

Review

Australian Tropical Marine Micromolluscs: An Overwhelming Bias

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Abstract: Assessing the marine biodiversity of the tropics can be overwhelming, especially for the Mollusca, one of the largest marine phyla in the sea. With a diversity that can exceed macrofaunal richness in many groups, the micro/meiofaunal component is one of most overlooked biotas in surveys due to the time-consuming nature of collecting, sorting, and identifying this assemblage. We review trends in micromollusc research highlighting the Australian perspective that reveals a dwindling taxonomic effort through time and discuss pervasive obstacles of relevance to the taxonomy of micromolluscs globally. Since a high during the 1970s, followed by a smaller peak in 2000, in 2010 we observe a low in micromolluscan collection activity in Australia not seen since the 1930s. Although challenging, considered planning at each step of the species identification pathway can reduce barriers to micromolluscan research (e.g., role of types, dedicated sampling, integration of microscopy and genetic methods). We discuss new initiatives to trial these methods in Western Australia, an understudied region with high biodiversity, and highlight why micromolluscs are worth the effort. A number of important fields that would benefit from increased focus on this group (e.g., ecological gaps) are considered. The methods and strategies for resolving systematic problems in micromolluscan taxonomy are available, only the desire and support to reverse the decline in knowledge remains to be found.

Keywords: biodiversity; tropical reefs; micromolluscs; marine; genetics; Australia; DNA taxonomy; morphospecies

1. What Is the Problem?

As we seek to understand and document global biodiversity, persistent challenges threaten that goal. Efforts to count and estimate the world's marine species vary significantly; 33%–91% of species in the ocean appear undescribed [1,2]. This sentiment is echoed in our understanding of Australian marine invertebrates, where the state of taxonomic, biological, and ecological knowledge for these groups is generally poor [3]. As we seek to improve our knowledge of undersampled groups and undersampled habitats, the 'perfect storm' emerges in molluscs. Molluscs are a hugely diverse taxonomic group with their highest diversity, in general, in the tropics [4]. Here we focus attention on the smaller size fraction of molluscan biodiversity that often escapes the eye of traditional biodiversity campaigns and is essentially unrepresented in many studies. These groups have shown high diversity, and even dominance, over millennia [5,6]. These knowledge gaps around micromolluscs exacerbate conservation concerns; without a clear understanding of species and their distributions, it is impossible to assess whether assessment or action is required.

The term “micromollusc” has been loosely applied to represent any mollusc where a microscope or loupe is needed for their observation (Figure 1). Geiger et al. [7] suggested applying a definition based on an adult maximum dimension limit of 5 mm, although its arbitrary nature is acknowledged [8]. For example, many groups have species in both micro and macro categories (e.g., Turridae, Galeommatidae), while other groups just exceed that range (e.g., 0.5–1 mm, Condylorcardiidae, Rissoidae). Obviously, most molluscs are micromolluscs as juveniles [9], but there are many molluscan groups that are entirely micromolluscan throughout their life and these span phylogenetic diversity. According to the Australian Faunal Directory [10], of the 10 most diverse families of marine molluscs, only three are strictly macroscopic (Muricidae, Veneridae, and Conidae), and four are essentially micromolluscan (Rissoidae, Triphoridae, Eulimidae, and Cerithiopsidae). Although many micromolluscs occupy deep sea environments and temperate areas (reviewed for Japan in [9]), the focus of this review are tropical reefs; these latter four families are all common inhabitants of coral reef habitats.



Figure 1. Diversity of small molluscs from recent Western Australian field trips (2011–2015). 1–2. Condylorcardiidae. 3. Neoleptonidae. 3–6. Galeommatidae. 7. Scissurellidae. 8. Skeneidae. 9–10. Pickworthiidae. 11. Trochidae. 12. Cerithiidae. 13. Dialidae. 14–20. Rissoidae. 21–22. Triphoridae. 23–24. Cerithiopsidae. 25. Epitoniidae. 26. Lithiopidae. 27–30. Eulimidae. 31–36. Cystiscidae/Marginellidae. 37. Raphitomidae. 38. Clathurellidae. 39–40. Haminoidea. 41–43. Juliidae. 44–46. Rissoellidae. 47–49. Omalogyridae. 50–51. Orbitestellidae. 52. Pyramidellidae. 53. Neomemiomorpha. 54. Gadilidae. Individual images scaled to 1 mm (see scale bar). Photos P. Middelfart.

Micromolluscs are often hard to find and collect, laborious to sort from sediment, difficult to identify, and expensive to illustrate (SEM or CT scanning). They are often missed in many ecological studies, which utilize a mesh size of ~2 mm [11]. Dissection of soft anatomy can be tedious and require tremendous skill, and special techniques may be necessary for understanding some organ systems (e.g., 3D reconstruction). Geiger et al. [7] provided a comprehensive handbook of practical techniques for working with micromolluscs, and this remains a valuable resource. However, tackling this fauna from a logistical perspective is simply daunting and beyond the means of many museum programs today (however, see [8,11]).

2. Collection Activity in Australia, a Telling Measure

Although many papers argue that taxonomic expertise is diminishing [1,12], the occasional paper holds the opposite opinion—that there are more taxonomists than ever before [13]. The idea that the golden age of taxonomy peaked in the 1970s holds true when examining collecting activity in databases, such as the Atlas of Living Australia (ALA). Collection activity encompasses collection effort, sorting, identification, and databasing. Examination of the year of collection over the past century for a diversity of micromolluscan families (exemplars chosen here to reflect gastropods and bivalves, highly diverse, and less diverse groups, as well as better known and less well known groups) according to the Australian Faunal Directory [10] reveals a disturbing trend (Figure 2). Although highs and lows are apparent, with a pronounced peak in the 1970s and a smaller peak in 2000, at 2010 we observe a low not seen since the 1930s. This unfortunate trend is not exclusive to micromolluscs; macromollusc groups also exhibit a similar downward progression.

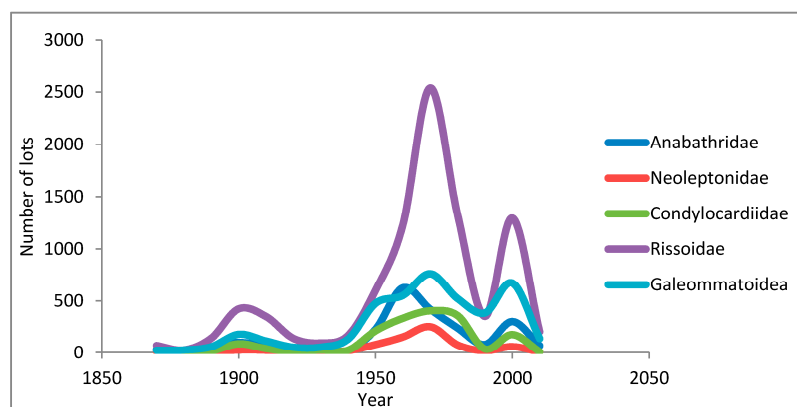


Figure 2. Declining collection activity for micromollusc groups (Neoleptonidae, Condylorcardiidae, Rissoidae, Anabathridae) or those containing significant micromollusc representatives (e.g., superfamily Galeommatoidae) through time in Australia [14].

