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Morphology of crab predation scars on Recent and fossil turritellid gastropods

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A B S T R A C T

When nonlethal attempted predation breaks the aperture of a gastropod shell, the break is preserved as a scar which is frequently visible in the fossil record. Such scars are very frequently observed on fossil and living Turritellidae, a family of high-spired marine gastropods, but little is known about which predators make such scars or how they do so. If the form of these scars on fossil shells could be better interpreted biologically, a large data set of predation scars might become available for analysis. We experimented with live turritellids (*Turritella banksi*) and four species of crabs from the family Xanthidae (*Panopeus* sp., *Eurypanopeus planus*, *Leptodius taboganus*, *and Xanthodius sternberghii*) in Panama in order to investigate factors contributing to the breakage morphology resulting from crab predation on turritellid shells. Qualitative examination of scar morphology resulting from attacks by different crab species shows that particular crab species can cause distinctively-shaped scars, although some shapes of scars can be created by more than one crab species. Multivariate analysis of these scars reveals that scar morphologies arising from different crab species fall on overlapping continua in morphospace. Incorporating the shapes of fossil scars into these analyses reveals that fossil scars are similar to many of those created in the aquaria, and that scar shape can be accurately predicted by predator species. In particular, scars caused by *Panopeus* can be very similar to some fossil scars. Although the particular crab species used in the experiments probably do not prey on turritellids in the wild, the data on causes of break scar morphology and crab-turritellid predation behavior allow information of predation stored in the scars on fossil turritellids to be used to explore the history of predation on this important group of gastropods.

1. Introduction

Gastropod shells frequently function as defense against predation. Crabs (decapod crustaceans), in particular, are highly adapted for crushing and consuming hard-shelled prey, with crusher claws that have a high mechanical advantage (Vermeij, 1982b, 1987; Alexander and Dietl, 2003; Kosloski and Allmon, 2015). Crabs employ many methods to overcome the defenses of their gastropod prey, including outright crushing, piercing with the tip of the claw, and peeling and nipping at the aperture of the shell. The latter strategy is especially effective (and has been especially well-studied) in the family Calappidae, whose chelae have adaptations for breaking from the shell aperture in a predation method known as peeling (Vermeij, 1982a, 1982b, 1987; Ogaya, 2004, and references therein; Schweitzer and Feldmann, 2010), but (as demonstrated below) other crab families engage in similar behavior. When a gastropod survives this aperture-breaking attempt at predation, the mantle may resume shell growth at the edge of the break, thus preserving the shape of the break as a scar on the shell. These scars are commonly used as indicators of predation on fossil gastropods (e.g., Vermeij, 1987; Huntley and Kowalewski, 2007; Stafford et al., 2015).

Gastropods of the family Turritellidae have been abundant and diverse in the fossil record since at least the Late Jurassic (Das et al., 2018), occurring in great numbers in some beds, and are still abundant today in certain environments (Allmon, 1988, 2011). Throughout the group's entire stratigraphic range, many turritellid species show evidence of having survived durophagous, or shell-breaking, attempted predation, which leaves scars on the shell (Fig. 1). Predation scar frequency varies from 11% to 52% of individual turritellid shells in a fossil assemblage, with many individual shells showing multiple scars (Allmon et al., 1990). Attempted peeling predation thus appears to be an important factor in the life of an average turritellid. Despite this, very little is known about predation on turritellids, whose modern biology has not been well studied (Allmon, 2011). There are, for

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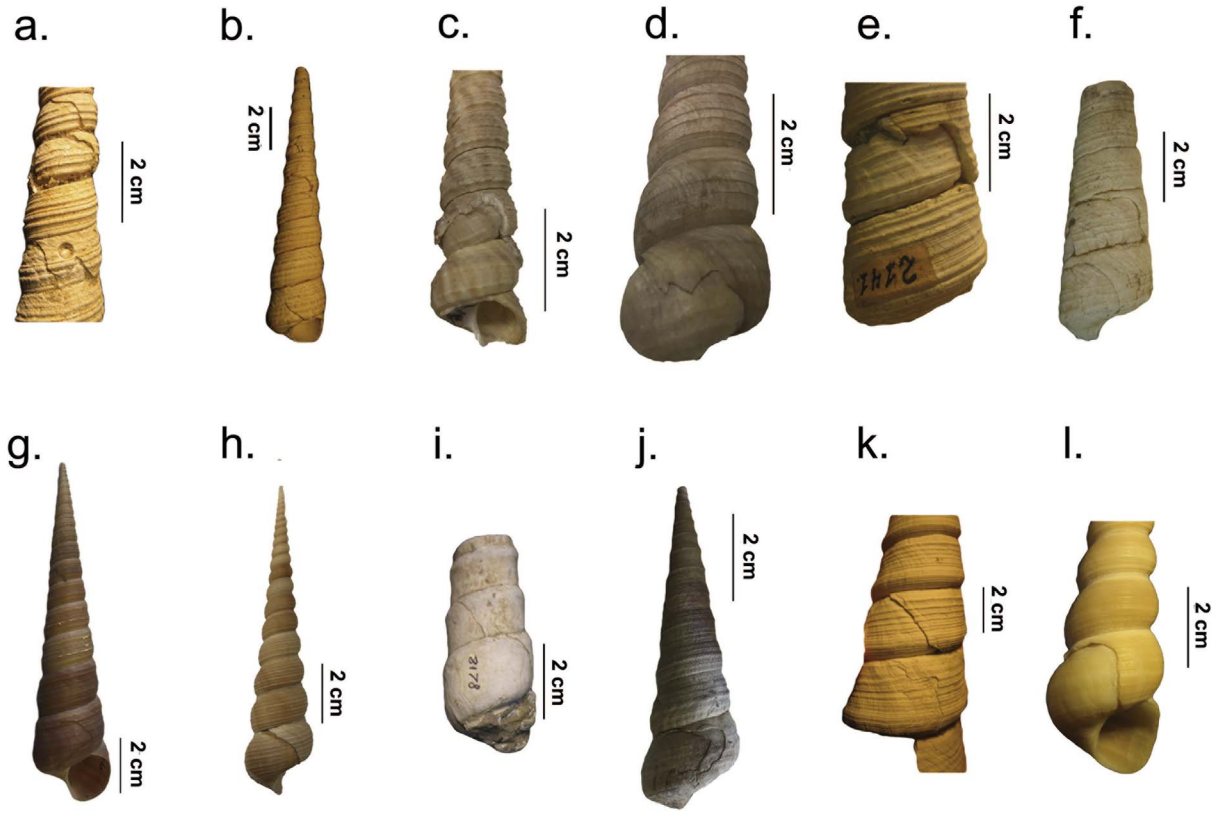

Fig. 1. Examples of scars of unsuccessful predation on living and fossil turritellid gastropods, showing diversity of scar shapes. a: *Turritella bipertita*, Pliocene, Williamsburg, VA, USNM 403444. b: *Turritella pilsbryi*, Pliocene, James River, VA, USNM 325457. c: *Turritella cochlea*? Recent, Gulf of Oman, MCZ 266723A. d: *Turritella bacillum*, locality unknown, MCZ 49743. e: *Turritella variegata*, Pleistocene, Cabo Blanco, Venezuela, NHMB. f: *Turritella* sp., Plio-Pleistocene, Williamsburg, VA, USNM. g: *Turritella bacillum*, Recent, Sri Lanka, AMNH 49029. h: *Turritella terebra*, Recent, Philippines, MCZ 360460. i: *Tropicolpus milleri*, Miocene, New Zealand, NZGS j: *Turritella carinifera*, Recent, South Africa, AMNH 205998. k: *Turritella pontoni*, Pliocene, Florida, USNM. l: *Turritella cerea*, Recent, northern Australia, PRI. (Repository abbreviations: AMNH – American Museum of Natural History, New York, NY, USA; NHMB – Naturhistorisches Museum Basel, Basel, Switzerland; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; PRI – Paleontological Research Institution, Ithaca, NY, USA; USNM – National Museum of Natural History, Smithsonian Institution, Washington, DC, USA).

example, apparently no published observations of a crab attempting to eat a turritellid. The efficacy of the shell at resisting breakage, the behaviors used by the crab predators, and even the size of predator necessary to create the observed breaks and scars have therefore all remained unknown.

