# Mollusca: an evolutionary Cornucopia

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**The World Congress of Malacology 2001 was held at the University of Vienna, Austria, from 19 to 25 August 2001.**

Squid, snails, scallops… even biologists might have gastronomic rather than scientific associations with the Mollusca. And yet, as transpired during the recent World Congress of Malacology 2001, snails and their kin are ideal subjects for a range of ecological and evolutionary research fields. Students of sexual selection and adaptive radiation, in particular, could do worse than selecting this phylum for their organisms of choice.

Molluscs cannot seriously be termed an obscure group. They have played a crucial role in morphological and molecular attempts to unravel the phylogeny of major animal groups [1], land-snail genera, such as *Cepaea*, have contributed to our understanding of population genetics [2], and shell fossils form one of the major sources of data for paleontologists [3]. Nevertheless, a large part of the potential of molluscs remains untapped. For example, studies of evolutionary radiations have been dominated by vertebrates and insects, whereas the fossil record for snails is much better, as Frank Wesselingh (National Natural History Museum, Leiden, The Netherlands) and Ellinor Michel (University of Amsterdam, The Netherlands) pointed out.

### Ancient lakes: laboratories and archives

Wesselingh and Michel were the conveners for the congress symposium on ancient lakes, in which a range of paleontological and neontological studies explored mollusc radiations in long-lived lakes. At 28 million years old, Lake Baikal in Siberia is the Methuselah of lakes [4]. Tanya Sitnikova (Limnological Institute of SD RAS, Irkutsk, Russia) and Peter Röpstorf (Free University, Berlin, Germany) reported on two endemic families of snails, the Baicaliidae and the Benedictiidae. Analyses of gut contents and experimental staining of food items showed that the species-rich Baicaliidae (43 species) are filter feeders, whereas the species-poor Benedictiidae (17 species) are grazers. Differentiation among species appears to be primarily by depth. Molecular phylogenies suggest that the groups diverged at the very origin of the lake, 20–25 million years ago (Mya), but that two lineages within the baicaliids experienced major burst radiations at 2.5 Mya. These radiations coincide with the cessation of a period of glaciation when massive amounts of clay particles ended up in the lake. Paleontological records show that diatom abundance plummeted at that time and most ancestral baicaliids went extinct, probably because of starvation (E.B. Karabanov, PhD thesis, Russian Academy of Sciences, 1999). Subsequently, when diatom abundance increased dramatically, snail diversity followed suit.

Less old, but equally famous (although mostly for their cichlid fish species), the Great African Lakes were the subject of no less than 15 papers. Ellen Strong (Museum für Naturkunde, Berlin, Germany) provided new anatomical data that gave an insight into the amazing diversity of alimentary and reproductive structures in the 17 endemic genera of freshwater snails in Lake Tanganyika. One of these, *Lavigeria*, looks set to become an important model system for evolutionary radiation. Once considered a single variable species, it is actually a flock of at least 30 species, each defined by subtly different sets of shell characters. Jonathan Todd (The Natural History Museum, London, UK) and Leonard Papadopoulos (University of Amsterdam) reported on detailed conchological investigations, which underscore the fact that painstaking morphological study is still the best way for recognizing the disjunct genetic constitutions that we call species. That the freshwater thiarid radiations in Lake Tanganyika have a 'marine' appearance has been linked to the presence of crab predation in the lake [5]. Peter McIntyre (Cornell University, Ithaca, NY, USA) used stable isotope data to show that the specialized snail-eating crab *Platytelphusa armata* feeds on the genera *Reymondia* and *Spekia*, but not on *Lavigeria*. Nevertheless, up to 70% of *Lavigeria* snails in a population carry scars of crab attack, which suggests that attempted predation might be a strong selection pressure on shell armour. This was tested by Megan Phifer (Duke University, Durham, NC, USA), who reported that the development of shell characters (e.g. aperture size, wall thickness and sculpture) was correlated with the degree of crab predation in *L. nassa*. Karen Hinkley (University of Washington, Seattle, WA, USA) showed that *Lavigeria* shells get their toughness from plywood-like, crossed lamellar layers of shell material.

Although these studies of mollusc species flocks in ancient lakes have not yet reached the same level of detail and understanding as those of cichlids, there is reason to believe that, eventually, they will. The wealth of morphological characters, the ease of field sampling and laboratory experimentation, combined with the presence of a fossil record (in Lake Tanganyika, a large core-drilling programme is in the planning stages: http://malawidrilling.syr.edu/report2.html) will set the stage for successful multidisciplinary research programmes into freshwater snail radiations.