A comparative approach is useful to further illustrate the bias against micromolluscs. Here we examine the difference between mollusc groups with medium and high diversity. Firstly, the Condylorcardiidae and Cardiidae have very similar medium-level diversity in Australia with 64 and 68 recorded species, respectively. However, the magnitude of difference in collection activity varies dramatically (Figure 3A). In the past decade, databased collections of macroscopic cardiids have exceeded those for microscopic condylorcardiids up to 37-fold. In the so-called golden age of taxonomy (1950–1970) this difference was least pronounced (1.5–3.6x) for these two taxa.

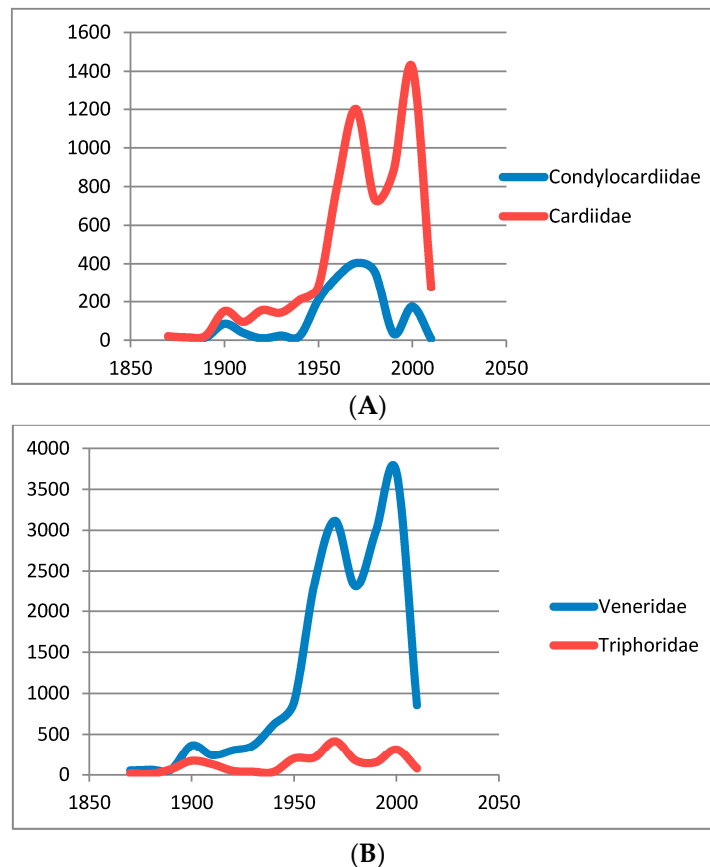


Figure 3. A micromollusc bias. (A) Comparison of Condylorcardiidae and Cardiidae collection activity per decade in Australia; and (B) comparison of Veneridae and Triphoridae collection activity per decade in Australia [14].

The second comparison, between highly diverse groups, compares Veneridae with Triphoridae (Figure 3B). These groups have 193 and 186 recorded species, respectively. In the last decade, the collection activity for the micromolluscan Triphoridae has been up to 22 times less than the macroscopic Veneridae. Again, in the ‘golden age’ this difference was reduced to about 10. Predictably, many of the major monographs and revisions emerged during those decades as well. Since this time, decreased collection activity has been absolute; not only has it slid in micromolluscan, but also in macromolluscan collections. It is clear that our capacity to discover diversity among micromolluscan groups has been steadily decreasing over the last few decades.

It is unclear why interest and collection activity for micromolluscs was historically high in Australia in the first place. It may have been a serendipitous accident, where workers with a keen interest had opportunity to follow this through, or whereby interest was really on all molluscan groups, and the diverse micromollusc fauna was simply numerically greater. Whatever the reason, major works by Laseron were foundational for many Australian micromollusc groups [15–29]. Subsequent works by Ponder [30–39] also yielded a strong baseline for a still poorly understood fauna. Despite these foundations, the bulk of the micromolluscan fauna remains untreated.

3. The Dreaded Taxonomic “Cul-De-Sac”

The seemingly simple task of identifying a micromollusc to the species-level can take taxonomists down a tricky path. Most will compare their species to literature for the local region, and if it appears different in any way, two things can happen. It will either remain in the collection as an unidentified species, thus not contributing to any resolution, or it will be described, in isolation, as new. It is

problematic to continue the singular or additive alpha-taxonomy of micromolluscs, when revisionary works are what is needed. This is especially true when the material is represented only by shells, either extant or fossil. In many cases, like Galeommatoidea, the shells can be very similar within a given genus, but the anatomical morphology is diagnostic at the species-level (Figure 4A–D). The simplification of external anatomy is common with miniaturization [40], and convergent evolution can result in similar, non-informative shells. Therefore, progress in understanding biodiversity in these situations must incorporate collection and examination of fresh material. In many cases, the insight afforded by anatomy and genetics can assist the re-assessment of dry material (which represents much of the material in museum collections). In many cases, confident assignment of dry material is not possible, and should be excluded, rather than introducing errors in distribution.

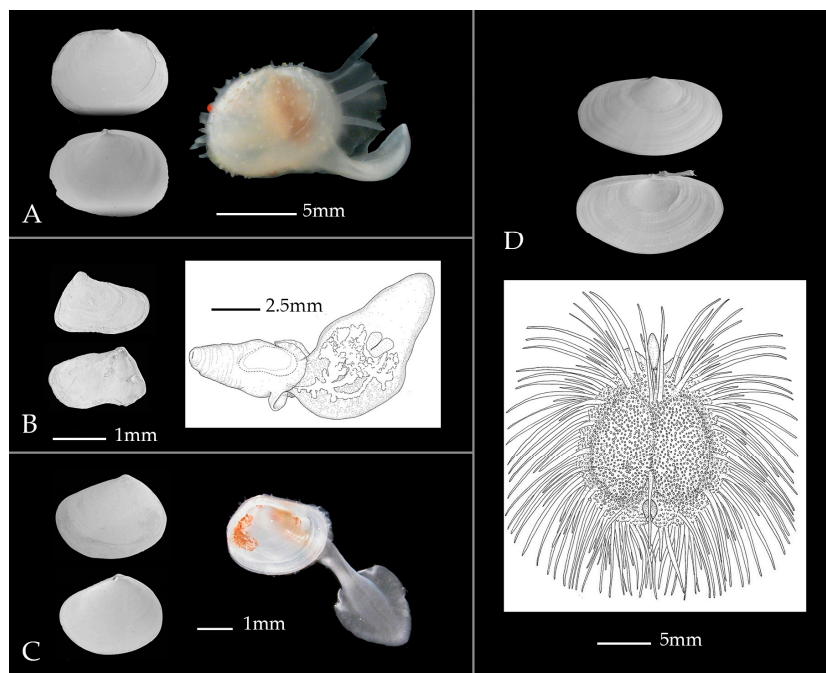


Figure 4. Simple shells and complex animals in species of Galeommatoidea from Eastern and Northeastern Australia. (A) *Scintilla anomala*; (B) *Entovalva* sp.; (C) *Austrodevonia sharnae*; and (D) *Ephippodantomorpha hirsutus*.