The scars observed on fossil turritellids are present not only in great numbers, but also in great variety of shapes, from shallow divots to jagged scalloped/embayed breaks (Allmon et al., 1990; Alexander and Dietl, 2003) (Fig. 1). This variation in scar morphologies, coupled with the ubiquity of scarring and sheer numbers of these gastropods in the fossil record, suggests that a large data set on predator-prey interactions could be encoded in these scars. If particular predators cause distinctive scar shapes, then the shape of each scar records the details of its particular predation event - perhaps even details such as predator identity or size.

Crabs, particularly calappids, are the major culprits behind these scalloped/embayed scars in other gastropods (Alexander and Dietl, 2003; Ogaya, 2004). In fact, predation by calappid crabs is thought to be a key factor in the evolution of small or narrow apertures and tall spires of gastropods of the family Terebridae, since these traits defend against peeling in that group (Vermeij, 1982a, 1982b; Vermeij et al., 1980; Signor, 1985). Ascribing the scalloped/embayed scars seen on equally high-spired and relatively small-apertured turritellids to crabs therefore seems plausible.

Through experimentation with live crabs and turritellids, and quantification of the resulting shell breakage scars, this study attempts to provide preliminary answers the following questions: Will crabs attack turritellids given the opportunity? What break shapes result from such attacks, and do these shapes correlate to the species of the predator? How do the modern, experimentally-created break shapes compare to scars observed in the fossil record?

2. Methods

2.1. Experimental

We collected approximately 130 living and 200 dead specimens of *Turritella banksi* from tidal zone among mangroves on sandy substrate at low tide near Bahia Bique, southwest of Panama City, Republic of Panama (Fig. 2). A number of the shells collected showed signs of previous survived breakage (Fig. 3). We also collected 27 xanthid crabs of different sizes, including four species (*Panopeus* sp., *Xanthodius sternberghii*, *Eurypanopeus planus*, *Leptodius taboganus*), from Bahia Bique, Playa Farfan, and the intertidal zone of Naos Island at low tide. These crab species were selected purely for their availability and are not necessarily representative of all crabs in the area or of those that feed on turritellids in the wild.

Length, width, and aperture diameter of each gastropod shell were recorded; for the crabs, carapace width and length, width, thickness, and dactyl length of each crab were measured. *T. banksi* ranged from 15 to 50 mm in length, with a median of 35 (Fig. 4a). Crabs ranged from 16 to 44 mm in width, with *L. taboganus* the smallest and *Panopeus* the largest. *Panopeus* and *X. sternberghii* dominated the crabs collected, and most crabs were 26 to 36 mm in width (Fig. 4b). Xanthid crabs such as these are equipped with disproportionately large crushing claws and are very active predators (Williams, 1984). *Panopeus* in particular is a

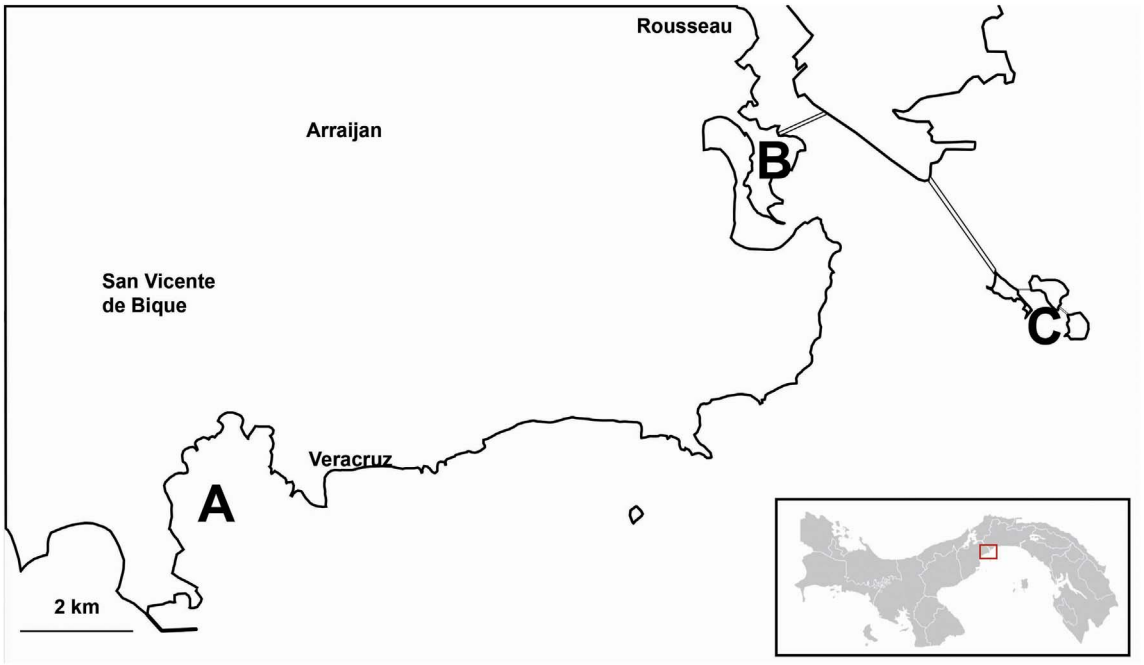

Fig. 2. Map of collection sites in Panama. A - Bahia Bique; B- Playa Farfan; C - Naos Island.

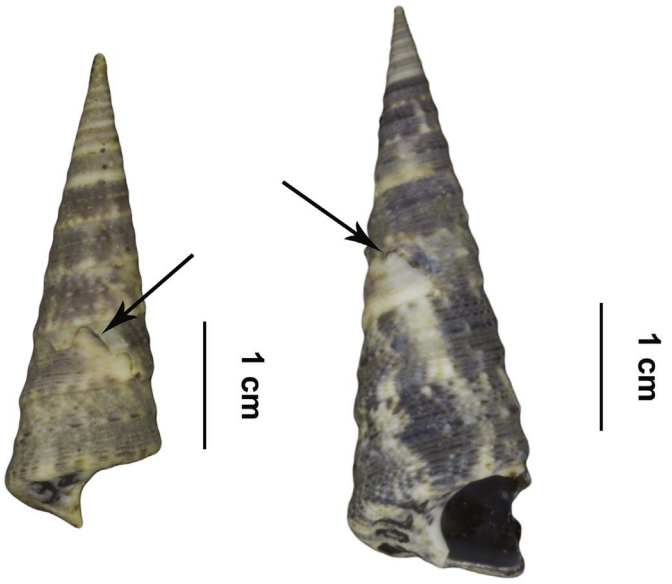

Fig. 3. Beach-collected dead specimens of *Turritella banksi*, showing unsuccessful predation scars (arrows).

robust crab, with a carapace approximately as wide as long and thick chelae with short dactyls. Its chelipeds are highly mobile, capable of reaching in many directions and grasping with strength. *Eurypanopeus* is similarly shaped to *Panopeus* but smaller; its chelae, similar in dimensions to those of *Panopeus*, are slightly weaker but still capable of pinching strongly. *Leptodius*, one of the smaller crab species used, has a carapace wider than long and chelae of intermediate thickness which, though large compared to the size of the crab, are neither especially large nor strong. *Xanthodius*, also wider than long, has slender dactyls and long, narrow chelae. Its claws have neither the strength nor the range of motion of *Panopeus.* All the crabs were right-handed in terms of claw size, but aside from the size difference between crusher claw on the right and cutter claw on the left, there were no notable asymmetries.

