Mauritian snail shells show evidence of extinct predators (#120137)

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Mauritian snail shells show evidence of extinct predators

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Shells of several species of *Tropidophora* land snails of the volcanic island of Mauritius (Mascarenes, SW Indian Ocean), all dated between ~1426BCE and ~1090 CE predating the earliest confirmed human discovery (1519) and settlement (1638) of the island have been found with characteristic predatory holes. These are either large, irregular holes on the underside of *T. carinata*, or circular holes 0-9-3.3 mm in diameter, in almost the exact same place in *T. ligata*, *T. icterica* and *T. michaudi*. The former have been suggested to be evidence of predation by the extinct red rail *Aphanapteryx bonasia*, which we consider to be probable. The circular holes have not been reported previously, examination of these shows them to be very regular in shape and size, to be in the centre of a shallow depression marked by two sets of fine grooves at right angles to one another. These holes were compared to damage caused by predators reported to have 'bored' into shells: *Drillus* elaterid beetles, *Poiretia* spiraxid snails and rathouisiid slugs. The damage is most similar to that caused by rathouisiids and we postulate that the holes were caused by a now extinct predator of that family. The only extant members of the family in the Mascarene islands are too small to be the predators. There is no evidence of such predation in recent shells; this is an extinct interaction between an extirpated predator and its prey.

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Abstract

Shells of several species of *Tropidophora* land snails of the volcanic island of Mauritius (Mascarenes, SW Indian Ocean), all dated between ~1426BCE and ~1090 CE predating the earliest confirmed human discovery (1519) and settlement (1638) of the island have been found with characteristic predatory holes. These are either large, irregular holes on the underside of *T. carinata*, or circular holes 0-9-3.3 mm in diameter, in almost the exact same place in *T. ligata*, *T. icterica* and *T. michaudi*. The former have been suggested to be evidence of predation by the extinct red rail *Aphanapteryx bonasia*, which we consider to be probable. The circular holes have not been reported previously, examination of these shows them to be very regular in shape and size, to be in the centre of a shallow depression marked by two sets of fine grooves at right angles to one another. These holes were compared to damage caused by predators reported to have ‘bored’ into shells: *Drillus* elaterid beetles, *Poiretia* spiraxid snails and rathouisiid slugs. The damage is most similar to that caused by rathouisiids and we postulate that the holes were caused by a now extinct predator of that family. The only extant members of the family in the Mascarene islands are too small to be the predators. There is no evidence of such predation in recent shells; this is an extinct interaction between an extirpated predator and its prey.

Introduction

The island of Mauritius has only been occupied by humans since 1638 but this has been sufficient to result in a devastating ecological impact due to a combination of hunting, invasive species and habitat destruction (Cheke & Hume 2008). As a result, an unusually large number of species are known to have become extinct on the island, famously including the dodo *Raphus* *cucullatus*. The known extinction rate is 41% for native bird species, 53% for reptiles (Cheke & Hume 2008; Florens 2013) and 34% for native snail species (Griffiths & Florens 2006). The extinction rate in insects is much less well known but can be assumed to be comparable.

The high levels of species extinction will inevitably also have led to extinction of species interactions (Albert *et al.* 2021; Heinen *et al.* 2023). This is most obvious in the case of seed dispersing giant tortoises, and for these surrogate species introductions of other species of tortoise provide some means of restoring lost interactions (Griffiths *et al.* 2011). As these 'lost interactions' are behavioural they usually leave no direct evidence, unless they were described by early observers. The exceptions to this are interactions involving hard structures: wood, bones or shells. As these can be durable in suitable preservation conditions they can retain evidence of interactions indefinitely. No notable marks have been observed on wood or bone in Mauritius, but interesting marks have been found on snail shells. In 2006 holes in the large extinct snail *Tropidophora carinata* (Born, 1780) were proposed to have been made by the extinct red rail *Aphanapteryx bonasia* (Griffiths & Florens 2006his snail species is known only from subfossil shells other than the report of an apparently fresh shell collected in the 1870s (Nevill 1881), although the shell is now lost and so the record cannot be verified. Very distinct circular perforations are found in three smaller *Tropidophora* species: *T. icterica* (Sowerby, 1847) (subfossil only), *T. michaudi* (Grateloup, 1841) and *T. ligata* (Muller, 1774) (both now very rare but abundant as old shells). These perforated shells have not been reported previously. The abundance of apparently predator damaged shells in these rare or extinct species and the absence of similar damage in any fresh shells suggests that the predator may also be extinct. These observations prompted a review of the damaged shells in an attempt to determine their cause. This review is presented here.

Materials & Methods

Mauritian predated shells

Shells with damage typical of rat predation (large gnawed holes on the body whorl or apex) are widely distributed across the island and found in all relatively large snail species. These were disregarded and shells with other forms of damage were ascribed to two different categories of damage (Fig. 1):

1. Smashed body whorl – an irregular hole in the shell, taking up at least half the diameter of the whorl
2. Drilled shell – small, roughly circular holes in the shell

Mauritian shells showing potential predator damage were examined from collections made in several localities (Fig. 2):

1. – *Tropidophora icterica* (2 specimens, sample A5693). Subfossil and old dead in sandy soil exposed by clearing, E side of Av Victory, Albion, W Mauritius. S20˚12'8.57", E57˚24'16.50". O Griffiths, July 2021.

2. – *Tropidophora ligata* (5 specimens, sample A4054). In sandy excavations, approx. 0.5 m deep, 50m inland, next to Klondike Hotel, Flic en Flac, W. Mauritius. S20˚16’20.73”, E57˚22’19.75”. O Griffiths, June 2012.

3. – *Tropidophora ligata* (24 specimens, sample A3912). Subfossil. In sandy trenches in construction site, next to Clinique Occident, N end of Flic en Flac beach, approx. 250 m from sea. O Griffiths, October 2010.

4. – *Tropidophora michaudi* (6 specimens, sample A4106). Deep under piles of rocks in small patch of native dry forest between Riviere Papayes and Rivière du Rempart, just E of village of Cascavelle, Médine SE, W. Mauritius. S20˚17’14.07”, E57˚25’16.90”. O Griffiths, January 2013.

5. – *Tropidophora michaudi* (10 specimens, sample A5512). Dead in scree and under rocks in recently exposed bulldozed area within alien vegetation dominated by *Senegalia rugata* and *Hiptage benghalensis*, on east scarp of Riviere du Rempart valley, 500 m SW of Beaux Songes, Mauritius. S20˚17’06.70”, E57˚25’22.00”. elevation 216-219m. FBV Florens, C Baider, OL Griffiths et al., March & June 2020.

6. – *Tropidophora michaudi* (4 specimens, sample A5587). Under rocks in dry forest at summit of Tourelle du Tamarin, W. Mauritius. Alt 485m. S20˚20’50.65”, E57˚22’37.67”. O Griffiths, June 2021.

7. – *Tropidophora carinata* (5 specimens, sample A965). In sandy excavations just inland from beach, Riambel, Mauritius. S20˚31’01.65”, E57˚29’43.40”, OL Griffiths, 1985.

The frequency of damaged and intact shells at these localities and elsewhere was recorded from collected shells (OL Griffiths collection).

Measurements were taken of each shell (maximum diameter), the holes (height along shell axis and along direction of coiling), their position (number of whorls from the aperture, height from shell base and height from the resting plane of the shell – Fig. 3). All holes were measured using digital callipers, accurate to 0.1 mm.

The edges of the holes were examined microscopically: microscopic grooves were measured and the angle of the grooves measured relative to growth lines in the shells. Angles were measured using a transparent protractor, accurate to 1 degree. One specimen of *T. ligata* (A3912) was examined using scanning electron microscopy at the Cambridge Imaging Centre.

One specimen from each of the main species was dated at the Cambridge University Department of Earth Sciences Radiocarbon Laboratory using methods of Freeman *et al.* (2016): *Tropidophora carinata* A965; *T. ligata* A3912; and *T. michaudi* A5512. Approximate sample size varied from 0.47 to 0.87 mgC.

<u>Distribution of drilling predation marks on *Tropidophora michaudi* shells</u>

To gather further insights on the ecology of the drilled *Tropidophora michaudi*, we examined the distribution of drilled predation marks (both complete and partial) at a site that yielded a particularly large number of shells, sufficient to allow for meaningful statistical testing.

The choice of a single site (Rivière du Rempart river valley) also avoided the possible confounding effects that might have arisen from inter-site differences in predation frequency. Of the many individuals found, 230 shells were sufficiently well preserved to allow for both the determination of the snail life stage (adult: with the shell lip expanded; versus non-adult: lacking an expanded lip) along with the detection of presence of successful or attempted shell drilling. We used χ^2 tests to compare the percentages of shells that had completed predation marks (large drilled hole) or attempted predation marks (evidence of initiation but incomplete shell drilling at the usual spot), as well as the percentages of these predation instances on adults versus non-adult shells. We were also able to compare the frequency of drilled predation marks between shells of animals strewn on the ground or under scree at the site, with animals that died during aestivation (as evidenced by their shells being found jammed between sharp edges of rock in the cavities within a dry layer of undisturbed vesicular volcanic scoria in the ceiling of a thick basaltic rock overhang, where no shell could have fallen from above, but where instead, the snails must have crawled, before dying *in-situ*).

