

# UC Davis

## UC Davis Previously Published Works

### Title

Why do chitons curl into a ball?

### Permalink

<https://escholarship.org/uc/item/9k16n9kq>

### Journal

Biology Letters, 15(10)

### ISSN

1744-9561

### Authors

Sigwart, Julia D  
Vermeij, Geerat J  
Hoyer, Peter

### Publication Date

2019-10-01

### DOI

10.1098/rsbl.2019.0429

Peer reviewed

## Research



**Cite this article:** Sigwart JD, Vermeij GJ, Hoyer P. 2019 Why do chitons curl into a ball? *Biol. Lett.* **15**: 20190429.  
<http://dx.doi.org/10.1098/rsbl.2019.0429>

Received: 6 June 2019

Accepted: 6 September 2019

### Subject Areas:

behaviour, evolution, palaeontology, taxonomy and systematics

### Keywords:

trade-off, functional morphology, conglobation

### Author for correspondence:

Julia D. Sigwart

e-mail: [j.sigwart@qub.ac.uk](mailto:j.sigwart@qub.ac.uk)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4682516>.

# Why do chitons curl into a ball?

Julia D. Sigwart<sup>1</sup>, Geerat J. Vermeij<sup>2</sup> and Peter Hoyer<sup>1</sup>

<sup>1</sup>Marine Laboratory, Queen's University Belfast, 12–13 The Strand, Portaferry, Northern Ireland BT22 1PF, UK

<sup>2</sup>Department of Earth and Planetary Science, University of California, Davis, CA 95616, USA

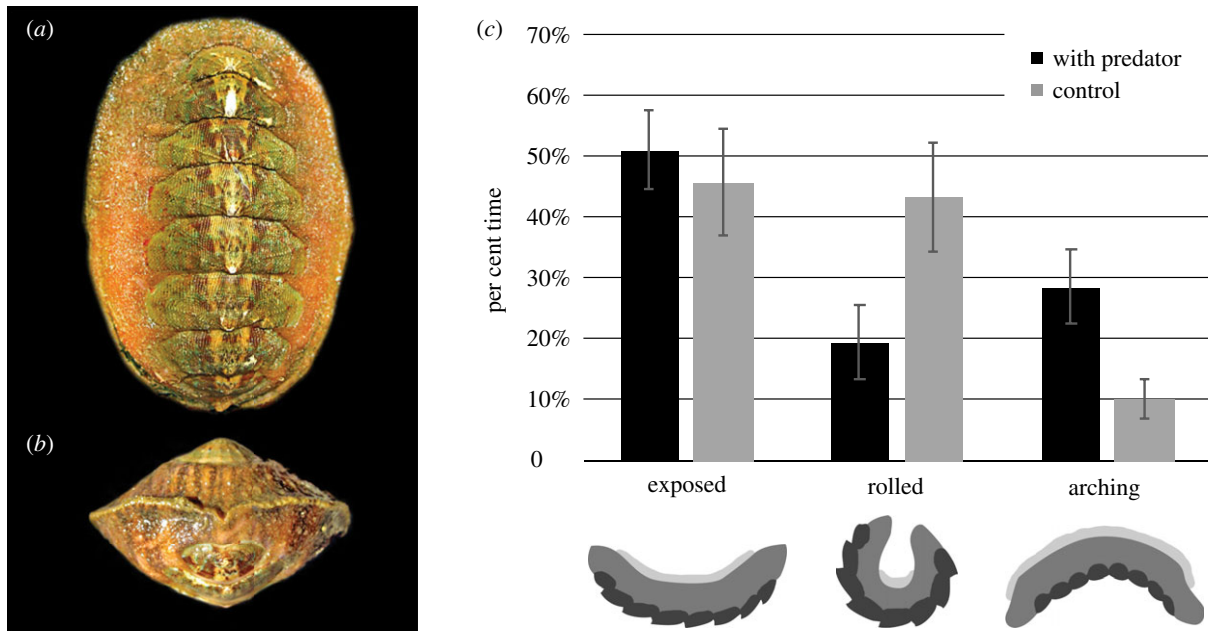
JDS, 0000-0002-3005-6246; GJV, 0000-0002-6450-5687

