Mechanisms, ultrastructure and behavioral flashing in *Ctenoides ales*: ‘disco clams’

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Dynamic visual displays throughout the animal kingdom are often bright and dramatic. They can be produced through a variety of photic processes including bioluminescence, the use of chromatophores, and structural coloration. Here I describe the mechanism underlying the striking display of the ‘disco’ or ‘electric’ clam *Ctenoides ales* (Limidae), the only species of bivalve known to have a behaviorally mediated photic display and whose flashing is so vivid that it has been repeatedly confused for bioluminescence. The flashing display occurs on the mantle lip, where electron microscopy revealed two distinct tissue sides; one highly scattering side containing dense aggregations of spheres composed of silica, and one side containing a strongly absorbing pigment. High-speed video confirmed that the two sides of the mantle lip act in concert to create a vivid broadband reflectance that rapidly alternates with strong absorption in the blue region of the spectrum. Optical modeling suggests that the diameter of the spheres, but not their packing density, is nearly optimal for scattering visible light. This simple mechanism produces a remarkable optical effect that may function as a signal.

The photonics of structural coloration are of particular interest in biomimetics, where nanostructure influences countless technologies derived from natural design. The use of structural coloration and scattering by various taxa in the ocean’s euphotic zone is especially interesting as long wavelengths are absorbed rapidly with depth, light attenuates with suspended solids, and available light varies between habitats. *Ctenoides ales* lives as deep as 50 m underwater and inside small crevices, where ambient light is dim and wavelength-restricted. Despite this, the species evolved a reflective mantle edge that emits vivid light, resulting in the common name ‘disco’ or ‘electric’ clam. Preliminary research in spectrometry (Fig. 2), high speed video, electron microscopy (Fig. 3), elemental analysis (Fig. 4) and particle modeling (Fig. 5) has deduced how the photic display is produced; tissue composed of silica nanospheres is rapidly exposed then concealed to create a dynamic broadband reflectance that is optimized for a light-restricted environment. However, the behavioral purpose of the flashing display remains unknown. Three hypotheses are being tested: that the display acts as: (i) a signal facilitating the recruitment of conspecifics, (ii) a phototaxic prey lure, and/or (iii) a deimatic anti-predator display. Research interests center around (i) the proximate mechanisms that produce the display (how) and (ii) the ultimate behavioral purpose of the flashing display (why).

(Continued on page 3)
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Abdopus aculeatus brooding eggs. Photo: R. Caldwell.
Behavioral observations and ecological analysis in 2013 provided a solid context within which to conduct follow-up experiments in the field in 2014. Behavioral observations showed that organisms lived in clumped situations, which may result from conspecific recruitment. Predatory encounters were never observed, although valves with obvious whelk or octopus predation were common. The study sites, population densities, operational setup plans and data analyses were cemented after exploratory dives last summer. Additionally, the 2013 summer field season resulted in several new collaborations, including stable isotope analysis of silica origins and optical research into the clams’ visual abilities.

In addition to the field work on behavior, a collaboration investigating the optical capabilities of the species has been established with researchers at the University of Wisconsin and the University of Maryland. Transmission electron microscopical analysis of the eyes, and molecular testing for the expression of opsins will be conducted. The visual abilities of the clam are important when considering potential communication with conspecifics.

Optical biomimetics focuses on structurally-based coloration produced by photonic nanostructures. Research in this area has broad applications including anti-reflective lenses, solar panel surfacing, polarization and angular anti-counterfeiting devices, paints, coatings, tuneable lasers and cell culturing for nanostructures. Behavioral uses of structural colours are diverse, including species and sex recognition, mate choice, ornamentation, aposematic coloration, and orientation, schooling and flocking behavior. Structural colours have also been proposed to result in non-communicative functions, including thermoregulation, friction reduction in burrowing organisms, water repellency, structural strengthening, photoprotection and vision enhancement. There is a wide diversity of organisnal light use in the euphotic zone of the ocean, ranging from circularly polarized light signals in stomatopods, which led to the commercial development of quarter-wave retarder plates, to the use of reflective proteins by *Tridacna* giant clams to optimize the photosynthesis of symbiotic algae.