The live snails and crabs were housed in aquaria at Naos Island Marine Laboratories, Smithsonian Tropical Research Institute. Each crab was kept in its own aquarium for the duration of the experiments; snails were kept together in a holding aquarium until needed. Aquaria were approximately 30 l in volume each, fitted with polystyrene lids to prevent escapes, and connected to a running seawater system. Each aquarium contained one or two large rocks to provide cover for the crab; otherwise the bottom was bare glass in order to keep the snails from burrowing to escape the predators. Crabs were not fed for 5–7 days prior to introducing the first turritellid. Crabs were fed shrimp to satiety half-way through the experiments, at the two-week mark, because of their extremely low predation success rate.

Live turritellids were placed one at a time in a tank with a single crab and left there until the crab either successfully consumed the gastropod or completed an unsuccessful predation attempt. Unsuccessful attempts resulted when the crab attempted to break the shell and discarded it while the snail was still alive (Fig. 5). The resulting break was photographed, any remaining soft parts removed, and the shell kept, together with a record of which crab produced the break. (To supplement the live turritellids, additional prey was simulated using small pieces of shrimp inserted more than one full whorl inside unbroken, empty turritellid shells. Encounters involving prey simulated in this way were only used for observation of behavior and not included in counts of predation success because simulated prey was more susceptible to successful predation due to lacking muscle attachments and an operculum.) Some predation encounters were captured on video using a digital camera positioned for the clearest view, based on the location of the crab under examination; this was only possible with attacks by *Panopeus*, which was more willing to attack prey in daylight than the less aggressive crab species were.

Breakage scars on the shells were drawn by hand in a standard orientation (Fig. 6). We do not believe this drawing method introduced systematic biases because the shells selected were chosen randomly regardless of which crab had caused the scar. We were testing for separation of groups and so at worst, imprecise drawings would blur the groups together. A fixed vertical distance represented the width of the aperture attacked, and a horizontal axis represented the degrees of shell broken backwards from the aperture. This flattened the 3-dimensional break shapes on the conical turritellids into 2-dimensional curves which could be digitized and analyzed using standard morphometric

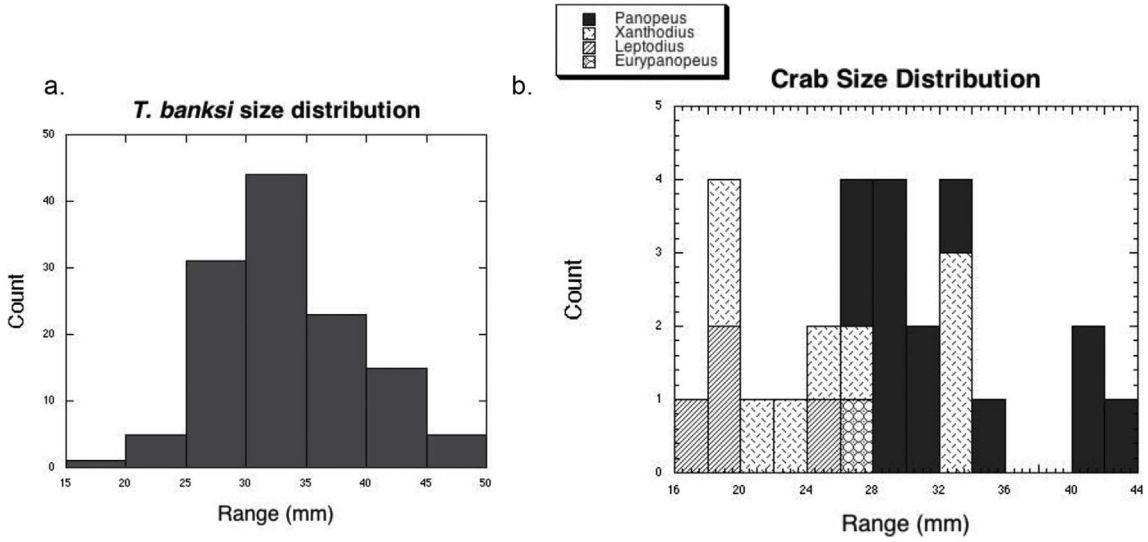

Fig. 4. Size distribution of (a) *T. banksi* gastropod specimens and (b) crab specimens used in the experiments.

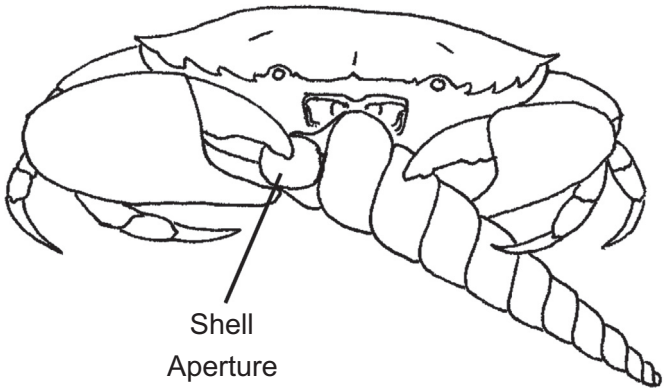

Fig. 5. Drawing of a crab (*Panopeus* sp.) grasping a *Turritella banksi*, and beginning to peel it at the aperture. Drawn from video images. Snail is about 3 cm long.

techniques.

2.2. Analysis of video

The filmed crab-turritellid encounters were divided into intervals of 30 s. The first and last intervals included the first and last observed physical contact between crab and turritellid. Recognizable behaviors observed in each 30-s interval were tallied into four categories (Fig. 8): **manipulation** of the shell using pereiopods and tips of right or left chelae, **grasping** of the spire or aperture in the right or left chelae, periods in which the crab exhibited **no motion** but remained in contact with the shell, and periods in which the crab or shell remained visible in the frame but **no contact** between the two was observed. Intervals in which the crab and shell moved out of the frame of the video were also recorded and excluded from analysis. Of these behaviors, only grasping is likely to leave damage that is visible in the fossil record as breaks or scars.

2.3. Fossils

For comparison with living *Turritella banksi*, we chose the fossil species *Turritella wagneriana* from the Pliocene (Pinecrest Sand/Tamiami Formation and Caloosahatchee Formation) of Florida (Fig. 7). This species was selected for analysis because it shows one of the highest break/repair frequencies seen in fossil *Turritella* (Allmon et al., 1990), and because their relatively large shell sizes (up to 60 mm in length) render any scars clearly visible. A total of 54 specimens of *T. wagneriana* from the Upper Pliocene Pinecrest Sand in Sarasota County, Florida were examined from the collections of the Paleontological Research Institution in Ithaca, NY. Of the 54 specimens examined, 36 (66.7%) displayed a total of 91 repair scars indicative of attempted predation; the remainder of the specimens were undamaged. These scars were drawn in the same flattened orientation as those on *T. banksi*. In addition to scar shape, whorl number (counted from the apex) was recorded for breaks on complete specimens.

