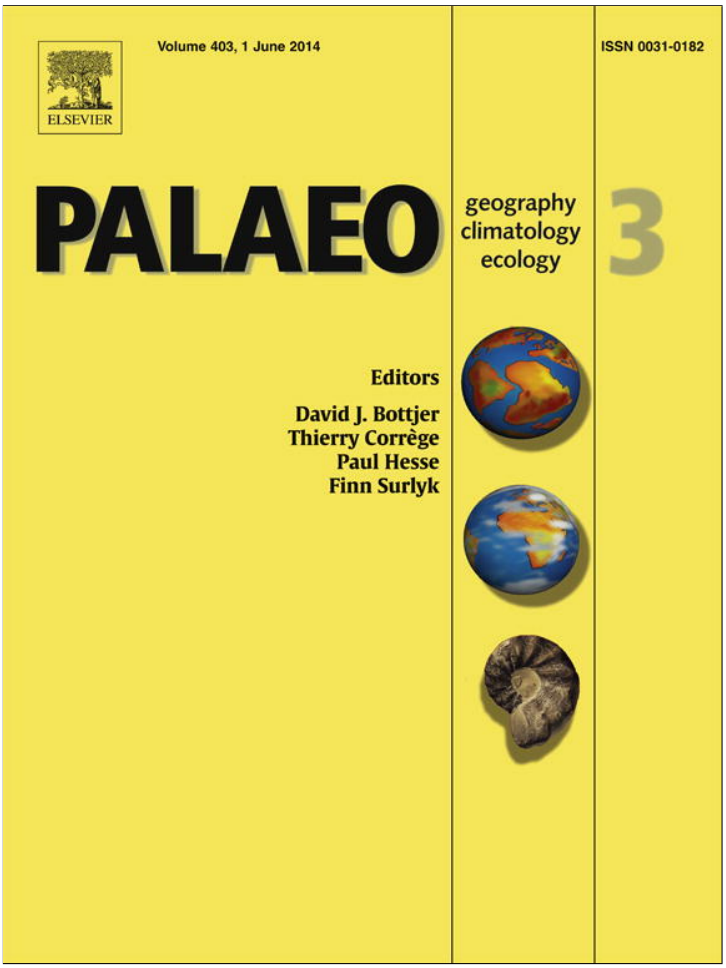

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How subtle are the biases that shape the fidelity of the fossil record? A test using marine molluscs

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ABSTRACT

Biases in preservation shape the fossil record, and therefore impact on our reconstructions of past environments and biodiversity. Given the intensive recent research in the general fields of taphonomy and exceptional preservation, surprisingly, fundamental questions remain unanswered about species-level variation in skeletal preservation potential at low taxonomic levels (*e.g.* between genera from the same family, or between taxa from related families) across myriad groups with multi-element skeletons. Polyplacophoran molluscs (chitons *sensu lato*) are known from the late Cambrian to Recent, and possess a distinctive articulated scleritome consisting of eight overlapping calcareous valves. The apparent uniformity of living chitons presents an ideal model to test the potential for taphonomic biases at the alpha-taxon level. The vast majority of fossil chitons are preserved as single valves; few exhibit body preservation or even an articulated shell series. An experimental taphonomic programme was conducted using the Recent polyplacophorans *Lepidochitona cinerea* and *Tonicella marmorea* (suborder Chitonina) and *Acanthochitona crinita* (Acanthochitonina). Experiments in a rock tumbler on disarticulated valves found differential resistance to abrasion between taxa; in one experiment 53.8–61.5% of *Lepidochitona* valves were recovered but 92% of those from *Tonicella* and 100% of elements from *Acanthochitona*. Chiton valves and even partly decayed carcasses are more resistant to transportation than their limited fossil record implies. Different species of living chitons have distinctly different preservation potential. This, problematically, does not correlate with obvious differences in gross valve morphology; some, but not all, of the differences correlate with phylogeny. Decay alone is sufficient to exacerbate differences in preservation potential of multi-element skeletons; some, but not all, of the variation that results is due to specimen size and the fidelity of the fossil record will thus vary intra-specifically (*e.g.* between ontogenetic stages) as well as inter-specifically.

1. Introduction

It has long been recognised that the principal cause of bias in the fossil record is the discrepancy between the greater fossilisation potential of biomineralised tissues ('hard parts') and that of non-biomineralised tissues ('soft parts'). In practice, many taxa comprise a combination of both, thus a comprehensive understanding of their taphonomy (*i.e.* the processes responsible for their preservation) requires elucidating the processes that reduce the fidelity of each. Such studies have significant wider implications, not least the requirement that the data yielded by the fossil record is sufficient to address evolutionary and ecologic questions centred around the history of life of Earth (*e.g.* Behrensmeyer et al., 2000; Kosnik et al., 2011). Our understanding of the taphonomy of both biomineralised and non-biomineralised tissues has improved markedly over recent decades as a result of both investigation of the taphonomy of fossils, and experimental programmes using extant taxa designed to identify the physical, chemical and biological processes responsible for fossilisation.

The relative recalcitrance (resistance to decay) of non-biomineralised tissues has been established by experimental decay of modern animals. Different non-biomineralised tissues vary in their recalcitrance, but the same tissue can also vary as a result of subtle differences in physical and biochemical structure, or similar tissues can also vary between different parts of the body in an individual or taxon (Orr et al., 2008; Sansom et al., 2013).