Comparative predator damage

Predator damaged shells were examined similarly in the Natural History Museum, London (NHM); potential predators were identified by comparison to published descriptions and figures of damage attributed to specific predators (Schilthuizen *et al.* 1994; Baalbergen et al. 2014; Helwerda *et al.* 2014; Helwerda & Schilthuizen 2014; Liew & Schilthuizen 2014). Shells apparently predated by *Drilus* sp. beetles (Elateridae) and *Poiretia* sp. snails (Spiraxidae) were found in samples of *Alinda biplicata* (Clausiliidae) (NHMUK 202000133-4), and Rathouisiidae slug bored shells were found in *Plectostoma austeni* (Diplommatinidae) (NHMUK FF Laidlaw colln.).

Results

Mauritian shell damage

Shell damage and frequency are summarized in Tables 1-2 and described below.

1. Smashed body whorl – 5 *Tropidophora carinata* had irregular holes on the underside of the shell (Fig. 4), next to the aperture or ¾ of a whorl from the aperture. The holes had jagged edges and measured 10.7-13.1 mm high. Width was difficult to determine due to fragmentation in that direction. The shape of the hole suggested a single puncture caused by an external impact. This damage was found only in *T. carinata* which is the largest of all *Tropidophora* species recorded from Mauritius, and occurs throughout the species' range, except for the very humid central highlands. Damaged shells were found in coastal dunes or in scree. In upland areas shells were only found in caves. This may reflect a genuine difference in distribution of smashed shells or a preservation bias, with broken shell persistence only when buried.
2. Drilled shell – large numbers of shells of *T. icterica* (2), *T. michaudi* (20) and *T. ligata* (28) had almost identical holes (Fig. 4). Holes were almost circular, almost always at least as wide as high (41/50), with a few higher than wide (9/50). Holes were wider than high by up to

44%, but higher by no more than 22%. In *T. michaudi* (and one *T. ligata*) the holes were surrounded by a narrow depression where the substance of the shell had been thinned (Fig. 5-6). The surface of this depression was covered by irregular parallel grooves measuring 12-29 µm wide. These were in two layers: irregular, deep grooves (Fig. 7e) at 12-26˚ (19.90±5.09) to the radial sculptural ridges of the shell and more regular, shallow grooves (Fig. 7c, g) at 87-110˚ (95.83±7.44). The deeper grooves were at 83-115˚ (97.69±9.44) to the shallow grooves. In one *T. michaudi* (A4106) the superficial grooves extended a small distance onto the next whorl (Fig. 8), and in three others (A5512) the eroded and grooved area extended onto two further whorls of the spire (Fig. 8b). This was only superficial but in two cases it extended around approximately half of a whorl (Fig. 8b). In one *T. michaudi* (A5512) and one *T. ligata* (A4054) the depressed eroded area was deepest towards the spire, in other specimens the depression was regular. Drilled shells come from a restricted area of the prey species' ranges (Fig. 2): throughout the ranges of *T. ligata* (western lowland coastal dry forest) and *T. icterica* (central west coast) in the lowland west of Mauritius, but just the lowland area of *T. michaudi*'s range in the south-west from coast to ridge top.

Dating

All specimens pre-date recorded human occupation of the island by between about half to three millennia (Table 3).

Distribution of drilling predation marks on *Tropidophora michaudi* shells

Of the sample of 230 shells of *Tropidophora michaudi* examined from the Rivière du Rempart site, juveniles had sustained significantly higher successful predation (69.2%) than adults (37.5%) ($\chi^2 = 20.694$; df = 1; P = 0.00001). The smallest confirmed juvenile bearing the drilled predation marks was 15.6 mm high, which is between 56-68% of the size of the adult. Among shells that displayed failed predation attempts (initiated, but incomplete shell boring), most were adults (91.7%, n = 12) ($\chi^2 = 15.998$; df = 1; P = 0.00006). When attempted, the rate of successful predation on adults and juveniles differed significantly and were respectively of 83.8% and 98.2% ($\chi^2 = 7.100$; df = 1; P = 0.00771). Of the 14 snails that can be confirmed to have died *in-situ* within their aestivating hideouts, none bore drilled predation marks, whereas predation marks occurred in 111 (48.3%) of the 230 other shells found ($\chi^2 = 12.363$; df = 1; P = 0.00044).

Comparative predator damage

Poiretia-made holes in *Alinda biplicata* (Fig. 9a-b) measured 1.5-2.0 x 0.8-1.2 mm, taking up most of the height of a whorl, sometimes extending into another whorl. The edges of these holes were smooth, lacking notable scratches and surrounded by very extensive etched areas.

Drilus-made holes in *Alinda biplicata* (Fig. 9c-d) extended across two or three whorls measuring 3.2-4.5 x 1.5-2.0 mm. The edges of these holes were jagged, marked with irregular scratches and had only a small area of etched surface around them.

Rathouisiidae-made holes (Fig. 9e) were minute, semi-circular and with a narrow etched border. The maximum dimension of the hole was 0.4 mm. No other details could be detected on the very small shells concerned.

Discussion

The shell damage identified here can be ascribed to two different types of predation: large external punctures (*Tropidophora carinata* and some *T. michaudi*) and small drilled holes (*T. icterica, T. michaudi* and *T. ligata*). The external punctures appear to have been made by an object about 10 mm wide, which corresponds to the beak diameter of the extinct red rail *Aphanapteryx bonasia* which has been speculated to be the predator (Griffiths & Florens 2006; Hume 2017, 2019). It had the largest beak of any of the Mauritian rails, reach about 10 cm wide at its midpoint, making it the most likely predator of the family. The Mauritius night heron *Nycticorax mauritianus* is also a possibility, but no beaks of that species are known. Red rails were first proposed as snail predators in 1868 (Milne-Edwards 1868, 1869a, b), although as crushing shells in the manner of oystercatchers. The only *T. carinata* populations that lacked evidence of predation were those of the central highlands, outside of the recorded range of the red rail (Hume 2019). The upland populations of *T. carinata* were also smaller than those from the lowlands (maximum dimension 21 mm compared to 35 mm), making them less attractive prey. Lowland shells are found mainly in dune environments that preserve the thick calcareous shells well. In contrast the upland ones are found in sheltered overhangs where they are protected from the more acidic forest leaf-litter. Thus the absence of evidence of predation in the uplands may be due to the absence of predators, avoidance of low value prey or poor preservation. Similar damage is caused by the weka *Gallirallus australiae* (Meads *et al.* 1984) on the thin shells of *Powelliphanta* snails in New Zealand. This is usually by pecking out the spire but high spired shells may be penetrated on the underside, through the wide umbilicus which “stops the weka’s beak from glancing off” (Meads *et al.* 1984). A similar pattern is seen in shells broken by the Okinawa rail *G. australae* (Miyazawa & Shimada 2017). The positioning of holes in *T. carinata* is comparable. Meads *et al.* (1984) also described predation by New Zealand parrots which made holes 15-30 mm across, “through the outer whorl near the aperture and through all the successively decreasing inner whorls”, “on larger, thicker shells there were pairs of vertical scratches around the side of the shell presumably where several attempts were made to penetrate the shell”. However, this damage is now known to have been caused by possums (K. Walton pers. comm.). The Aldabra rail (*Dryolimnas cuvieri*) has been observed *in-situ* repeatedly hitting an object with the tip of its closed beak with force, apparently in attempts to crack it open (FBVF, pers. obs., May 2023) in a behaviour reminiscent of what would have cracked the shell of *T. carinata* to create the kind of holes observed on the underside of the shells. Accordingly, we consider it highly probable that the *T. carinata* shells were predated by red rails.

The drilled holes differed slightly in the different species, being almost vertical sided and usually lacking grooves in *T. ligata* and being always accompanied by a grooved depression in *T.*

michaudi. This difference can be explained by the relative thickness of the shells (0.3 mm in *T. ligata,* 0.6 mm in *T. michaudi*). The thicker shells of *T. michaudi* would have been harder to penetrate and require more effort by the predator. Stereotypically positioned holes in shells are known to be produced by human consumption of snails, but these holes are sharp and jagged edged (Hutterer *et al.* 2014), unlike the thinned and smoothed edges of most of the holes in the Mauritian shells. Additionally, the radio-carbon dating shows that the damaged shells predate human occupation of Mauritius by between about half to three millennia. These shells, especially in the case of *T. michaudi* show evidence of the holes being made by a combination of secretion of an acidic substance onto the shell and the scraping away of the softened material to form a small hole.

Acidic secretions are known to be used by *Drilus* elaterid beetles to thin the shells prior to penetration. Entrance holes are small (0.38-0.77 mm) and bevelled by acid dissolution, whereas exit holes are vertical without such dissolution, oval and wider: 0.92-1.38 mm (Orstan 1999; Schilthuisen et al. 1994). These are not generally abraded, and the holes have sharp vertical edges caused by the mandibles (Baalbergen *et al.* 2014). Carabid ground beetles create distinctive spiral biting patterns running from the shell mouth towards the apex around the spiral (Němec & Horsák 2019; Millar & Waite 2004; Hayashi & Sugiura 2021). Similar damage can be created by opilionids (Martens 1965).

