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Introduction to the James H. Lee symposium, "Great Unanswered Questions in Malacology," 77th annual meeting of the American Malacological Society.

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Humans have been asking questions about mollusks for tens of thousands of years, and many of those questions have been answered. However, despite extensive study, many gaps remain in our knowledge about mollusks.

This issue of *American Malacological Bulletin* includes eight papers from the 11 presentations in the James H. Lee symposium, "Great Unanswered Questions in Malacology," held at the American Malacological Society meeting in Pittsburgh, Pennsylvania, 23–27 July 2011 (Sturm *et al.* 2011). Experts from North America and Europe report on various groups of mollusks, discussing recent developments in these groups as well as known unknowns that are ripe for future exploration. Our goal is for these reports to provide stimulating ideas for future directions, perhaps inspiring graduate students and others with topics for projects.

The seed for this symposium had been planted in Tim's mind in 1985 when he was a student at the University of California at Berkeley. For a Paleontology Department seminar class led by Carole Hickman, we listed major questions about mollusks. Twenty-four years later in 2009, while returning to Pittsburgh from the Mid-Atlantic Malacologists meeting in Delaware, Charlie and Tim were dining at the Lost Cajun Kitchen in Columbia, Pennsylvania. Charlie would be president of AMS in two years for the Pittsburgh 2011 meeting so we discussed meeting plans including the president's symposium. The idea of the major questions exercise evolved into this symposium addressing unanswered questions. We invited a speaker for each extant class of Mollusca (assuming a single class of Aplacophora), and because Bivalvia and Gastropoda are large in numbers of species and amount of research, we divided them by realm to have separate speakers on both marine and freshwater bivalves, and on marine, freshwater, and terrestrial gastropods.

James H. Lee, a retired healthcare executive, had a keen interest in Malacology. Jim was Charlie's father-in-law and accompanied Charlie on numerous mollusk-focused field trips in Pennsylvania, Maryland, North Carolina, and Florida. In addition to his activities in the field, he also supported malacology at the Carnegie Museum of Natural History. He participated in the publication of the AMS book, *The Mollusks* (Sturm *et al.* 2006), serving as one of the amateur reviewers, reading and commenting on most of the chapters and he helped fund the book's publication. Had Jim not passed away, he would have been involved with this annual meeting. In recognition of his interests, his dear wife Dolores made a contribution to help support this symposium named in his honor.

Presenters in the symposium were Robert A. D. Cameron, Robert T. Dillon, Jr., Douglas J. Eernisse, Daniel L. Graf, Gerhard Haszprunar, Carole S. Hickman, Kevin M. Kocot, Paula M. Mikkelsen, Elizabeth K. Shea, Gerhard Steiner, and Christiane Todt (Fig. 1).

We might expect a creature as intriguing as the giant squid, which has captured our imaginations over the centuries and appears in our fiction and movies, to have been thoroughly studied by scientists. Considerable literature does enlighten us about cephalopods. Octopus intelligence is legendary, surpassing that of any other non-vertebrate (and many vertebrates); squid axons facilitate studies of neurobiology, and squids are commercially harvested for food. In a clever approach to identifying unanswered questions, Clyde **Roper** and Liz **Shea** refer to the charismatic giant squid as a model demonstrating many gaps in our knowledge about systematics and basic biology of cephalopods. Of the species that have been studied, these intelligent creatures reproduce once then die. This non-overlap of generations seems unfortunate because they have no opportunity to pass their acquired knowledge to their offspring, but Roper and Shea present evidence that giant squids might have an extended spawning time. Although adult and juvenile giant squid occupy different depths, we speculate the possibility that older giant squid might be able to pass knowledge to younger ones.

The Bivalvia is the second largest class of mollusks, yet as Rüdiger **Bieler**, Paula M. **Mikkelsen**, and Gonzalo **Giribet** point out in their paper about marine bivalves, debate continues regarding exactly how many of them there are. The Bivalvia, charming despite their acephalic nature, have not been utilized as a research model to the same extent as the Gastropoda and Cephalopoda. Bieler *et al.* discuss some of the reasons for this. The sister-group for the Bivalvia and how they fit into a molluscan phylogeny is still an area ripe with

Figure 1. Participants in the Symposium. Left to right, front row: Timothy A. Pearce, Daniel L. Graf, Robert A.D. Cameron, Carole S. Hickman, Douglas J. Eernisse, Kevin M. Kocot, Elizabeth K. Shea; back row: Robert T. Dillon, Jr., Gerhard Haszprunar, Paula M. Mikkelsen, Christiane Todt, and Gerhard Steiner. Photo by Fabio Moretzsohn.

research potential. Moreover, some fruitful areas include the soft tissue anatomy and morphology of the bivalves. Few bivalves have been studied extensively and features of most species, genera, and families have not been described except for their shell morphology. While a few bivalves are cultivated or harvested for food, and thus are relatively well known, we know little, if anything, regarding the anatomy of the vast majority of bivalves. These authors implore us to start exploring the anatomy, morphology, and ecology of these fascinating organisms.