The preservation of taxa that possess multi-element skeletons (for example, echinoderms, vertebrates, and molluscs, including bivalves and chitons) as highly articulated and near-complete remains is obviously favoured *via* certain taphonomic pathways and in specific

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environmental contexts: rapid burial, ideally entombment while alive, and deposition of carcasses in quiet water, low oxygen environments are obvious factors that inhibit disarticulation and following it, loss of completion. Outside of such settings, carcasses will inevitably be subjected to various biostratinomic processes before incorporation into the sediment column. Almost invariably, these, and subsequent diagenesis, result in loss of the skeletal fidelity of the biomineralised tissues of any carcass.

Dispersion patterns of isolated skeletal elements have been investigated in field-based (typically fluvial settings), or laboratory settings (flume tanks). In such cases, the entire skeleton or an assemblage of selected bones (in the cases of vertebrates), and individual valves (for example, in brachiopods and bivalves) are used. Such data reveal the complexity of the processes that govern the loss of skeletal fidelity. Even subtle differences in a single parameter can induce variation, and results can sometimes be counter-intuitive. The difference in current velocity required to entrain the corresponding pedicle and brachial valves of a brachiopod is not unexpected given the difference in mass (Messina and LaBarbera, 2004). A difference in abundance between left and right valves of bivalves, the mass of each of which is identical, has been reported previously by different authors, and ascribed to differences in the hydrodynamic properties of the two valves (see review by Chattopadhyay et al., 2013). Paradoxically, a light porous skeleton may be abraded rapidly *in situ* but fragment little during transport; as a result of its low density the skeleton may be carried suspended in the water column, not as part of the bedload, and thus impacted little or not at all by components of the bedload.

Experimental studies generally work within a framework where: (a) autolysis and decay of the non-biomineralised tissues has been completed fully before any transport occurs; and (b) that the skeleton has thus been reduced to individual, associated elements (for example, isolated bones, two separated valves or in the case of crinoids, ossicles and plates). This is clearly a potential over-generalisation in comparison to natural settings, as transport may occur before death, at the time of (and be the cause of) death, or at any stage after death and before initial burial. Experiments confirm the effects of transport depend strongly on how much decay the carcass has experienced beforehand: the transport of fresh and decayed carcasses of the same taxon will almost invariably result in markedly different products in the fossil record (Allison, 1986; Kidwell and Baumiller, 1990). Non-biomineralised in this context extends to the organic matrix present within many biomineralised tissues, including shells and bones. Microbial degradation of this may leave the mineralised component more susceptible to fragmentation. The post-mortem fate of both biomineralised and non-biomineralised tissues is therefore often strongly coupled, although rarely, for practical reasons, investigated together experimentally (although there are exceptions: Allison, 1990; Kidwell and Baumiller, 1990; Davis and Briggs, 1998).

The geochemistry of the depositional and burial environments can also be a significant control on the taphonomy of biomineralised tissues (*e.g.* Powell et al., 2012). The two principal polymorphs of calcium carbonate are aragonite and calcite; typically, the former dissolves or inverts to the latter during diagenesis. Dissolution of carbonate may occur before burial; Walker et al. (2013) conclude that at current rates the high Mg calcite of the vertebral ossicles of ophiuroids would dissolve completely in between 6 and 105 years on the surface of the Antarctic shelf, a figure that may decrease given predicted rates of oceanic acidification in the 21st century. The impact on these differences in preservation potential on the fidelity of a fossil assemblage can be dramatic (Cherns and Wright, 2000). Short-term changes in environmental conditions can (*e.g.* Barton and Wilson, 2005) but do not always (*e.g.* McNamara et al., 2012) result in differences in the fidelity of skeletal preservation of taxa.

Despite these complexities, it is now possible, for most fossil groups, to generate reasonably robust *a priori* models that predict the taphonomic pathway between death and incorporation into the geological record in a specific set of environmental conditions. Critically, however, implicit in such general models is the further assumption that closely related taxa that share a similar body plan will behave similarly. This is, however, essentially untested: *i.e.* it remains uncertain how subtle the biases that shape the fidelity of the fossil record are. Put another way: in how much more detail do palaeobiologists need to understand taphonomic processes?

To investigate this, we integrated decay experiments and tumbling experiments for representative taxa from three different families of polyplacophoran mollusc (chitons) that naturally occur in similar environmental settings. The specific null hypothesis tested is that the response of each group to decay and simulated transport, as evidenced by the fidelity of preservation of the valves of the multi-element skeleton, will be identical.

Chitons are distinctive members of the rocky intertidal marine invertebrate fauna; a series of eight aragonite shell plates or valves is arranged on the dorsal surface, protecting the soft molluscan foot that grips onto the hard substrate (Schwabe, 2010). The modern chiton scleritome ('skeleton') consists of three distinct elements that can be distinguished easily: the head valve (I), intermediate valves (II–VII) and tail valve (VIII). Valves vary in shape and morphology. Among the intermediate valves, valve II is typically longer. Valve II covers the radula bolster in life position, but this is nearly impossible to distinguish in the absence of the complete valve set for comparison; the intermediate valves must be considered effectively interchangeable in a palaeontological context. The valve series is surrounded by a muscular girdle covered by a cuticle bearing small scales, bristles, or other armature. An exposed series of valves is the more common condition, though some species have largely or entirely internalised shells (*e.g.* the wandering meatloaf, *Cryptochiton stelleri*).

Chitons are an ideal model organism to investigate whether subtle differences in the biology of taxa may impact on their preservation potential. With some exceptions, extant chitons are morphologically conservative; they and all fossil chitons *sensu stricto*, have an essentially equivalent anatomy. Their intrinsic preservation potential, *i.e.* that controlled by their biology, would thus be expected to be both identical among extant taxa, and unchanged over geological time.