The parallel microscopic grooves in the etched area of the Mauritian bored shells are indicative of rasping by a mollusc radula. Scraped holes of a similar size are known to be caused by Zonitidae such as *Aegopinella nitidula*, the holes formed this way are irregular ovals with a broad worn area around it (Preece 1998; Myzyk 2014). The irregularity of the worn area and the hole, the lack of the etched depression and the varied angles of the scrape marks distinguish zonitid predation from the Mauritian holes. The scraping of the Mauritian holes is very regular, with a superficial scraping at 20˚ (12-26) to the axis of the shell, followed by rotation through 113˚ (105-123) to give deeper penetrative gauging at an almost right angle to the axis (96˚, 87-110).

Species in four families of molluscs have been identified as secreting acid solutions in predation. The most specialized are the marine Muricidae and Naticidae. Both secrete acid from an accessory boring organ and are able to rotate the odontophore (through 180˚ in Muricidae and 90˚ degrees in Naticidae) to make a cylindrical hole with what appears to be a random rasping pattern (Carricker 1981). Of terrestrial species, the Spiraxidae *Poiretia dilatata* secretes acid from a pedal gland over a two-day period, causing a wide etched area and a large irregular hole. There is no rasping in this species (Helwerda & Schilthuizen 2014; Helwerda 2015). More specialist boring is carried out by Rathouisiidae: *Atopos* spp. produce drill holes that resemble those in Mauritian shells, with a narrow scraped margin and measuring 0.13-0.33 µm diameter (Liew & Schilthuizen 2014). The drill hole size corresponds to proboscis diameter (Liew & Schilthuizen 2014). *Rathouisia leonina* predating snail eggs made smaller holes up to 0.62 mm in diameter (Wu *et al.* 2006). The presence of an acid etched area, its scoring by parallel grooves and the width of the grooves measuring 12-29 µm all suggest that the predator is likely to be a mollusc, feeding in the same manner as Rathouisiidae. Rathouisiids are known from south-east Asia and Australasia, with undescribed species in Mauritius (Griffiths & Florens 2006) and Réunion (Griffiths, pers. obs.). These species are only 12 mm long, so are unlikely to be able to produce large enough holes to be the predator. Asian species are known to reach 85 mm long (Wiktor 2003), so it is possible that a large Mascarene rathouisiid may have existed in the past.

Stereotypical positioning of boring holes, as in the present case, is known from naticid whelks (Berg & Nishenko 1975; Kitchell *et al.* 1981; Archuby & Gordillo 2018; Kingsley-Smith *et al.* 2003) with the position being selected to minimise energy expenditure in drilling (Mondal *et al.* 2014). The stereotypical position of the bored holes could indicate that the predator approached the shell in a stereotypical manner while also taking into consideration the accessibility of the animal when maximally retracted within the shell as a defensive response to the attack. The latter inference is demonstrated by the existence of a few shells that had slightly misplaced drill holes that fell just over the suture onto the body whorl, instead of their characteristic predatorily successful position on the penultimate whorl. These misplaced drill holes were all invariably abandoned as soon as the shell was pierced and therefore as soon as the predator would have sensed the absence of the prey's flesh, leaving only a very small unfinished hole. The predator would then readjust the position of the drilling to create a second and definitive full hole in the correct place, thereby completing the predation event. The fact that exactly the same point on the penultimate whorl was attacked in *T. michaudi* and *T. ligata*, despite the species being of very different sizes, supports the inference that the predator drilled the hole both at a point beyond which the snail could not have retracted in defensive response, and also in a position that is accessible to the predator when the shell is upright on the substratum (incidentally suggesting also that the predator may not have been handling and turning the prey during attack, but instead simply position itself on top of it before starting to drill the hole).

Orientation of the grooves suggests that the gauging started at the suture with the body whorl and moved towards the spire; grooves start in a straight line at the suture, with no evidence of scraping onto the body whorl (except in the rare instances of originally misplaced drilling mentioned above), whereas at the spire end the groves are irregular. This would indicate that in this stage of feeding the forepart of the predator was oriented along the shell axis, head-up towards the spire, and that the snail was in the normal resting position with the shell's mouth against the stratum. The depth of the depression in two cases indicates that the gauging may have been from the basal end towards the apex, with the deepest part reflecting maximum impact where the rasping came up against the suture. It was not possible to determine the direction of the superficial grooves. From this we deduce that the predator first positioned itself towards the apex of the shell with its head approaching the lip. This would mean that the proximity of the shell's peristome would indicate the boring position. It probably then started scraping at the surface whilst releasing an acidic secretion. The beginning of the shell surface eroding probably then stimulated the predator to change the angle of attack, rotating the odontophore by 90˚ and gauging along the direction of coil of the shell until a hole was formed. The small number of specimens where the abraded area extended beyond the immediate surroundings of the hole (Fig.

8) may indicate predators with an inefficient technique, either younger animals or ones affected by different environmental conditions or the position of the prey with the apex pointing down such that some of the secreted acidic substance may have flowed downwards under gravity.

The restriction of the bore holes to just *Tropidophora* species may be explained by the fact that non-operculate species can be attacked faster and with minimal energy expenditure through the aperture, without having to incur the time and energy costs of shell boring. The absence of bore holes on the smaller operculate species (Cyclophoridae, Assimineidae and smaller *Tropidophora* spp.) may have been the consequence of these species being too small to be worth the energetic expenditure of boring when other prey were available (indeed, there exists a large number of non-operculated snail species that could be potential prey and that are smaller than the shells bearing the drilled holes). Of the other Pomatidae *T. carinata* is probably too thick-shelled for this means of predation, but seven other species were large enough and thin-shelled enough to have been potential prey. Three are known from a small number of individuals from single localities, so the lack of predated shells may be uninformative (*T. eugeniae, T. lienardi* and *T. vincentflorens*). One species, *Cyclotopsis conoidea*, being at most 9.3 mm high, is much smaller than the smallest predated juvenile *T. michaudi* suggesting it would not make an interesting prey for the undescribed predator. The three remaining species (*T. fimbriata, T. mauritiana* and *T. scabra*) all appear to be potential prey in terms of size and geography; the lack of predated shells in these species appears to reflect the abundance of other species of comparable sizes which are non-operculated, and thus easier and less energetically costly to predate.

The analysis of the distribution of drilling predation marks on *Tropidophora michaudi* shells relative to the snail's life stage suggest that juveniles were the preferred prey, presumably because their shells are thinner and therefore faster and less energetically costly to drill through. The advantageous trade-off over a smaller meal that this would represent appears supported by the fact that virtually all failed predation attempts observed (91.7%) had occurred on adult shells and that the vast majority (>98%) of attempted predation on juveniles were successful. It also appears that predation occurred predominantly if not solely on non-aestivating snails, therefore during the rainier season, suggesting that the predator may have been relatively short-lived, unless it could also feed on other food items to sustain itself during the dry season. Rathousiids are predominantly carnivorous but may also feed on plants and fungi (Barker 2001).

Conclusions

We conclude that the damaged subfossil shells of Mauritian snails preserve evidence of ecological interactions that have been lost with the decline in the snail populations and the probable extinction of the predators. These predators probably included unspecialised shell-smashing predation by the red rail *Aphanapteryx bonasia*, evidence of which is preserved only in the most robust of shells (*Tropidophora carinata*). In contrast, predation by a mollusc comparable to the Rathouisiidae was highly specialised. The only evidence for the existence of this species is the presence of the highly stereotypical bore holes in *Tropidophora* shells which are half to three millennia old. Given that several new species of molluscs continue to be discovered and described from Mauritius (Griffiths 2000; Griffiths and Florens 2004), it would not be too surprising that a native predatory slug would have existed on Mauritius and gone extinct within the last centuries, leaving no shell behind but leaving predatory marks on its prey, betraying its past existence.

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References

Albert, S., O. Flores, C. Baider, F.B.V. Florens & D. Strasberg. 2021. Differing severity of frugivore loss contrasts the fate of native forests on the land of the Dodo (Mascarene archipelago). *Biological Conservation* **257**: 109-131

Adams, H. 1868. Descriptions of some new species of land and marine shells. *Proceedings of the Zoological Society of London* (1868): 14-17.

Archuby, F.M. & S. Gordillo. 2018. Drilling predation traces on recent limpets from northern Patagonia, Argentina. *Palaeontologia Electronica* **36A**: 1-23

Barker, G.M. 2001. Gastropods on Land: Phylogeny, Diversity and Adaptive Morphology. In: Barker, G.M. (ed) *The biology of terrestrial molluscs*. CABI Publishing, Oxon, UK. 146pp.