Expected outcomes of this research include insight into the behavioral function of the photic display as well as comprehension of the molecular and evolutionary position and radiation of *C. ales*.
Fig. 4. Energy Dispersive X-Ray Spectroscopy (EDS). EDS elemental analysis shows the composition of the reflective spheres. Blue (Silicon) and red (Oxygen) combine to form the purple, amorphous silica spheres (SiO$_2$), while green (carbon) composes the underlying tissue. Both the outer shells (a) and the cores (b) of the spheres are composed of silica (silicon 1.70-1.80 keV, oxygen 0.40-0.60 keV).

This research involves a unique type of reflective structure that operates in conditions atypical of traditional reflectance, and it has the potential to advance the field in low-light and restricted wavelength reflectance potential. The widespread occurrence of structural colours, coupled with their diverse functionality, make this an important research area, contributing insight into biological function, physical optics, and biomimetic technological applications for society. With a broad array of biological and engineering applications and a study organism popular in aquaria and with associated conservation implications, this research appears to be of great public interest.

Acknowledgments
The authors thank the Lizard Island Research Station, J. Auchterlonie, R. Templin and J. Drennan at the Center for Microscopy and Microanalysis at the University of Queensland, M. Zelman of Surface Optics Corporation (San Diego, CA, USA), D. Elias for High Speed Video assistance and R. Zalpuri of the Electron Microscopy Lab, both of the University of California Berkeley. This work was supported by the University of California Museum of Paleontology Palmer Fund, the NSF East Asia and Pacific Summer Institutes (EAPSI) Award, the Australian Academy of Science, the Professional Association of Diving International (PADI) Foundation Award, the Animal Behavior Society Student Research Grant, the Conchologists of America Grant and the Lerner Gray Memorial Fund from the American Museum of Natural History.

Field work in Indonesia and Australia was conducted during the summer of 2013. Work in Australia was supported by the NSF EAPSI in collaboration with the Australian Academy of Science and the Australian Museum. Above is a description of lab and field work results obtained from my funding.

Reference

Fig. 5. The effect of sphere diameter and density on the total amount of 400 nm, 480 nm, 550 nm and 650 nm Angle-Weighted Scattered Light from a Dense Collection of Spheres (arbitrary units). The mean values (dots) and error bars show the range of the parameters found in C. ales tissue at four different wavelengths. The size of the spheres found in C. ales is close to optimal for maximal light scattering at 400 nm and 480 nm. Units are normalized to one for the maximum angle weighted scattering for 400 nm light.
Wanted: Australian *Penion* (Siphon Whelks)

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We appeal to members of the Malacological Society in Australia for help in sampling the Australian *Penion* species, *P. maximus* (Tyron, 1881) and *P. mandarinus* (Duclos, 1831).

The genus *Penion* (‘siphon whelks’) has a convoluted history of synonymy and heavy taxonomic revision (Ponder 1973, Powell 1947). Populations in Australia have been classified in *Megalotractus*, *Austrosipho* and *Berylma*, while New Zealand populations have previously been assigned to *Siphonalia*, *Veronella*, *Fusus*, and *Larysiphon*. At present, therefore, the current taxonomy of two extant species in Australia and seven in New Zealand within a single genus seems satisfyingly resolved. However, the relationship between described species is still not understood and there has been no attempt to test and analyse the group comprehensively using molecular data.

*Penion* is of interest for several reasons. First, populations are widely distributed (Dell 1956, Ponder 1973), although all of the species have direct development. Species occur throughout New Zealand from the far northern Three Kings Islands to the far southern Antipodes Islands, and individuals can be found from low tide level to at least two kilometres deep off the continental shelf. Populations also occur off south-eastern Australia, from Gulf St Vincent to southern Queensland, and surrounding Tasmania.

Species are large with an average shell length of 18 cm and width of 7 cm (the largest species can attain 26 × 11 cm) (Powell 1979). Specimens exhibit a variety of shell characteristics such as prominent axial ribs, shoulder angulations, spire nodules, heavy banding and ridging, and long siphonal canals (Powell 1929, Powell 1979). Intraspecific and interspecific morphological variation is very high. Little is known about the group’s ecology but they are benthic, carnivorous predator-scavengers that likely play a significant role alongside apex mollusc predators such as *Alatihoe* species, and sea stars.