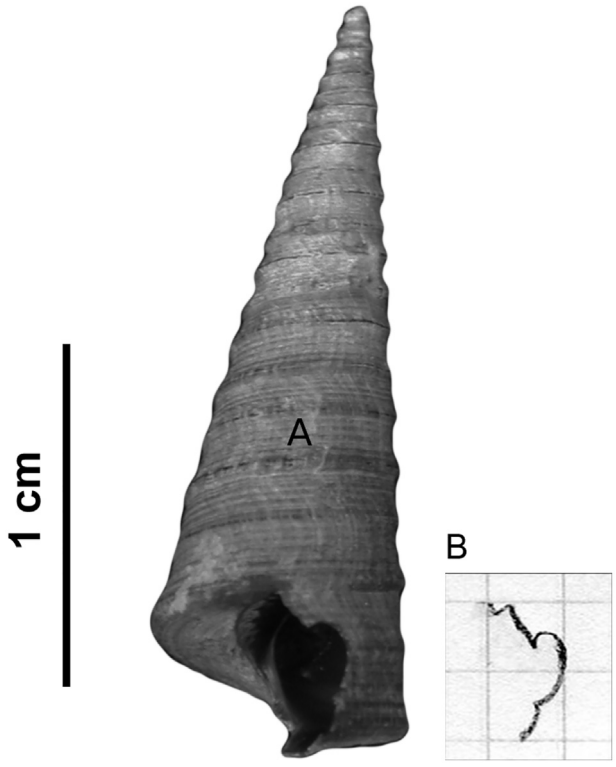

Fig. 6. (A) specimen of *T. banksi* with its aperture broken by a crab. (B) Trace of the broken aperture drawn flat.

2.4. Morphometric analysis

All flattened scar traces were scanned, then digitized using 50

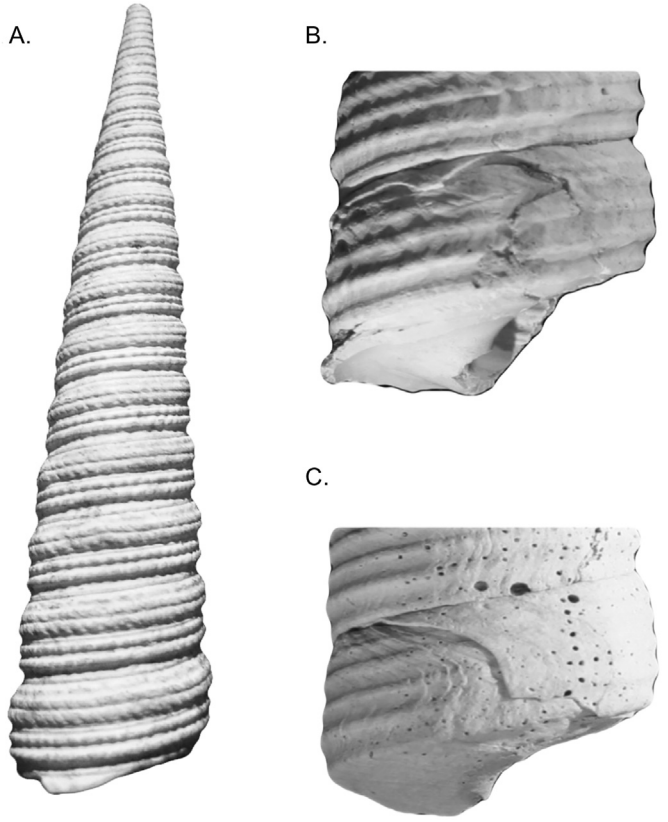

Fig. 7. *Turritella wagneriana* from the Pliocene of Florida. A. Shell is about 5 cm long. B, C. Unsuccessful predation scars. Each specimen is around 1 cm wide at base.

equally-spaced semilandmark curve points (Bookstein, 1997) in TpsDig2 (Rohlf, 2006). These points were imported into MorphoJ (Klingenberg, 2011) as landmarks. All subsequent analyses took place in MorphoJ. First, shape information was extracted from the semi-landmark data using a Procrustes superimposition (Dryden and Mardia, 1998). Principal components analysis of the breaks made by the four modern crab species was conducted to investigate the structure of the distribution of scar morphologies – whether the shapes plotted as distinct clusters of points, as overlapping continua of morphologies, or as an entirely undifferentiated scatter. A second principal components analysis incorporated the fossil scars into the above analysis to examine where the fossil scars plot in morphospace in relation to the Recent scars of known origin.

Discriminant function analyses of the partial warp scores from the four groups of experimentally-derived breaks – those caused by *Panopeus*, *Eurypanopeus*, *Xanthodius*, and *Leptodius* respectively – were conducted to examine how well predator crab type predicts scar shape. Finally, the group of scars recorded on fossil *T. wagneriana* were compared using the same techniques against each of the four groups of modern scars.

3. Results

Over the course of the experiments, 82.2% of snails were attacked, with 68.8% of the crabs making predation attempts and most crabs making multiple predation attempts (Table 1; Figs. 8,9,10). The smallest crabs, measuring 15 to 23 mm in width, made no attempts, and larger crabs made the most attempts (Fig. 10); 83.5% of those attempts were by *Panopeus*, which represented 48% of the crabs involved in the experiment. The great majority of predation attempts were unsuccessful: of the 103 attacks, only three were lethal. These three were performed by *Panopeus* on snail shells at the smaller end of the size distribution (15.1, 30.1, and 20 mm in length). Crabs accomplished the

Table 1
Summary of crabs and number of attacks in experiments.

	No. of crabs	No. of attacks	Attacks per crab	No. of successes	Success rate
Eurypanopeus	1	5	5	0	0
Leptodius	4	4	1	0	0
Panopeus	11	86	7.5	3	0.034
Xanthodius	9	8	0.8	0	0

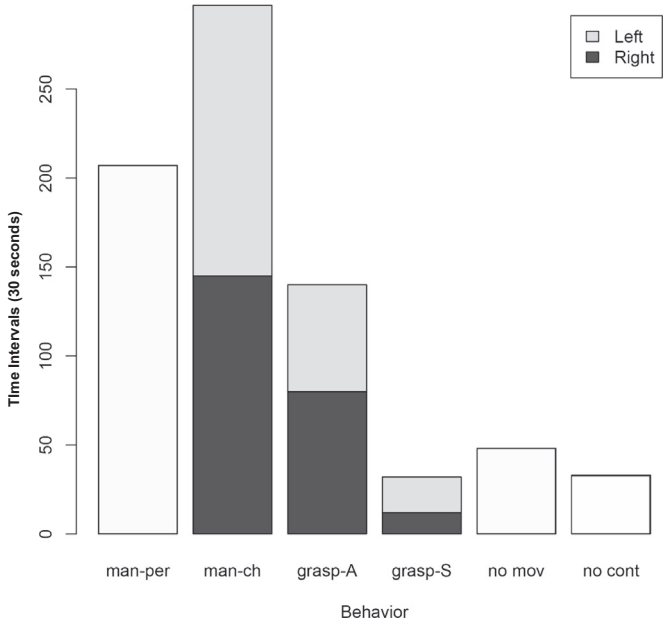

Fig. 8. Distribution of behaviors observed in crab-turritellid predation encounters. **Man-per**, manipulation with perpeiopods; **man-ch**, manipulation with chelae; **grasp-A**, grasping of the aperture with left or right chelae; **grasp-S**, grasping of the spire with left or right chelae; **no mov**, time intervals in which no movement was observed; **no cont**, time intervals in which to contact was observed.