We tested for the impact of biology on the fidelity of preservation of transported taxa using tumbling experiments ('*tumbling experiments*' herein). Previous studies have consistently demonstrated that transportation of freshly killed organisms rarely induces either rapid disarticulation or fragmentation of multi-element skeletons (see for example Allison, 1986; Kidwell and Baumiller, 1990). Thus, to exacerbate the effects of any difference in the biology of taxa, specimens were decayed in advance of being tumbled; the rate, and sequence, of valve disarticulation during decay and modification of valves during decay were assessed (referred to as '*decay experiments*' herein).

2. Methods

2.1. Study organisms

Animals were collected by hand in the low intertidal near the Queen's University Marine Laboratory (Strangford Lough, Northern Ireland). Three species that are locally abundant were selected: *Acanthochitona crinita* (n = 53), *Lepidochitona cinerea* (n = 26), and *Tonicella marmorea* (n = 44). *Lepidochitona* and *Tonicella* are morphologically similar in terms of basic valve architecture, and belong to the suborder Chitonina. *Acanthochitona crinita* (Suborder Acanthochitonina) is larger, but has relatively smaller valves that are more disc-like in outline and flattened in profile (Fig. 1).

All animals were acclimated in QML aquarium facilities prior to being sacrificed for experiments. Individual wet weights were recorded (after blotting dry) at experiment commencement. The same set of animals was used for both subsequent experiments. *Acanthochitona* was the largest of the three (0.27–1.02 g wet mass) with *Lepidochitona* (0.03–0.32 g) and *Tonicella* (0.02–0.58 g) rather smaller.

Fig. 1. Specimens in life and isolated valves of the three study species, from top to bottom Acanthochitonina: *Acanthochitona crinita*; Chitonina: *Tonicella marmorea*, *Lepidochitona cinerea*. Anterior is to the right in all pictures and total animal length is ca. 2 cm, valves show the tail (at left), example intermediate, and head elements.

2.2. Decay experiments

Animals were moved to individual screw-close plastic containers (25 mL) filled with filtered deoxygenated seawater and sealed underwater to prevent ingress of atmospheric oxygen. The total group of containers (n = 123) was kept in a waterbath cooled by a flowthrough seawater system, maintaining the chambers at the same temperature as ambient seawater conditions (10–13°C) for the duration of the experiment.

Specimens were inspected at intervals of 1–3 days over the first 50 days of the experiment (July–September 2011), after which time disarticulation of all but one taxon (*Acanthochitona*) was extensive (Fig. 2). Specimens were inspected again upon termination of the experiment (120 days). During inspection, animals were visually inspected (without removing them from the experimental chambers) for the extent to which the head valve, any of the intermediate valves, and the tail valve were detached from the body. These were recorded as 'attached', 'lifting' (as the valve came loose from the viscera) or 'removed' when the valve was separated completely. The former two categories are akin to what would be described as fully or entirely articulated, and partially or semi-articulated, respectively, in a fossil specimen.

The motion of removing chambers from the waterbath for inspection agitated the contents slightly, and made it less likely that a disarticulated valve resting in life position was not inadvertently scored as attached or lifting. Scoring of specimens at each inspection was without any reference to previous values, and not always by the same individual; none of the data show a reversal over time whereby a valve scored as either loose or removed is subsequently scored as attached, or attached or loose, respectively.

2.3. Tumbling experiments

The decay experiments were terminated after 120 days, and the specimens retrieved. Those *Acanthochitona* specimens that were still fully articulated (n = 32) were placed directly into a (1.5 L) rock tumbler in a treatment of medium-coarse sand (100 mL volume, 1–2 mm grain size) and 100 mL dH_2O and tumbled for 18 h. There were insufficient intact specimens in the other two taxa to repeat tumbling experiments on *Tonicella* or *Lepidochitona*. All tumbling experiments were conducted separately for each species, and the intact *Acanthochitona* separately from the set of disarticulated valves for that taxon, but individuals of each species were tumbled collectively.

The disarticulated specimens for all species were rinsed in dH_2O, tissue and organic matter were decanted from the experimental chamber, and the valves were dried in a ventilated drying oven at 40 °C. Some

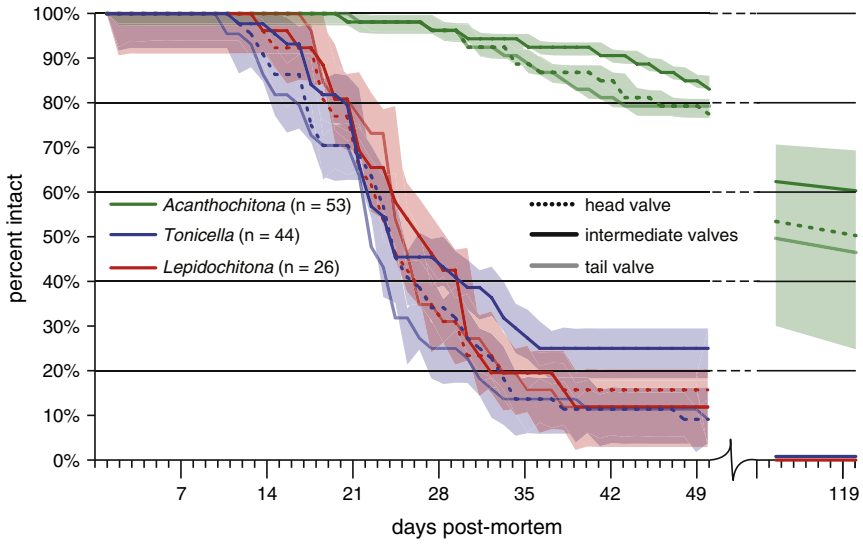

Fig. 2. Disarticulation of specimens during decay. The shaded areas are 95% confidence intervals for a forecast model for each valve dataset (forecast values not shown within days 1–50; lines indicate actual valves recorded as detached over time). The total shaded areas for each taxon indicate the spread for each species between a maximum percent intact (with any valve still attached, top) or disarticulated (with any valve even partially detached, bottom). At right, the forecast predictions for disarticulation at days 114–120, the final week of the experiment. Predicted values are shown for *Acanthochitona*; forecasts for the other two taxa are 0%. The actual proportion of completely intact *Acanthochitona* specimens at day 120 was 75.6%.