Of special significance is that the group has a good fossil record (Powell 1947, Beu and Maxwell 1990). In New Zealand 19 species have been described ranging as far back as 66 million years, while in Australia a further three or four species are documented, dating back as far as 27 million years. Further New Zealand species are yet to be described from the Miocene. The fossil record in New Zealand is very good and specimens of some species are locally abundant. Crucially existing collections of fossils allow for comparison with extant populations and accurate geological dating is available. Preservation of fossils is often excellent.

We are conducting integrated phylogenetics to improve our understanding of *Penion* systematics, and to use the evolutionary history of the group to test evolutionary hypotheses related to morphological change, divergence and speciation. Our primary aims are to define the limits of variation of the Recent species based on traditional morphological traits using (1) molecular data and (2) morphometric analyses, and (3) to reconcile relationships between extant and fossil taxa using integrated phylogenetics. Current taxonomy does not bridge fossil evidence with present data, and hypotheses regarding the ancestry of New Zealand and Australian taxa require investigation.

We appeal to members of the Malacological Society in Australia for help in sampling the Australian *Penion* species, *P. maximus* (Tyron, 1881) and *P. mandarinus* (Duclos, 1831). In particular, we require tissue samples of *P. maximus* and *P. mandarinus*. Since we are based in New Zealand, the main hindrance to sampling in Australia are the necessary government permits, and we are hopeful that malacologists based in Australia may be able to collect samples for us under their own permits. Given the distribution of *Penion*, clearly an Australasian approach is warranted.

All contributors will be duly acknowledged. None of the species are endangered. Tissue samples ideally should be 1–2 cm³ foot or columellar muscle clippings fixed in 95% ethanol. If collectors do not have access to high strength ethanol, specimens should immediately be deep-frozen and then forwarded to a nearby museum such as the Australian Museum or Museum Victoria. Please contact the email address above for further details. Shells are needed for our morphometric analysis, and we plan a visit in 2015 to conduct photography.

Final sequence data will be uploaded to GenBank and remaining tissue will be available for future research at Museum of New Zealand Te Papa Tongarewa, Wellington.

Penion maximus. Photo: F. Vaux.
Characterising Australian Molluscs Alive

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Observation and characterisation of living molluscs assumes new importance as a long-term investment in the increasingly threatened environments they inhabit. Most marine gastropods are known only by their shells, and only occasionally by preserved anatomy. In postmodern malacology the species can be reduced to a molecular sequence. How much is gained by characterising what the snail does: its functional morphology, feeding, locomotion, reproduction, life history, dispersal, interactions with congeners and predators, defenses, sensory reception, symbioses, and physiological responses? Although observational biology and natural history often are dismissed as merely ‘descriptive’ they are a rich source of new discoveries, questions, and testable hypotheses.

For more than 30 years I have studied Australian trochoidean gastropods from habitat observations, watching individuals in situ, photographing them alive, and making drawings in field notebooks while observing them under a binocular dissecting microscope. This article offers two examples of species in different families that are unable to retract into their shells and have evolved alternative behavioural responses to disturbance. Both were collected from the undersides of shallow subtidal rocks at Albany, Western Australia. Both have provided new questions and lines of integrative research. There is more in the notebooks than in the brief narrative that follows. Each encounter has had its own serendipity.

Granata imbricata (Lamarck, 1816) (Family Chilodontidae) remains firmly attached to rock when collected and is sometimes so difficult to dislodge that part of the rock adheres to the foot upon separation. When the shell is turned over with the ventral foot uppermost, the animal extends the anterior end of the foot as far as possible but is incapable of righting itself (Fig. 1). When the foot is prodded, the animal ejects a white milky fluid that appears in discrete pulses and is sufficiently viscous that individual fronts of exudate can be identified in relatively still water (Fig. 2). Subsequent dissection of a relaxed animal removed from its shell shows that the exudate is from the enlarged and prominent hypobranchial gland, and the unpleasant sulfurous smell is consistent with the hypothesis that it is a predator deterrent.