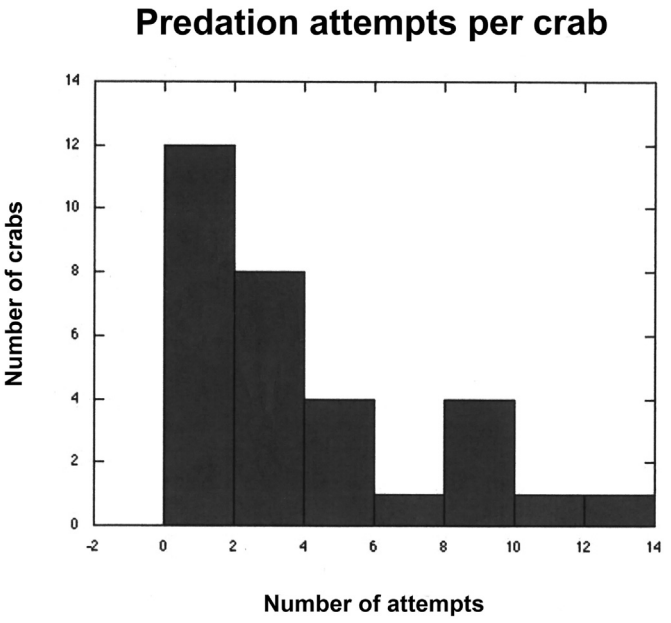

Fig. 9. Distribution of predation attempts per crab.

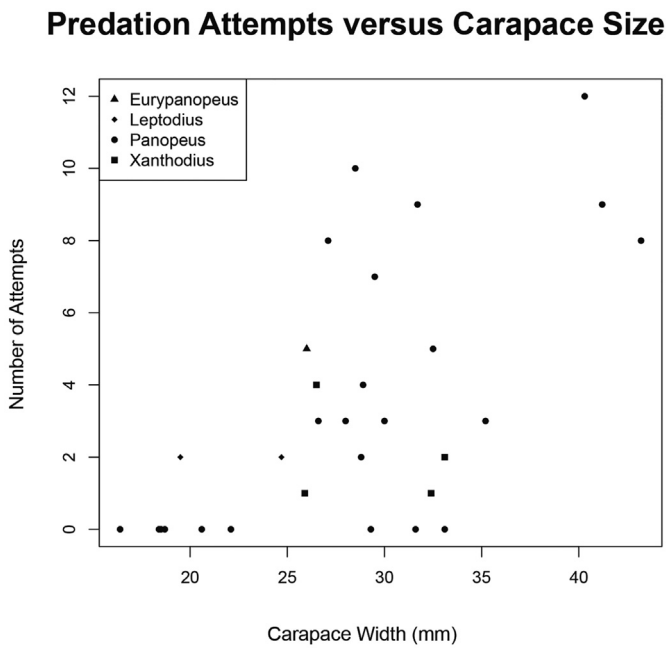

Fig. 10. Predation attempts versus crab carapace width, by species.

lethal predation attempts by crushing the entire shell into many gravel to sand-sized fragments. In unsuccessful predation attempts, all breakage was confined to the aperture.

All videos taken were of *Panopeus*, because these crabs were more willing to attack in daylight when it was possible to film them. Because the snails and crabs were approximately the same size (i.e., shell length ≅ carapace width), and the smooth, conical shells presented few easy opportunities for gripping, the crabs experienced difficulty in attacking the shells, spending much of their time trying to manipulate the shells into a position where shell breakage was possible (Fig. 5). The crabs' general approach was to stabilize the shell with the pereiopods and/or one of the chelae while chipping and reaching into the aperture with the remaining chela. The general pattern of attack following the introduction of a shell to the tank consisted of up to five seconds of inactivity, followed by a quick approach and then cycles of manipulation, grasping, and motionlessness for 2–30 min before rejection of the shell and resumption of inactivity. As indicated in the graph, manipulation with pereiopods or chelae was by far the most common behavior, with left and right chelae used close to equally. Behavior switched frequently, rather than continuing uninterrupted in one category. Grasping, the behavior that could result in scar damage, occurred predominantly at the aperture and less often on the spire. There was a slight preference for grasping the aperture with the right (larger) chela. This could be due either to the greater strength of the right chela; alternatively, the coiling direction of the shells could make it easier for the crab to attack with the right chela rather than the left.

3.1. Break shapes

We used several variables to describe break shape qualitatively. **Depth**, measured in degrees around the coiling axis, is 0 for an unbroken aperture and 360 for a break that removes an entire whorl. **Smoothness** describes the curvature of the scar: a *smooth* scar changes curvature gradually, while *jagged* scar has abrupt changes in curvature, i.e. sharply protruding or indented points along the length of the scar. **Regularity** describes the repeating of shapes within the scar; irregular scars are composed of nonrepeating shapes.

Panopeus and *Eurypanopeus* produced distinctive shapes on the snails that they attacked (Fig. 11a,b). Drilling was unique to larger *Panopeus* (carapace width ≥ 40 mm), while *Panopeus* in general produced deep, jagged, sometimes-regular breaks (Fig. 11c-e). Within *Panopeus*, larger crabs did not necessarily create deeper breaks. *Eurypanopeus* produced a distinctive smooth hook shape at the end of shallow to deep, jagged, regular breaks (Fig. 11a); within these constraints, breaks from each crab species exhibited a high degree of variability. *Leptodius* and *Xanthodius*, on the other hand, both produced shallow breaks which, lacking characteristic morphologies such as hooks, marked shell protrusions, or regular stairstep shapes, were very similar to each other (Fig. 11). *Panopeus* and *Eurypanopeus* also produced a few such simple breaks. Thus, two of the four crab species produced distinctive scar shapes; however, not all scar shapes were indicative of a particular species, as shallow, irregular break morphologies were created by all species in the experiment. In general, deep and jagged shapes were more likely to be indicative of a particular species.

No fossil scar examined (Fig. 7) had morphology identical to an experimentally-derived one, and there were some general differences in morphology observed. The deepest fossil scar penetrated approximately 450° from the aperture, while the deepest *Panopeus* scar penetrated 360°. Fossil scars tended to have a lower degree of regularity. Fossil scar shape varied more than single experimental scar groups: where *Panopeus* produced breaks > 90° deep in most cases and *Leptodius* only made breaks < 90°, scars on *T. wagneriana* were evenly split between shallow ones of < 90° and deep ones which penetrated a complete whorl. Furthermore, scar shape overall was more variable in the fossil scars than in any single experimental group. In details, however, many of the fossil scars were similar to the experimental ones. For instance, deeper fossil scars often displayed high regularity along their length. A few repeating scar morphologies, such as a deep one with regularity and a rectangular end which is found on two separate fossil gastropods, could indicate a particular species of crab, just as sub-apertural puncturing indicates *Panopeus*.

