



Systematics, Phylogeny and Biology of Polyplacophora

FOREWORD

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The last two of three highly successful previous workshops in Menfi had focused on opisthobranchs and neogastropods, respectively, and this emphasis on a particular taxon proved to be a tremendously successful format. Each brought together leading authorities on the particular taxon together with other less-established workers and allowed them the rare opportunity to exchange ideas and expertise in a friendly and productive setting. Thus it was natural to plan a fourth workshop that would likewise focus on a particular taxon, in this case the chitons or Polyplacophora. Chitons are an ancient molluscan lineage with a generally conservative appearance and grazing habit yet are a group that has generated considerable interest among diverse scientists. Researchers investigating topics as diverse as molluscan evolution and comparative anatomy (Wingstrand, 1985; Baxter *et al.*, 1987; Eernisse and Reynolds, 1994; Gowllett-Holmes *et al.*, 1998), biomineralization (Kirschvink and Hagadorn, 2000; Webb *et al.*, 2001; Brooker *et al.*, 2003) and marine community ecology (Dethier and Duggins, 1984; Duggins and Dethier, 1985) have featured chitons in their studies. So it came to be that the Scientific Committee (Bruno Dell'Angelo, Marco Oliverio, and Renato Chemello) and the Organizational Committee (Vanna Rotolo) extended invitations to five leading authorities on diverse aspects of the study of Polyplacophora. Their successful promotion of the event, aided by considerable support from the community of Menfi, attracted many other polyplacophoran researchers. The diverse nature of the international attendees, the many natural attractions in Sicily, and especially the ceaseless efforts of the local organizers all contributed to make this workshop truly memorable.

Eight lectures by the five invited speakers and 19 other communications or posters covered a diversity of topics that can be roughly categorized as follows:

1. Phylogenetic analyses across chitons or within specific genera.
2. Biogeographic or reproductive patterns emerging from regional faunal surveys of living or fossil chitons
3. Dietary or ecological characterization of specific chiton species
4. Investigations of chiton radular teeth biomineralization

Nine papers have been finally accepted for the publication in

the present proceedings volume, and these represent all but the last of the above categories.

1. Phylogenetic analyses across chitons or within specific genera

My own presentation at the meetings was the only attempt to address the current state of higher-level chiton phylogenetic estimates, and I summarized the recent progress made in better resolving relationships, especially employing gill placement, egg hulls, and sperm characteristics (Eernisse, 1984; Sirenko, 1993; 1997; Buckland-Nicks, 1995). The only new analyses I presented in Menfi demonstrated that the sparse (mostly 18S ribosomal DNA) gene sequences available for chitons at that time were woefully inadequate to contribute to a better resolution of higher-level chiton phylogeny. The good news is that this situation is now much improved. Since the workshop, our much more ambitious study of five gene loci representing over 40 genera of chitons, and multiple outgroups, has appeared (Okusu *et al.*, 2003). My own subsequent sequencing efforts (D. J. Eernisse, in prep.) have yielded approximately 150 additional sequences, and these have given me renewed optimism that higher-level chiton phylogenetic estimates will continue to be improved with continued molecular sequence comparison. Moreover, these results are already generally congruent with ongoing parallel phylogenetic analyses of morphological data sets (D. J. Eernisse, J. Buckland-Nicks, and A. N. Hodgson, in prep.).

Continued morphological study will also certainly contribute to improving chiton phylogenetic estimates. Here, Hiroshi Saito elegantly demonstrates the utility of comparisons of the radula for a specific test case, Cryptoplacoidea, and his results suggest that similar studies are expected to have great potential in sorting out other groups of chitons. It might surprise those readers more familiar with gastropods how little utilized the radula has been for chitons. The chiton radula is certainly much more conservative than for gastropods, with nearly invariant 17 teeth per row, with the second lateral pair of teeth per row used as the major working teeth for scraping or biting, and always coated with the hard magnetic iron mineral, magnetite. Yet the historical reluctance of many chiton specialists to use the radula is also partly a quirk of historical timing. In one of his earliest publications, the renowned German malacologist, Johannes Thiele, happened to have bad timing and flawed specimen iden-



tifications when he published his 1893 study of chiton dentition, entitled “Das Gebiss der Schnecken zur begründung eine natürlichen Classification.” In it, he proposed 23 new chiton genera based on radular distinctions, of which only one has survived to present classifications (as a subgenus). This happened to be the same year that Henry Pilsbry published his monumental “Monograph of the Polyplacophora.” Pilsbry completed his monograph with little knowledge of Thiele’s radular comparisons, and he primarily relied on shell, girdle, and gill attributes. Thiele later (1909–1910) published “Revision des Systems der Chitonen,” which was much more refined than his 1893 study. For example, he began by listing and correcting the numerous misidentifications that had compromised his earlier study. He then continued to give primary emphasis to the radula throughout his newer revision. Summarizing his results, in 1910, he acknowledge the important contributions made by Carpenter, Pilsbry, and Plate, but firmly objected to Pilsbry’s categorical dismissal of his radular distinctions as mere slight variations of a single organ. He then went on to provide an elaborate description of which radular distinctions he considered to be most generally valuable, with many specific examples. Now, Saito has renewed this call to employ the radula as a rich source of characters, especially as it can now be studied with the combined approach of both scanning electron and light microscopes. Thiele would have enjoyed this contribution as much as I did!