Some groups, like the small galeommatooid bivalves *Scintilla*, have seven out of eight recorded species [10] described over a hundred years ago, only from shells. The species names remain linked to shells, which are simple and possess few characters, but the animals themselves display clear, diagnostic features, like those illustrated in Figure 4A–D. Any worker who moves forward with only dry material can easily find themselves in a taxonomic “cul-de-sac”, or blind alley, where few can progress. It takes a great investment of labour, both taxonomic and descriptive, to get the taxonomic foundation laid for future work. This has not yet been carried out for many micromollusc groups. The alternative would be to declare many names as nomina dubia, which should not be undertaken lightly.

Even sensible starting points, such as describing the soft anatomy of the type species of *Scintilla*, *S. philippinensis* Deshayes, 1856 [41], did little to assist the overall problem, because of the numerous other species only known from shells. For some other groups (see Table 1), no baseline information (e.g., no revision or monograph) coupled with relatively uncommon/inaccessible taxa, offer almost insurmountable barriers to advancement.

Table 1. Some micromolluscan groups with documented representatives in tropical coral reef environments. * = no recent revision in tropical coral reefs; NZ = New Zealand; NSW = New South Wales; IP = Indo Pacific.

Higher Level Systematics	Family (Unless Stated Otherwise)	Key Literature
Class Aplacophora		[42] *
Class Bivalvia	Neoleptonidae	[19] NSW focus *
Class Bivalvia	Condylocardiidae	[43,44] Australian focus
Class Bivalvia	Cyamiidae	[19] NSW focus *
Class Bivalvia	Superfamily Galeommatoidea	*
Class Gastropoda, Caenogastropoda	Superfamily Cerithioidea, Pickworthiidae	[45] *
Class Gastropoda, Caenogastropoda	Superfamily Cerithioidea, Scaliolidae	[39] *
Class Gastropoda, Caenogastropoda	Superfamily Cerithioidea, Dialidae	[38] *
Class Gastropoda, Caenogastropoda	Superfamily Cingulopsoidea	[31,46] Australian Eatoniellidae *
Class Gastropoda, Caenogastropoda	Superfamily Eulimoidea, Eulimidae	[47] *
Class Gastropoda, Caenogastropoda	Superfamily Triphoroidea, Cerithiopsidae	[48,49] NZ
Class Gastropoda, Caenogastropoda	Superfamily Triphoroidea, Triphoridae	[50] Southern Australia
Class Gastropoda, Caenogastropoda	Superfamily Rissoidea	[16,24,30,34,35,46,51] Rissoidae NSW, [33] Barleeidae
Class Gastropoda, Caenogastropoda	Superfamily Truncatelloidea	[52] Australian and East Timorese Stenothyridae, [30] Australian and tropical IP Tertiary and Recent species of <i>Pisinna</i> (= <i>Estea</i>), [53] <i>Ctiloceras</i> and some comparative genera, [54] Caecidae, [55] Caecidae, Southwest Pacific, [56] NZ and NSW, Tornidae
Class Gastropoda, Caenogastropoda	Superfamily Vanikoroidea, Vanikoridae	Very limited information *
Class Gastropoda, Heterobranchia	Cimidae	[57] Very limited information *
Class Gastropoda, Heterobranchia	Tofanellidae	[58] Very limited information *
Class Gastropoda, Heterobranchia	Murchisonellidae	[59,60] Very limited information *
Class Gastropoda, Heterobranchia	Rhodopidae	[61–63] Southern Australia
Class Gastropoda, Heterobranchia	Omalogyridae	[21] NSW, [28] Dampierian Zoogeographical Province
Class Gastropoda, Heterobranchia	Orbitestellidae	[21,36] NSW, [28] Dampierian Zoogeographical Province, [56] NZ and NSW
Class Gastropoda, Heterobranchia	Pyramidellidae	[17] NSW Pyramidellidae, <i>Mathilda</i> , [29] Northern Australia, [64] Tropical South Pacific, [65,66] <i>Odostomella</i> and <i>Herviera</i>
Class Gastropoda, Heterobranchia	Rissoellidae	[31] Australia
Class Gastropoda, Heterobranchia	Ringiculidae	[67] Very limited information
Class Gastropoda, Heterobranchia	Cornirostridae	[37] Very limited information *
Class Gastropoda, Vetigastropoda	Scissurellidae	[68] Anatomidae, Larocheidae, Depressizonidae, Sutilizonidae, Temnocinclidae
Class Gastropoda, Vetigastropoda	Superfamily Trochoidea, Skeneidae	[56] NZ and NSW
Class Gastropoda, Vetigastropoda	Superfamily Trochoidea, Liotiidae	[21] NSW

For some taxa (e.g., cerithiopsids, triphorids, condylocardiids), shell characters such as protoconch/prodissoconch and teleoconch/dissoconch can be highly informative, and may assist some progress. Alternatively, groups like the Pyramidelloidea are overwhelming diverse worldwide (over 2800 extant species [69], with an entire career seemingly needed to make any revisionary progress. As each group is faced with a unique set of constraints, finding a straightforward approach suited to many is challenging.

As well as the need for description of informative soft characters and photography of live animals, proper morphological description and detail of the important taxa (e.g., types) in a group is also required. An example of this is case of the Condylocardiidae (Bivalvia), which contained numerous poorly illustrated genera and species described from Australia. Until that Australian fauna was redescribed [43,44] it was almost impossible for other regions to sensibly place and describe the taxa they had. For this group, the minute size of the taxa necessitated the use of scanning electron microscopy (SEM) to detail important shell characters (Figure 5). The application of that technology was the only way to re-ignite taxonomic research on Condylocardiidae [70]. In the same way that thorough taxonomic work on any group of molluscs requires time, effort, and access to the largest and oldest natural history collections in the world, micromolluscs additionally require high powered microscopes, high resolution photography, and/or SEM. These days, genetics can also be used to initiate the understanding of groups and offer a way out of the cul-de-sac, where the classical tools have failed or are confusing.