Baalbergen, E., R. Helwerda, R. Schelfhorst, R.F. Castillo Cajas, C.H.M. van Moorsel, R. Kundrata, F.W. Welter-Schultes, S. Giokas & M. Schilthuizen. 2014. Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. *PLoS ONE* **9**(6): e100366

Berg, C.J. & S. Nishenko. 1975. Stereotypy of predatory boring behavior of Pleistocene naticid gastropods. *Paleobiology* **1**: 258-260

Carriker, M.R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* **20**(2): 403-422

Cheke, A. & J. Hume. 2008. *Lost Land of the Dodo: The ecological history of Mauritius, Réunion and Rodrigues.* T & AD Poyser, London

Florens F. B. V. 2013. Conservation in Mauritius and Rodrigues: Challenges and achievements from two ecologically devastated oceanic islands. In: Sodhi N., L. Gibson & P. Raven (Eds.) *Conservation Biology: Voices from the tropics*. Pp. 40-50, Wiley Blackwell

Griffiths, O.L. 2000. Nine new species of Mascarene land snails (Mollusca: Gastropoda). *Molluscan Research* **20**: 37-50

Griffiths, C.J., H. Dennis, C.G. Jones, N. Zuel & S. Harris. 2011. Resurrecting extinct interactions with extant substitutes. *Current Biology* **21**(9): 762-765

Griffiths, O.L. & V.F.B. Florens. 2004. Ten new species of Mascarene landsnails (Mollusca: Gastropoda) and their conservation status. *Molluscan Research* **24**: 161-177

Griffiths, O.L. & V.F.B. Florens. 2006. *Non-Marine Molluscs of the Mascarene Islands*. Bioculture Press, Mauritius

Heinen, J.H., F.B.V. Florens, C. Baider *et al.* 2023. Novel plant–frugivore network on Mauritius is unlikely to compensate for the extinction of seed dispersers. *Nat. Commun.* **14**: 1019

Hayashi, M. & S. Sugiura. 2021. Shell-breaking predation on gastropods by *Badister pictus* (Coleoptera, Carabidae) with strikingly asymmetric mandibles. *ZooKeys* **1044**(2): 815-830

Helwerda, R.A. 2015. Predatory *Poiretia* (Stylommatophora, Oleacinidae) snails: histology and observations. *Vita Malacologica* **13**: 35-48

Helwerda, R.A. & M. Schilthuizen. 2014. Predation on Greek *Albinaria* (Pulmonata: Clausiliidae) by *Poiretia* (Pulmonata: Oleacinidae) and by an unknown organism making circular holes: Possible drivers of shell evolution. *Journal of Molluscan Studies* **80**(3): 272-279

Hume, J.P. 2017. *Extinct Birds*. 2nd Edition. Helm, London, 608 pp

Hume, J.P. 2019. Systematics, morphology and ecology of rails (Aves: Rallidae) of the Mascarene Islands, with one new species. *Zootaxa* **4626**: 1-107

Hutterer, R., J. Linstädter, J. Eiwanger & A. Mikdad. 2014. Human manipulation of terrestrial gastropods in Neolithic culture groups of NE Morocco. *Quaternary International* **320**: 83-91

Kitchell, J.A., C.H. Boggs, J.F. Kitchell & J.A. Rice. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology* **7**(4): 533-552

Kingsley-Smith, P.R., C.A. Richardson & R. Seed. 2003. Stereotypic and size-selective predation in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. *Journal of Experimental Marine Biology and Ecology* **295**(2): 173-190

Kubicka, A.M., Z.M. Rosin, P. Tryjanowski & E. Nelson 2017. A systematic review of animal predation creating pierced shells: implications for the archaeological record of the Old World. *PeerJ* **5**: e2903

Lamont, T.A.C., E. Wilding & D.C. Aldridge 2016. Predation of freshwater gastropods (*Viviparus viviparus*) by brown rats (*Rattus norvegicus*). *Journal of Molluscan Studies* **82**(3):eyw012

Liew, T.-S. & M. Schilthuizen. 2014. Association between shell morphology of micro-land snails (genus *Plectostoma*) and their predator's predatory behaviour. *PeerJ* 2:e329

Martens, J. 1965. Verbreitung und Biologie des Schneckenkankers *Ischyropsalis hellwigi. Nat. Mus.* **95**: 143–149.

Meads, M. J., K.J. Walker & G.P. Elliott. 1984. Status, conservation, and management of the land snails of the genus *Powelliphanta* (Mollusca: Pulmonata). *New Zealand Journal of Zoology* **11**(3): 277–306

Millar, A.J. & S. Waite. 2004. Patterns of shell damage among snails from a coppice woodland in Sussex, England. *J. Conchol.* **38**: 421–440

Milne-Edwards, A. 1866–1873. *Recherches sur la faune ornithologique éteinte des iles Mascareignes et de Madagascar.* G. Masson, Paris, 147pp.

Milne-Edwards, A. 1869a. Researches into the zoological affinities of the bird recently described by Herr von Frauenfeld under the name of *Aphanapteryx imperialis. Ibis* **11**(3): 256–275

Milne-Edwards, A. 1869b. On the ancient fauna of the Mascarene Islands. *Annals and Magazine of Natural History* (4) **4**(20): 129–132

Miyazawa, K. & Shimada, M. 2017. Anvil use by Okinawa Rail *Gallirallus okinawae. Jpn. J. Ornithol.* **66**: 153–162

Mondal, S., J.A. Hutchings & G.S. Herbert. 2014. A note on edge drilling predation by naticid gastropods. *Journal of Molluscan Studies* **80**(2): 206-212

Myzyk, S. 2014. The predator *Aegopinella nitidula* (Draparnaud, 1805) and its prey *Perforatella bidentata* (Gmelin, 1791) (Gastropoda: Pulmonata). *Folia Malacologica* **22**(3): 225-227

Němec, T. & M. Horsák. 2019. Specific damage recognised on land snail shells as a tool for studying predation intensity: differences related to habitat and predator types. *Contributions to Zoology* **88**: 277-296

Nevill, G. 1881. New or little-known Mollusca of the Indo-Malayan fauna, Part II. *The Journal of the Asiatic Society of Bengal.* **50**(3): 125-167

Orstan, A. 1999. Drill holes in land snail shells from western Turkey. *Schr. Malakozoo.* **13**: 31-36

Preece R.C. 1998. Mollusca. Pp 158-212 in: Preece, R.C. & D.R. Bridgland. 1998. *Late Quaternary Environmental Change in North-west Europe: Excavations at Holywell Coombe, South-east England*. Chapman & Hall, London

Rosin, Z.M., P. Olborska, A. Surmacki & P. Tryjanowski. 2011. Difference in predatory pressure on terrestrial snails by birds and mammals. Journal of *Biosciences* **36**: 691-699

Schilthuizen, M., T.C.M. Kemperman & E. Gittenberger. 1994. Parasites and predators in *Albinaria* (Gastropoda Pulmonata: Clausiliidae). *Bios* **2**: 177-186

Freeman, E., L. Skinner, R. Reimer, A. Scrivner & S. Fallon. 2016. Graphitization of Small Carbonate Samples for Paleoceanographic Research at the Godwin Radiocarbon Laboratory, University of Cambridge. *Radiocarbon* **57**: 1-10.

Wiktor, A. 2003. Terrestrial gastropods (Mollusca) of Province Madang in Papua-New Guinea. Part III. Pulmonata: Rathouisiidae, Ellobiidae, Succineidae, Agriolimacidae, Endodontidae (partim), Ariophantidae, Euconulidae, Subulinidae, Streptaxidae. *Folia Malacologica* **11**(1/2): 1-21

Wu, M., J.-Y. Guo, F.-H Wan, Q-L. Qin, Q. Wu & A. Wiktor. 2006. A preliminary study on the biology of the predatory terrestrial mollusk *Rathouisia leonina. The Veliger* **48**(2): 61-74

Table 1(on next page)

Mauritian shells examined and measurements of damage.

Abbreviations: a – adult, d – diameter; h – height; j – juvenile; sa – subadult. Hole position is number of whorls from the aperture. Distance from substrate in mm, groove widths in µm

Species	**n**	**sample**	**shell diameter**	**hole position**		**hole dimensions (hxd)**	**groove width**
				whorls	**substrate**		
T. icterica	1a	A5693	24.3	2.0	10.8	2.0 x 1.3	-
	1sa		18.1	1.1	6.7	1.1 x 1.3	-
T. michaudi	6a	A4106	23.3-30.8	1.1-1.2	6.5-13.2	2.3-3.8 x 2.2-4.3	15-29
	4a	A5587	18.1-24.0	1.1-1.2	7.0-7.2	1.8-1.9 x 2.1-2.6	26
	5a, 1sa, 4j	A5512	12.7-25.6	(0.1) 1.1-1.2	5.8-10.6	0.9-3.3 x 1.6-3.3	16-25
T. ligata	4a	A4054	15.5-18.1	1.1	6.3-7.3	2.5-2.8 x 2.3-3.2	22
	21a 2sa	A3912	15.9-19.9	1.0-1.2	4.6-9.5	2.1-3.1 x 1.9-3.3	15-28
T. carinata	5a	A965	33.1-34.5	under	-	h 10.7-13.1	-

Table 2(on next page)

Frequency of damaged shells at different locations showing proportions with the damage considered here and also shells considered to be gnawed by rats

Species	Locality	Sample	% intact or damaged				N
			intact	rail damaged	drilled	rat damaged	
T. carinata	La Cambuse	A5544	57.1	42.9	0	0	28
	Bassin Blanc	A1831	71.4	28.6	0	0	14
	Mare aux Songes	A2649	61.8	38.2	0	0	55
	St Felix	A5574	68.2	31.8	0	0	22
	Snail Rock	-	41.7	0	0	58.3	12
	Riambel	A965	71.6	28.4	0	0	95
	Nouvelle Decouverte cave	-	100.0	0	0	0	40
T. michaudi	Cascavelle	A4106	28.2	32.5	15.4	23.9	117
	Tourelle du Tamarin	A5587	25.0	13.9	36.1	25.0	36
	Flic en Flac	A3921	49.3	10.4	6.0	34.3	67
T. icterica	Albion	A5693	84.8	1.5	3.0	10.6	66
T. ligata	Flic en Flac	A3912	70.1	0	29.9	0	488

1

Table 3 (on next page)

Radio-carbon dates of predated Mauritian shells, 14 C age in years before 1958.