specimens were discarded if single valves remained attached to the viscera and could not be isolated without dissection. Broken valves were discarded. These were not broken during experimental procedures: they were broken before or at the time of collection but remained held in place by the muscular girdle. The unbroken valves were used in a 1 : 6 : 1 ratio (head : intermediate : tail), as per a living animal.

The dried valves were scored on seven features to generate an *a priori* 'total taphonomic grade' (TTG) the maximum value for which (12) is the cumulative score for the seven categories (Table 1). The scheme is modified from that designed for chiton valves by Puchalski and Johnson (2009). Scores were assigned based on visual inspection under a dissecting microscope at 30× magnification. Sets of valves from the three species were subjected to experimental abrasion in a rock tumbler for 18 h (repeated separately for each species) with a mix of sand (as above) to which a limited amount of 5–6 mm gravel and 100 mL dH_2O was added. The combination of gravel and sand approximates the intertidal substrate in Strangford Lough. A subset of *Tonicella* valves was treated in sand only; to distinguish the two treatments this is referred to as 'sand' and the former, sand plus gravel mixtures, as 'gravel'. This resulted in eight experimental groups: *Acanthochitona* carcasses in sand (n = 32), *Acanthochitona* valves in gravel (n = 11), *Tonicella* valves in sand (n = 15), *Tonicella* valves in gravel (n = 16), and *Lepidochitona* valves in gravel (n = 13).

Following treatment, the whole volume of the rock tumbler was transferred to a drying oven, and then sorted under a dissecting microscope to remove all valves and chiton elements from the matrix, and scored again according to the TTG (Table 1).

2.4. Analysis

In most cases a Kruskal–Wallis test was used to investigate differences in mean score between treatments, with a non-parametric multiple comparison (npmc) to determine pairwise differences (Helms and Munzel, 2011; R Core Development Team, 2011). To test for differences in skeletal disarticulation during decay, and the trends of disarticulation during the unmonitored extended experiment (days 50–120) we implemented low-order autoregressive integrated moving average (ARIMA) models for each of the nine datasets (3 valve elements × 3 taxa) in SPSS (IBM, USA). Based on the behaviour of the time series and inspection of variance and autocorrelations, a 0-order exponential smoothing with growth, ARIMA (0,1,1), was determined to be the most appropriate for the measured data. These nine models were then used to forecast disarticulation to day 120 and compared with actual observations.

3. Results

3.1. Decay experiments

The different species showed statistically significant variation as to how they disarticulated during decay. Over the course of the experiment *Acanthochitona* disarticulated less than the other two (Table 2; Fig. 2). The time to the first valve disassociating from the body mass was significantly longer in *Acanthochitona* (day 21) than in *Tonicella* or *Lepidochitona* (days 11 and 14, respectively) separated by a 95% confidence interval for each taxon (Fig. 2). In *Acanthochitona*, and in *Tonicella*, terminal valves disassociate significantly more rapidly than intermediate valves. In *Lepidochitona* there is no difference between the 3 valve types. Over the first 50 days of the experiment, a significantly greater percentage of specimens of *Tonicella* or *Lepidochitona* experience disarticulation than do those of *Acanthochitona* (*circa* 90%, as opposed to 23% respectively).

There is no significant difference in total disarticulation between *Tonicella* and *Lepidochitona*, which are both members of the suborder Chitonina (as opposed to Acanthochitonina, represented by *Acanthochitona*). However this also coincides with a significant difference in body wet weight of the experimental animals. An ANCOVA analysis indicated a significant interaction between size and length of time to disarticulation ($F_{2,74} = 4.18$, $p = 0.02$).

At the end of decay experiments, a substantial number of specimens remained partially articulated (Table 2), although all *Tonicella* specimen valve series had disassociated completely. A large proportion of the *Lepidochitona* specimens (42.4%) included partially articulated valve series but no specimens remained fully articulated. The majority of *Acanthochitona* specimens (75.6%) were, however, fully articulated animals after 120 days' decay; these specimens were transferred to the sand tumbling experiment intact (Figs. 3, 4D). The forecast model prediction for the number of intact intermediate valves closely corresponds to the actual proportion of fully articulated specimens (Fig. 2) although the model slightly over-estimates the tempo of disassociation of terminal valves. The forecast model estimated total disarticulation by day 62 for *Lepidochitona*, and day 68 for *Tonicella*, relatively shortly after regular recording was stopped, and broadly consistent with the results of the latter.

A small number of valves recovered from the decay experiments were fragmented (attributable to injuries suffered in life), but the total number of intact valves recovered after decay did not differ statistically between species nor from the expected 1:6:1 ratio ($\chi^2 = 0.191$, df = 6 $p = 0.995$).

The taphonomic scores (TTG) for the valves in each species after decay, recalculated as percentage values, are shown in Fig. 4A–C. In each taxon the TTG scores for the intermediate valves are significantly different from the other two (Mood's test of medians: *Acanthochitona*, $\chi^2 = 6.93$, $p = 0.03$; *Lepidochitona*, $\chi^2 = 24.27$, $p < 0.001$; *Tonicella*, $\chi^2 = 10.54$, $p = 0.005$). The TTG scores for the tail and head valves are not statistically significantly different from each other in any taxon.