Many animals with external armour, such as hedgehogs, isopods and trilobites, curl into a protective ball when disturbed. However, in situations where predators would engulf an exposed animal whole, regardless of position, conglobation may provide limited added defence and the benefits were previously unclear. We show that polyplacophoran molluscs (chitons) are three times less likely to spend time curled into a ball in the presence of a predator. When the cue of a potential predator is present, animals instead spend significantly more time in active, high risk, high reward behaviours such as arching, balancing on the head and tail ends of their girdle and pushing the soft foot up into an exposed position. Arching increases vulnerability, but also can increase the likelihood of rapidly encountering new substratum that would allow the animal to right itself. In some other animals, the ability to roll into a ball is associated with rolling away from danger. Curling into a ball would improve mobility, to be rolled on to a safer position, but reattachment is the higher priority for chitons in the face of danger.

## 1. Introduction

The ability of armoured animals to roll into a defensive ball is known from many disparate groups [1]. This ability, called conglobation or enrolment, is known from mammals such as pangolins (Manidae) and hedgehogs (Tenrecinae), and echidna (Tachyglossidae), arthropods including some isopods, trilobites, pill millipedes and larvae of other groups [2], and, among molluscs, the multi-shelled chitons [3]. These animals have the flexibility to curve their entire body and touch the anterior to the posterior end, such that the hard dorsal elements cover the whole outer surface and the softer, ventral parts are protected inside the ball. Species with this ability span a broad variety of ecological niches and both terrestrial and aquatic environments; while the ability to display protective armour in every direction is doubtless beneficial to defence, the ability to become more spherical may have additional and more relevant implications in terms of functional morphology.

Chitons are unusual among ball-forming invertebrate animals in that they entirely lack mechanisms that lock the body in the enrolled position. By contrast, many trilobites, oniscoid isopods and millipedes have intricate locking (or coaptive) devices that are modifications of the exoskeleton [4–10]. Many of these ball-forming taxa with coaptive devices protect legs, antennae and reproductive structures, and at least some develop spines that protrude outward when the animal is in the enrolled position. Spines provide an additional defence against gape-limited predators, and in aquatic contexts may affect hydrodynamic dispersal [1,2]. Conglobation with coaptive devices is common among living terrestrial arthropods, but is essentially unknown in living adults in the sea, perhaps implying that passive defence in the form of coaptive rolling up into a ball is no longer as effective as it once was during the Paleozoic heyday of the trilobites [1].



**Figure 1.** (a) A chiton in normal position (dorsal view, *Mopalia swanni*, a species not used in this experiment but shown for illustrative purposes); (b) the same individual in (a), rolled into a ball, anterior is at top in both images; (c) time spent by experimental animals in different positions in the presence or absence of a predator cue; 'exposed' here combines any position not tightly curled (rolled), or actively lifting off the substratum (arching). Values are mean ( $\pm$ s.e.) per cent time among 12 trials in each treatment group. (Online version in colour.)

A chiton attached to the substratum by its soft foot is well defended by its dorsal scleritome and will respond to disturbance by holding fast to the surface [11]. The chiton scleritome and its overlapping plates have been analysed as an armour that optimizes a trade-off between defence and mobility [12]. When rolled into a ball, the valves and girdle together provide a complete armour, although much of the 'ball' is muscular tissue covered only by a thin cuticle (figure 1b). The potential predators in modern shallow marine settings, including fish, seastars, birds and crabs, are likely to consume an unattached chiton whole. Anecdotal speculation has suggested the primary advantage of curling into a ball could instead be mobility, to allow chitons to roll to a better position [3]. This implies that enrolment is not a passive defence against attack, but perhaps a strategy to improve circumstances.

Here, we applied an experimental approach to test the response of dislodged chitons with and without exposure to the threat of potential predation. If the tendency of armoured marine animals to roll into a ball is a passive defensive behaviour, then we would expect chitons to spend relatively more time curled up in the presence of a predator.

## 2. Material and methods

Live chitons were collected from the intertidal at Pinnacle Gulch, Bodega Bay, California and held in aquaria on flow-through seawater at the University of California, Davis, Bodega Marine Laboratory. Chitons used in these experiments included three species: *Mopalia hindsii* (Sowerby in Reeve, 1847) ( $n = 17$ ), *M. muscosa* (Gould, 1846) ( $n = 4$ ) and *Lepidozoma mertensii* (Middendorff, 1847) ( $n = 3$ ). These species co-occur in the rocky intertidal in Northern California and are broadly distributed on the Pacific coast of North America. *Pisaster ochraceus* (Brandt, 1835) was selected to produce the predator cue as it is a co-occurring predator known to consume chitons [13].