Species	**Sample ID**	**^{14}C Age**	**δC^{13}**	**$F^{14}C$**	**uAC**
Tropidophora carinata	A965/1	1304±26	-13.5	0.8501±0.0028	14.1
	A965/2	1216±19	-12.2	0.8595±0.002	23.7
T. ligata	A3912/1	3254±21	-5.2	0.6669±0.0017	21.1
	A3912/2	3363±21	-11.7	0.658±0.0017	20.8
T. michaudi	A5512/1	895±27	-32.3	0.8945±0.003	13.8
	A5512/2	900±17	-10	0.894±0.0019	22

Figure 1

Shell damage in the different taxa.

(A) *Tropidophora carinata* (smashed body whorl, underside view). (B) *T. icterica* (bored). (C) *T. ligata* (bored). (D) *T. michaudi* (bored). Not to scale.

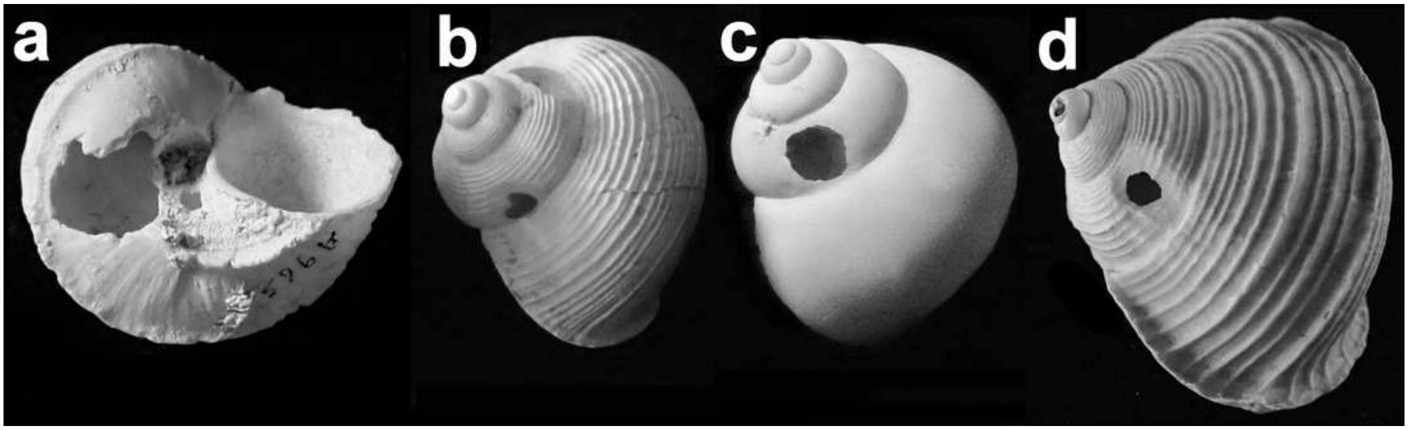


Figure 2

Localities mentioned in the text, distribution of damaged shells and ranges of the species concerned (distributions from Griffiths & Florens 2006).

(A) Localities numbered in the text. (B) *Tropidophora carinata*. (C) *T. icterica.* (D) *T. ligata*. (E) *T. michaudi*. (F) Location of the Mascarene islands in the western Indian Ocean. Key to b-e: shading - approximate original ranges; stars – smashed body whorl; points – drilled shells.

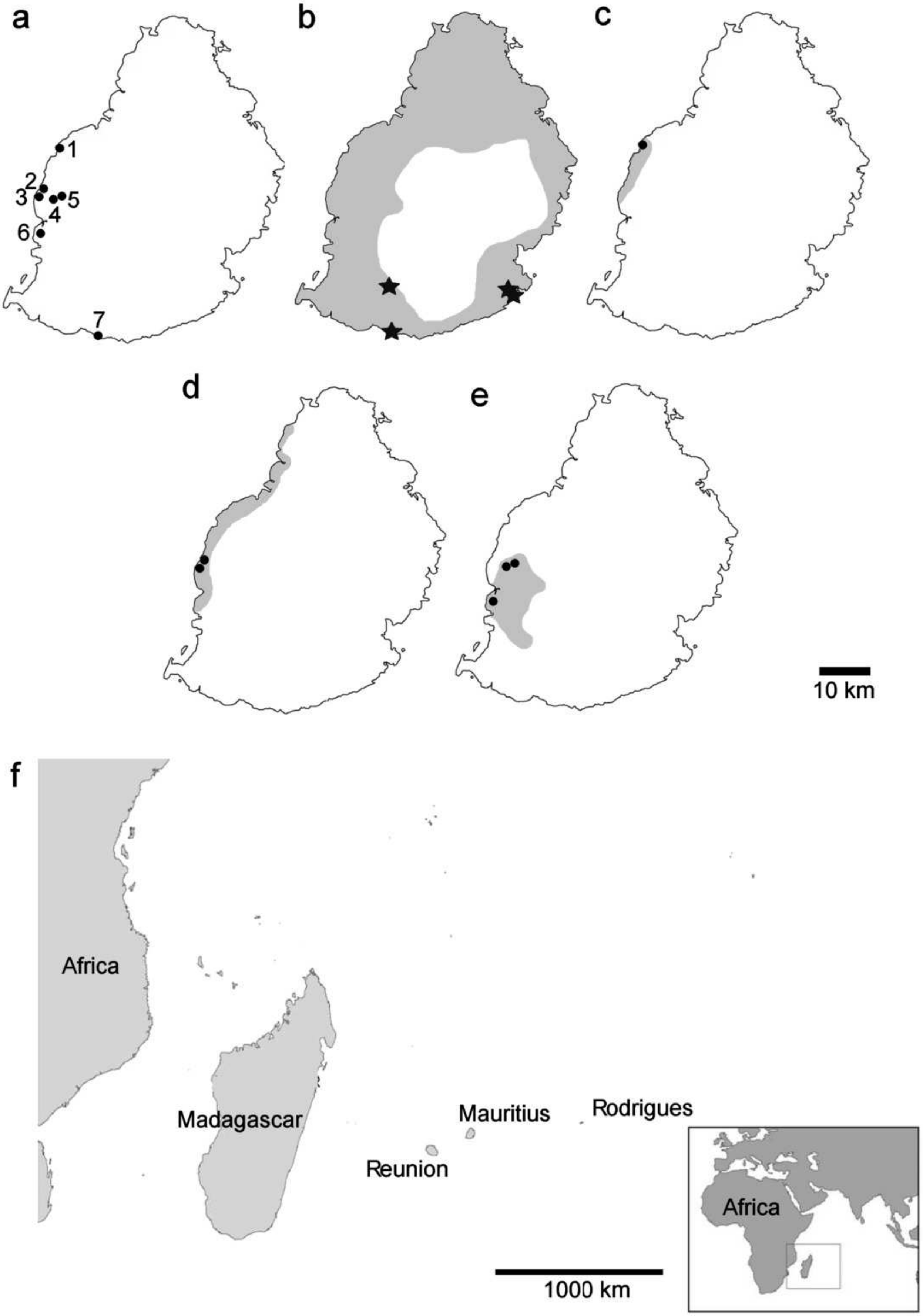

a
1
2
3
5
4
6
7
b
c
d
e
10 km
f
Africa
Madagascar
Mauritius
Rodrigues
Reunion
1000 km
Africa

Figure 3

Shell measurements showing the dimensions recorded in an example of *Tropidophora ligata.*

(A) Shell: s – distance from substrate to centre of hole. (B) Detail of hole, d – diameter in direction of whorl coiling, h – height along shell axis.

