



A Special Issue of selected papers from the conference: ‘Bivalves 2023—Where are we going?’,  
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## Bivalves 2023—Where are we going? An overview of an international meeting

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During an unexpected heatwave, just over 100 scientists, from more than 15 different countries attended ‘*Bivalves 2023—Where are we going?*’ held at the University of Cambridge (UK) between 5 and 8 September 2023, a meeting organized by Liz Harper, John Taylor, Emily Glover and Katie Collins (Fig. 1). This was the first international meeting specifically focussed on bivalves since Barcelona in 2006, itself a successor of previous bivalve meetings that took place in London (1977), Drumheller (1995) and Cambridge (1999). Just as significantly, it occurred after the restrictions of the global pandemic and a key aim was to provide an open, relaxed, in-person meeting where old interests could be rekindled and new collaborations and friendships forged. Pleasingly 28% of the attendees were undergraduate or postgraduate students.

The conference title posed a question: ‘*Bivalves—where are we going?*’ During the nearly 20 years since we had all last met, there have been exciting developments—new methods, most obviously the advances in molecular phylogeny but also novel morphometric techniques, quality-controlled databases, new discoveries and increasingly detailed sampling. We deliberately did not solicit specific contributions and aimed to welcome all. Instead, we wanted to focus on what has been achieved recently. Where is the active research? Where, perhaps, has there been less activity but promise of new breakthroughs?

We had a full programme, and it was heartening to see a wide variety of topics, with marine, freshwater, fossil and living taxa well represented. This special issue is a collection of 20 papers associated with just some of the 69 oral and 29 poster contributions presented at the meeting. They represent the diversity of approaches explored at the meeting.

### CLASSIFICATION AND PHYLOGENY

Twenty years ago molecular phylogenies were beginning to provide a broader understanding of relationships between major bivalve groups and there was an appetite for assembling detailed and comprehensive morphological characters which could be used for phylogenetic analyses of modern and fossil forms. The revolution

in molecular methodologies and increasingly sophisticated analyses has continued with earlier challenges to prior classifications rapidly absorbed into the consensus. It is apparent that these are now part of the basic tool kit.

In an example of the use of molecular phylogenies, Tan & Tan (2024) tackle marine mussels of the Mytiloidea, perhaps the most ecologically and economically important group of bivalves worldwide. They range in habitat from high intertidal rocky shores and salt marshes to the deep sea with some venturing into freshwater. Despite the global interest, the classification and phylogenetic relationships of the 57 living genera are hotly debated and conflict with a plethora of poorly defined subfamilies. In a critical analysis, Tan & Tan use publicly available DNA data together with their own sequences to produce the most comprehensive analysis of mytiloidean relationships to date. This new phylogeny will act as a framework for exploring the distribution of shell morphological and anatomical characters as well as the ecological diversification of mussels. In a separate study of mussels, Tan *et al.* (2024) examine *Brachidontes*, a problematic genus of small, ribbed mussels which are often highly abundant in the tropics. Using both molecular and anatomical characters, Tan *et al.* (2024) establish eight frequently co-occurring species in the Indo-West Pacific and, significantly, provide morphological characters with the potential to differentiate between them.

Establishing the phylogenetic positions of extinct taxa is particularly difficult. Zhang *et al.* (2024) use a detailed study of the hinge morphology of *Yunfuconcha bimenta* n. gen. n. sp. from the Ordovician of China that shows a combination of palaeotaxodont and heteroconch hinge elements, and indicate it is either a stem-archiheterodont or stem-heteroconch. This conclusion is incompatible with current molecular phylogenies which find actinodontoid-descendant groups to be basal to the archiheterodonts.