3.2. Tumbling experiments

Acanthochitona was the most robust to abrasion (compare Fig. 4F with 4G–H). In all treatments, all valves were recovered with relatively few elements broken. Remarkably, some of the specimens (n = 32) treated in coarse sand after 120 days' decay emerged lacking most or all valves, but otherwise entire, with intact body muscle blocks (n = 3, all with radulae still in place; Fig. 3); the disassociated girdle armature of a further 17 animals and 15 radulae were recovered. The median TTG was significantly higher for terminal valves (TTG = 5) than intermediate valves (TTG = 4; Mood's test of medians, $\chi^2 = 93.7$, df = 2, $p < 0.01$). By contrast, in gravel treatments, *Acanthochitona* valves (n = 11) show no statistical difference between terminal and intermediate valves ($\chi^2 = 0.24$, df = 2, $p > 0.10$). Following treatment, many valves (intermediate and terminal alike) of *Lepidochitona* were fragmented severely; a large proportion of valves (16%) were not recovered, *i.e.* they were broken into fragments smaller than the grain size of the sand matrix.

The *Tonicella* specimens provide the strongest evidence for sand and gravel treatments having different effects, with a clear pattern of increasing damage between the two levels of abrasion (Fig. 4). In both abrasion treatments, the intermediate valves of *Tonicella* showed the highest median level of damage, and were most susceptible to increasing levels of damage through the two separate treatments.

The intermediate valves provide the largest sample size and the most appropriate proxy to make interspecific comparisons. Among the three taxa studied, there is no significant difference in median damage score between the three samples of pre-treatment valves ($\chi^2 = 93.7$, df = 2, $p = 0.14$); after tumbling in gravel, there is a significant difference ($\chi^2 = 205.2$, df = 2, $p < 0.002$) and there are significant differences separating all three groups.

Table 1
Scoring system to assess total taphonomic grade of isolated chiton plates. The aspects are additive, with a maximum potential total score of 12 (a score of 2 in fragmentation makes other aspects inapplicable).

	Score		
Aspect	0	1	2
Fragmentation	Intact or whole	Fragment larger than 50% or original	Fragment less than 50% of original size
Posterior margin	Intact, or not applicable (fragment without posterior aspect)	Apex chipped	Apex eroded or polished
Apophyses	Intact, or not applicable (head valve or fragment)	Margins of apophyses chipped or broken	Margin of apophyses eroded or apophyses missing entirely
Insertion plates	Insertion plates pristine	Insertion teeth eroded	Insertion plates eroded to base, insertion teeth not protruding from margin
Tegmentum	Dorsal surface pristine	Dorsal layer thinned, sculpture eroded	Dorsal layer more than half eroded, patches missing
Ventral surface	Ventral surface pristine	Ventral surface sanded, muscle scars eroded	Ventral surface eroded and pitted
Further edge modification	No breaks, fresh, or fragment without clear shape	Edge erosion causing change in outline	

4. Discussion

Our model organisms, chitons, have a patchy fossil record (Puchalski et al., 2008; Smith, 1960). This, in combination with previous studies of their taphonomy (Puchalski and Johnson, 2009) suggests taphonomic processes may be impacting on the fossil record. Chiton disparity was clearly much greater in the Palaeozoic with forms including 17 plates instead of the usual 8 (Vendrasco et al., 2004) or with an armoured body lacking a foot (Sigwart and Sutton, 2007). There are many specimens and many species of these strange forms, which are important evidence in debates about molluscan evolution and disparity (Sutton et al., 2012); however, our present experimental framework is restricted to the morphologically conservative Neoloricata, the clade including all living chitons.

Most articulated fossil chitons, in the sense of those with the shell structure of modern chitons, are Palaeozoic in age, and total twelve taxa but several specimens are incompletely described (Table 3). Most of them are from the Carboniferous of Europe and USA. A specimen of *Glauphurochiton concinnus* from the Mazon Creek Formation (Carboniferous, Middle Pennsylvanian, Illinois) is an internal mould, but preserving the outline of the girdle and with a mould of the radula on the ventral side of the valve series (Baird et al., 1985: Fig. 6.3). This is the oldest known fossil of a neoloricate chiton with either girdle or radula preservation, others are only skeletal elements. There are four Mesozoic taxa with articulated specimens. *Chiton beskidensis* Plička, 1981 is preserved as an internal mould of the valve series but includes what is probably an impression of part of the girdle, from the Upper Cretaceous of Nydek, Czechoslovakia. There are only a handful of published records of articulated chitons from the Cenozoic. The best known, *Craspedochiton altavillensis*, from the Pliocene of Italy (Dell'Angelo et al., 2003), is preserved as valve series (*i.e.* lacking soft tissue preservation), in life position attached to a large pectinid shell. This is in almost identical position to the unnamed Eocene *Leptochiton* sp. from the La Mesta Formation of Antarctica, which is preserved on a brachiopod shell (Cabrera and Oliviero, 2011). An unidentified polyplacophoran was reported from the Eocene of Florida with the specimen on seagrass rather than a shell, though it has not been figured (and not seen by the present authors; Ivany et al., 1990). Two other articulated specimens of *Leptochiton* spp. are known from the Oligocene of Washington, USA (Squires and Goedert, 1995; Peckmann et al., 2002) and a third from the Miocene of Aichi Prefecture, Japan (as '*Lepidopleurus*' *morozakiensis* Itoigawa et al., 1977).

