

Introduction to the symposium “Advances in Chiton Research”*

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The present volume features contributions from participants of the symposium, “Advances in Chiton Research,” in Seattle, Washington on 31 July 2006. As the organizer for this symposium, I was impressed with the willingness of national and international authorities or students whose diverse research involves chitons to participate in these meetings. The symposium was a tremendous success and compared favorably to four previous meetings of international scope that were devoted to chitons: (1) 1987 AMS symposium on “Biology of the Polyplacophora” in Key West, Florida (see *American Malacological Bulletin* 6(1), 1988); (2) 1st International Chiton Symposium, 1991, Adelaide, Australia (see *Journal of the Malacological Society of Australia* 13, 1992); (3) the 4th International Workshop on Malacology devoted to Polyplacophora, 2001, Menfi, Sicily, Italy (see *Bollettino Malacologico* Supplemento 5: I-IV, [2003] 2004); and (4) 2nd International Chiton Symposium, 2003, Tsukuba, Japan (see *Venus* 65(1-2), 2006). The participants of the present symposium (Fig. 1) featured 14 speakers, of whom half were international, and 10 posters devoted to chitons. Including all co-authors, there were 39 total contributors to the symposium and about a third of these were students.

Research on chitons is central to many aspects not only of malacology but also of zoology, paleontology, evolutionary biology, molecular systematics, molecular evolution, physiology, and ecology (reviewed by Schwabe and Wanninger 2006, Eernisse 2007, Todt *et al.* 2008). The present collection of articles reflects this integrative role for contemporary chiton research. Some of the symposium speakers are not represented here because they have already published articles related to their talks in other journals, including Jean-Bernard Caron (Caron *et al.* 2006a, 2006b), Ryan Kelly (Kelly and Eernisse 2007, 2008, Kelly *et al.* 2007), and Enrico Schwabe (Schwabe 2008). Lesley Brooker (“Genes and biomineralization in the radular teeth of chitons”) and Bruce Runnegar (“Paleontological evidence for the origin of valves in polyplacophoran molluscs”) gave insightful presentations and have contributed as co-authors on articles in this volume. Bernie Lieb and his coauthors have continued to

elucidate the molecular evolution and systematics of molluscan hemocyanin (*e.g.*, Bergmann *et al.* 2007), and his forthcoming collaborative studies on chiton hemocyanin as a promising new phylogenetic marker are eagerly anticipated. Those who have contributed articles for the present volume still represent an impressive cross-section of the diverse, ongoing research on chitons.

Pojeta and DuFoe (this volume) have extended what is known about the earlier described Ordovician spiny chiton, *Echinochiton dufoei* Pojeta, Eernisse, Hoare, and Henderson, 2003. This fossil has already figured prominently in the ongoing debate on the disparity of Paleozoic chitons, including whether the geologically younger multiplacophorans diverged from within chitons or from an earlier “stem chiton” ancestor, and whether certain Cambrian “problematica” with disputed affinities, such as *Wiwaxia* Walcott, 1911, halkierids, and *Odontogriphus* Conway Morris, 1976 could potentially be close relatives of chitons. The four previously known *E. dufoei* specimens were already remarkable for their articulated preservation but details of the anterior portion of the animal were still unknown. After additional monumental collecting effort by co-author Jimmie DuFoe, resulting in the discovery of even better fossil examples that were also displayed in a special session at the symposium, Pojeta and DuFoe are now able to provide details of the anterior portion. They show that the anterior portion has the same striking hollow girdle spines found surrounding the rest of the animal. The authors also reconsider the significance of *E. dufoei* in discussions of molluscan and polyplacophoran evolution.