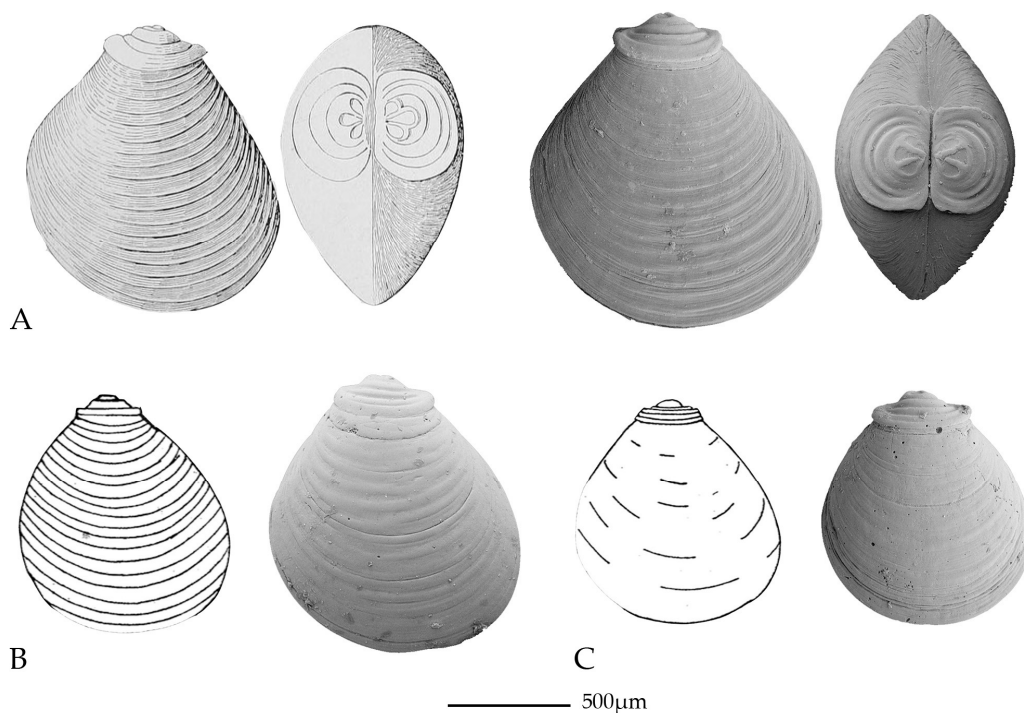


Figure 5. The utility of SEM for harvesting rich micromolluscan character data. Synonymised types of *Austrocardiella trifoliata* (from [71]). (A) Original drawings of *Condylocuna trifoliata* (from [71]); (B) *Condylocuna cambrica* (in [19]); and (C) *Benthocardiella vitrea* (from [19]), compared with SEM [43].

Lastly, because of the colonization history and population distribution in Australia, research efforts have mostly centred on east coast micromolluscan diversity, largely completed at east coast institutions. Most material was collected from the east coast of Australia, and is deposited at museums there, specifically the Australian Museum, Sydney (AMS) (or historically in European institutions). When querying databases for select micromolluscan taxa (Figure 6, Rissoellidae, Eatonellidae, Eulimidae, Neoleptonidae), the trends reveal different biases. Some groups, like Rissoellidae (Figure 6A) show

poor sampling across the continent as a whole, whereas Eatoniellidae (Figure 6B) are particularly poorly represented in the tropics. Although that family's diversity is centred on southern areas, several species occur in the north of Australia and at least one is known to be widespread. The east coast bias is evident in records for Eulimidae and Neoleptonidae (Figure 6C,D). Most significantly, the type localities of most described micromolluscan species are found at historically well-collected sites on the east coast of Australia (e.g., Port Jackson = Sydney Harbour). When a study of a new and distant region is undertaken, such as tropical Western Australia, the need for comparison to this type material is critical.

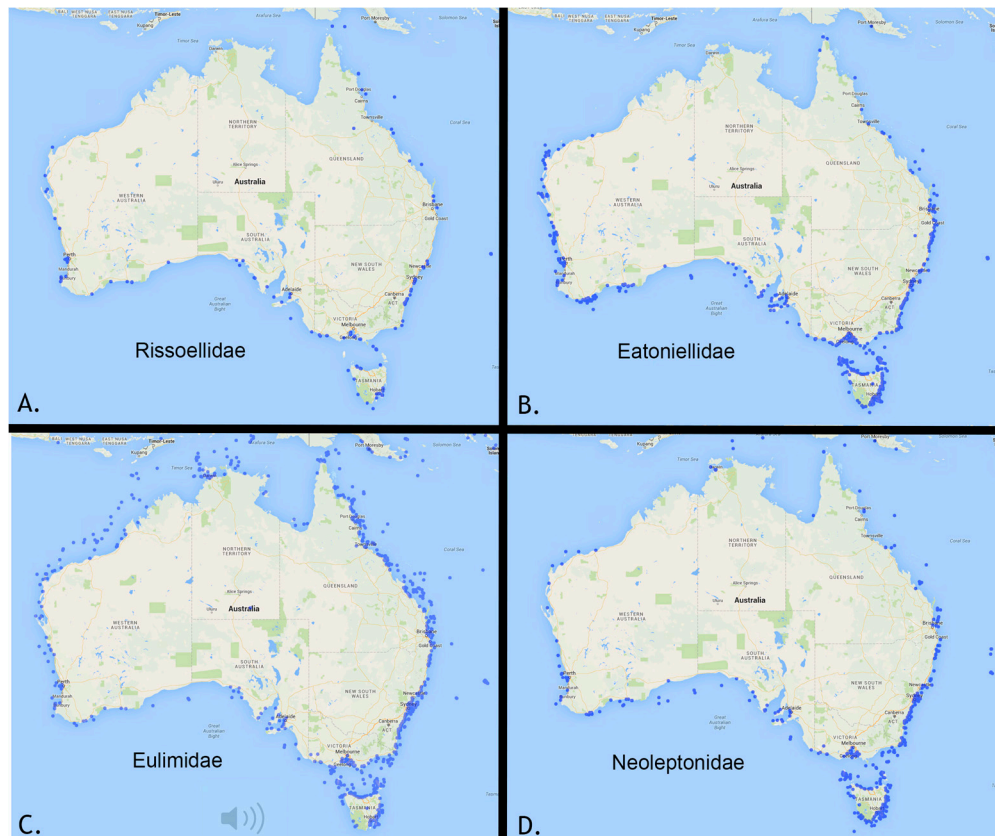


Figure 6. Regional biases for micromolluscs in Australia. An east coast bias is apparent in some groups (e.g., (C) Eulimidae; and (D) Neoleptonidae) while a southern bias (e.g., (B) Eatoniellidae) typifies the trend in others. Some groups have received little attention Australia-wide (e.g., (A) Rissoellidae). The highly diverse tropical reefs have overall received less attention than temperate ecosystems. Each dot represents an identified lot in a collection in Australia [14].

4. Connecting Parallel Taxonomies—Species Names, Morphospecies, and DNA Taxonomy

Since most micromolluscs have had discontinuous attention, historical species names are not readily resolved to contemporary faunal knowledge. In most operational surveys, there is a mix of taxa for whom species names are confidently known, and those that are known by a morphospecies name. Most checklists from coral reefs do not include molluscs less than 10 mm, even though these are just as rich, if not more so, than the macroscopic fraction [72]. The main reason besides the need of specialised tools, and in some cases handling skill, is the lack of review literature dealing with those groups. The work required to even attempt to put names on rissoideans, eulimids, or pyramidelloideans from coral reefs is quite daunting [9]. Most faunistic studies are done by small groups of museum scientists, with various specialist knowledge, but not pan-molluscan knowledge and, therefore, favoured groups receive more attention than other groups. The remaining organisms are often hard to place at all,

and are either not attended to, or are considered prime candidates for DNA sequencing to aid with identification. Thus, a DNA taxonomy is also emerging. In large countries like Australia, with several climatic zones and high endemism, the emergence of multiple taxonomies is not surprising. It can be the only practical way forward with immense and overwhelming faunas (Moorea Biocode Project [73]). Now, in the age of integration, connecting these three taxonomies requires a strategic approach.