Both the principal components (PCA) and the discriminant function analyses (DFA) confirm these qualitative observations. PCA of the breaks caused by the four crab species (Fig. 12a) shows the morphologies plotting as overlapping continua inside of a shared morphospace. Incorporation of the fossil data (Fig. 12b) shows that fossil breaks plot as a scatter of points distributed throughout the Recent ones. Thus, the fossil breaks represent shapes that are not only quantitatively similar to the Recent breaks, but also contain a similar amount of variation overall.

Examining pairwise differences between the experimental scar groups described above (in Methods) with DFA (Fig. 13) confirms the qualitative observation that *Panopeus* created some markedly distinctive scars, while *Leptodius* and *Xanthodius* caused break morphologies that were indistinguishable from those caused by other species. *Panopeus* scars on *T. banksi* were substantially different from those of *Eurypanopeus*, *Xanthodius*, and *Leptodius*. On the other hand, the characteristic hook shape of *Eurypanopeus* scars that made them qualitatively distinguishable from those caused by both *Leptodius* and *Xanthodius* was not strongly reflected in the DFA, perhaps because most scars from these three taxa had a similar depth. In addition, *Xanthodius,* and *Leptodius* scars, which looked similar to each other, did not show any marked quantitative separation in the DFA. Overall, results from the DFA indicate that scar morphologies caused by *Panopeus* separate strongly from those caused by other crabs, but scar morphologies from the other three crab taxa grade into each other. Confounding this result may be the small sample size of break shapes caused by *Eurypanopeus*, *Xanthodius*, and *Leptodius*, but the pronounced difference between the breaks caused by these species and those caused by *Panopeus* is consistent regardless of which group the *Panopeus* group is compared to.

DFA of the fossil breaks on *T. wagneriana* against each of the experimental groups (Fig. 14) also supports the qualitative observations. Breaks on *T. wagneriana* were quantitatively different from those caused by *Eurypanopeus*, *Leptodius*, and *Xanthodius*. Meanwhile, scars on *T. wagneriana* and those caused by *Panopeus* on *T. banksi* had overlapping distributions of discriminant scores, showing that these two categories

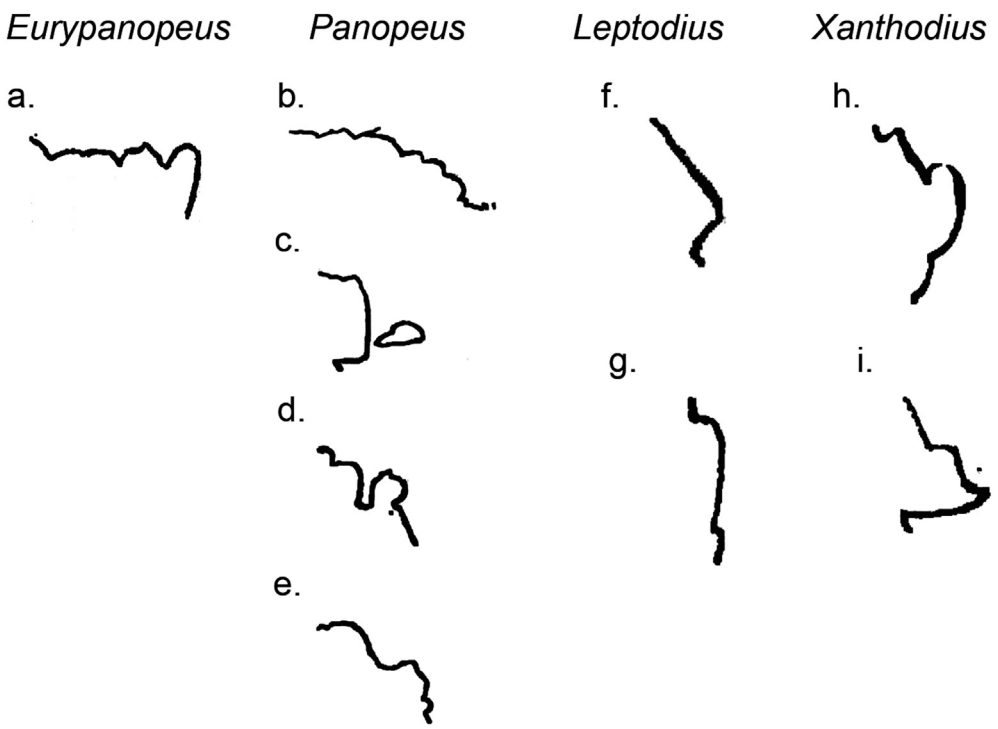

Fig. 11. Representative scar shapes on the aperture of *Turritella banksi* (see Fig. 6). (a) *Eurypanopeus*; (b) *Panopeus*; (c–e) Breaks in various stages of sub-apertural drilling by *Panopeus*, from (c) newly drilled, to (d) semi-open, and (e) completely broken. (f,g) *Leptodius*. (h,i) *Xanthodius*.

contain some similar shapes; in particular, this may reflect the shared presence of deep scars in the *Panopeus* and fossil groups.

4. Discussion

The case study of the four living crabs presented here is preliminary, but provides sufficient information to begin decoding the information contained in the morphology of repair scars on fossil turritellid shells. First, however, it is important to note that these experiments are artificial in several respects. In addition to the animals being in captivity in a non-natural setting, we do not know if these particular crab species prey on this particular turritellid species in nature. It is also possible that if the prey were novel to the crabs used, the crabs may have had a harder time feeding on them or be less inclined to attack. Given the paucity of information available on crab-turritellid interaction, we nevertheless believe that the data reported here provide a valuable first step toward improved understanding.

The results of these experiments indicate: 1) that different crab species can produce distinctive break morphologies on turritellid shells, and 2) that the same scar shapes, especially shallower ones, can be produced by different species of crabs even when those species are very different in claw shape and physical capabilities. This means that deep fossil scar shapes with distinctive morphology (such as jaggedness or repeating shape structures) likely correspond to particular predatory

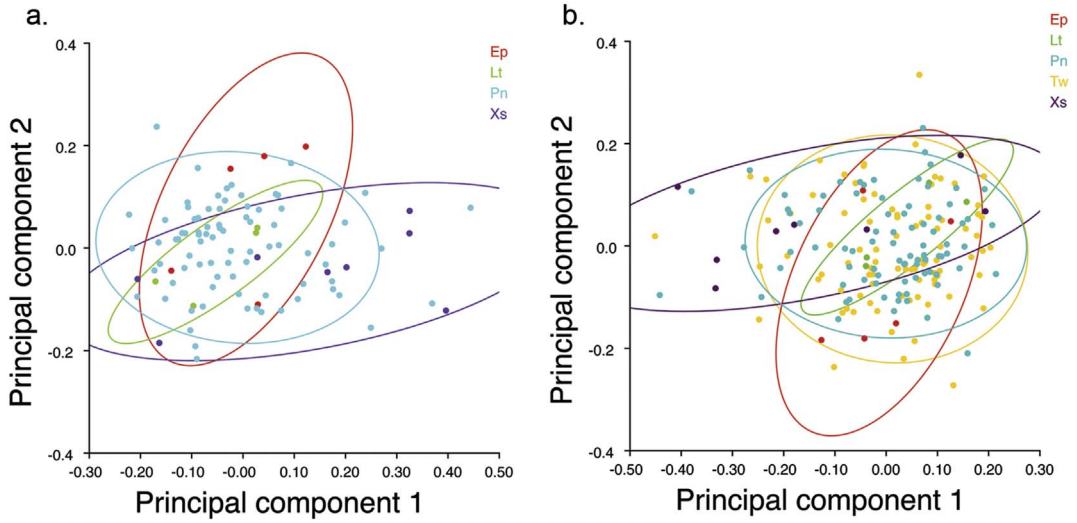

Fig. 12. Principal components analysis of scar shapes at the broken aperture of individuals of *T. banski*, a. without and b. with fossil scars. Initials indicate the crab that created the scar: Lt, *Leptodius*; Ep, *Eurypanopeus*; Pn, *Panopeus*; Xs, *Xanthodius*; and Tw, scars on *T. wagneriana*, caused by unknown fossil crab taxa. Scar morphology samples are surrounded by 95% confidence intervals for each group. There is substantial overlap between groups and all crab taxa were variable in the break morphologies that they created. Breaks created in this study plot in the same region of morphospace as breaks found on fossil *Turritella* (b).

