



Abrasion provides clues on a chiton taphonomic conundrum

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ABSTRACT

Chitons are common marine invertebrates found worldwide that use aragonite to form their shell and are rare in the sedimentary and fossil records. Their rarity in the fossil record is interesting due to how abundant live chitons are. Previous work suggests that chitons resist dissolution, which appears inconsistent with their rarity in the sediment and fossil records and aragonite composition. This result warrants examination of other taphonomic processes on chiton skeletal material since other taphonomic processes may play a larger role in removal than previously thought. As many chitons are intertidal, mechanical abrasion of chiton valves is likely to occur; its extent is largely unknown and yet necessary to provide insight to the taphonomy of chiton material. Eight species of chitons were collected from the Otago Peninsula, South Island, New Zealand. A total of 129 valves were isolated, cleaned, weighed, and tumbled in a Lortone 3A rock tumbler for 96 h. The valves from each species lost an average of between 9 and 44% of their weight; damage varied among species. *Leptochiton inquinatus* (the sole lepidopleuran) lost the most material while the acanthochitonids (*Acanthochitona zelandica*, and *Notoplax violacea*) and the chitonids (*Chiton glaucus*, *Onithochiton neglectus*, *Sypharochiton pelliserpentis*, and *S. sinclairi*) were more resistant to abrasion. The dorsal layer of the valves (the tegmentum), which is penetrated by aesthete tissue and has a granular crystal microstructure, was the most damaged by abrasion in all species. The ventral layer (the articulamentum), which has a highly-organised crystal structure with fewer organic components than the tegmentum, showed the least signs of abrasion. Since abrasion reduces the tegmentum and changes the valve shape, it is likely that abraded chiton material is present but unrecognisable in the fossil record. The valves are estimated to last about seven years when in the intertidal zone when enduring abrasion alone, which is much less than the hundreds to thousands of years material is exposed.

1. Introduction

Chitons are common molluscs worldwide. They are exclusively marine and are characterised by their eight-part shell, composed of overlapping aragonite plates called valves. There are an estimated 930 extant species and 430 fossil species, most of which are found in the intertidal zone (Fontoura-da-Silva et al., 2013; Puchalski et al., 2008; Schwabe, 2008). New Zealand has a large and diverse chiton population, with over 8.5% of the world's chiton species live in its Exclusive Economic Zone (Gordon et al., 2010). Population densities of the very common chiton *Sypharochiton pelliserpentis* may reach 228 individuals/m², but most species are found in New Zealand at population densities of 3–8 individuals/m² (Boyle, 1970). Creese, 1988 shows other mollusc abundances to be typically lower than those of chitons (see Table 1; Creese, 1988).

Despite being locally common, chitons rarely appear in the sediment and fossil records (Cherns, 1999; Puchalski et al., 2008; Cherns and Wright, 2009). The vast majority of carbonate shelf deposits are

skeletal material, yet literature describing carbonate sediments from New Zealand has no mention of chitons, despite bivalves and gastropods comprising over 20% of the deposit (Ashby, 1930; Andrews, 1973; Nelson, 1978; Probert et al., 1979; Nelson and Hancock, 1984; Nelson et al., 1988; Hayton et al., 1995). Fossilised New Zealand chitons are discussed only in some of the literature detailing the fossil records of New Zealand (Beu and Maxwell, 1990; Crampton et al., 2006).

Although the live-to-dead fidelity of molluscs is generally high for intertidal, sub-coastal and open shelf habitats (Kidwell and Flessa, 1995; Behrensmeier et al., 2000), chitons also rarely appear in the fossil record (Cherns, 1999; Vendrasco et al., 2012). Extinct chiton species are generally represented by only a few valves and are rarer than other taxa even when reported as abundant (Puchalski et al., 2008). The tegmentum and valve shape are used to identify chiton species, so the valve must be in good condition to be recognised and identified. However articulated chiton valves are rare in the fossil record (Dell'Angelo et al., 2003; Sigwart and Sutton, 2007). For example, Cherns (1999) reported that chitons from the Silurian of Gotland,

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Table 1
Average valve weight loss in the control and experimental treatments.^a