Despite a generally extensive fossil record, the number of examples of chitons preserved as articulated shell series is extremely limited. The more continuous, but depauperate, fossil record provided by isolated, even fragmentary, valves, is thus critical to reconstructing the evolutionary history of the group in any detail. There are thus significant wider implications as to whether (or not) the corresponding valves have similar preservation potential in different taxa.

The paucity of articulated shell series in the fossil record is perhaps somewhat surprising in the light of the results of the experiments herein, in particular, the resilience to tumbling exhibited by some of the previously decayed specimens of *Acanthochitona*. In these cases most, usually all, the valves were absent; in others the girdle armature remained intact but disassociated from the rest of the carcass. Neither phenomenon has been reported from the geological record.

The possibility of systematic taphonomic variation between taxa is indicated by the results of the study by Puchalski and Johnson (2009). Their (*op. cit.*) study of the taphonomy of two extant taxa was based on collections of valves recovered from different localities on San Juan Island, Washington, USA. The physical environment at each of the two localities is markedly different as is valve shape and size between the taxa; the variation Puchalski and Johnson (2009) observed is thus potentially the combination of both intrinsic (*i.e.* linked to the animals' biology; McNamara et al., 2012) and extrinsic (*i.e.* environmental) variables.

The experiments herein thus reveal that differences between taxa develop even if the number of variables is significantly reduced; for example, each taxon was subjected to identical transport in the tumbling experiments. Most notably, the experiments identify, for the first time, that the effects of decay alone are sufficient to impact differently on the preservation potential of valves among the taxa. Three variables are considered potentially significant: the size of specimens, the structure, including shape, of the valves and related to the latter, the systematic positions of the taxa. *Acanthochitona* is extremely robust, the other two taxa markedly less so. Given the significant interaction between size and length of time to disarticulation the larger mass of *Acanthochitona* apparently influenced this aspect of the decay tempo. Other variation in the data is not explained by this difference. For example, terminal valves disassociate more rapidly than do intermediate valves in *Acanthochitona* and *Tonicella*, than in *Lepidochitona*. The TTG scores overall are not statistically different among the three taxa after the decay experiments. A similar pattern emerges when the valves are considered separately. TTG scores after decay for the head and tail valves are the same for each taxon; the TTG values for the intermediate valves differ significantly from those for the other two types of valve in all three taxa.

Fossil assemblages of chiton valves almost invariably differ from the element ratio *in vivo*. There is, however, little consistency. Death assemblages collected from a modern beach had a significantly lower

Table 2
Number of specimens intact (fully articulated) during decay experiments.

	Day 0	Day 50	Day 120
Acanthochitona	53	41	32
Lepidochitona	44	4	0
Tonicella	26	3	0

rate of terminal (head plus tail) valves than expected (Puchalski and Johnson, 2009). In contrast in their study of a large single-species Paleocene assemblage of isolated plates of *Leptochiton faksensis* from Fakse, Denmark, Sigwart et al. (2007) found intermediate valves to be less, and tail valves more abundant, than expected. Larger assemblages show variation among species, but essentially all species deviate from expected valve ratios, including examples in which intermediate valves are less, and tail valves more abundant than expected, but also examples where the opposite is the case (Vendrasco et al., 2012: Fig. 22). Others are dominated by intermediate valves over and above the natural ratio of 1 : 3 :: terminal : intermediate valves (Dell'Angelo and Giusti, 1997, 2000; Puchalski and Johnson, 2009).

Such *a posteriori* studies of individual taxa hint at the potential complexity of the taphonomy of polycoplachorans. The preferred life habitat of chitons, high energy shores, is an environment with intrinsically poor preservation potential (Johnson, 1988; Hayes et al., 1993). The most common lithologies in which articulated remains are preserved, limestones and fine-grained siliciclastic sediments (Dell'Angelo et al., 2003; Table 3), implies that transportation, rather than burial *in situ*, routinely forms part of the taphonomic history of individual examples.

Transport in water currents is a recurrent cause of the loss of fidelity in multi-element skeletons; its effects have been researched extensively, primarily for terrestrial vertebrates in fluvial settings. The process is also important in marine environments; fossil crinoids, for example, exhibit a spectrum of preservational states spanning fully articulated, complete, individuals through to assemblages of isolated abraded ossicles sorted by size (*e.g.*, Gahn and Baumiller, 2004; Thomka et al., 2012). Both current and wave activity are potential agents; they induce sorting, plus abrasion and fragmentation as the skeletal elements interact with each other and any other load being transported. Sorting of

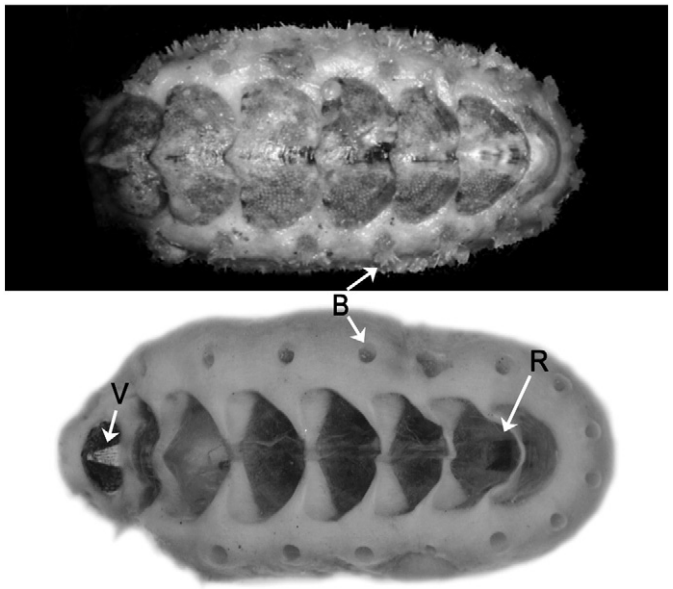

Fig. 3. *Acanthochitona crinita*: top, intact specimen; bottom, body muscle block of one specimen following 120 days' decay and 18 h in a rock tumbler. Note most valves are removed but the tail valve (V) still attached to the muscle (at left, posterior), and the radula (R) still *in situ*; small holes at the valve interstices are points where tufts of girdle bristles have detached.