In each trial, a single randomly selected chiton was placed up-side-down in the centre of the experimental aquarium (4 l). Seawater was siphoned continuously from one of two sources, selected by a coin flip: the 40 l holding aquarium with captive chitons (control condition), or a separate 20 l aquarium holding a single *Pisaster* (predator treatment). These two source aquaria were fed continuously with flow-through seawater. Time lapse images were taken from one side of the experimental aquarium with a GoPro Hero5 camera every 30 s for a 2 h period. For analysis, the time lapse series were classified frame by frame into five *a priori* position categories: curled into a ball, half curled, curled slightly, flat or arching. Tendencies in position were analysed as the proportion of time (percentage of valid frames). We excluded frames in portions of 10 out of 24 experiments where frames could not be scored because of obstruction (condensation or splashing), or early termination of the experiment if the animal made contact with the wall and righted itself. Two to three trials were conducted per day (at least one control, and one treatment) over an 11-day period. Animals were not re-used. To compare the occurrence of different behaviours, we calculated the odds ratio of each behaviour's frequency with and without the predator cue. We also used a Dirichlet Regression implemented in R (package DirichReg [14]) to compare the distribution of time spent arching, in a ball, or otherwise, with and without the predator cue. Because the assumptions of the Dirichlet regression require proportional behaviours to sum to 1 for each individual and do not allow for zero values [15], we substituted a small term (0.001) and calculated proportions of time among frames scored for each individual.

## 3. Results

Chitons left up-side-down on a flat surface were never able to right themselves, except by manoeuvring close enough to the wall to contact and attach to the vertical surface (electronic supplementary material, Video [16]). This occurred four times in 24 trials, three of which were in the presence of the

predator cue; the control animal that made contact with the side did so only after 109 min of a 120-min trial, while animals in the predator treatment that manoeuvred themselves to the side did so relatively much faster, after 43–87 min (electronic supplementary material, table S1 [16]).

Left in a prone orientation, chitons adopted the enrolment position around 30% of the time overall; however, there was a strong positive association between the predator cue and time spent arching. The odds of an individual spending time in a ball are 2.85 times higher without a predator cue (95% confidence interval of the odds ratio, 2.52–3.23 times higher). In the presence of a predator cue, the odds of an individual chiton spending time arching are 2.93 times higher (95% CI, 2.51–3.41). We considered arching, curled in a ball and exposed (all other categories) as response variables in the Dirichlet regression; the predator cue was a strong predictor of arching behaviour ( $p = 0.0006$ ). Although chitons also spent less time curled into a ball in the presence of the predator cue (figure 1), time curled into a ball or other exposed positions was not predicted by the treatment group ( $p > 0.3$  for both categories).

The sample sizes for *L. mertensii* ( $n = 3$ ) and *M. muscosa* ( $n = 4$ ) were too small to allow robust comparison among species, although these trends were apparently broadly consistent in all three species used. We noted that *L. mertensii* spent more time overall curled into a ball, compared to the total group, and spent considerably more time rolled in the control condition (63% of frames in two trials, compared to an overall average of 44% per trial) than in the presence of a predator cue (25% of frames in one trial for *L. mertensii* compared to an overall average of 20%) (electronic supplementary material, table S1 [16]).

#### 4. Discussion

In the presence of the chemical cue of a distant predator, the urgent pressure to reattach to the substratum prompted more exposed positions in chitons, but that would (and in a few cases did) enable the animal to reattach to the substratum and regain normal posture. Chitons are not able to right themselves on an isolated, flat surface such as the bottom of an experimental aquarium. But extended flat surfaces and still water are unusual in the context of rocky marine benthos. The articulating armour of chitons is flexible [12], and the inability of chitons to right themselves is generally limited to environments with flat surfaces and no current. In normal circumstances, on a rugose surface in a dynamic environment with moving water, a rolled-up chiton can expect to be transported to a new position very rapidly [3], and an arching chiton might also be buffeted more rapidly toward a potential safe haven. Although chitons are often considered ‘primitive’, there is mounting evidence for neurological complexity [17] and this behaviour suggests a certain level of strategic response.