Shaw *et al.* (this volume) have contributed an extremely useful description of methods they used to analyze radular tooth formation and biomineralization, ensuring minimum deformation of the fragile associated tissue layers involved in biomineralization processes. Based on Jeremy Shaw’s Ph.D. research, the authors have employed multiple state-of-the-art electron microscopy approaches to analyzing biomineralization processes in chitons, the results of which are being published elsewhere (*e.g.*, Shaw *et al.*, 2008). The exquisite results achieved by these authors reflect not only the con-

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Figure 1. Attending participants in the “Advances in Chiton Research” symposium, 31 July 2006 in Seattle, Washington. Numbers correspond to the inset key: 1. Stephaney Puchalski; 2. Albert Rodriguez; 3. Jeremy Shaw; 4. John Pojeta, Jr.; 5. Roger Clark; 6. Ryan Kelly; 7. Alejandro Herrera-Moreno; 8. Liliana Betancourt; 9. Donald Cadien; 10. Hiroshi Saito; 11. Lesley Brooker; 12. Doug Eernisse; 13. Mike Vendrasco; 14. John Buckland-Nicks; 15. Jimmie DuFoe; 16. Julia Sigwart; 17. Anel Ramirez Torres; 18. Klaus Streit; 19. Bernie Lieb; 20. Christine Fernandez; 21. Bruce Runnegar; and 22. Jean-Bernard Caron.

siderable contributions by Shaw but also the high quality of the electron microscope facility at Murdoch University, Perth, Western Australia, headed by co-author David Macey, and notably drawing on the considerable expertise of Shaw’s mentor, co-author Lesley Brooker. Besides a detailed examination of potential fixation artifacts, with implications for interpreting electron micrographs, I was especially impressed by the simple method for cleaning a radula using a high-pressure jet of water. The clever adaptation of a dis-

posable pipet tip not only allows for avoiding artifacts associated with applying alkaline treatment but also results in the most pristine images of a chiton radula that I have ever seen.

Sigwart (this volume) has extended what has long been recognized as a phylogenetically informative set of traits, the position of the gill rows relative to the foot, the nephridiopores, and the gonopores, and also characteristics and the number of the gills within each gill row, to reveal unexpected variation in the most poorly known of all chiton taxa: the

mostly deep-water Lepidopleurida (*sensu* Sirenko, 2006; alternatively as Lepidopleurina). Her present contribution and her ongoing molecular and morphological investigations are welcome additions to the scant literature on lepidopleurid chitons.

Vendrasco *et al.* (this volume) have investigated the phylogenetic utility of the aesthete (or esthete) canal morphology in Mopaliidae, testing between different expectations implied by either its conventional classification or the conflicting arrangement predicted by molecular results (Kelly and Eernisse 2008, Eernisse, unpubl. data). This is a significant change because it implies that Mopaliidae, as recently reformulated (*e.g.*, Eernisse *et al.* 2007), had a relatively recent origin and a dramatic subsequent diversification while largely confined to the northern Pacific Ocean. Based on the pattern of innervation of esthetes, Vendrasco *et al.* provide independent corroboration generally agreeing with the molecular arrangement. Moreover, they have further demonstrated the phylogenetic utility of considering esthete innervation patterns across chitons.

Clark (this volume) has contributed two significant taxonomic articles here, the first clarifying the taxonomic status a north/south species pair of common, but confusing, shallow-water chitons found along western North America. In agreement with recent morphological and molecular treatments (Eernisse *et al.* 2007, Kelly and Eernisse 2008), he has formally revived *Mopalia kennerleyi* Carpenter, 1864 from obscurity for the northern species (Alaska to northern California) and has restricted *Mopalia ciliata* (Sowerby, 1840) to the south, occurring no further north than northern California. Clark's second contribution introduces two new species discovered by recent exploration of the deep-water habitat of the Monterey Sea Canyon and also restores full generic status for members of *Tripoplax* Berry, 1919, to which the new species are assigned.

Puchalski *et al.* (this volume) have assembled a comprehensive database of nominal fossil chiton species, made available on-line (<http://biology.fullerton.edu/deernisse/fossilchitons/>) in association with this publication. They have used this database to investigate potential sampling biases that have likely affected perceptions of the chiton fossil record.

Buckland-Nicks (this volume) provides an overview and new analysis, reviewing phylogenetic inferences that have been drawn from comparing chiton eggs, egg hull coverings, sperm morphology, and egg-sperm interactions during fertilization. As he and his colleagues have continued to demonstrate in publications featuring splendid electron microscopy (*e.g.*, Buckland-Nicks and Brothers 2008), attention to chiton gametes and their interaction is highly informative for chiton phylogenetics.

Saito *et al.* (this volume) have provided a thorough

description of three newly discovered chiton species found near hydrothermal vents and cold seeps around Japan. The authors also consider whether these and other chitons reported from similar habitats are necessarily associated with these chemosynthetic environments.