The first and most important step should be consideration of primary type material. Most of the older names are represented by dry types, which may have been lost, or degraded through processes such as Byrne's disease and Glass disease [7]. Both of these cause efflorescence on the shells, which eventually crumble. Additionally, for wet specimens, even slightly acidic formalin or ethanol can quickly destroy shells. If still intact, these types should be digitised whenever possible. Advances in microCT scanning [74] have meant that high-quality 3D images can be easily shared without loaning types (which many museums are understandably reluctant to do) and without damaging the specimens. These images are key to connecting names with morphospecies concepts. Original drawings may or may not be informative, depending on whether the shell or anatomy was depicted in the primary description (Figure 5). If all of these avenues of accessing type information are not productive, then re-collection from the type locality is critical. Freshly-collected material then allows DNA sequencing, and connects the species' name with a DNA taxonomy; it might also allow for further anatomical investigations. The danger here is that the newly re-collected material does not match the type material; only a stringent assessment of identification can be satisfactory.

DNA sequences can then also connect morphospecies collected from outside the type locality to the species name. This introduces a new problem, as most micromollusc shells dissolve with DNA lysis methods, so imaging pre-DNA lysis is absolutely critical. Using images and DNA sequences to coalesce species concepts is important for bringing these taxa to the attention of the wider community, a process that will ultimately lead to a worldwide effort in unifying taxonomies. Although linking all of these methodologies will require a long and concentrated effort, it is possible to achieve this goal. Once historical names can be confidently applied, and revisions have highlighted valid taxa and informative character sets, it is then possible to move forward with descriptions of unknown species. Even the micromollusc fauna of Indo-West Pacific is finite.

The Western Australian Museum (WAM) and partners have surveyed marine invertebrate biodiversity along the northwest shelf coral reef habitats over the last five decades (summarized for molluscs recently in [75]), and like many other surveys, largely ignored micromolluscs. The northwest coast of Australia can show strong links to the west-Pacific [76] and is an intriguing region to study. The Woodside Collection project (Kimberley) is one of the more recent field-based initiatives in the Kimberley region (2009–2012), with the novel introduction of a micromolluscan survey for the final two years (2013–2014). This has offered an important new collection resource for the Western Australian Museum, which has traditionally avoided micromolluscan groups. The opportunity to extend this micromollusc work to the Pilbara has emerged with Gorgon Project's Barrow Island Net Conservation Benefits Fund. The focal area of WAM's project abuts the Kimberley to the north and extends to Shark Bay in the south. Although both studies are making significant headway, both studies are now facing major roadblocks as they move from estimates of morphospecies diversity to assessing regional diversity through comparative methods, as well as to the description of new species. This shift requires ground-truthing newly-collected taxa with type material, almost exclusively from outside WA.

5. Why Would Anyone Care?

Our knowledge of tropical micromolluscan biodiversity is grossly underestimated relative to macromolluscs. A comprehensive molluscan survey in New Caledonia reported that over 33% of recovered species were smaller than 4.1 mm [8]. Even less is known about aspects of biology, ecology, and evolution in these groups. The basic biology of most taxa is largely undescribed (e.g., nutrition, reproduction mode, cues, or timing, behaviour, dispersal, ontogeny) [9] even though it is recognized that such assemblages have great potential for measuring changes in Australian

marine biodiversity [77]. In many instances, knowledge of micromollusc families is derived from European taxa (e.g., much of the rissoidean ecology is based on European material) [51], but sparse to non-existent in mostly endemic families (e.g., in Australia such as Anabathridae, Emblanidae, and Pickworthiidae) [78]. For the rest of the thousands of known taxa, we are not able to examine experimentally, or even anecdotally, the role of any of these groups in systems biology, including food web dynamics, genetic connectivity, or faunal turnover. Olabarria and Chapman [77] highlight a complete absence of quantitative descriptions of spatio-temporal patterns of variability in Australian microgastropods. Thus, we are not able to confidently assess the importance of micromolluscs in terms of their role in ecosystems at this stage. As many groups must underpin tropical coral reef and other systems (as food for juvenile fish and macroinvertebrates, including commercially important taxa) this is hugely problematic. One of the major aims of the Moorea Biocode project was to connect trophic levels and identify predator/prey linkages via ecological genotyping of stomach contents, in essence to document who was eating who [79]. These results will not only be important to begin to test the importance of the small size fraction across microinvertebrates (not just micromolluscs) as food for larger predators in reef settings, but also as a novel method to apply elsewhere. This type of work is being carried out more commonly as a monitoring tool by government departments [80]. Partnerships between groups that can make differential use of these large datasets should be encouraged.

From an evolutionary perspective, phylogenomic work incorporating micromolluscs has a long way to go, since the relatively large quantities of genomic material needed is best sourced from a single individual, which is not always practical for micromolluscs. However, incorporating key micromollusc taxa in direct sequencing studies has overturned our perspective on traditional relationships when attempted (e.g., [81]). Many micromolluscs are reduced in size to facilitate a parasitic or symbiotic lifestyle [47,82] and some of the most exciting evolutionary work on micromolluscs is to begin to tackle how these relationships evolved, how they are maintained and, for mutualisms, whether coevolution is supported. Work on these groups, although not yet encompassing the full taxonomic diversity of any group, has yielded major breakthroughs into understanding how taxa can exploit new habitats [83] and, as such, symbioses can be considered a key innovation [84,85].

The so-called meiofaunal paradox, which involves taxa that have predicted low dispersal potential but that show wide distributions, applies strongly to micromollusc groups. This paradox appears ultimately driven by scarce information and records, combined with difficult to identify organisms, and may not be upheld after intensive study [86]. Recent efforts have been combating this problem by using a multi-marker phylogeny with multiple independent methods of species delimitation [87]. When the microscopic lifestyle has led to real absence of characters (not just poorly studied), and cryptic radiations, using a DNA taxonomy has offered some promise. This method has been used for cryptic species in general [88,89] and for cryptic micromolluscs [90]. All robust works using DNA characters for species delimitation must also incorporate evidence that the species are truly cryptic and demonstrate a lack of morphological characters before going down that path.

6. How Do We Move forward?

Fundamentally, to address sampling gaps and increase available information on poorly-known micromollusc groups, especially in the hyperdiverse tropical reef environments, requires nothing new [11]. With appropriate methods of sampling, global approaches, live observation, and documentation where practicable, high-resolution imaging, and integration of genetic data, systematic problems can be resolved. Part of the revisionary process should include highlighting long-forgotten names and associated type material to aid modern re-identification. We cannot emphasize enough the resampling of type localities for DNA sequencing—this practice creates a long-lasting bridge between historical literature and contemporary barcoding approaches. All of these methods are improving the knowledge of molluscs worldwide and groups, such as micromolluscs, simply require equal attention. Our call for attention to this issue is neither novel nor the first to point out neglect—so why has little progress been made?