elements will decrease the fidelity of the overall assemblage. Sorting also impacts indirectly on the fidelity with which individual single skeletal elements are preserved. It is difficult to make *a priori* predictions as to its effects. For example, elements transported farthest will experience a longer time interval in which their fidelity can be reduced by other biostratinomic processes. Conversely, those elements deposited first may be subjected longer to surface abrasion *in situ* from other particles carried in the flowing water. The most obvious possible cause of any biases in fossil chiton valve assemblages would be sorting during transport in response to variation in valve mass, density, size and shape (see for example, experiments by Vendrasco, 1999). Although simulating the effects of transport, our tumbling experiments do not separate isolated valves spatially (in effect generating an autochthonous or parautochthonus assemblage). The experiments indicated that deviations from the ratio between valve types *in vivo* can be generated *in situ*, *i.e.* by mechanisms other than sorting during transport. In such assemblages, the relative preservation potential of different valve types is thus likely to be more significant. This in turn will be controlled by differences in robustness (density is more likely to be important than absolute size or shape) and microstructure among the valves. Clearly, these parameters will vary between taxa, and potentially even between individuals (for example depending on ontogenetic stage) and even between parts of an individual skeleton. For example, tail valves are positioned to protect the posterior pericardium, and often substantially thicker than other valves (Sigwart per obs).

The TTG scores are statistically different between taxa after the tumbling experiments using gravel (Fig. 4). The scores are lowest for valves of *Acanthochitona*; there are, however, differences between the two similarly sized, smaller, taxa *Tonicella* and *Lepidochitona*, in which the valves are the same size. The effect of differences in substrate (gravel compared to 'sand') is, not unexpectedly, significant; for *Tonicella*, fragmentation is exacerbated in gravel (Fig. 4H) compared to sand (Fig. 4E). However, the experiments did not reproduce breakage patterns that have been observed in fossil valves. In the experiments, valves eroded around their edges or broke along the ventral perforation of the natural shell pores (aesthetes) in a diagonal line to the insertion slit on the lateral edge. In *Leptochiton faksensis*, a large number of the intermediate valves recovered were broken first along the midline ridge longitudinally, then fragmented further (Sigwart et al., 2007).

In the most dramatic example of resistance to disarticulation in this study, some *Acanthochitona crinita* specimens remained articulated with foot and girdle muscle block intact after prolonged decay, but after simulated transportation the whole spicular cuticle (perinotum) sloughed off as an intact unit and this tissue was recovered from the matrix during sorting. There is only one reliable example of a fossil neoloricate chiton with any putative girdle preservation (Baird et al., 1985). Interestingly, living species with dorsal girdle spicules in life have been recovered in death assemblages after transportation with their girdle elements totally absent (Dell'Angelo et al., 2004). The converse of this point is that there are no recognised fossils of isolated perinota nor radulae despite this empirical evidence for their potential for fossilisation alongside disarticulated valves.

The taphonomic variation observed among the taxa in these experiments does not correspond precisely to, but is broadly sympathetic with, their phylogeny. The taxonomic classification of individual taxa within the Chitonina and Acanthochitonina and their organisation into phylogenetic clades is still the subject of extensive debate (Okusu et al., 2003; Sirenko, 2006). Nonetheless as its stands at present, there is a strong correlation of apparent resistance to decay and the recorded fossil diversity of each suborder. Both suborders contain 35 valid genera each (Sirenko, 2006), but of that total across living and extinct taxa, the fossil record preserves only two genera of Chitonina but seven genera in Acanthochitonina. Intriguingly, and perhaps significantly, this general pattern may be indicative of differential preservation potential.

