonal deposits that were deposited in warm well-oxygenated water (Michaud 1988; Vega *et al.* 2001). Calcareous algae, large rudists, other bivalves and gastropods, such as aporrhaids and turritellids, are abundant in the outcrops, which indicate a productive setting. Benthic foraminifera and stratigraphic position indicate an Early Maastrichtian age for the Ocozocoautla Formation (Vega *et al.* 2001).

3. RESULTS AND DISCUSSION

Megaxantho zoque is one of the largest species of fossil brachyuran crabs described for the Cretaceous (carapace width approx. 127 mm; figure 1; Vega *et al.* 2001). The right claw is large in this species, measuring approximately 108 mm in length and approximately 57 mm in height on the holotype specimen (IHNCH-3421; figure 1*c*). The movable finger (dactyl) of the right claw is lined with four broad, blunt teeth on the occlusive surface and has a large curved basal tooth (lobule; figure 1*c*,*e*), which articulates with a large sub-basal tooth, arising on the distal margin of the palm of the claw (Vega *et al.* 2001). The fixed finger of the right claw is also armed with five blunt teeth on the occlusive surface (figure 1*c*). The left claw is more slender (half the height of the right claw; Vega *et al.* 2001) and is also armed with blunt teeth on the occlusive surface (figure 1*d*).

While Vega *et al.* (2001) described the claw morphology of *Megaxantho*, they did not consider the functional significance of the claws. *Megaxantho*'s large claws would have translated into increased force-generating potential (Schenk & Wainwright 2001); among modern durophagous crabs, increased claw strength is generally associated with increased claw size, particularly in the height dimension (Vermeij 1977*b*; Schenk & Wainwright 2001). Increased claw size, however, has also been associated with success in sexual and agonistic interactions (Lee 1995), such that large claw size by itself is not enough to establish a strong link between claw morphology and durophagy. Other elements of claw morphology need to be examined before we can accept the interpretation that the claws of *Megaxantho* functioned in crushing hard-shelled prey. First, claw dimorphism in *Megaxantho* is consistent with an asymmetry based on a force–speed trade-off that allows the crab one 'strong', 'crusher' and one 'fast', 'cutter' claw, which is

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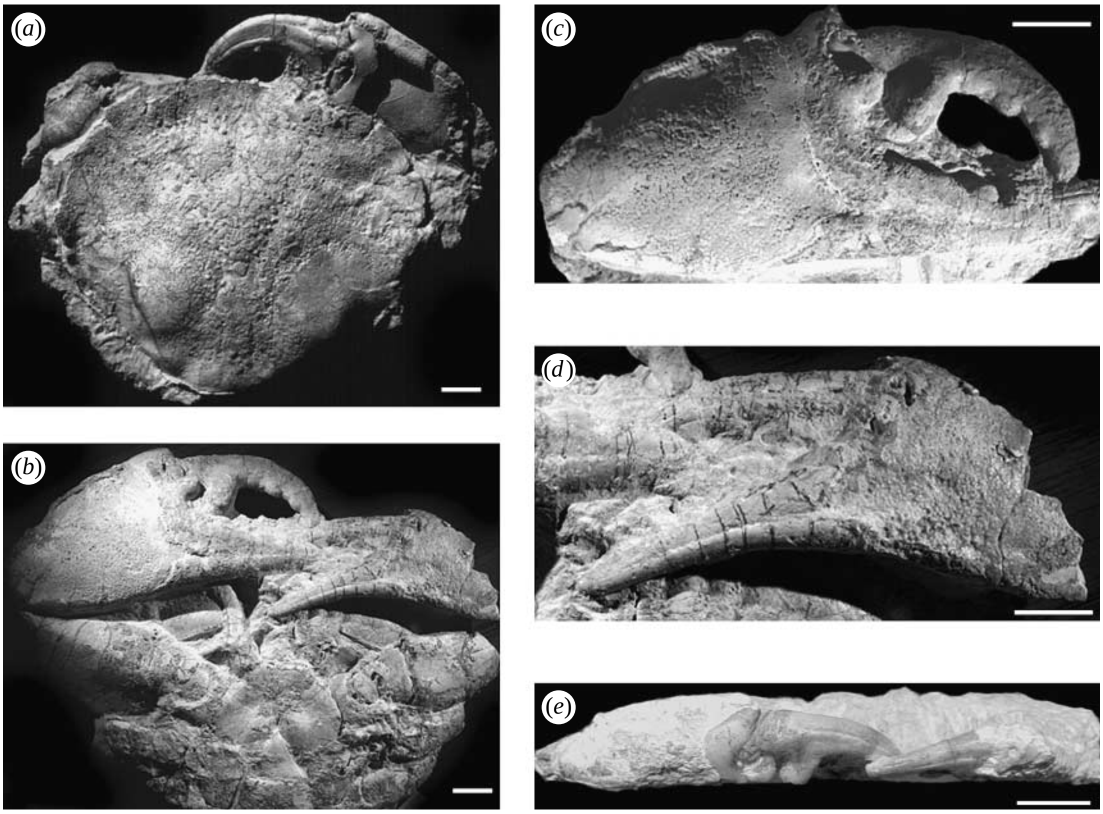