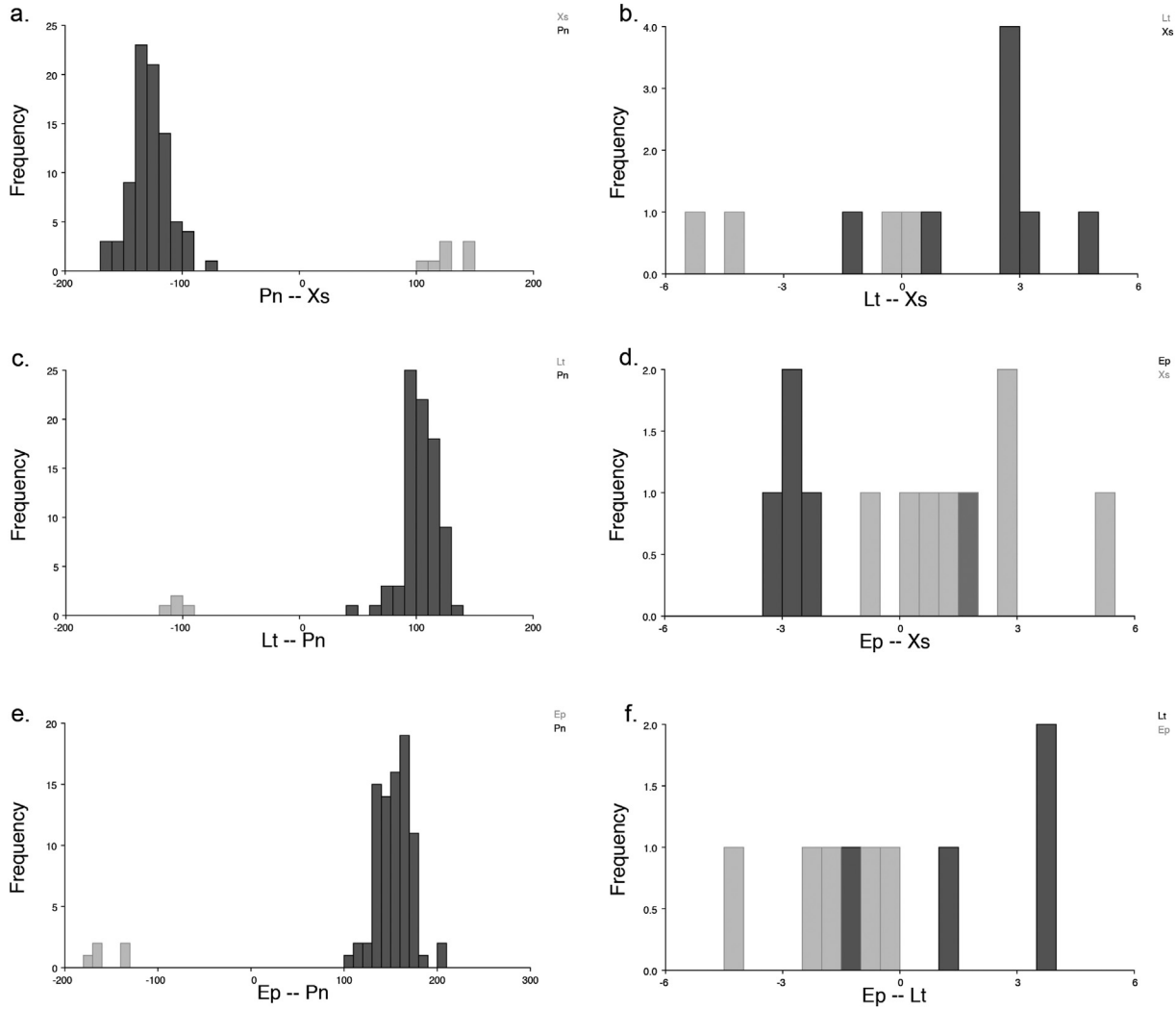

Fig. 13. Discriminant function analysis of all groups of modern breaks, comparing separation between pairs of scar groups. Initials in the upper right of each graph indicate the crab that created the scar: Lt, *Leptodius*; Ep, *Eurypanopeus*; Pn, *Panopeus*; Xs, *Xanthodius*; and Tw, scars on *T. wagneriana*, caused by unknown fossil crab taxa. In pairwise comparisons scars from the *Panopeus* group separate from the other three groups, but morphologies of scars in the *Xanthodius, Leptodius*, and *Eurypanopeus* groups grade into each other and cannot be clearly separated.

crab species, while simpler and shallower scars are less likely to hold any recoverable information about predator type. Further work on the subject would thus do well to focus on the more complex and distinctive scar shapes (see, for example, Fig. 1). For future experiments, researchers could also target living decapods similar in taxonomy or morphology to those known from particular stratigraphic units of interest. Experimental work using crabs with similar claw morphology from different genera could also evaluate whether scar shapes correspond directly to chela shape or whether there are genus-specific differences in shell-breaking behavior that result in different scar shapes.

Morphometric analysis of the 90 scars on fossil *T. wagneriana* confirms that the fossil scars overall are quantitatively similar to some of those caused by crabs in our experiments (Figs. 12b, 14b). While the DFA reveals marked differences between the fossil scars and those caused by *Eurypanopeus*, *Leptodius*, and *Xanthodius*, the fossil and *Panopeus* scars represent overlapping categories of morphology (Fig. 14). Not all morphological differences were resolved by the DFA; *Eurypanopeus* caused some qualitatively characteristic scars (Fig. 11b), but did not quantitatively separate from the *Leptodius* or *Xanthodius* scar groups to an appreciable degree (Fig. 13). Since breaks and scars lack homologous landmarks and are highly variable within and between experimental groups, geometric morphometrics may only be able to resolve gross morphological differences such as scar depth. If that is the case, then careful observation of scar morphologies and semi-qualitative metrics (such as relative degree of smoothness or regularity) might be more reliable methods of linking different species of crabs to particular scars on modern and fossil gastropods. More robust quantitative patterns may also emerge with larger sample sizes.

The overlapping discriminant score distributions of the *Panopeus* and *T. wagneriana* groups (Fig. 14b) could be explained in several ways. The “single crab” model posits that the fossil predation scars were caused by one crab species which created break morphologies with a similar range of variation as *Panopeus* but a different median shape, resulting in an overlap of break morphologies on the tail of the distribution; because some shallow, simple shapes were caused in common by *Panopeus*, *Eurypanopeus*, *Leptodius*, and *Xanthodius* in this study, we know that different crabs with very different claw morphologies can cause quantitatively similar breaks.