Stomatella auricula Lamarck, 1818 (Family Trochidae, Subfamily Stomatellinae) is more tentative in its attachment to rock. Several individuals often shelter under the same rock. The head and anterior portion of the foot of a crawling animal are mostly covered by the shell, but the long posterior end of the foot is fully exposed (Fig. 3).
Intact individuals must be collected carefully, with as little disturbance as possible when picking up rocks. The typical response of an individual is to drop immediately from the rock, autotomizing the posterior half of the foot. The sole of the foot is white, and the two pieces oscillate similarly in the water as they descend. The response is consistent with the hypothesis that a swimming predator is 50% more likely to capture the autotomized foot, allowing animal to survive and regenerate. A line of autotomy is not visible on a whole animal, but after autotomy the foot has a characteristic shape (Fig. 4).

Fig. 3. *Stomatella auricula* crawling with long posterior foot fully extended. Photo: C. Hickman.

Fig. 4. Lab notebook drawings and observations of extended foot before and after foot autotomy. C. Hickman.

Penion mandarinus (originally described as *Largisipho spectanda*). See article ‘Wanted’ on page 5. Australian Museum specimen. Photo: M. Allen.
Progressive change in dermal pigmentation in the intertidal dorid nudibranch *Dendrodoris guttata* (Odhner, 1917)

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The dorid nudibranch *Dendrodoris guttata* (Odhner, 1917), distributed across the Indo-West Pacific (Rudman 2000), is a conspicuous and distinctive animal with characteristic aposematic colouration (Fig. 1). Although it has been previously recorded from northern NSW (Allan 1947; Buchanan 1989; Rudman 2000), sightings have been few and far between. In December 2013, MN commenced regular surveys of intertidal rock pools in the Solitary Islands Marine Park, north of Coffs Harbour, NSW as part of an undergraduate research project quantifying temporal variation in opisthobranch assemblages. Individuals of *D. guttata* were regularly observed at most sites.

Each specimen of *D. guttata* was photographed over the period from December 2013 to February 2014 and chronologically-ordered photographs revealed a change in dermal pigmentation over this period. Animals observed in December (Fig. 1A) and early January (Fig. 1B) had the characteristic solid apricot mantle colour punctuated with black spots surrounded by a diffuse white halo. In early February, an individual was found with reduced pigmentation such that the white areas around each black spot had begun to coalesce (Fig. 1C). Two weeks later, three animals were observed with increasingly greater areas of white (or reduced pigmentation) (Figs. 1D–F), one considerably so (this animal was also missing the tip of its left rhinophore: however, it retained some proximal lamellae) (Fig. 1D). Despite regular searches, no further animals were found between Feb. to Aug. 2014.

It is likely that these observations of reduced pigmentation are symptomatic of senescence in this species. Senescent changes recorded for other nudibranch species include: spontaneous ceratal autotomy (Christensen 1977, Wagner *et al.*, 2009); mantle margin autotomy (Avila 1996); and a general contraction in crawl length (Folino 1993, Wagner, *et al.* 2009). In many *in vitro* observations, death was also preceded by behavioural change, primarily cessation of oviposition (Schlesinger *et al.*, 2009, Wolf and Young 2012).

Further field observations will provide a test of the hypothesis that these changes, observed at multiple locations, are indicative of regional seasonality in this species. This forms one of the objectives of the year-long project documenting temporal variation in intertidal opisthobranch assemblages.

**References**


Molluscan Research Grants 2014: Outcomes

As usual, the 2014 Molluscan Research Grant applications were extremely competitive with a number being of a very high standard. The project proposals encompassed a diverse range of molluscan research, including responses to climate change, ecology, taxonomy, fisheries management and conservation. The grant selection committee decided to award $1500 to the two equal top ranked projects, as follows:

Priscila Goncalves, Macquarie University, was awarded a general Molluscan Research Grant for her very innovative project on ‘Understanding climate change impacts on oysters’.

Jonathan Parkyn, Southern Cross University was awarded the Molluscan Taxonomy Grant for his highly significant proposal to study ‘The systematics of the speciose landsnail genus Gyrocochlea (Mollusca: Charopidae)’.

Congratulations to these dedicated early career malacologists. We look forward to hearing a project summary from the successful applicants in future issues of the MSA Newsletter.