There were a number of contributions on systematics and biogeography. Notably, Utrilla, Gofas & Salas (2024) provide a critical review of the confused taxonomy of the tiny Atlantic species of *Kelliella* with detailed descriptions, images and distributional data based on intensive deep-water sampling in the eastern Atlantic and Caribbean. They also present characters to distinguish *Kelliella* from



**Figure 1.** The conference delegates in front of the Gate of Honour, Gonville & Caius College, Cambridge University. Picture by Sarah Humbert.

the confusingly similar shells of *Vesicomya*. Mitra & Halder (2024) present a comprehensive analysis of Eocene bivalve palaeobiogeography and its relationship with the evolution of a global ocean current system. Of particular interest here is the legacy left by the former circumtropical Tethyan ocean in modern bivalve faunas. Further back in time, evidence for oceanic connections during the Jurassic between landmasses of the Southern Hemisphere is provided by the study by Saha *et al.* (2024) of the archiheterodont genus *Seebachia* in India.

## ECOLOGY AND PALAEOECOLOGY

Several papers consider the ecology of modern or fossil bivalves. These include Peck, Colman & Clarke (2024), who examined larval development times in the protobranch *Aequiyoldia eightsi* in the extreme cold of Antarctica. As with previous polar studies, they discover rates much slower than might be predicted for low temperatures alone, suggesting additional factors at play.

The unexpected ‘winner’ in the popularity stakes was the number of contributions on symbiotic ecologies of bivalves ranging from photosymbiosis, chemosymbiosis and commensalism. Galeommatoida is probably the most species-rich group of all bivalves with many species living in commensal associations with a wide range of other invertebrate phyla. Live animals show extraordinary external mantle features in contrast to the often rather featureless shells. Bouchet & Strong (2024) illustrate some of these spectacular bivalves and provide a comprehensive review table documenting the known habits and associations of all living genera. Galeommatoids also feature in a paper by Campbell (2024) who documents bivalve micro species and the end of Carolinian endemism from the Waccamaw Formation (basal Pleistocene, USA). This study shows how painstaking collection of small specimens can significantly alter our understanding of the taxonomic composition of a palaeocommunity. In another contribution on symbioses, Goto *et al.* (2024) discuss the relationships of the unusual oyster *Anomiostrea* which has the surprising habit of cementing to dead coral deep within the burrows of the callichirid shrimp *Neocallichirus jousseaumei*.

Johnston *et al.* (2024) provide a revision and re-description of the Ordovician genus *Shaninopsis* Isberg, 1934, reducing the original 18 described species to just 3. A detailed study of the morphology combined with lithological interpretations of the environment suggests that *Shaninopsis* had an epifaunal or semi-infaunal habit perhaps with a foot that probed through the anterior gape into the underlying sediment.

## BIVALVES AND THE ENVIRONMENT

Modern concern for the environment has obvious implications for bivalves and we had several talks on the effects of microplastics and the need to understand and conserve diversity. Neo (2024) describes the use of citizen scientists to collect data on the occurrence and distribution of tridacnids around Singapore, highlighting the benefits and effectiveness of mobilizing such a force in allowing long term monitoring over comprehensive areas to assess and inform conservation efforts.

The use of shells as archives of environmental change is an expanding field, with several talks presenting data from sclerochronological analyses to document changes such as in temperature, salinity or primary productivity. Such approaches can be used, and ground-truthed, in modern environments but also, in well preserved fossil material, be used to understand environmental change in deep time. Cudenec *et al.* (2024) discuss a stable oxygen isotope analysis of various bivalve taxa from the Early Pliocene Coralline Crag Formation, UK to reveal that both warm- and cold-adapted species can co-occur at the same stratigraphic horizon. This in turn has important implications for how we interpret palaeoclimatic conditions from molluscan assemblages.

## MORPHOMETRICS AND SHAPE ANALYSIS

During the last 20 years, new and increasingly sophisticated ways to describe and analyse shell shape have emerged which have yielded new insights into both recognizing environmental controls on

bivalves and to understand morphological changes that occur over evolutionary timescales. [Telesca et al. \(2024\)](#) characterize patterns of shell shape, thickness, microstructural and biomechanical property differences in populations of *Crassostrea virginica* across a range of sites with different environmental parameters in the Hudson River Estuary (USA), finding that salinity is a key control. [Doyle \(2024\)](#) finds that the bivalve fauna at the Southern Hemisphere polar region has a significantly smaller median body size than its Northern Hemisphere counterpart. The persistence of this pattern across clades and climate zones suggests the operation of fundamentally different evolutionary pressures on the two faunas.