The “multiple crab” model requires a variety of predator crabs in the fossil record, each with a small range of variation of break morphology, summing up to a distribution which overlaps somewhat with that of *Panopeus*. The ultimate limit of this model is that of having a one-to-one correspondence between individual scars and predator types; since no two fossil scars are identical, this boundary case would require a unique predator for every single scar.

These two models represent two extremes of a continuum. In the

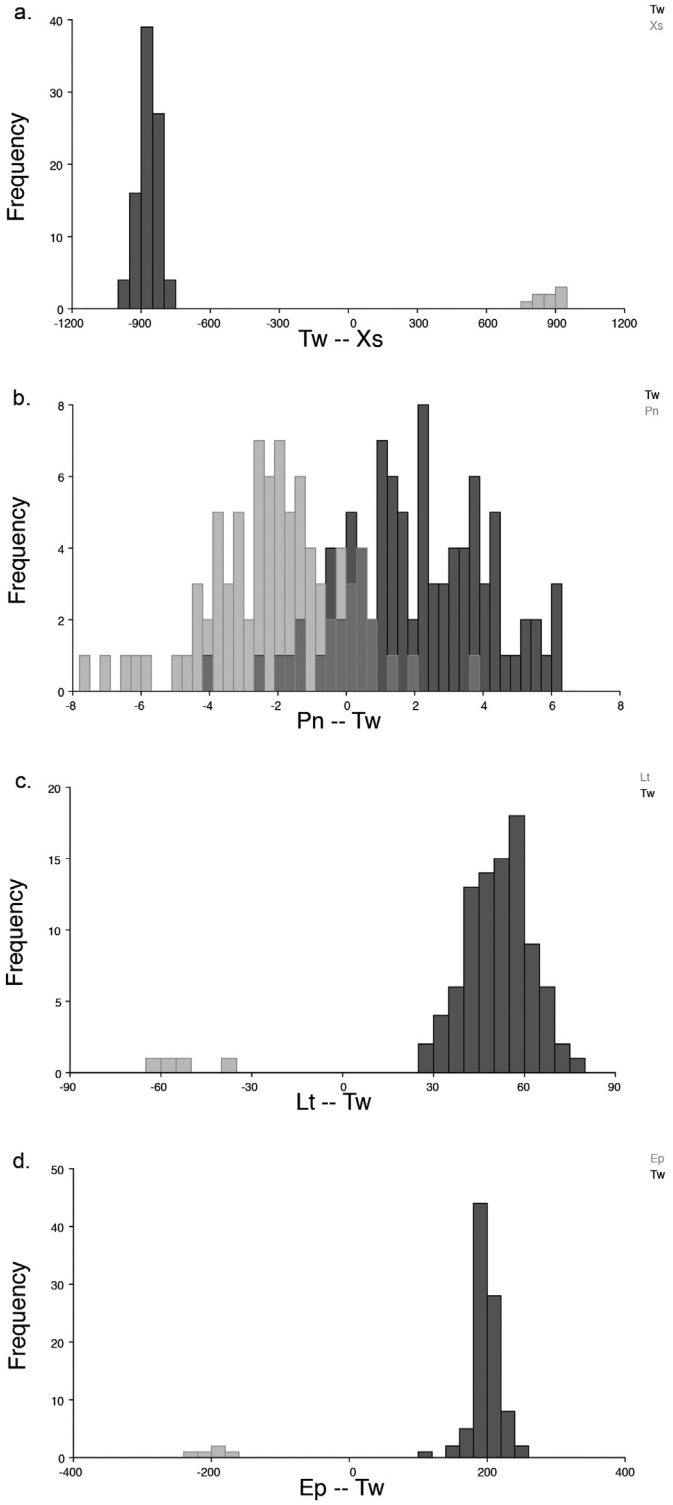

Fig. 14. Discriminant function analysis comparing fossil scars on *Turritella wagneriana* to each of the four groups of modern breaks (see Fig. 12 caption for identifiers). There is substantial overlap between the *Panopeus* and *T. wagneriana* groups indicating that there is a set of scar morphologies that is shared between these groups.

productive, nutrient-rich environment that caused the turritellid-rich beds known throughout the fossil record of the group (Allmon, 2007), it is unlikely that only one type of predator crab would ever try to eat the abundant turritellids. A one-to-one correspondence between scar morphology variation and predator identity variation, however, is also unlikely, given the range of variation in break morphology arising from a single crab species that we observed in the experiment. An intermediate state of the multiple-predator model, incorporating several predator crab species, each capable of producing some range of variation in scar morphology, thus is more likely for most fossil turritellid assemblages that show ranges of repair scar shapes similar to those shown here by *T. wagneriana*. This interpretation is supported by the fossil record: the Pliocene deposits in which *T. wagneriana* occurs (the Pinecrest Sand, part of the Tamiami Formation, and the Caloosahatchee Formation) do contain crab fossils, although they are generally rare. Portell and Agnew (2004) list 10 or 11 crab species in the Caloosahatchee and 2 in the Pinecrest (Table 2).

Table 2
Taxa of crabs reported from the Plio-Pleistocene Pinecrest and Caloosahatchee formations of Florida by Portell and Agnew (2004). Species marked with (?) are listed by Portell and Agnew as "problematic or doubtful".

	Family	Genus/species
Caloosahatchee Formation	Callianassidae	*Callichirus major*
		Neotrypea sp.
		Sergio trilobatus
	Diogenidae	*Petrochirus bouvieri* (?)
	Leucoslidae	*Persephona mediterranea*
	Majidae	*Libinia* sp.
	Parthenopidae	*Parthenope charlottensis*
	Portunidae	*Ovalipes stephensoni*
		Portunus gibbesii
	Menippidae	*Menippe mercenaria*
		Menippe nodifrons (?)
Pinecrest (Tamiami) Formation	Porcellanidae	*Petrolisthes myakkensis*
	Calappidae	*Calappa* sp.

We do not know what crabs actually prey on *T. banksi* in the wild, and so we do not know whether the real predators bear any resemblance in morphology or behavior to the *Panopeus* crabs used in the experiment. At least 20 species in 14 genera of decapod crustaceans are recorded in Pacific Panamanian mangroves and 78 species in 48 genera in the corresponding rocky intertidal, with most species represented by only a few individuals (Abele, 1976). Many of the most common such crabs, such as *Clibanarius albidigitus* and *Petrolisthes* sp., are not predators, but there are nevertheless many different possible predators on *T. banksi.* The differing collection locations of crabs (rocky intertidal) and snails (soft sediments, mangroves) also argues against *Panopeus* and the other crabs used in the experiment being the primary predators of *T. banksi* in the wild; it is unlikely that the particular crabs in the experiments encounter turritellids frequently enough for the gastropods to form a routine part of their diet. *Goniopsis pulchra* is a possible candidate predator of *T. banksi* (see Beever et al., 1979). In any case, the occasional breakage scars on modern living and dead *T. banksi* (Fig. 3) support the idea that predator crabs encounter these gastropods from time to time, but exactly which crabs remains unknown. Regardless of whether or not *Panopeus* attacks *T. banksi* in the wild (*P. herbstii* in the western Atlantic is known to be a generalized carnivore, feeding on bivalves and occasionally other crabs; Seed, 1980; Stachowicz and Hay, 1999), these experiments document crab predation on turritellid gastropods, demonstrate that different crab species produce a variety of break morphologies on the shells of their prey, and support the idea that at least some particularly distinctive scar shapes observed on fossils may be characteristic of particular crab taxa.

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