Figure 1. (*a*) Dorsal and (*b*) ventral views of *M. zoque* (Vega *et al.* 2001; IHNCH-3421); occlusive geometry of (*c*) right and (*d*) left claws. Note the blunt teeth and curved tooth at base of dactyl on the right claw. (*e*) Orientation of curved tooth directed slightly to the outside of the palm of the claw. Scale bar, 1 cm.

typical of most living durophagous crabs (Vermeij 1977*b*; Seed & Hughes 1995); the crusher claw is used to apply compressive force to break the prey's shell, while the cutter claw functions to manipulate the prey (Seed & Hughes 1995). Right handedness, with the crusher on the right side of the body (perhaps for more effective manipulation of dextrally coiled snail prey; figure 1*b*; Dietl & Hendricks 2006), is thus likely to be a character shaped by selection pressures associated with foraging requirements (Lee 1995).

Also consistent with this line of reasoning are estimated values for the mechanical advantage of *Megaxantho* claws. Mechanical advantage, calculated as the ratio of the distance between the pivot and the point of insertion of the apodeme (muscle attachment point) on the dactyl divided by the distance from the pivot to the tip of the dactyl, is often closely related to the degree of development of crushing teeth on the occlusive surface of the claw in living durophagous brachyurans (Vermeij 1987); estimated values for *Megaxantho* crusher claws fall within the range reported for living durophagous crabs (*Megaxantho* approx. 0.4; living brachyurans = 0.22–0.55; Seed & Hughes 1995). With only two specimens known so far (one known to be male), it is not possible to determine unequivocally whether claw dimorphism in *Megaxantho* is equally developed in male and female crabs. If evident once more specimens are available, such a pattern would also support the major role of claw dimorphism in feeding, rather than sexually based aggression.

Second, the presence of specialized occlusive regions (*sensu* Brown *et al.* 1979), which influence force distribution (the focus of stress against an object; Schenk & Wainwright 2001), is also highly indicative of durophagous behaviour. The curved tooth structure found on the right claw of *Megaxantho* is similar to the one observed on claws of many living durophagous crabs, which use it as a weapon to peel, crush or chip the edges of the shells of hard-shelled prey. Some portunid species, for instance, *Necora puber* and *Thalamita danae*, and many xanthid crabs, including species of *Panopeus*, *Eriphia* and *Ozius*, have a pronounced tooth at the base of the dactyl of the right claw that enhances the mechanical advantage of the claw. This tooth is usually directed slightly to the outside of the claw's palm, as it is in *Megaxantho* (figure 1*e*). This alignment enables shearing and compressive forces to be applied to the prey's shell (Seed & Hughes 1995). In some menippids, such as *Lydia annulipes* and *Epixanthus dentatus* the curved tooth is similar in its development to that of some calappids (Ng & Tan 1984). Calappids also possess two blunt teeth on the propodus of the claw that form a socket into which the curved tooth can fit. This 'socket' in calappids is less well developed or absent in other crabs, including *Megaxantho*, but that does not diminish the significant increase in power for claws armed with a basal curved tooth.