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The pumice-associated *Litiopa limnophysa* Melvill & Standen, 1896 (Gastropoda: Litiopidae) and two species of pearl-oyster (Bivalvia: Pteriidae: *Pinctada* Röding, 1798) drift down to Tasmania

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Australian litiopids are best known for the species in the genus *Alaba* H. & A. Adams, 1853, whose small shells can be abundant on beaches fringing shallow-water seagrass or macroalgal beds, where the living animals feed. But a second genus, *Litiopa* Rang, 1829 is also present in eastern and northern Australia, and has recently turned up in Tasmania.

According to Healy and Wells (1998 pages 714–715), members of the genus *Litiopa* are semipelagic, living in floating *Sargassum* weed or associated with algae attached to floating pumice. The authors illustrate a shell very similar in appearance to Fig. 1a (below), but do not venture specific names for any Australian *Litiopa*. Globally, the genus comprises four named species (Bouchet and Goufas 2014); the only named species in Australian waters, according to Wilson (1993, p. 127), is *L. limnophysa* Melvill & Standen, 1896, a species that was originally described from the Loyalty Islands (now part of New Caledonia). Wilson (1993) gives its Australian distribution as North Queensland to central NSW — a distribution echoed by the occurrence records for unspecified *Litiopa* in the online Atlas of Living Australia (ALA). The ALA additionally shows a Northern Territory record; all these ALA records are from the Australian Museum collections. Strangely, there is no entry for any *Litiopa* species in the *Seashells of New South Wales* web-site (Beechey 2014).

The species’ original description (Melvill and Standen, 1896, page 305) is brief and not very informative, but is accompanied by a drawing of the 5 mm long shell (Plate XI, figure 72), copied here and slightly digitally enhanced as Fig. 1b.

In March this year, I spent ten days on Flinders Island, carrying out fieldwork surveying terrestrial invertebrates as part of the *Bush Blitz* program. In my spare time I visited a few beaches, collecting samples of shell-grit for later examination. In samples from two west-coast localities I later found a total of three specimens of *Litiopa*, which I take to be *L. limnophysa*. Fig. 1a is a montaged photo of one of these.

The presence of this species in Tasmanian waters represents a considerable southward extension of its known distribution. Its appearance in March 2014 was associated with the arrival of large quantities of pumice that had been transported, eventually via the East Australian Current, from an undersea volcanic eruption of the Havre Seamount on the Kermadec Ridge, situated 800 km northeast of New Zealand (Carey et al. 2014). The original pumice raft, first spotted on 31st July 2012, spanned an area of about 23 000 km². By November or December 2013 local media were reporting large quantities of pumice washing up on Sydney’s beaches, and by mid-March it was being reported off Tasmania’s east coast, with at least some pumice making it into Bass Strait and onto northern Tasmanian beaches such as Low Head at the mouth of the Tamar River (Rebecca Carey pers. comm.) and even Stanley (pers. obs.). Shells of *Litiopa*, associated with the Havre pumice, have appeared in recent months on beaches from Far North Queensland (Prince of Wales Island, Torres Strait) south at least to northern New South Wales (Eleanor Velasquez pers. comm.). Though I did not see pumice on the two west-coast Flinders Island beaches where I found *Litiopa*, it had been reported there by locals in previous weeks (Rebecca Carey, pers. comm.), and during my visit it was still washing ashore along the east coast of the island in vast quantities. It generally comprised heavily weathered fist-sized to marble-sized balls, encrusted with goose-barnacles and algae; ideal conditions, it would appear, for a pelagic *Litiopa*. I surmise that, as the pumice continued to break up and beach, its cargo of *Litiopa* and other organisms would often have ended up stranded too, eventually finding its way into the shell-grit that I then collected.

Pumice provides a convenient settlement substrate for a wide range of marine organisms with a

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**Fig. 1. Litiopa linophysa. a: 2.0 mm, Killiecrankie, Flinders Island, March 2014, coll. Simon Grove; b: 5 mm, illustration of type from Loyalty Islands, coll. James Hadfield (in Melvill and Standen, 1896, plate XI figure 72).**
planktonic larval stage, including many species of mollusc, which can be transported vast distances across oceans over the space of just a few months (Bryan et al. 2012). This paper refers to *Recluzia* (Janthinidae) as being one of the commonly encountered molluscs on pumice in eastern Australia originating from an eruption off Tonga in 2006. However, following recent discussions with author Scott Bryan and with Denis Riek, who took the photo in Fig. 2 showing a live *Litiopa* on Hayre pumice from northern New South Wales, it seems that these shells may well have been misidentified, and were probably *Litiopa* instead (*Recluzia* is entirely pelagic and free-living, like *Janthina*).