Saito has focused on Cryptoplacoidea (*sensu* Sirenko, 1997) as a test case for examining the potential utility of employing radular characters. This contribution is particularly welcome because members of Cryptoplacoidea (approximately equivalent to Acanthochitonina in Van Belle, 1983, 1999) were among the approximately 20 percent of chiton species not covered in the incomplete recent monograph series on chitons by the late Piet Kaas and Richard Van Belle (1985–1998). Cryptoplacoidea includes speciose genera such as *Acanthochitona* and *Notoplax*, but also morphologically divergent genera such as *Choneplax*, *Cryptoconchus*, and *Cryptoplax*. Saito first considers the variation he has noted “tooth by tooth” and then treats each genus. His comparisons have led to important inferences about the evolution of traits within this group. For example, he concludes that the tegmentum (the unique dorsal “living” shell layer found only in chitons) has been reduced through convergent evolution no fewer than three times within Cryptoplacoidea. He has sorted out the members of *Acanthochitona* and *Notoplax* into provisional species groups based on their radular affinities, and has also proposed affinities of other genera with each of these. Specifically, he would group *Choneplax* and *Cryptoplax* with *Acanthochitona*, and the type species of *Cryptoconchus* with *Notoplax*. Other species currently included in *Cryptoconchus* are regarded as closer to *Acanthochitona*, instead, so that their inclusion within *Cryptoconchus* should be abandoned. Saito also hints at the probable misplacement of *Hemiarthrum* and *Cryptochiton* within Cryptoplacoidea. The case of *Cryptochiton* has recently been confirmed by DNA sequence comparisons (Okusu et al., 2003; Eernisse, in prep.); *Cryptochiton* instead shows sequence

affinities with northern Pacific members of Mopaliidae. Interestingly, Thiele (1910) concluded the same based on his described radular affinities of *Cryptochiton* and *Amicula* (Mopaliidae). Adults of *Amicula* spp. also show striking similarity to juveniles of *Cryptochiton*.

2. Biogeographic patterns emerging from regional faunal surveys of living or fossil chitons

Bruno Anseeuw and Yves Terryn have presented the results of their first-hand survey and detailed description of an estimated 22 to 24 species of chitons collected from the intertidal zone along the coast of Jordan, Red Sea, significantly increased from the 13 intertidal species previously known to occur in Jordan. Besides the thorough redescriptions and synonymies provided for each species, most notable is the description of a new species of *Parachiton* Thiele, 1909.

As a follow-up to a previous study (Reyes-Gómez and Salcedo-Vargas, 2002), Adriana Reyes-Gómez has contributed an updated literature-based review of the chitons that have been reported from Mexican waters. The Mexican coastline includes shores in multiple Caribbean and Pacific biogeographical provinces so its chiton fauna is understandably diverse, and these contributions have helped set the stage for future investigations. Because the Gulf of California is a geologically-young sea, it is particularly interesting that Reyes-Gómez found it to have the greatest chiton species diversity, including a substantial number of endemic species.

Bruno Dell’Angelo, Antonio Bonfitto, Marco Taviani, and Bruno Sabelli have contributed a survey of chiton valves recovered from coarse-grained bioclastic sands forming around coral reefs in the Ifaty-Tulear back reefs of Madagascar, western Indian Ocean. These samples were collected in 1995 by a European team of SCUBA researchers involved the E.U. TESTREEF project. Altogether they treat 16 chiton species identified from these samples, and their thorough scanning electron microscope (SEM) study has provided new details for several of these species that were poorly known.

In another excellent and comprehensive treatment of regional fossil chitons, Bruno Dell’Angelo, Bernard Landau and Robert Marquet report here their findings of the Early Pliocene chitons from Estepona in southwestern Spain. This represents a substantial undertaking based on the careful study of over 400 fossil valves. Of 18 species treated, two are new species described herein, and 12 are still living on the Atlantic coast of Europe or in the Mediterranean Sea. Most live in rather shallow water but there are at least two extant species only known from relatively deep collections. As the authors point out, this tremendous diversity greatly exceeds any other reported diversity of Pliocene chitons from a single European locality.