Taken together, the large dimorphic claws armed with several broad teeth, including a curved tooth positioned at the base of the dactyl on the right claw point to a durophagous mode of life for *Megaxantho*.

This conclusion presents an opportunity for a re-evaluation of the role that brachyurans played in the restructuring of shallow marine benthic communities during the Mesozoic marine revolution, particularly the marked increase in shell armour (e.g. internally thickened and narrowed apertures) of gastropods, which occurred in the Cretaceous (Vermeij 1987).

Our results also suggest that durophagous innovations evolved more than once within the brachyuran clade. This study has shown that minor innovations in occlusive geometry of the claw (e.g. a curved tooth), which increase competitive performance, evolved at least once in the Early Maastrichtian. The phenotype was evolutionarily lost when *Megaxantho* became extinct at the end of the Cretaceous (Vega *et al.* 2001). Throughout the Cenozoic, however, the phenotype evolved again independently within some of the major living durophagous crab families. For instance, the first record of the curved tooth on calappid claws is in the Oligocene (Bellwood 1998); but the trait is likely to have evolved as early as the Eocene, given the appearance of characteristically peeled prey shells (Vermeij 1987). A similar (?) structure present on the claws of other extinct crabs from the Cretaceous, such as an undescribed species of *Ophthalmoplax* from Mexico and *Binkhorstia ubaghsii* (van Bakel *et al.* 2003) suggest tentatively that the trait may have been more widespread even in the Cretaceous. There is no robust phylogeny for the infra-order Brachyura (both living and fossil), however, which limits our ability to infer the number of times the trait might have evolved in living durophagous groups, such as the Xanthidae and Portunidae, but it is clear with the data at hand that the trait evolved more than once.

This repeated evolution permits a comparative approach to ask where, when and under what circumstances innovations are acquired and secondarily lost (Vermeij 2002). As indicated above, the data are too sparse at this point to address these questions rigorously, but emerging patterns in other clades with similar traits (e.g. labral spines in predatory gastropods; Vermeij 2001) that improve competitive performance put forward a testable hypothesis: evolutionary innovations that increase competitive performance appear at times and in places where resources are abundant and accessible (i.e. where energetic constraints on functional improvement are low), and where predators and competitors impose intense selection (Vermeij 2002).

In other words, because crushing, chipping or peeling the edges of the shell of molluscan prey involves a substantial structural (and energetic) investment in the form of powerful claws, innovation should be concentrated during productive and competitive times and places. This outcome is expected because, as with most adaptive improvements, the evolution of specialized elements of the claw that underlie durophagy entails trade-offs relative to other competing functions. For instance, the claws of living durophagous crabs function in multiple ways, including foraging, agonistic interactions (intraspecific competition for dominance, refuge and food) and competition for mates (Lee 1995). Thus, the structure and size of the claw among living durophagous brachyurans is a complex balance between at least three broad selection pressures. Trade-offs among these competing functions enforce ecological constraints on functional improvement, and are only lessened when individuals gain greater access to resources—these conditions enable trait combinations to become established that would otherwise have been selected against.

With only a single data point in the Early Maastrichtian, it is not possible to evaluate whether availability of resources is a consistent factor associated with the evolution of specialized claws in brachyurans as a whole, but it is interesting to note that the Late Cretaceous is often portrayed as a time of abundant resources (Vermeij 2001), which is consistent with our hypothesis.

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