Daniel **Graf** reviews the current state of our knowledge of freshwater bivalve diversity and evolution, explicitly defining what is a freshwater bivalve. While he mentions a number of bivalve groups that have invaded freshwater environments, he discusses three in depth: Unionoida, Sphaeriidae, and Cyrenidae (formerly Corbiculidae). He discusses the problems with the phylogenetic relationships in these groups and the implications for future research. He briefly mentions the unusual larval biology of Unionidae and conservation needs in these organisms that are part of the ongoing extinctions in freshwater ecosystems. He discusses the implications of convergent evolution among these groups and their adaptation to life in a hypoosmotic medium. In addition, he elucidates a number of biological phenomena that cause us to look at mollusks in a new light. Specifically, he highlights doubly-uniparental inheritance of mitochondria, genome duplication, and androgenetic reproduction.

Molluscan shell formation involves biological, chemical, and physical processes that can result in different or similar structures. Carole **Hickman** focuses on marine gastropods, noting that similar structures are usually regarded as either homologous or analogous, she then offers a third explanation: constructional morphology. In showing how constructional morphology can lead to similar shell structures, she draws attention to the observation that shell mineralization does not always require presence of mantle or periostracum (*i.e.*, remote biomineralization), she discusses shell reorganizations such as the filling of deep velar notches at metamorphosis (heterotectonic construction), and she shows how the property of shells by which they record past events (funeous structure) can lead to recurring patterns. Her elegant illustrations include larval and metamorphosed marine gastropods as well as an abiotic example.

Studying diversity of land snails could start with enumerating species and figuring out why they have the forms they do and why they live where they do, but Robert **Cameron**'s paper notes that numerous unknowns complicate these tasks. What is a species anyway, how comparable is a minute species to a large snail having nearly 100,000 times greater mass, or how do ecological and evolutionary forces affect snails and slugs differently? Cameron recognizes as controversial the question whether interspecific competition structures faunas or even exists among land snails. We know that land snails have gotten to places to which they cannot walk (*e.g.*, Hawaii), but how they got there remains largely unknown. He presents a wealth of unknown questions relating to land mollusk diversity.

The Aplacophora differ from other Mollusca morphologically, have relatively few species, and are not commonly encountered, but they are relevant to understanding molluscan relationships and evolution. Christiane **Todt** outlines the current status of aplacophoran research and discusses unknowns as areas for future studies. Their diversity is often underappreciated, but they can range in size from minute interstitial creatures up to 30 cm long, they occur throughout ocean depths from the surface to 9000 m, and they can be very numerous at hydrothermal vents. Acknowledging the ongoing debate about whether the two major types of Aplacophora are sister groups, Todt in either case considers their differences profound enough to call them separate classes. In addition to systematic questions, she identifies aspects of basic biology that remain unknown.

Although Monoplacophora contain relatively few species, the class is of great interest because it is highly relevant to understanding phylogeny of all Mollusca. Gerhard

Haszprunar and Bernhard **Ruthensteiner** bring us up to date on new developments in monoplacophoran systematics and biology. On the debate whether serially-repeated structures are shared with the ancestor of all Mollusca or whether they are independently-derived in Monoplacophora and Polyplacophora, the authors conclude that both positions are correct, with some repeated structures being plesiomorphic and others autapomorphic. Of the many remaining gaps in our knowledge, they focus on ontogeny as the unknown of greatest importance for understanding morphology and evolution of Monoplacophora.

Resolving how molluscan classes are related is becoming clearer with the application of molecular techniques, especially multi-gene and whole-genome analyses. Some malacologists became concerned that Mollusca wasn't monophyletic after an analysis by Goloboff *et al.* (2009) recovered most traditional phyla as monophyletic, but Mollusca came out polyphyletic (Scaphopoda and Bivalvia were successive sister-groups to several other phyla and the rest of Mollusca was separately monophyletic). Fear not; evidence exists that Mollusca is once again monophyletic as shown by Kevin **Kocot** who reviews recent analyses of the deep relationships among the molluscan classes. He sheds light on sister group relationships of the difficult-to-pin-down Aplacophora and Monoplacophora, and intriguingly, suggests that the relatively complex brains of gastropods and cephalopods might have evolved independently.

Three other presentations in the symposium did not result in print manuscripts. Douglas J. **Eernisse** summarized recent advances in systematics of Polyplacophora, pointed out that phylogenetic questions remain, and inferred that a slit posterior valve might be polyphyletic. Robert T. **Dillon**, Jr. presented a talk by himself and John D. **Robinson** on freshwater gastropods and suggested that analysis of 10 allozyme loci using 30 individuals at each of 15 localities can recognize cryptic taxa better than one mitochondrial gene from one individual per locality. Gerhard **Steiner** pointed out ample gaps in our knowledge of Scaphopoda, focusing primarily on systematic questions, but also noting how scarce our knowledge is about their development.

The papers in this symposium point out numerous unknowns about mollusks, reflecting the current state of our understanding and giving fruitful directions for future research. Many of the papers focus on systematics including molecular results, while some focus on other topics, for example, Cameron centered on ecology, Hickman focused on morphology, and Haszprunar and Ruthensteiner emphasized ontogeny. Had this symposium been held a couple of decades ago, discussions might have included topics such as why there is torsion, why shells have the colors and patterns they have, how changes in soft part morphology affect hard part morphology (and vice versa), environmental influences on phenotype, and what the real hypothetical ancestral mollusk looked like. We don't hear much about those topics these days, but potential improvements about our understanding of them remain. The unknown questions identified in this symposium have far-reaching ramifications beyond malacology. Addressing many of them will require ingenuity and hard work; malacologists are poised to address these questions.

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