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References

- Mora, C.; Tittensor, D.P.; Adl, S.; Simpson, A.G.; Worm, B. How many species are there on Earth and in the ocean? *PLoS Biol.* **2011**, *9*, e1001127. [[CrossRef](#)] [[PubMed](#)]
- Appeltans, W.; Ahyong, S.T.; Anderson, G.; Angel, M.V.; Artois, T.; Bailly, N.; Bamber, R.; Barber, A.; Bartsch, I.; Berta, A.; et al. The magnitude of global marine species diversity. *Curr. Biol.* **2012**, *22*, 2189–2202. [[CrossRef](#)] [[PubMed](#)]
- Ponder, W.; Hutchings, P.; Chapman, R. Overview of the Conservation of Australian Marine Invertebrates. Report for Environment Australia 2002. Available online: http://malsocaus.org/marine_invert/ (accessed on 10 June 2016).
- Valentine, J.W.; Jablonski, D. A twofold role for global energy gradients in marine biodiversity trends. *J. Biogeogr.* **2015**, *42*, 997–1005. [[CrossRef](#)]
- Hausmann, I.; Nützel, A. Diversity and palaeoecology of a highly diverse Late Triassic marine biota from the Cassian Formation at the Stuoeres Wiesen (North Italy, Dolomites). *Lethaia* **2015**, *48*, 235–255. [[CrossRef](#)]
- Nützel, A.; Kaim, A. Diversity, palaeoecology and systematics of a marine fossil assemblage from the Late Triassic Cassian Formation at Settsass Scharte, N Italy. *Paläontologische Z.* **2014**, *88*, 405–431. [[CrossRef](#)]
- Geiger, D.L.; Marshall, B.A.; Ponder, W.F.; Sasaki, T.; Warén, A. Techniques for collecting, handling, preparing, storing and examining small molluscan specimens. *Molluscan Res.* **2007**, *27*, 1–50.
- Bouchet, P.; Lozouet, P.; Maestrati, P.; Heros, V. Assessing the magnitude of species richness in tropical marine environments: Exceptionally high numbers of molluscs at a New Caledonia site. *Biol. J. Linn. Soc.* **2002**, *75*, 421–436. [[CrossRef](#)]
- Sasaki, T. Micromolluscs in Japan: Taxonomic composition, habitats, and future topics. *Zoosymposia* **2008**, *1*, 147–232. [[CrossRef](#)]
- Australian Faunal Directory (AFD). Available online: <http://www.environment.gov.au/biodiversity/abrs/online-resources/fauna/> (accessed on 2 April 2016).
- Bouchet, P. From specimens to data, and from seashells to molluscs: The Panglao Marine Biodiversity Project. *Vita Malacol.* **2009**, *8*, 1–8.
- Haas, F.; Häuser, C.L. Taxonomists: An endangered species. In *Success Stories in Implementation of the Programmes of Work on Dry and Sub-Humid Lands and the Global Taxonomy Initiative*; Secretariat of the Convention on Biological Diversity: Montreal, Canada, 2005; volume 87.
- Costello, M.J.; May, R.M.; Stork, N.E. Can We Name Earth's Species Before They Go Extinct? *Science* **2013**, *339*, 413–416. [[CrossRef](#)] [[PubMed](#)]
- Atlas of Living Australia (ALA). Available online: <http://www.ala.org.au> (accessed on 26 April 2016).
- Laseron, C. New South Wales Marginellidae. *Rec. Aust. Mus.* **1948**, *22*, 35–48. [[CrossRef](#)]
- Laseron, C.F. Review of the Rissoidae of New South Wales. *Rec. Aust. Mus.* **1950**, *22*, 257–287. [[CrossRef](#)]
- Laseron, C. The New South Wales Pyramidellidae and the genus *Mathilda*. *Rec. Aust. Mus.* **1951**, *22*, 298–334. [[CrossRef](#)]
- Laseron, C. Revision of the New South Wales Cerithiopsidae. *Aust. Zool.* **1951**, *11*, 351–368.
- Laseron, C. Minute bivalves from New South Wales. *Rec. Aust. Mus.* **1953**, *23*, 33–54. [[CrossRef](#)]
- Laseron, C. Revision of the New South Wales Triphoridae. *Rec. Aust. Mus.* **1954**, *23*, 139–158. [[CrossRef](#)]
- Laseron, C. Revision of the Liottiidae of New South Wales. *Aust. Zool.* **1954**, *12*, 1–25.
- Laseron, C. Revision of the New South Wales eulimoid shells. *Aust. Zool.* **1955**, *12*, 83–107.