While sophisticated shape analyses have been illuminating in many groups, for some taxa, which lack obvious landmarks and which show a high degree of plasticity, have remained challenging. [Nagel-Myers, Walrath & Bowdish \(2024\)](#) approach the problem in unionids, looking at shape variation between reservoir and river populations of *Elliptio complanata* in New York State (USA). They supplement a traditional 2-D landmark analysis with 3-D landmark data derived by the non-expensive approach of photogrammetry. Computed tomography (CT) images are providing new ways of looking at 3-dimensional morphologies. [Edie, Collins & Jablonski \(2024\)](#) use CT images to explore the different volumes in separate components of the animal (i.e. soft tissue, shell thickness and sculptural elements) in species from the Florida Keys. The aim was to understand the resource allocation between the mineralized and soft-parts of the animal. They found a high degree of overlap between major bivalve clades in this ‘allocation-space’ but in an interesting contrast between anomalodesmatan and imparident bivalves, [Deng \(2024\)](#) finds high levels of disparity are recorded in those anomalodesmatan taxa that diversified into novel life modes such as carnivory that differ from the infaunal, suspension-feeding lifestyle of their ancestors.

In a more evolutionary context of analysing shell shape, [Roopnarine & Goodwin \(2024\)](#) develop a geometric model of bivalve shell growth that requires only minimal assumptions on ontogeny and anatomy. They use it to examine the origin of coiling and of the bivalved shell form, testing three different hypotheses of the origin of Bivalvia and suggest that there may have been multiple groups displaying laterally compressed morphologies in early molluscan evolution. The pleurothetic life habit of laying with one valve next to the substrate, in the manner of oysters or rudists, has evolved many times in the history of bivalves and is typically accompanied by an asymmetry between the valves. [Palmer \(2024\)](#) conducts a careful analysis of the direction of valve asymmetry across a wide range of modern and fossil pleurothetic bivalves. He investigates how frequently instances arose as a direct consequence of genetic novelty (“genes as leaders”) as opposed to randomly that subsequently became genetically fixed (“genes as followers”).

## AFTERTHOUGHTS

Molecular phylogenies push forward into the genomic era but there are still major gaps. For instance, comprehensive analyses of the Anomalodesmata, Galeommatoidea and Tellinoidea are lacking, with only a fraction of their diversity sequenced. The positions of Chamoidea, Gastrochaenoidea and Thyasiroidea are still equivocal. There is an ongoing need to increase the integration of fossils into phylogenies and more rigorous choices of fossil data for tree calibration.

Bivalves have figured strongly in analytical marine biogeography and the approach is now expanding from simple counts of taxa against latitude and longitude to incorporate more sophisticated features such as bivalve traits. All depend on the taxonomic underpinning as in new regional compilations such as [Cosel & Gofas \(2019\)](#) for western Africa and comprehensive taxonomic monographs ([ter Poorten, 2024](#)). These will open up more areas for critical analyses and augment global diversity assessments.

Increasing access to the deep sea and new sampling protocols are revealing large numbers of undescribed species, integrating morphology and molecular sequencing from the onset. We still have much to learn about the ecology of vent faunas and substantiation of diversity gradients is a high macroecological priority.

With their diversity of shell microstructures and mineralogy, bivalves have long been the focus of biomineralization studies and in recent years, a wealth of new techniques have become available for their detailed study. With new genomic methods focussing on the genes of mantle cells coupled with high resolution microscopy of crystal structures there is the potential to gain greater understanding of the calcification process. This should feed into studies of the mechanical and adaptive significance of different microstructures and their phylogenetic pattern.

With so many exciting developments in the fields of bivalve biology and palaeobiology, we hope that we do not have to wait another 19 years for the next symposium. The floor is now open for a small group of dedicated bivalve specialists to set plans in motion for another interdisciplinary meeting in the not-too-distant future.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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