Finally, I have contributed (Eernisse, unpubl. data) a preliminary phylogenetic analysis of worldwide chitons based on about 350 partial sequences of the mitochondrial 16S ribosomal DNA gene. While this is planned to be the first phase before an eventual multi-locus analysis including these same taxa, the 16S gene appears to be relatively effective in both separating chiton species and in providing a higher-level inference of relationships that agrees well with recent cladistic morphological analyses. The taxon sampling in this study is much more extensive than in the only previous DNA-based analysis of chiton phylogeny (Okusu *et al.* 2003). This has allowed a more complete inference of relationships across chitons, with important phylogenetic implications that mostly agree with, but also challenge, certain aspects of our best available classifications of living chitons (*e.g.*, Sirenko 2006).

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LITERATURE CITED

- Bergmann, S., J. Markl, and B. Lieb. 2007. The first complete cDNA sequence of the hemocyanin from a bivalve, the protobranch *Nucula nucleus*. *Journal of Molecular Evolution* **64**: 500-510.
- Buckland-Nicks, J. and E. Brothers. 2008. On fertilization in *Chaetopleura apiculata* and selected Chitonida. *Biological Bulletin* **214**: 184-193.
- Caron, J.-B., A. H. Scheltema, C. Schander, and D. Rudkin. 2006a. A soft-bodied mollusk with a radula from the Middle Cambrian Burgess Shale. *Nature* **442**: 159-163.
- Caron, J.-B., A. H. Scheltema, C. Schander, and D. Rudkin. 2006b. Reply to Butterfield on stem-group "worms": Fossil lophotrochozoans in the Burgess Shale. *BioEssays* **29**: 1-3.
- Eernisse, D. J. 2007. Chitons. In: M. W. Denny and S. D. Gaines, eds. *Encyclopedia of Tidepools and Rocky Shores*. University of California Press, Berkeley, California. Pp. 127-133.
- Eernisse, D. J., R. N. Clark, and A. Draeger. 2007. Polyplacophora. In: J. T. Carlton, ed., *Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon*, 4th Ed. University of California Press, Berkeley, California. Pp. 701-713.
- Kelly, R. P. and D. J. Eernisse. 2007. Southern hospitality: A latitudinal gradient in gene flow in the marine environment. *Evolution* **61**: 700-707.
- Kelly, R. P. and D. J. Eernisse. 2008. Reconstructing a radiation:

- The chiton genus *Mopalia* in the north Pacific. *Invertebrate Systematics* **22**: 1-12.
- Kelly, R. P., I. N. Sarkar, D. J. Eernisse, and R. Desalle. 2007. DNA barcoding using chitons (genus *Mopalia*). *Molecular Ecology Notes* **7**: 177-183.
- Okusu, A., E. Schwabe, D. J. Eernisse, and G. Giribet. 2003. Towards a phylogeny of chitons (Mollusca: Polyplacophora) based on combined analysis of five molecular loci. *Organisms, Diversity and Evolution* **3**: 281-302.
- Schwabe, E. 2008. Discovery of the South African polyplacophoran *Stenosemus simplicissimus* (Thiele, 1906) (Mollusca, Polyplacophora, Ischnochitonidae) in the Southern Ocean. *American Malacological Bulletin* **24**: 71-77.
- Schwabe, E. and A. Wanninger. 2006. Polyplacophora. In: C. F. Sturm, T. A. Pearce, and A. Valdés, eds., *The Mollusks: A Guide to their Study, Collection, and Preservation*. American Malacological Society and Universal Publishers, Boca Raton, Florida. Pp. 217-228.
- Shaw, J. A., D. J. Macey, and L. R. Brooker. 2008. Radula synthesis in three species of iron mineralizing mollusc: Production rate and elemental demand. *Journal of the Marine Biological Association of the United Kingdom* **88**: 597-601.
- Sirenko, B. 2006. New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus* **65**: 27-49.
- Todt, C., A. Okusu, C. Schander, and E. Schwabe. 2008. Solenogastres, Caudofoveata, and Polyplacophora. In: W. F. Ponder and D. R. Lindberg, eds., *Phylogeny and Evolution of Mollusca*. University of California Press, Berkeley, California. Pp. 71-96.

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