Chiton species	Control		Experimental			n
	mg	%	mg	%	%/km	
<i>Acanthochitona zelandica</i>	0.02 ± 0.02	0.13 ± 0.02	2.1 ± 1.6	15.2 ± 4.9	0.21 ± 0.07	16
<i>Notoplax violacea</i>	0.01 ± 0.002	0.85 ± 0.01	4.9 ± 1.2	14.7 ± 2.7	0.20 ± 0.04	17
<i>Chiton glaucus</i>	0.05 ± 0.01	0.14 ± 0.01	4.9 ± 2.0	9.2 ± 1.8	0.12 ± 0.02	16
<i>Onithochiton neglectus</i>	0.02 ± 0.01	0.21 ± 0.01	3.5 ± 1.4	13.0 ± 1.1	0.18 ± 0.01	15
<i>Sypharochiton pelliseptentis</i>	0.04 ± 0.03	0.20 ± 0.01	10.6 ± 7.8	18.8 ± 2.5	0.25 ± 0.03	15
<i>Sypharochiton sinclairi</i>	0.02 ± 0.01	0.07 ± 0.01	5.1 ± 1.8	20.2 ± 5.4	0.27 ± 0.07	13
<i>Ischnochiton maorianus</i>	0.02 ± 0.01	0.40 ± 0.01	16.4 ± 3.0	21.1 ± 4.6	0.28 ± 0.06	15
<i>Leptochiton inquinatus</i>	0.001 ± 0.0004	6.77 ± 0.02	0.6 ± 0.1	44.0 ± 21.8	0.59 ± 0.29	22

^a Values are reported as the average ± standard deviation. n is the number of individual valves tumbled for each species.

Sweden showed an “unusually abundant, diverse, and well-preserved assemblage”, but Paleoloricata valves were 7% as common as bivalves. In a rare exception, [Cherns and Wright \(2009\)](#) described a lagerstätten with Paleoloricata fossils representing 3.5% of silicified molluscs in the Devonian period and dominating in the Ordovician period (18% of molluscs). [Hoare and Farrell \(2004\)](#) also found both Paleoloricata and Neoloricata from the Devonian period in the Garra Formation in New South Wales. In all, however, chitons accounted for only 3.5% of the silicified molluscs from the Paleozoic to Early Mesozoic in this area ([Cherns and Wright, 2009](#)). [Hoare and Pojeta \(2006\)](#) collected 55,000 silicified mollusc fossils from the several localities in the USA and only 1.9% (1083) of them were chitons. [Sigwart et al. \(2007\)](#) collected 458 chiton valves from Denmark, which is was the first reported occurrence of chitons from the region. The only report of chiton fossils that number above 10,000 comes from the San Diego Formation, with > 15,000 chiton valves from 22 species. The large numbers of intact chiton valves in the San Diego Formation are most likely a result of rapid burial at the relatively shallow depth of 25 m ([Vendrasco et al., 2012](#)).

The relative absence of chitons in the fossil records is apparent even in New Zealand, which has the most complete Cenozoic molluscan fossil record in the Southern Hemisphere ([Crampton et al., 2006](#)). Other molluscs, particularly bivalves and gastropods, are common throughout the record and both cephalopods and opisthobranchs make regular appearances ([Stilwell, 1993](#); [Stilwell and Grebneff, 1996](#); [Beu et al., 2012](#); [Beu, 2012](#)). [Beu \(2012\)](#) and [Stilwell \(1993\)](#) reported on molluscs in the Cenozoic, but listed no chitons. [Beu et al. \(2012\)](#) reviewed data collected in 1865 and did not list any chitons. [Beu and Maxwell \(1990\)](#) listed only 28 species of chitons in the checklist of New Zealand Cenozoic molluscs. *Notoplax rubiginosa* is the most common chiton in the Pliocene-Pleistocene. *Acanthochitona flebilis*, *Notoplax* sp., and *Chiton* sp. are representative species of the Pliocene. *Cryptoplax* sp. was found in sediment washings from the Early/Mid Miocene. Isolated chiton valves were found in the base of the Kauru formation and in faunules from Waitakian and Cenozoic periods but were not identified to species.