The behaviour associated with conglobation has been studied most closely in arthropods, especially the terrestrial pill bug *Armadillidium*, which can roll into a completely sealed ball. In experimental exposure, isopods were marginally more likely to be attacked when extended rather than when rolled into a ball, and the animals do use conglobation as an active response to attack by potential predators [18]. Likewise, a dislodged chiton, if physically prodded, would

also roll up rather than arch and leave the foot exposed. Conglobation in isopods has secondary advantages in that it may help prevent desiccation as well as predation [19], which would only be relevant for chitons in the rare event of dislodgement when exposed to air at a low tide. There are certainly protective benefits to curling into a ball, but the ball configuration in chitons and other animals is entirely incompatible with normal feeding and locomotion.

Some arthropods lack coaptive devices that lock the ball configuration, including a few terrestrial caterpillars and spiders. These animals roll into a wheel-like configuration and use powerful appendages to propel themselves away from danger [20,21]. This situation, and the observation that the ability to roll into a ball is associated with rolling away from a disadvantageous situation rather than with direct or even indirect contact with a predator, is mirrored in our observations of chitons. Whether energy-intensive as in these terrestrial arthropods, or more passive, as in chitons, rolling away evidently does not require coaptive devices and is more a temporary measure.

In chitons, the action of enrolment is controlled by the diagonal dorsoventral muscles that connect the eight shell valves to the ventral foot. All chitons are able to use anterior–posterior flexing, including species with reduced or internal shells (e.g. *Cryptochiton stelleri* (Middendorf, 1847)). This muscular arrangement and additional longitudinal muscles also cause the typical curled posture in aplacophoran molluscs, which are anatomically and phylogenetically related [22]. This is in contrast to the coaptive interlocking exoskeletal elements involved in the conglobation postures of arthropods [2]. Although the shell-less condition in aplacophorans is derived, curling does not require an exoskeleton and does not require physical coaptive devices.

The ability of animals to transform into a defended sphere is a solid defence with multiple benefits [23]; however, the results here suggest that anti-predatory defence is not the principal merit for chitons. Chitons demonstrate behavioural decision-making when faced with the threat of a potential predator, to enable it to right itself and regain a safe foothold. By contrast, some other species with coaptive mechanisms resist attack by a predator through special morphological features that strengthen the exoskeleton and make it difficult to manipulate for a gape-limited or skeleton-breaking predator [1]. The rolled-up configuration in chitons and other animals without coaptive devices is superficially convergent, but the similarity in these different forms of rolling up may hide fundamentally different approaches to defence.

**Data accessibility.** The datasets generated during and/or analysed during the current study are available on the Dryad Digital Repository at: <https://doi.org/10.5061/dryad.3s31f7n> [16].

**Authors' contributions.** J.D.S. and P.H. conducted the experiments and analysed the data; J.D.S. and G.J.V. interpreted the data and wrote the manuscript. All authors contributed to writing the article, approved the final version of the manuscript, and agreed to be held accountable for the content of this.

**Competing interests.** We declare we have no competing interests.

**Funding.** This work was funded by the European Union's Horizon 2020 Research and Innovation Programme (grant agreement no. H2020-MSCA-IF-2014-655661 to J.D.S.) and by Unitas Malacologica (student research award to P.H.).

**Acknowledgements.** The authors thank the director and staff of the UC Davis Bodega Marine Laboratory, in particular Kitty Brown, Carol Vines, Jackie Sones and Eric Sanford for support in the laboratory and advice on specimen collection.