23. Laseron, C. The Family Cerithiopsidae (Mollusca) from the Solanderian and Dampierian Zoogeographical Provinces. *Aust. J. Mar. Freshw. Res.* **1956**, *7*, 151–182. [[CrossRef](#)]
24. Laseron, C. The families Rissoinidae and Rissoidae (Mollusca) from the Solanderian and Dampierian zoogeographical provinces. *Aust. J. Mar. Freshw. Res.* **1956**, *7*, 384–484. [[CrossRef](#)]
25. Laseron, C. A Revision of the New South Wales Leptonidae. Mollusca: Pelecypoda. *Rec. Aust. Mus.* **1956**, *24*, 7–21. [[CrossRef](#)]
26. Laseron, C. A new classification of the Australian Marginellidae (Mollusca), with a review of species from the Solanderian and Dampierian Zoogeographical Provinces. *Aust. J. Mar. Freshw. Res.* **1957**, *8*, 274–311. [[CrossRef](#)]
27. Laseron, C. The Family Triphoridae (Mollusca) from Northern Australia, also Triphoridae from Christmas Island (Indian Ocean). *Aust. J. Mar. Freshw. Res.* **1958**, *9*, 569–658.
28. Laseron, C. Liotiidae and allied molluscs from the Dampierian Zoogeographical Province. *Rec. Aust. Mus.* **1958**, *24*, 165–182. [[CrossRef](#)]
29. Laseron, C. The family Pyramidellidae (Mollusca) from northern Australia. *Aust. J. Mar. Freshw. Res.* **1959**, *10*, 177–267. [[CrossRef](#)]
30. Ponder, W.F.; Yoo, E.K. A revision of the Australian and tropical Indo-Pacific Tertiary and Recent species of *Pisinnna* (= *Estea*) (Mollusca: Gastropoda: Rissoidae). *Rec. Aust. Mus.* **1976**, *30*, 150–247. [[CrossRef](#)]
31. Ponder, W.F.; Yoo, E.K. A revision of the Australian species of the Rissoellidae (Mollusca: Gastropoda). *Rec. Aust. Mus.* **1977**, *31*, 133–185. [[CrossRef](#)]
32. Ponder, W.F.; Yoo, E.K. A Revision of the Eatoniellidae of Australia (Mollusca, Gastropoda, Littorinacea). *Rec. Aust. Mus.* **1978**, *31*, 606–658. [[CrossRef](#)]
33. Ponder, W.F. Review of the genera of the Barleeidae (Mollusca: Gastropoda: Rissoacea). *Rec. Aust. Mus.* **1983**, *35*, 231–281. [[CrossRef](#)]
34. Ponder, W.F. A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). *Rec. Aust. Mus. Suppl.* **1985**, *4*, 1–221. [[CrossRef](#)]
35. Ponder, W.F. The truncatelloidean (= Rissoacean) radiation—A preliminary phylogeny. *Malacol. Rev. Suppl.* **1988**, *4*, 129–166.
36. Ponder, W.F. The anatomy and relationships of the Orbitestellidae (Gastropoda: Heterobranchia). *J. Molluscan Stud.* **1990**, *56*, 515–532. [[CrossRef](#)]
37. Ponder, W.F. The anatomy and relationships of a marine valvatoidean (Gastropoda: Heterobranchia). *J. Molluscan Stud.* **1990**, *56*, 533–555. [[CrossRef](#)]
38. Ponder, W.F. The anatomy of *Diala*, with an assessment of its taxonomic position (Mollusca: Cerithioidea). In Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia, Perth, Australia, 11–18 January 1991; Wells, F., Ed.; Australian Marine Sciences, Western Australian Branch: Perth, Australia, 1991; Volume 2, pp. 499–519.
39. Ponder, W.F. The anatomy and relationships of *Finella* and *Scaliola* (Caenogastropoda: Cerithioidea: Scalioidae). In *The Malacofauna of Hong Kong and Southern China*, 3rd ed.; Morton, B., Ed.; Hong Kong University Press: Hong Kong, China, 1994; pp. 215–241.
40. Hanken, J.; Wake, D.B. Miniaturization of body size: Organismal consequences and evolutionary significance. *Annu. Rev. Ecol. Syst.* **1993**, *24*, 501–519. [[CrossRef](#)]
41. Lützen, J.; Nielsen, C. Galeommatid bivalves from Phuket, Thailand. *Zool. J. Linn. Soc.* **2005**, *144*, 261–308. [[CrossRef](#)]
42. Todt, C. Aplacophoran Mollusks—Still Obscure and Difficult? *Am. Malacol. Bull.* **2013**, *31*, 181–187. [[CrossRef](#)]
43. Middelfart, P. A revision of the Australian Condyllocardiinae (Bivalvia: Carditoidea: Condyllocardiidae). *Molluscan Res.* **2002**, *22*, 23–85. [[CrossRef](#)]
44. Middelfart, P.U. Revision of the Australian Cuninae *sensu lato* (Bivalvia: Carditoidea: Condyllocardiidae). *Zootaxa* **2002**, *112*, 1–124.
45. Le Renard, J.; Bouchet, P. New species and genera of the family Pickworthiidae (Mollusca, Caenogastropoda). *Zoosystema* **2003**, *25*, 569–591.
46. Criscione, F.; Ponder, W.F. A phylogenetic analysis of rissooidean and cingulopsoidean families (Gastropoda: Caenogastropoda). *Mol. Phylogenet. Evol.* **2012**, *66*, 1075–1082. [[CrossRef](#)] [[PubMed](#)]

47. Warén, A. A generic revision of the family Eulimidae (Gastropoda, Prosobranchia). *J. Molluscan Stud. Suppl.* **1984**, *13*, 1–96. [[CrossRef](#)]
48. Marshall, B.A. Cerithiopsidae (Mollusca: Gastropoda) of New Zealand, and a provisional classification of the family. *N. Z. J. Zool.* **1978**, *5*, 47–120. [[CrossRef](#)]
49. Nützel, A. Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berl. Geowiss. Abh. E* **1997**, *26*, 1–229.
50. Marshall, B.A. A revision of the Recent Triphoridae of southern Australia (Mollusca: Gastropoda). *Rec. Aust. Mus. Suppl.* **1983**, *2*, 1–119. [[CrossRef](#)]
51. Criscione, F.; Ponder, W.F.; Kohler, F.; Takano, T.; Kano, Y. A molecular phylogeny of Rissoidea (Caenogastropoda: Rissooidea) allows testing the diagnostic utility of morphological traits. *Zool. J. Linn. Soc.* **2016**, 1–18. [[CrossRef](#)]
52. Golding, R.E. Molecular phylogeny and systematics of Australian and East Timorese Stenothyridae (Caenogastropoda: Truncatelloidea). *Molluscan Res.* **2014**, *34*, 102–126. [[CrossRef](#)]
53. Iredale, T.; Laseron, C.F. The systematic status of *Ctiloceras* and some comparative genera. *Proc. R. Zool. Soc. N.S.W.* **1957**, 1955–1956, 97–109.
54. Bandel, K. Phylogeny of the Caecidae (Caenogastropoda). *Mitteilungen Geol.-Paläontologischen Inst. Univ. Hambg.* **1996**, *79*, 53–115.
55. Pizzini, M.; Raines, B.K.; Vannozzi, A. The Family Caecidae in the South-West Pacific (Gastropoda: Rissooidea). *Bollettino malacologico* **2013**, *49* (Suppl. 10), 1–78.
56. Marshall, B.A. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *J. Nat. Hist.* **1988**, *22*, 949–1004. [[CrossRef](#)]
57. Warén, A. New and little known Mollusca from Iceland and Scandinavia. *Sarsia* **1993**, *78*, 159–201. [[CrossRef](#)]
58. Grindel, J.; Nützel, A. Evolution and Classification of Mesozoic mathildoid gastropods. *Acta Paleontol. Pol.* **2013**, *58*, 803–826. [[CrossRef](#)]
59. Warén, A. Murchisonellidae: Who are they, where are they and what are they doing? (Gastropoda, lowermost Heterobranchia). *Vita Malacol.* **2013**, *11*, 1–14.
60. Brenzinger, B.; Wilson, N.G.; Schrödl, M. Microanatomy of shelled *Kolonella* cf. *minutissima* (Laseron, 1951) (Gastropoda: 'lower' Heterobranchia: Murchisonellidae) does not contradict a sister-group relationship with enigmatic Rhodopemorpha slugs. *J. Molluscan Stud.* **2014**, *80*, 518–540.
61. Haszprunar, G.; Heß, M. A new *Rhodope* from the Roscoff area (Bretagne), with a review of *Rhodope* species (Gastropoda: Nudibranchia?). *Spixiana* **2005**, *28*, 193.
62. Brenzinger, B.; Wilson, N.G.; Schrödl, M. 3D microanatomy of a gastropod 'worm', *Rhodope rousei* n. sp. (Heterobranchia) from Southern Australia. *J. Molluscan Stud.* **2011**, *77*, 375–387. [[CrossRef](#)]
63. Brenzinger, B.; Haszprunar, G.; Schrödl, M. At the limits of a successful body plan—3D microanatomy, histology and evolution of *Helminthope*. (Mollusca: Heterobranchia: Rhodopemorpha), the most worm-like gastropod. *Front. Zool.* **2013**, *10*, 1–27. [[CrossRef](#)] [[PubMed](#)]
64. Peñas, A.; Rolán, E. *Deep Water Pyramidelloidea of the Tropical South Pacific: Turbonilla and Related Genera*; Gofas, S., Ed.; Mémoires du Muséum National d'Histoire Naturelle: Paris, France, 2010; Volume 26, pp. 1–436, In *Tropical Deep Sea Benthos*; 200.
65. Schander, C.; van Aartsen, J.J.; Corgan, J.X. Families and genera of the Pyramidelloidea (Mollusca: Gastropoda). *Boll. Malacol.* **1999**, *34*, 145–166.
66. Schander, C.; Hori, S.; Lundberg, J. Anatomy, phylogeny and biology of *Odostomella* and *Herviera*, with the description of a new species of *Odostomella*. *Ophelia* **1999**, *51*, 39–76. [[CrossRef](#)]
67. Kano, Y.; Brenzinger, B.; Nützel, A.; Wilson, N.G.; Schrödl, M. Ringiculid bubble snails recovered as the sister group to sea slugs (Nudipleura). *Sci. Rep.* **2016**, *6*, 30908.
68. Geiger, D. *Monograph of the Little Slit-Shells*; Volume 1: Introduction, Scissurellidae; Volume 2: Anatomidae, Larocheidae, Depressizonidae, Sutilizonidae, Temnocinclidae; Santa Barbara Museum of Natural History: Santa Barbara, CA, USA, 2012; p. 1291.
69. World Register of Marine Species (WoRMS). Available online: <http://www.marinespecies.org/index.php> (accessed on 20 April 2016).
70. Coan, E.V. The tropical eastern Pacific species of the Condylardiidae (Bivalvia). *Nautilus* **2003**, *117*, 47–61.
71. Hedley, C. The Mollusca of Mast Head Reef, Capricorn Group, Queensland. *Proc. Linn. Soc. N.S.W.* **1906**, *31*, 453–479. [[CrossRef](#)]