[Puchalski et al. \(2008\)](#) argue that the rarity of chitons in the fossil record may be due to sampling bias, since collector curves for Europe and North America are incomplete. A collector curve is a plot of the cumulative number of species compared to the total number of individuals sampled over time. The intention behind this method is to show when adequate sampling is achieved, a collector curve assumes sampling from an area where the biodiversity has not been fully described theoretically results in new species being recorded. The curve should approach a horizontal asymptote when all species have been found in an area; if the curve has not plateaued, it is likely there are additional species in the area that have not been recorded ([Weller, 1952](#); [Fountain et al., 2005](#)). While increased sampling may not reveal more species, the curve does not suggest that sampling is complete when the curve reaches an asymptote. It is possible that the rarity of chitons in the fossil record is due to lack of sampling, given that the main source of disagreement in the live and dead records is lack of

sampling over time for current environments. However, lack of sampling does not address chiton fossil rarity in the assemblages from Australasia, Africa, and South America since their collector curves appear to have reached a plateau ([Puchalski et al., 2008](#)). In fact, [Fleming \(1965\)](#) shows that the collector curve for New Zealand molluscs began to stabilise around 1945. While it remains to be seen if lack of sampling causes chitons to appear in the fossil record, the fact remains that they are hard to find ([Cherns, 1999](#); [Hoare and Farrell, 2004](#); [Cherns and Wright, 2009](#)). Therefore, it seems most likely that the sparsity of chitons in the sediment and fossil record is the effect of taphonomic processes removing them from these records or causing them to be unrecognisable, as suggested by [Puchalski and Johnson \(2009\)](#).

Taphonomic processes are non-random, since abrasion, breakage, dissolution, and bioerosion act differently on different shapes, sizes, and crystal structures of calcareous material ([Harper, 2000](#); [Sanders, 2003](#); [Smith and Nelson, 2003](#); [Cherns and Wright, 2009](#)). There is, for example, a bias in the fossil record against aragonite, as it either is removed by dissolution ([Sanders, 2003](#)) or is replaced by siliceous material which works against dissolution ([Cherns and Wright, 2000](#); [Wright et al., 2003](#)). Organisms that use calcite to form their skeletal components are more likely to be preserved than those that use aragonite. Since chiton valves are made of aragonite, it seems logical to conclude that dissolution is one of the main forces of removal, especially since silicified chiton fossils are found from the Devonian era ([Cherns, 1999](#); [Hoare and Farrell, 2004](#)). Strangely, however, chiton valves appear to resist dissolution when introduced to environments with a reduced pH of 7.5 ([Sigwart and Carey, 2014](#); [Sigwart et al., 2015](#)). Chiton valves were exposed to a pH of 7.5 for four weeks at three different temperatures (10, 15, and 20 °C) yet the valves remained undamaged ([Sigwart and Carey, 2014](#)). Valves also showed no reduction in fracture resistance after 10 days of treatment in a pH of 7.5 ([Sigwart et al., 2015](#)). However, [Sigwart and Carey \(2014\)](#) were primarily interested in the grazing behaviour under stressful conditions and neither study involved other molluscs or aragonitic shells; while the evidence that chitons may resist dissolution is equivocal it is important enough to consider examining other taphonomic forces since dissolution may not affect chiton valves as much as previously suspected. If chiton valves are indeed able to withstand dissolution, then either biological or physical forces may play a larger role than expected in removing them from the fossil record.

Chiton fossils have been shown to provide information on past salinity and temperature levels ([Rojas and Urteaga, 2011](#)) so understanding chiton taphonomy can aid in constructing palaeoceanographic conditions. Chitons also appear to have fossilisation potentials that vary among families ([Puchalski and Johnson, 2009](#); [Sigwart et al., 2014](#)), which adds to their importance as a study organism. If chitons are underrepresented in the fossil record, estimates of diversity through time may be biased. Since New Zealand has been isolated, its fossil record contains the only data from the southwestern Pacific region ([Crampton et al., 2006](#)). It is important to identify any potential

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