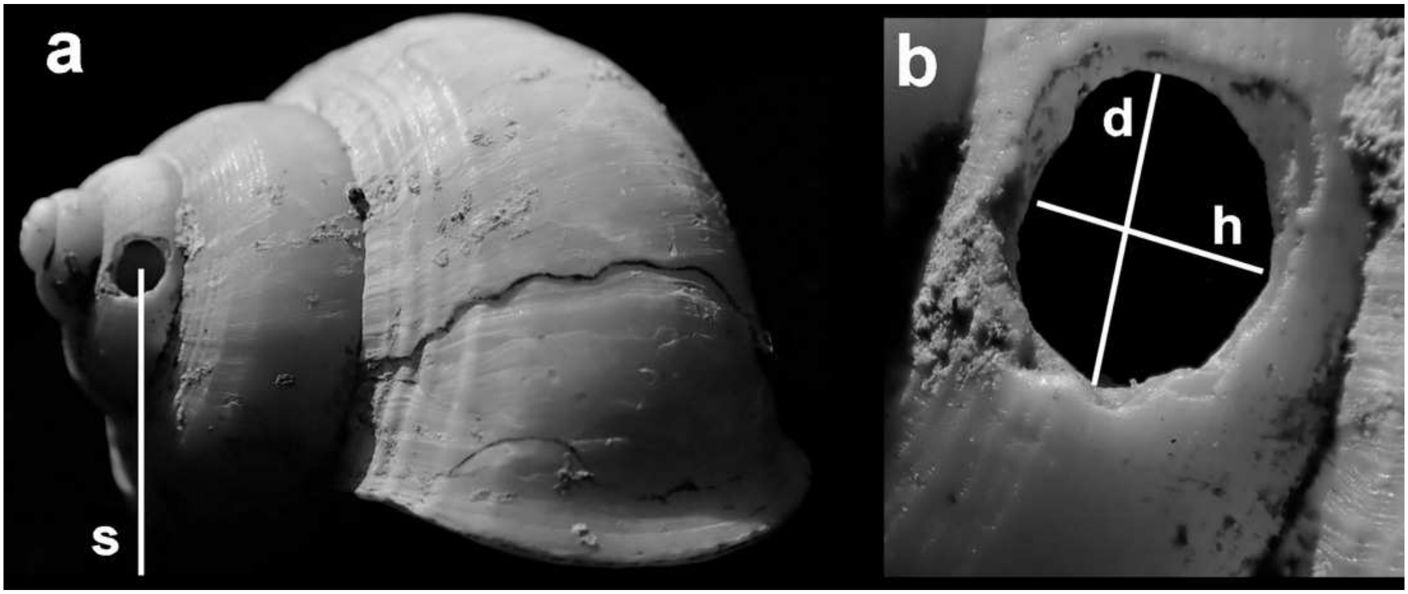


Figure 4

Variation in predated *Tropidophora.*

(A) Variation in irregular fractured holes in *T. carinata*. (B) limited variation in drilled holes in *T. ligata*. (C) exceptional position of a drilled hole in a *T. michaudi*. (D) Exceptional position of a drilled hole in a *T. icterica.* Not to scale.

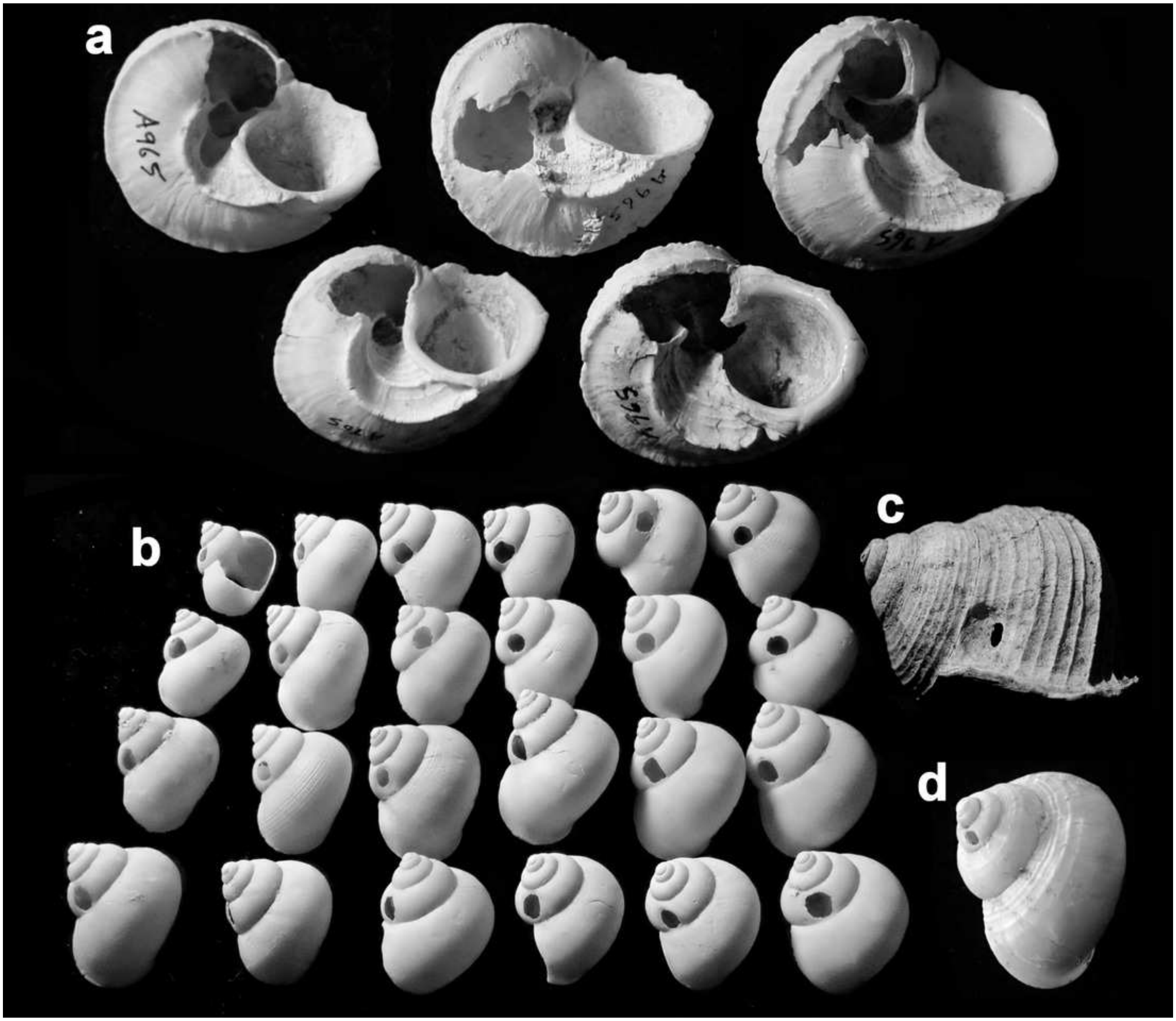


Figure 5

Details of bored holes in *Tropodiophora michaudi.*

Details showing grooves with shallow grooves denoted by up arrows, deep grooves by down arrow. Scale bar 1.0 mm.