Danilo Scuderi, Giovanni F. Russo, and Bruno Dell’Angelo have investigated the occurrence and ecological associations of seven chiton species in shallow water at two sites in the Bay of Catania,



in eastern Sicily. One notable observation is the report of a formerly rarely seen species, *Chiton phaseolinus* Monterosato, 1879. Scuderi and colleagues have also made the first observations of a brooding reproductive behavior in one of the species, *Lepidochitona monterosatoi* Kaas & Van Belle, 1981. Among Mediterranean chiton species, brooding was only previously reported from a congener, *L. caprearum* (Scacchi, 1836), as described in classic detail by Kowalevsky (1883). I have extensively studied chiton brooders classified in this genus myself, but emphasizing species from North American western shores (Eernisse, 1988). I did observe brooding chitons along the shores of Croatia in 1989 and, after hearing Scuderi deliver his talk, I was anxious to return home to see if I should have identified these Croatian brooders as *L. monterosatoi* instead of *L. caprearum*. This would have been strangely reminiscent of a confusing case all too familiar to me, a California brooder studied in detail by Stanford University Professor, Harold Heath (1905), whose specimen identifications as *Trachydermon raymondi* Pilsbry, 1894 [= *L. dentiens* (Gould, 1846)] came from the country's foremost chiton expert, Henry Pilsbry. Much later I discovered that the common *L. dentiens* was instead a free spawner and the rare, but locally abundant, brooder was an undescribed species, subsequently named *L. caverna* Eernisse, 1986. So was Kowalevsky's brooder really the much later described species, *L. monterosatoi*, now demonstrated to be a brooder by Scuderi *et al.*, and could *L. caprearum* really be a free spawner, or are there two separate species that brood in the Mediterranean? Upon returning home, I was able to reexamine the brooding specimens I collected in Croatia. They appear to best match the description for *L. caprearum*, not *L. monterosatoi*, so it would appear that there really are two chiton species that brood in the Mediterranean. It is still curious why the brooding activities of *L. caprearum* have only rarely, if ever, been observed in Italy since Kowalevsky's detailed report, including by Scuderi *et al.* It also remains to be tested whether the two species that brood are sister taxa, in which case it would be likely that they were both derived from a common ancestor that also was a brooder. Alternatively, perhaps brooding has arisen convergently in each species.

Finally, I delivered a paper in Menfi that would have fit best in this category, but I already published it electronically just prior to the meeting. This was related to my "Chiton Images on the Web" website (<http://biology.fullerton.edu/deernisse/chitons/>) created especially for these meetings (and since maintained and updated) as a new report type by my "Chiton Stacks" software package. I have personally used this software for over a decade for managing a worldwide database of chiton species, including their range distribution records, nomenclature, and type material and locality. My goal is to eventually transfer other sorts of reports generated by this software to the Web.

3. Dietary or ecological characterization of specific chiton species

Boris Sirenko presented a comprehensive synthesis of his ongoing worldwide research program on deep water chitons that inhabit sunken wood. Sirenko postulates a provocative hypothe-

sis that such chiton lineages and their associations with sunken wood are ancient. For example, he draws parallels between Recent species of the genus, *Ferreiraella* and fossil chitons from the Middle Pennsylvanian of Illinois (approximately 300 Ma; see Yochelson & Richardson, 1979), which he considers to be not only very closely related but also similar in their ecology, both feeding on sunken plant material. The hypothesis rests on the current distribution of the genera of deep-water chitons with such habitats. In particular, Sirenko argues that their distributions are well enough known to be confident that they are truly absent from geologically younger ocean basins, despite the availability of abundant sunken wood there. Their restricted distribution in only older ocean basins is interpreted as evidence that they are relicts in those ocean basins. This is a productive hypothesis because it leads to testable hypotheses. For example, if Sirenko is correct, then *Ferreiraella* should have diverged from other extant chiton lineages over 300 million years ago, which should make it by far the most basal lineage of extant chitons. Molecular methods might provide such a test.

Stefano Schiaparelli, Bruno Dell'Angelo, Bruno Sabelli, Barbara Gualandi and Marco Taviani report new observations for the diet of the rare deep-water chiton, *Bathychiton biondii* Dell'Angelo & Palazzi, 1988. The discovery of a living specimen in close proximity to a particular sponge suggested to the authors the possibility that this species might feed on those sponges, as a sponge diet is not uncommon among other deep-water chitons [e.g., *Hanleya nagelfar* (Lovén, 1846); see Warén and Klitgaard, 1991]. Schiaparelli and coauthors report mixed results with respect to the diet of *B. biondii* and negative results for a second species from similar depths. Even though it does not appear that either species has an obligate specialization on sponges, the results are interesting and should be applied to other deep-water species that are live collected, whenever possible.

Shirou Nishihama has reported the size and density distribution patterns of a chiton, *Stenoplax alata*, observed in an intertidal to shallow subtidal cobble shore habitats in Japan. These measurements should help understand community and intraspecific interactions, especially because they have not been carried out for many chiton species, and are almost non-existent for chitons in the tropics.

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Speaking for all of those who attended the meetings in Menfi, we all were extremely grateful for everything Vanna Rotolo (Organizational Committee) did to ensure the meetings were a tremendous success, along with her legion of local helpers and sponsors who all worked long hours to make this meeting truly memorable. The Scientific Committee also put together an excellent program of invited speakers and contributed papers and made sure we had plenty of time to discuss ideas. Bruno Dell'Angelo was primarily involved in assembling this set of interesting articles on chitons, and I would like to thank him personally for all his help with this introduction and his generosity over the years.



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