72. Albano, P.G.; Sabelli, B.; Bouchet, P. The challenge of small and rare species in marine biodiversity surveys: Microgastropod diversity in a complex tropical coastal environment. *Biodivers. Conserv.* **2011**, *20*, 3223–3237. [[CrossRef](#)]
73. Moorea Biocode Project. Available online: <http://mooreabiocode.org/> (accessed on 10 April 2016).
74. Golding, R.E.; Jones, A.S. Micro-CT as a novel technique for 3D reconstruction of molluscan anatomy. *Molluscan Res.* **2007**, *27*, 123–128.
75. Willan, R.C.; Bryce, C.; Slack-Smith, S.M. Kimberley marine biota. Historical data: Molluscs. *Rec. West. Aust. Mus. Suppl.* **2015**, *84*, 287–343. [[CrossRef](#)]
76. Wilson, N.G.; Kirkendale, L.A. Putting the ‘Indo’ back into the Indo-Pacific: Resolving marine phylogeographic gaps. *Invertebr. Syst.* **2016**, *30*, 86–94. [[CrossRef](#)]
77. Olabarria, C.; Chapman, M.G. Comparison of patterns of spatial variation of microgastropods between two contrasting intertidal habitats. *Mar. Ecol. Prog. Ser.* **2001**, *220*, 201–211. [[CrossRef](#)]
78. Beesley, P.L. Mollusca: The southern synthesis. *Fauna of Australia*; Beesley, P.L., Ross, G.J.B., Wells, A., Eds.; Australian Government Publishing Service (with CSIRO): Melbourne, Australia, 1998; Volume 5, Part A xvi 563p, Part B viii 565–1234.
79. Leray, M.; Meyer, C.P.; Mills, S.C. Metabarcoding dietary analysis of coral dwelling predatory fish demonstrates the minor contribution of coral mutualists to their highly partitioned, generalist diet. *PeerJ* **2015**, *3*, e1047. [[CrossRef](#)] [[PubMed](#)]
80. Berry, O.; Bulman, C.; Bunce, M.; Coghlan, M.; Murray, D.C.; Ward, R.D. Comparison of morphological and DNA metabarcoding analyses of diets in exploited marine fishes. *Mar. Ecol. Prog. Ser.* **2015**, *540*, 167–181. [[CrossRef](#)]
81. Schrödl, M.; Jörger, K.M.; Klussmann-Kolb, A.; Wilson, N.G. Bye bye “Opisthobranchia”! A review on the contribution of mesopsammitic sea slugs to euthyneuran systematics. *Thalassas* **2011**, *27*, 101–112.
82. Valentich-Scott, P.; Foighil, D.Ó.; Li, J. Where’s Waldo? A new commensal species, *Waldo arthuri* (Mollusca, Bivalvia, Galeommatidae), from the Northeastern Pacific Ocean. *Zookeys* **2013**, *316*, 67–80. [[CrossRef](#)] [[PubMed](#)]
83. Li, J.; Foighil, D.Ó.; Middelfart, P. The evolutionary ecology of biotic association in a megadiverse bivalve superfamily: Sponsorship required for permanent residency in sediment. *PLoS ONE* **2012**, *7*, e42121. [[CrossRef](#)] [[PubMed](#)]
84. Heard, S.B.; Hauser, D.L. Key evolutionary innovations and their ecological mechanisms. *Hist. Biol.* **1995**, *10*, 151–173. [[CrossRef](#)]
85. Hunter, J.P. Key innovations and the ecology of macroevolution. *Trends Ecol. Evol.* **1998**, *13*, 31–36. [[CrossRef](#)]
86. Leasi, F.; Andrade, S.C.; Norenburg, J.L. At least some meiofaunal species are not everywhere. Indication of geographic, ecological and geological barriers affecting the dispersion of species of Ototyphlonemertes (Nemertea, Haploneurata). *Mol. Ecol.* **2016**, *25*, 1381–1397. [[CrossRef](#)] [[PubMed](#)]
87. Jörger, K.M.; Norenburg, J.L.; Wilson, N.G.; Schrödl, M. Barcoding against a paradox? Combined molecular species delineations reveal multiple cryptic lineages in elusive meiofaunal sea slugs. *BMC Evol. Biol.* **2012**, *12*, 245.
88. Halt, M.N.; Kupriyanova, E.K.; Cooper, S.J.; Rouse, G.W. Naming species with no morphological indicators: Species status of *Galeolaria caespitosa* (Annelida: Serpulidae) inferred from nuclear and mitochondrial gene sequences and morphology. *Invertebr. Syst.* **2009**, *23*, 205–222. [[CrossRef](#)]
89. Cook, L.G.; Edwards, R.D.; Crisp, M.D.; Hardy, N.B. Need morphology always be required for new species descriptions? *Invertebr. Syst.* **2010**, *24*, 322–326. [[CrossRef](#)]
90. Jörger, K.M.; Schrödl, M. How to describe a cryptic species? Practical challenges of molecular taxonomy. *Front. Zool.* **2013**, *10*. [[CrossRef](#)] [[PubMed](#)]