### Sex without sexes

Sexual selection is another field of research that is likely to feel an increased malacological influence. As many snails and slugs are hermaphrodites, malacologists and evolutionary biologists alike (including Darwin [6]) often proclaimed molluscs to be uninteresting from the viewpoint of sexual selection. However, in spite of the absence of separate sexes, the signature of sexual selection is found in many aspects of mollusc reproduction, from highly

divergent spermatophore and male genital morphologies to elaborate courtship rituals [7]. As long as sperm is cheap and ova are limiting, competition for access to ova will result in selection pressure on the male component of a hermaphrodite [8]. As a result, we can expect to find the equivalent of sexual dimorphism within a single hermaphroditic mollusc, with its female genitalia selected for choosing from the incoming (allo-) sperm, and its male genitalia simultaneously selected for giving its outgoing (auto-) sperm the best chances of success.

The helicid snail *Arianta arbustorum*, for example, is known to mate multiply, and there are some indications that they are able to select among the allosperm received [9]. Nenad Bojat (University of Basel, Switzerland), reported on an ultrastructure analysis of the tubules of the sperm storage organ, and showed that each of the up to nine tubules has a separate musculature, which might allow separate storage and retrieval of allosperm. As for the male function, helicid snails are famed for having a so-called 'love dart' [10], a large calcium carbonate needle that is pushed into the partner during courtship. Ronald Chase and David Rogers (McGill University, Montreal, Canada) presented new evidence that the love dart acts as a hypodermic needle to inject manipulative substances into the partner. They found that *Helix aspersa* snails that had been successfully hit during courtship would store twice as many allosperm from the partner as snails that had not been hit during courtship.

Finally, as a glimpse of what other bizarre reproductive behaviours molluscs might have in store for us, Martin Haase (University of Basel) described the unusual courtship of the sea-slug *Aeolidiella glauca*. In this hermaphroditic species, partners use their massive penes to place spermatophores on each other's dorsum. The allosperm then migrate across the surface of the skin towards the genital opening. Experimental evidence is consistent with the notion that this behaviour evolved to increase male fitness by reducing sperm competition: in a mate-choice test, slugs preferred partners that had the spermatophore experimentally removed from their backs over those that still carried it around.

### The presence of molluscs

The congress showed that molluscan presence in the evolutionary literature is likely to become more prominent. As an added benefit, this might have a positive effect on the survival of molluscan biodiversity. Winston Ponder (Australian Museum, Sydney, Australia) pointed out that 37% of all recorded animal extinctions are molluscs, which is more than all the observed bird and mammal extinctions combined. Thus, as familiarity with the victim is still the best protection against its ruthless extermination, it can be hoped that malacologists will heed Tony Whitten's (The World Bank, Washington, DC, USA) plea for more snail-oriented project proposals to the UN's multi-million-dollar Global Environment Facility.

### Acknowledgements

The congress was organized by Luitfried Salvini-Plawen, Gerhard Steiner, Christiane Todt (all of the University of Vienna, Austria) and Helmut Sattmann (Natural History Museum, Vienna, Austria). I gratefully acknowledge the financial support from Universiti Malaysia Sabah to attend this congress. The article was greatly improved by critical comments from Martin Haase and Ellinor Michel.

### References

1 Adoutte, A. *et al.* (2000) The new animal phylogeny: reliability and implications. *Proc. Natl. Acad. Sci. U. S. A.* 97, 4453–4456
2 Cain, A.J. (1983) Ecology and ecogenetics of terrestrial molluscan populations. In *The Mollusca*, Vol. 6, *Ecology* (Russell-Hunter, W.D., ed.), pp. 597–647, Academic Press
3 Vermeij, G.J. (1993) The biological history of a seaway. *Science* 260, 1603–1604
4 Sherbakov, D.Y. (1999) Molecular phylogenetic studies on the origin of biodiversity in Lake Baikal. *Trends Ecol. Evol.* 14, 92–95
5 West, K. and Cohen, A. (1996) Shell microstructure of gastropods from Lake Tanganyika, Africa: adaptation, convergent evolution, and escalation. *Evolution* 50, 672–682
6 Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*, Murray
7 Eberhard, W.G. (1985) *Sexual Selection and Animal Genitalia*, Harvard University Press
8 Greeff, J.M. and Michiels, N.K. (1999) Low potential for sexual selection in simultaneously hermaphroditic animals. *Proc. R. Soc. London B Biol. Sci.* 266, 1671–1676
9 Baur, B. (1994) Multiple paternity and individual variation in sperm precedence in the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Behav. Ecol. Sociobiol.* 35, 413–421
10 Pomiankowski, A. and Reguera, P. (2001) The point of love. *Trends Ecol. Evol.* 16, 533–534

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