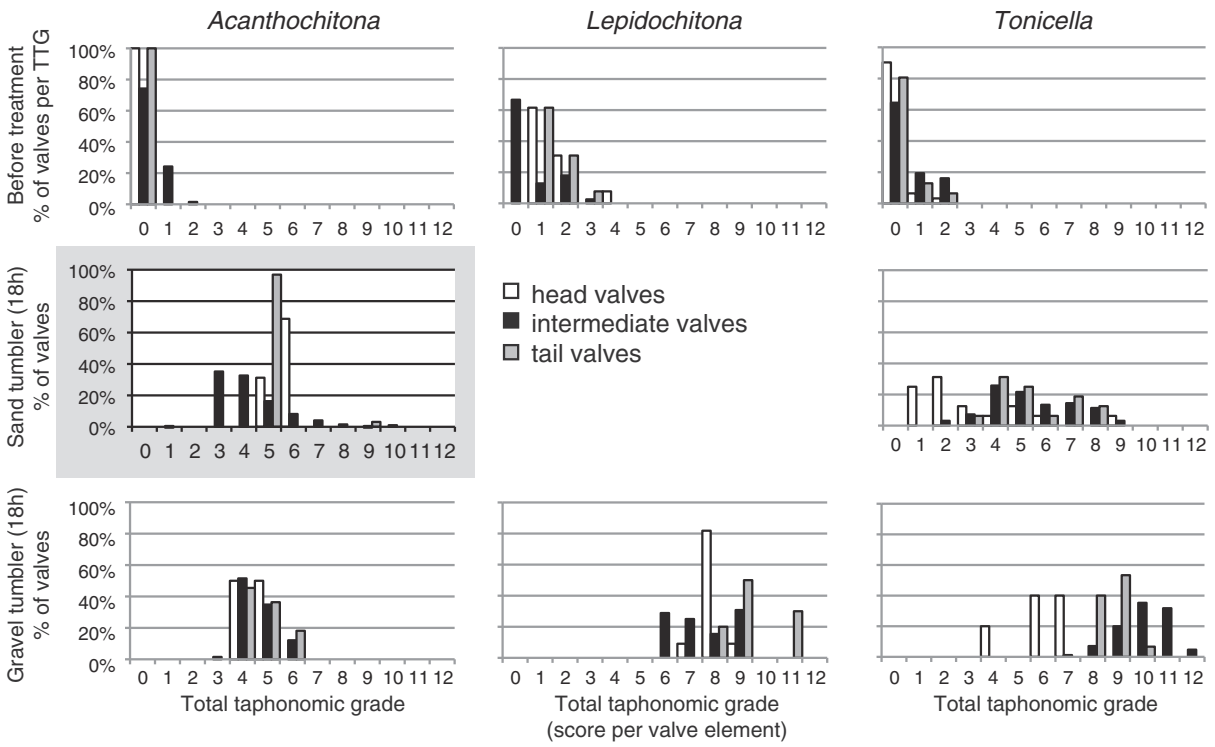

Fig. 4. Taphonomic score per valve for each of eight treatments in abrasion experiments. Treatment groups were exposed to 18 h in a rock tumbler with coarse sand, or gravel (treatments were not additive).

5. Conclusions

The taphonomic history of a fossil multi-element skeleton (whether vertebrate or invertebrate) is almost invariably complex, and the result of a series of different independent biostratinomic processes that acted in complex positive and negative feedback loops. There has been an extensive history of actualistic research including both observational data, and controlled experiments undertaken in both natural and laboratory settings. These recognise the importance of key variables such as the extent and timing of transport relative to how far decay of a carcass has progressed, and what biomineralised and non-biomineralised tissues were present at the outset and their preservational potential. As a result, generalised taphonomic models can now be erected for many types of skeleton. Implicit in these models is the assumption that for a specific set of environmental conditions the taphonomy of closely related taxa will be near-identical.

Our experiments revealed fundamental differences in the preservation potential of closely related chiton taxa. These differences occur between different polyplacophoran suborders, but, more surprisingly, between different, morphologically similar, taxa from the same clade. The cause is subtle variations in intrinsic factors (*i.e.* those linked to aspects of the biology of the animals), but it is impossible to isolate a single variable that is responsible. Decay alone is sufficient to exacerbate differences in preservation potential among taxa; some, but not all, of the variation that results is due to specimen size and will thus vary intra-specifically (*e.g.* between ontogenetic stages) as well as inter-specifically. The cause or causes of other variation among taxa remain unknown. Physical

Table 3
The record of complete articulated fossil neoloricate chitons from the Palaeozoic and Mesozoic.

Taxon	Age	Notes and references
Plasiochiton curiosus Hoare, 2000	Devonian of Pennsylvania	
Unidentified Neoloricata	Devonian of Pennsylvania, USA	Petzold et al. (1992)
Acutichiton allynsmithi Hoare et al., 1983	Carboniferous (Pennsylvanian) of Oklahoma	Hoare and Mapes (1989)
Glaphurochiton concinnus (Richardson, 1956)	Carboniferous of Mazon Creek, Illinois, USA	Known from a large number of specimens, impressions of dorsal and ventral side of valve series and many with impressions of the radula: *e.g.* Baird et al. (1985); Hoare and Mapes (1986); Yochelson and Richardson (1979)
Glaphurochiton carbonarius (Stevens, 1858)	Carboniferous of the central USA	Known from multiple incomplete specimens, dorsal impression: Hoare and Sturgeon (1972); Smith and Hoare (1987)
Rhombichiton laterodepressus (Bergenhayn, 1945)	Carboniferous of the Czech Republic	Lang et al. (1982)
Unidentified Neoloricata *cf. Pterochiton thomondiensis* (Baily, 1859)	Carboniferous of Ireland	Sigwart (2007)
Pterochiton kliazmensis Barskov & Morozov, 1996	Carboniferous of the Moscow Region, Russia	Two specimens
Permochiton australianus Iredale & Hull, 1926	Permian of Bundanoon, New South Wales, Australia	
Trachypleura triadomarchica Jaekel, 1900	Middle Triassic Muschelkalk, Rüdersdorf, Germany	
Ischnochiton marloffsteinensis Fiedel & Keupp, 1988	Jurassic (Middle Liassic) of Marloffstein near Erlangen, S. Germany	Two specimens

reworking of specimens *in situ*, for example within bedload, will alter the ratio of different valve types from that found *in vivo*; certain valve types are fragmented selectively. The negative effect of this on the fidelity of preservation of an assemblage of valves will potentially mimic the effects of sorting induced by transport. On the evidence currently available, it is considered likely that variation in the preservation potential of different taxa has impacted on the quality of the fossil record of chiton valves; it is, however, not possible to resolve how it has done so. The effects of extrinsic factors linked to variation in environmental context will be superimposed on this. Deciphering the effects of each in fossil assemblages will be challenging. More generally, this study reveals unexpectedly large variation in preservation potential at the alpha-taxon level; if repeated in other clades, the implications for estimating palaeodiversity are alarming.

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