In the weeks following my Flinders Island finds, I put the word out (initially via contacts provided by Rebecca Carey) that I was interested in examining pumice samples then washing up along Tasmania’s east coast. The response was enthusiastic, and between April and June I received samples from up and down the coast, from Flinders Island to Port Arthur. Dead *Litiopa* snails turned up, still attached to algal mats or embedded in pores and crevices, in several of these samples. Additionally, I found attached juveniles of four other mollusc species. Two of these (the oyster *Ostrea angasi* Sowerby, 1871 and the muricid *Diatahia orbita* (Gmelin, 1791)) are common locally occurring species; but the other two (the pearl-oysters *Pinctada margaritifera* (Linnaeus, 1758) and *P. sinuata* (Reeve, 1857) (the latter a tentative identification only)) have tropical or subtropical distributions. To the best of my knowledge, these records represent the first known occurrences of these species in Tasmanian waters — albeit of specimens that were dead on arrival.

**Collection details**

*Litiopa limnophysa*


*Pinctada margaritifera*

TAS: Schouten Island, 42.2997 S, 148.2786 E, 7 April 2014, 3 specimens, coll. A. Geard.

*Pinctada sinuata*

TAS: Schouten Island, 42.2997 S, 148.2786 E, 7 April 2014, 1 specimen, coll. A. Geard; Flinders Island, Trousers Point beach, 40.2275 S, 148.0296 E, 10 June 2014, 1 specimen, coll. R. Dallas.

**Acknowledgements**

I thank Lynnton Stephens, Melbourne, for his initial recognition of the photo that I sent him of my first find as a *Litiopa* species. Thanks, too, to Dr Rebecca Carey (University of Tasmania) for providing further information on the pumice raft and its origins, to Dr Scott Bryan and Eleanor Velasquez (Queensland University of Technology) for information and further discussions on the molluscan fauna of southeastern Pacific pumice, and to Denis Riek for more insights into *Litiopa* and *Recluzia*, including permission to reproduce the photo in Fig. 2. The pumice samples, minus the molluscan hitchhikers, have since been forwarded to Eleanor Velasquez to form part of her broader studies on pumice-borne biotic assemblages.

**References**


**Fig 2.** A live *Litiopa*, aboard a piece of pumice from the Hayre eruption that had been beached in northern New South Wales. Photo: Denis Riek.
Notice of the Malacological Society of Australasia
Annual General Meeting

Date: Wednesday 3rd December 2014
Time: 10.00 a.m. EDT
Venue: Via teleconference. Please contact me for details on how to join the teleconference.

Please forward any agenda items, nomination forms or proxy forms to me via mail or email by the 19th of November. If you cannot participate in the meeting and would like to appoint a proxy, please complete the form provided and nominate a person who will be participating in the meeting to vote on your behalf. If no suitable nominee is available, I, as secretary, can act as your proxy. Please contact me prior to the meeting to discuss your voting preferences.

Nominations are sought for MSA council positions (please use the following form, self nominations will be accepted).

If you would like to receive a copy of the agenda for the meeting and proposed council nominees, please contact me by the 19th of November.

Yours faithfully,

Carmel McDougall (Secretary), c.mcdougall@uq.edu.au
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Nomination form for council positions of the
Malacological Society of Australasia 2014–2015

Nominee: ____________________________________________
Position: __________________________________________
Nominated by: (name) ______________________________ (signature) ______________________________
Seconded by: (name) ______________________________  (signature) ______________________________
* nominations may also be seconded by participants during the meeting

Proxy Form

I, ____________________________________________, hereby appoint ____________________________ as my true and lawful proxy to vote on my behalf at the Annual General Meeting of the Malacological Society of Australasia to be held via teleconference on the 3rd of December, 2014.

Signed ___________________________ Date ___________________________

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