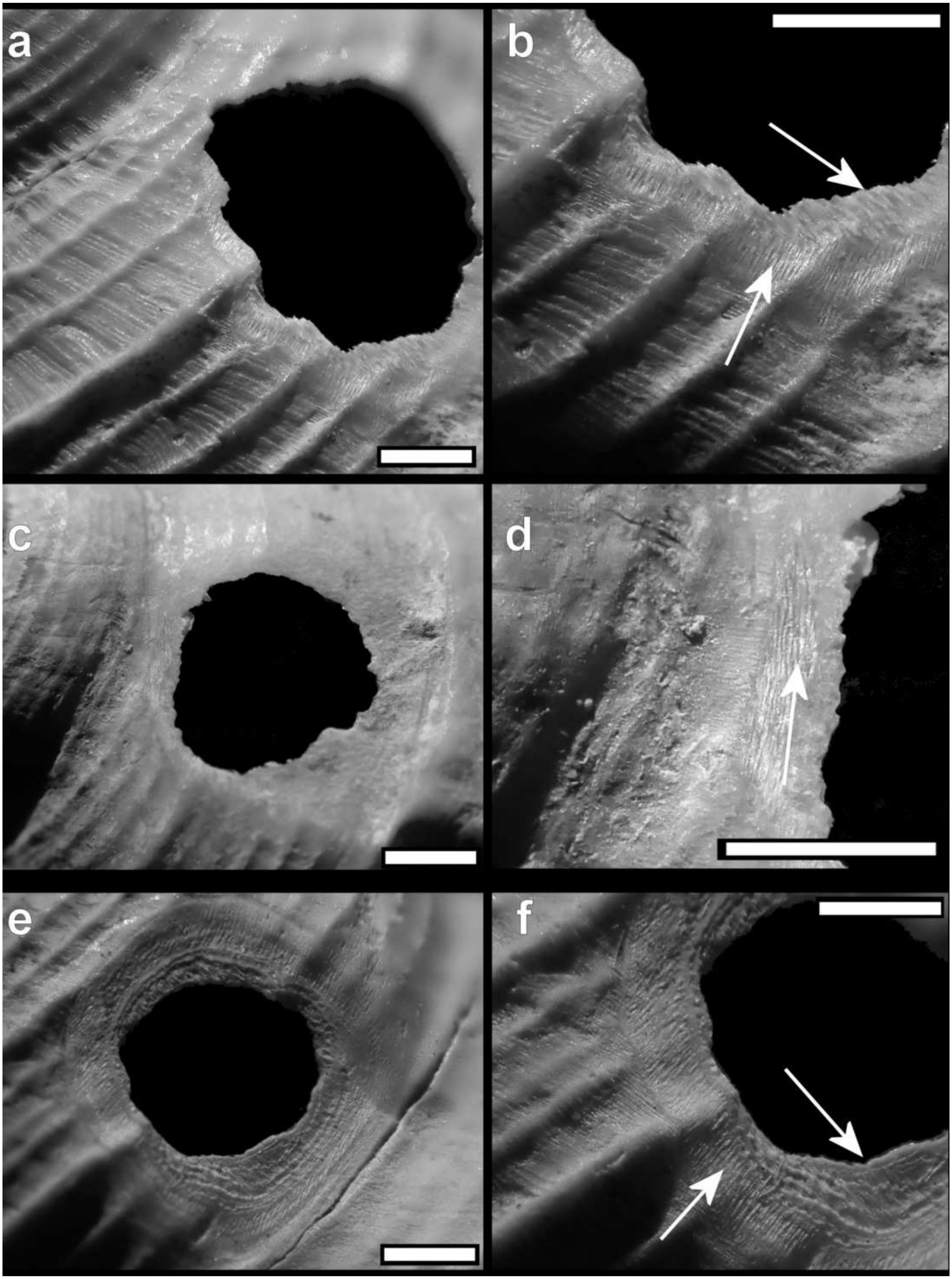

a
b
c
d
e
f

Figure 6

Details of bored holes.

(A) *Tropidophora icterica*. (B-C) *T. ligata:* (C) Detail showing shallow grooves denoted by up arrows, deep grooves by down arrow (these are worn and less distinct than the shallow ones). Scale bar 1.0 mm.

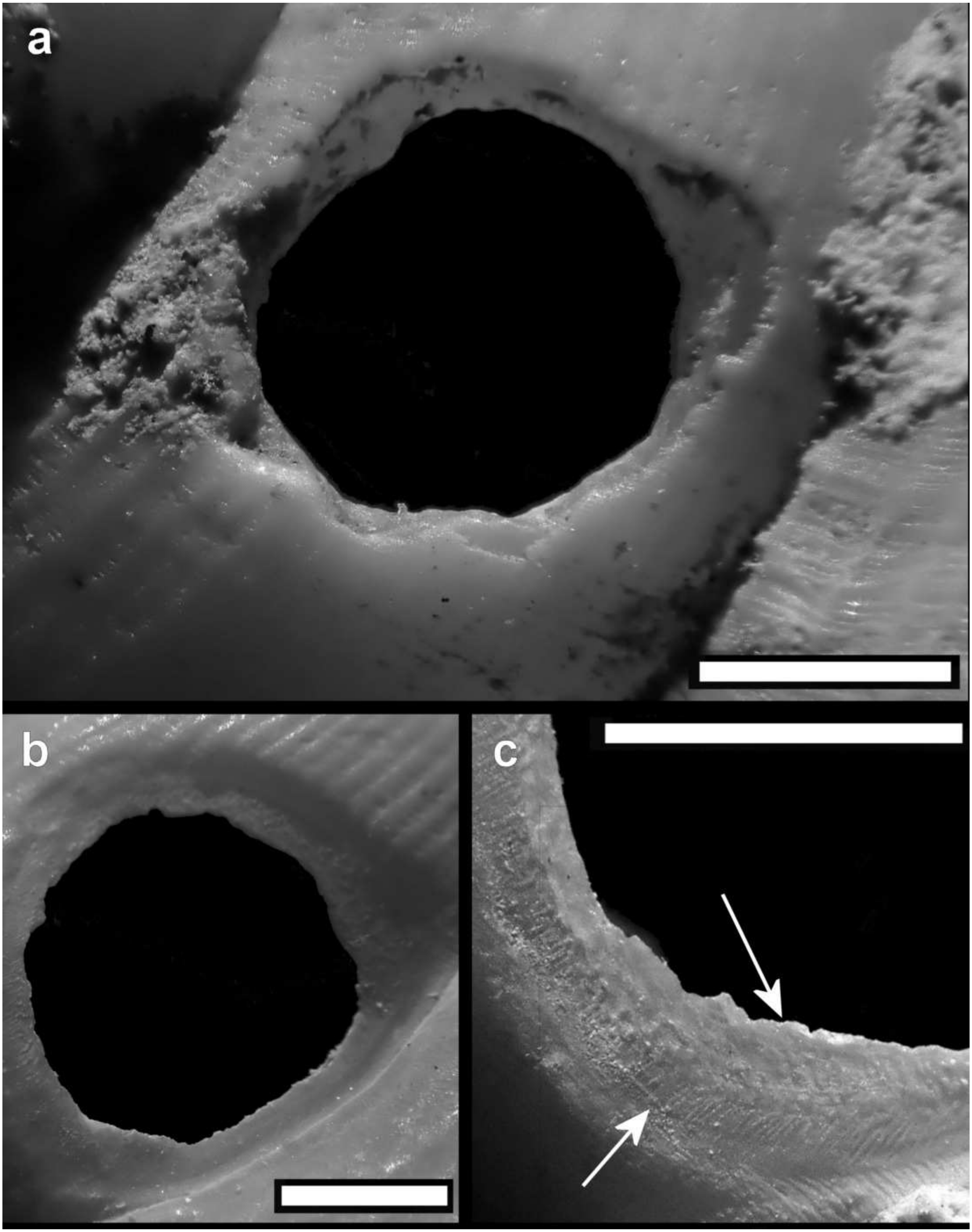

a
b
c

Figure 7

Scanning electron micrographs of *Tropidophora ligata* (A3912).

(A) Hole showing location of detailed views. (B) margin of hole showing vertical and horizontal grooves. (C) detail of shallow grooves. (D) border between different grooves. (E) detail of deep grooves. (F) lower grooved area. (G) detail of shallow grooves. Scale bar: A) 325 µm; b) 400 µm; C) 30 µm; D) 100 µm; E) 30 µm; F) 300 µm; G) 30 µm.

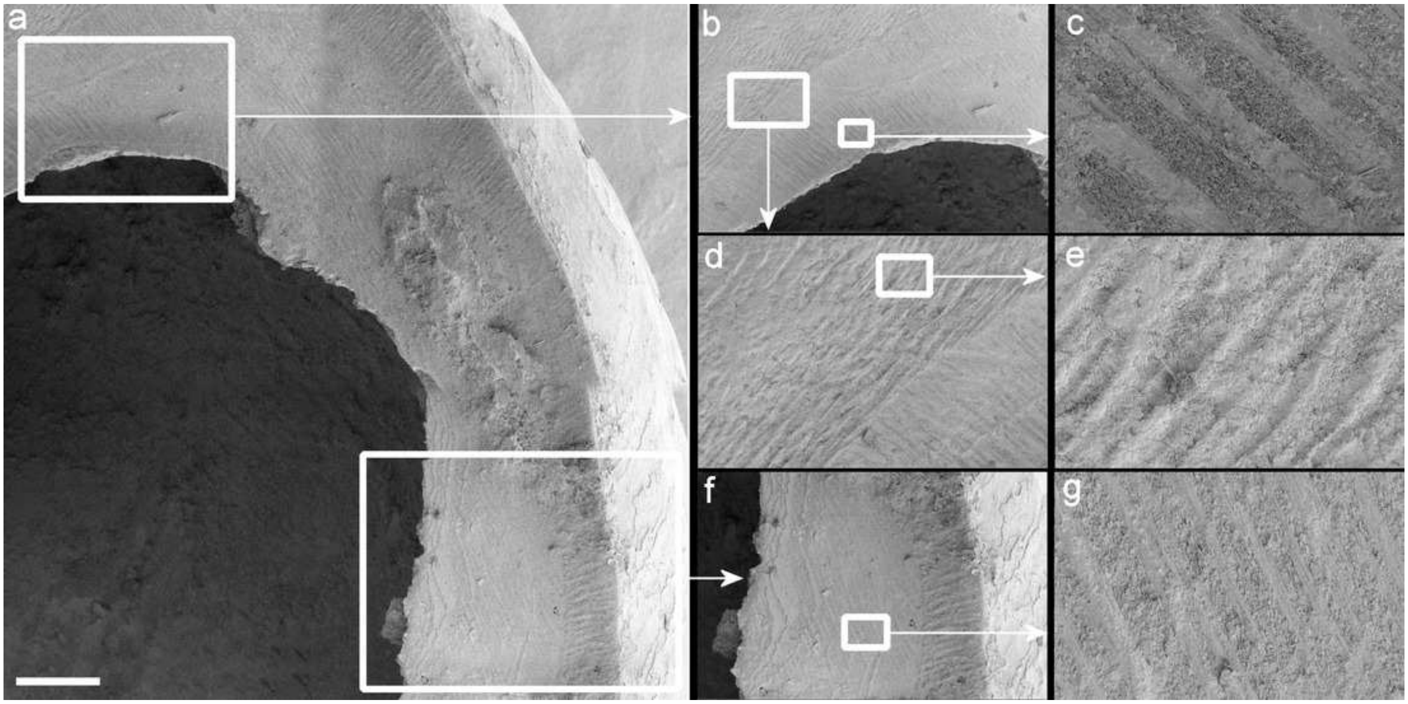


Figure 8

Superficial grooves (a) and deep gauges (c) extending onto spire in *Tropidophora michaudi* (A4106 and A5512).