1. Vermeij GJ. 1987 *Evolution and escalation: an ecological history of life*. Princeton, NJ: Princeton University Press.
2. Haug C, Haug JT. 2014 Defensive enrolment in mantis shrimp larvae (Malacostraca: Stomatopoda). *Contrib. Zool.* **83**, 185–194. (doi:10.1163/18759866-08303003)
3. Eernisse DJ, Clark RN, Draeger A. 2007 Polyplacophora. In *Light and smith manual: intertidal invertebrates from central California to Oregon*, 4th edition (ed. JT Carlton), pp. 701–713. Berkeley, CA: University of California Press.
4. Clarkson ENK, Henry J-L. 1973 Structure coaptatif et enroulement chez quelques trilobites Ordoviensiens et Siluriens. *Lethaia* **6**, 105–132. (doi:10.1111/j.1502-3931.1973.tb01186.x)
5. Esteve J, Gutiérrez-Marco JC, Rubio P, Rábano I. 2018 Evolution of trilobite enrolment during the Great Ordovician Biodiversification Event: insights from kinematic modeling. *Lethaia* **51**, 207–217. (doi:10.1111/let.12242)
6. Manton SM. 1954 The evolution of arthropodan locomotory mechanisms. Part 4. The structure, habits and evolution of the Diplopoda. *J. Linn. Soc. (Zool.)* **42**, 299–368. (doi:10.1111/j.1096-3642.1954.tb02211.x)
7. Vandel A. 1943 Essai sur l'origine, l'évolution et la classification des Oniscoidea (isopodes terrestres). *Bull. Biol. France Belg. Suppl.* **30**, 1–136.
8. Vandel A. 1948 Les isopodes volvationnels exoantennés et la genèse de leurs coaptations. *Bull. Biol. France Belg.* **82**, 388–428.
9. Vandel A. 1954 L'évolution considérée comme phénomène de développement. *Bull. Soc. Zool. France* **79**, 341–356.
10. Vandel A. 1959 Nouvelles recherches sur les isopodes volvationnels exoantennés et la genèse de leurs coaptations. *Bull. Biol. France Belg.* **93**, 121–139.
11. Speiser DI, Eernisse DJ, Johnson S. 2011 A chiton uses aragonite lenses to form images. *Curr. Biol.* **21**, 665–670. (doi:10.1016/j.cub.2011.03.033)
12. Connors MJ, Ehrlich H, Hog M, Godeffroy C, Araya S, Kallai I, Gazit D, Boyce M, Ortiz C. 2012 Three-dimensional structure of the shell plate assembly of the chiton *Tonicella marmorea* and its biomechanical consequences. *J. Struct. Biol.* **177**, 314–328. (doi:10.1016/j.jsb.2011.12.019)
13. Feder HM. 1959 The food of the starfish, *Pisaster ochraceus*, along the California coast. *Ecology* **40**, 721–724. (doi:10.2307/1929828)
14. Maier MJ. 2019 DirichletReg: Dirichlet Regression in R. R package version 3.1. See <https://cran.r-project.org/web/packages/DirichletReg>.
15. Douma JC, Weedon JT. 2019 Analyzing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. *Methods Ecol. Evol.* **10**, 1412–1430. (doi:10.1111/2041-210X.13234)
16. Sigwart JD, Vermeij GJ, Hoyer P. 2019 Data from: Why do chitons curl in to a ball? Dryad Digital Repository. (doi:10.5061/dryad.3s31f7n)
17. Sumner-Rooney L, Sigwart JD. 2018 Do chitons have a brain? New evidence for diversity and complexity in the polyplacophoran central nervous system. *J. Morphol.* **279**, 936–949. (doi:10.1002/jmor.20823)
18. Castillo ME, Kight SL. 2005 Response of terrestrial isopods, *Armadillidium vulgare* and *Porcellio laevis* (Isopoda: Oniscoidea) to the ant *Tetramorium caespitum*: morphology, behavior and reproductive success. *Invert. Reprod. Dev.* **47**, 183–190. (doi:10.1080/07924259.2005.9652158)
19. Smigel JT, Gibbs AG. 2008 Conglobation in the pill bug, *Armadillidium vulgare*, as a water conservation mechanism. *J. Insect Sci* **8**, 1–9. (doi:10.1673/031.008.4401)
20. Brackenbury J. 1999 Fast locomotion in caterpillars. *J. Insect. Physiol.* **45**, 525–533. (doi:10.1016/S0022-1910(98)00157-7)
21. Jäger P. 2014 *Cebrennus* Simon, 1880 (Araneae: Sparassidae): a revisionary up-date with the description of four new species and an updated identification key for all species. *Zootaxa* **3790**, 339–356. (doi:10.11646/zootaxa.3790.2.4)
22. Sigwart JD, Sutton MD. 2007 Deep molluscan phylogeny: synthesis of palaeontological and neontological data. *Proc. R. Soc. B* **274**, 2413–2419. (doi:10.1098/rspb.2007.0701)
23. Tenaza RR. 1975 Pangolins rolling away from predation risks. *J. Mammal.* **56**, 257. (doi:10.2307/1379632)