Arrows mark the areas of extended abrasion. Scale bar A) 1mm (0.3 mm detail), B) 2 mm.

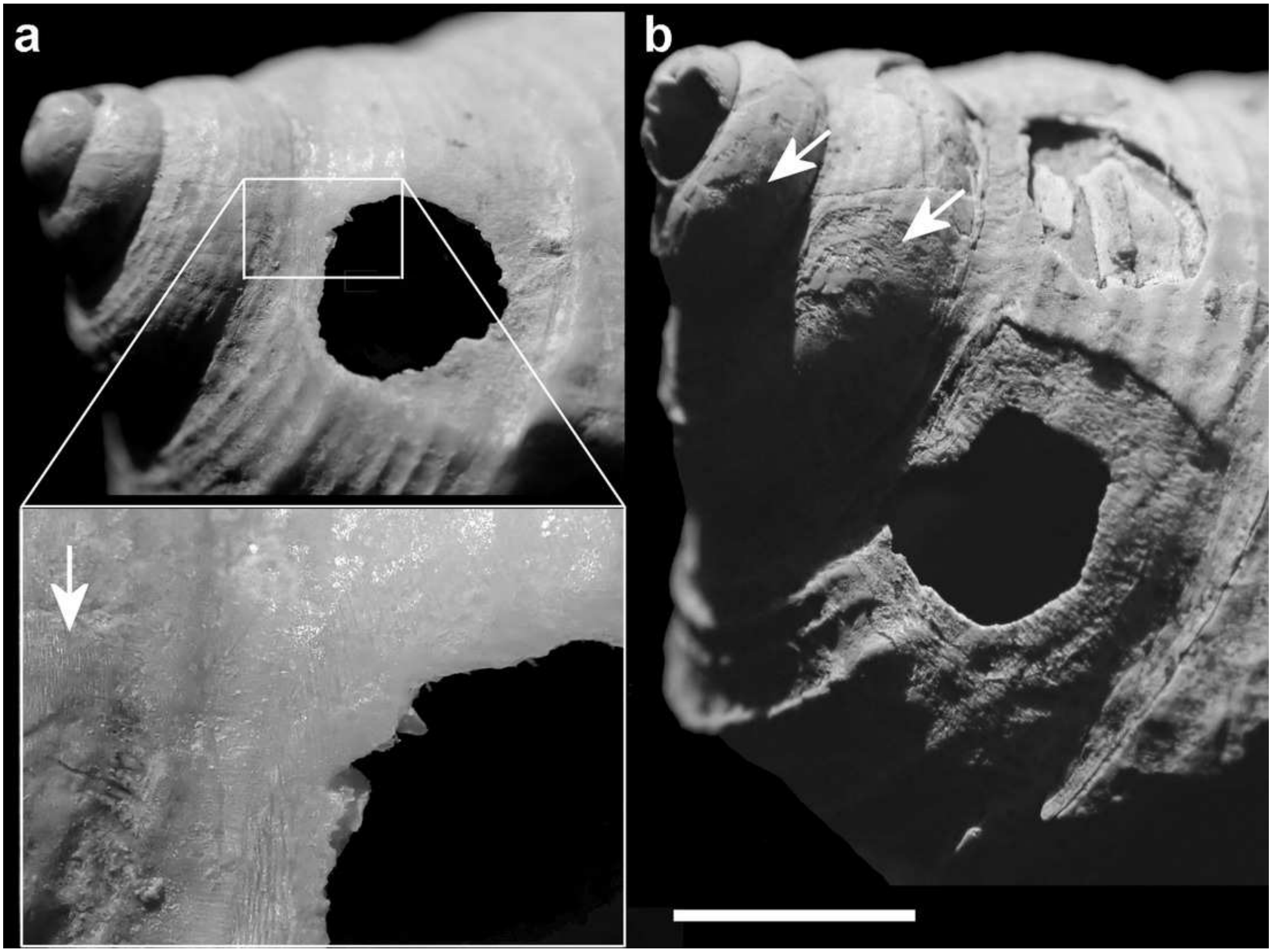
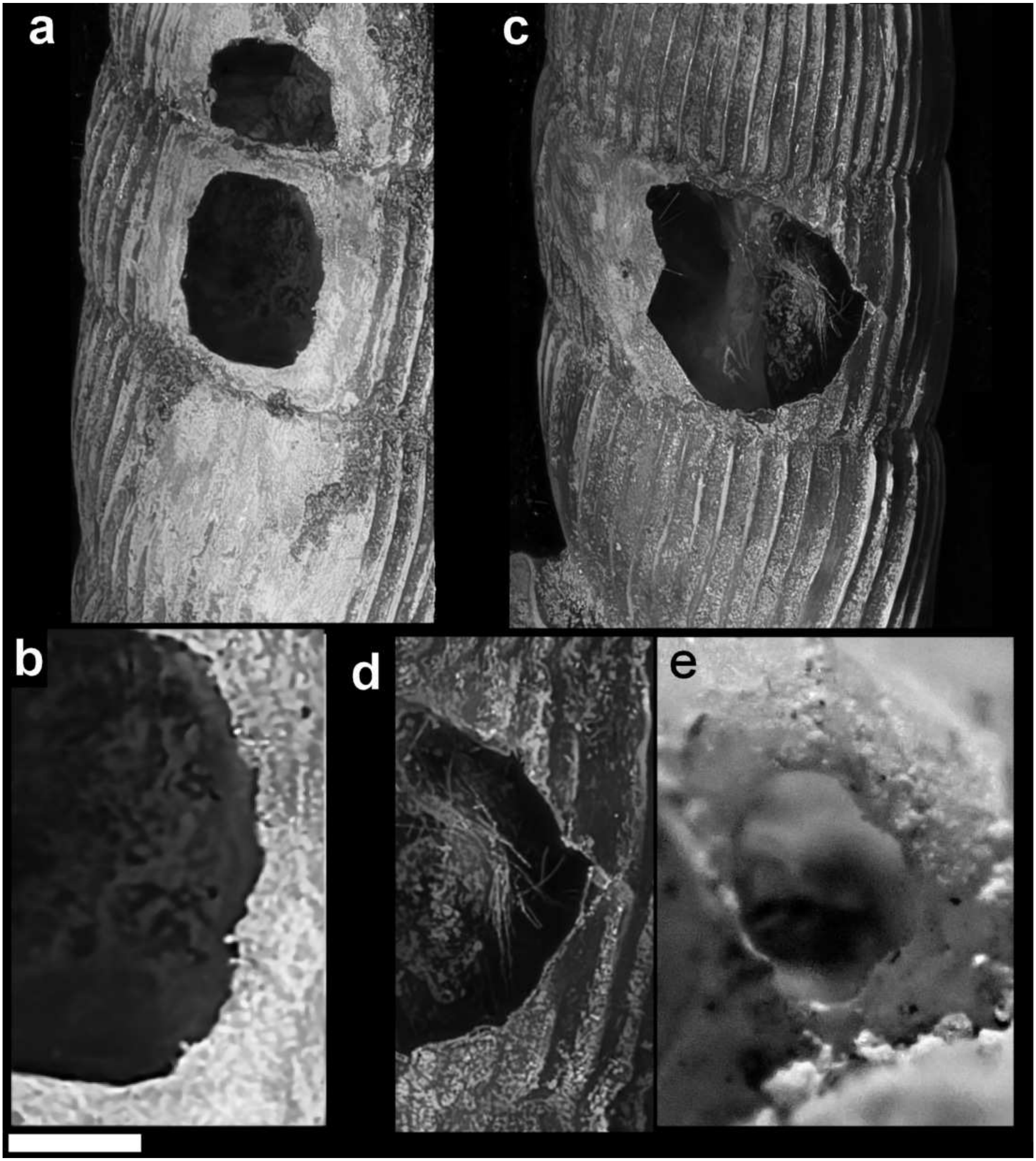


Figure 9

Details of comparative predated shells.

(A-B) *Alina biplicata* shells (NHMUK 202000133-4) predated by *Poiretia*. (C-D) spame predated by *Drilus.* (E) *Plectostoma austeni* (NHMUK FF Laidlaw colln.) predated by Rathouisiidae. Showing broad eroded areas caused by *Poiretia* (A) and irregular scape marks (B), and splintered edges made by *Drilus* (C) and irregular mandibular scratches (D). Scale bar 1 mm (A & C), 0.2 mm (B & D), 0.1 mm (E).


a
c
b
d
e