

A Modern Overview of Crustacean Biogeography: *Evolution and Biogeography* Review

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Martin Thiel continues his ambitious and successful role as series editor for Oxford's *Natural History of the Crustacea*. Volume 8 (*Evolution and Biogeography*) includes 18 chapters that discuss crustacean evolution and emergent patterns (and causal mechanisms) underlying the biogeography of Crustacea in marine, freshwater, terrestrial, and subterranean habitats. As is often the case with edited volumes, some chapters are stronger than others, but overall, this is a book most invertebrate zoologists, marine biologists, and biogeographers will want on their shelves. Because of its emphasis on review chapters, the volume will be especially useful for beginning researchers and those who are not crustacean specialists.

Five chapters focus on the evolution of Crustacea. Among the strongest is Shane Ahyong's summary of current views on crustacean evolution ("Evolution and Radiation of Crustacea"), noting that over the past two decades, our phylogenetic perspective has shifted from a long-bodied, serially homonomous ancestry (as seen in remipedes and cephalocarids; an idea promoted by Howard Sanders, Bob Hessler, and Fred Schram and one that many of us "cut our teeth on") to a short-bodied, possibly ostracod-like ancestry similar to Cambrian stem- and crown-group fossil forms. Ahyong correctly acknowledges the importance of the Orsten fauna as a key lens through which to understand the early evolution of Crustacea, noting that the oldest definitive crustacean fossils are upper Cambrian Orsten of Sweden—small, just millimeters in length, but exquisitely preserved specimens owing to their phosphatic preservation. Earlier ideas of long, serially homonomous ancestry had been influenced by two scientifically flawed lines of reasoning. First was an underlying notion that evolution moves from simple toward more complex. Second was a reliance on largely untestable narratives of ur-crustacean body morphology as a starting point (i.e., the hypothetical ancestor approach). The new view, of Pancrustacea comprising the two great clades Oligostraca and

Altocrustacea, places long-bodied groups like cephalocarids and remipedes far from the ancestral root of Crustacea.

The chapter by Björn von Reumont and Gregory Edgecombe ("Crustaceans and Insect Origins") provides an excellent discussion of current thinking on the origin of Hexapoda from Crustacea. They review proposed apomorphies of "Crustacea" and Hexapoda and recount the recent work that has firmly positioned the latter within the former. The idea that insects arose from within Crustacea dates back to Hanström (1926) drawing on neuroanatomical similarities, work revived by Nick Strausfeld beginning around the turn of this century (e.g., Strausfeld 2009; Strausfeld and Andrew 2011). Comparative neuroanatomy had pretty consistently suggested that Hexapoda was the sister group of Malacostraca, and a significant list of putative synapomorphies (e.g., the 19/20-segmented body plan, uniramous walking legs, aspects of the morphogenetic development of the compound eyes, anatomy of the optic lobes, several features of the cerebral ganglia) has been proposed (for a review, see Brusca 2000). Beginning with Ertas et al. (2009), molecular studies have favored a remipede-hexapod sister-group relationship, and this has achieved increasing support since, notably, von Reumont et al. (2012), Oakley et al. (2013), and Schwentner et al. (2017). The remipede-hexapod clade has been called Labiocarida, recognizing the functional labium in both groups (the strongest candidate sister group of Labiocarida is Branchiopoda). However, no fossils have yet been found that unambiguously suggest a hexapod stem group or that definitively link hexapods and crustaceans—the still-missing holy grail. Despite the lack of "missing link" fossils, elegant new research in gene patterning, using knockout methodology (e.g., Bruce and Patel 2020), backs a hundred years of comparative anatomy and embryology in support of the hypothesis that insect wings arose from crustacean leg segments that fused with the body wall in the evolutionary past (crustacean proximal leg segment exites evolved into body wall lobes, then into wings).

In the classical tradition, Stefan Richter and Christian Wirkner ("What the Ur-crustacean Looked Like") search for the hypothetical ur-crustacean, the putative ancestor of Pancrustacea, an exercise episodically fashionable for many decades. The authors set out to construct this hypothetical creature in the same way that generations of zoologists before them have—through a process of informed storytelling (as opposed to any empirical or testable methodology). The bulk of this chapter is a narrative about various traditional morphological characters among crustacean higher

taxa. Although the authors acknowledge strong support for the Myriapoda as the sister group of Pancrustacea (i.e., the clade Mandibulata), they do not overtly rely on the features of myriapods in their assessment of what the first crustacean might have looked like. They point out that their focus on crown-group Pancrustacea has the advantage of allowing the use of characters such as gene expression, yet they do not actually employ gene expression data in their “analysis.” Unsurprisingly, their hypothetical ur-crustacean was marine; had a distinct head covered by a dorsal shield, with five pairs of appendages, but may or may not have had a carapace; “probably” lacked maxillipeds; had a complex brain, with a lateral protocerebrum containing at least two optic neuropils, with or without a central complex, and a protocerebrum connected to a nauplius eye as well as to compound eyes; had ommatidia with tetrapartite crystalline cones and pigmented corneagenous cells; and had a nauplius larva. It might have had a uniformly segmented trunk, or it might have had a limb-bearing thorax and a limbless abdomen. This seems a rather unhelpful diagnosis of free-living crown-group Crustacea and the variability seen therein, and the authors make no attempt to fit their hypothetical beast into one of the three great Pancrustacean clades (i.e., Oligostraca, Multicrustacea, Allotriocarida). With the exception of the nauplius larva, none of their ur-crustacean attributes belong to the traditional list of synapomorphies that define the paraphyletic group Crustacea (e.g., naupliar eye, restriction of nephridia to two cephalic segments, various characters proposed from Cambrian fossils by Walossek and Müller [1990, 1998], Walossek [1999], Haug et al. [2012], and others). This chapter might be considered an example of why the search for hypothetical ancestors yields little that is of use to phylogenetic research.

In a misleadingly titled chapter (“The Fossil Record of the Pancrustacea”), Thomas Hegna and colleagues provide an overview of the older known fossils assigned to the paraphyletic group Crustacea *sensu stricto*. They do not provide an overview of hexapodan fossils. Hegna et al. argue that the three “epic clades” (Oligostraca, Multicrustacea, Allotriocarida) all have Cambrian (540–485 Ma) roots and that the pancrustacean stem lineage likely arose in the Ediacaran Period (635–541 Ma). Their composite photographic plates of representative fossil groups will be useful for beginning students even though the image quality is suboptimal. The earliest likely fossil crown-group pancrustaceans are three-dimensionally phosphatized larvae (*Yicaris*) from the Series 2 Cambrian Orsten deposits of south China, but these are not depicted in any of the figures. The oldest members of the Oligostraca, now thought to be one of the earliest-diverging clades of Pancrustacea and represented in the fossil record, include stem-group pentastomids from the upper Cambrian of Sweden (specific dates not given), crown-group myodocopid ostracods from the late Ordovician (~450 Ma), and podocopid ostracods from the early Devonian (~420–390 Ma) of Ukraine (although their fig. 2.1 shows stem-group podocopids extending back to the middle Ordovician). While being a worthwhile review, precise chronostratigraphic names and dates are often incorrect or ambiguous, and dates in the text do not always match those in figure 2.

Hegna et al. place the earliest ostracod fossils in the Ordovician, not trusting Harvey et al.’s (2012) report of a crown-group ostracod from the western Canada Cambrian Series 3 to the Furongian (~488–510 Ma). Although the authors seem to imply their lack of trust in this ostracod identification is based on Wolf et al. (2016), the latter did not expressly discount Harvey et al.’s (2012) claim (Wolf et al. [2016] suggest a maximum age of ostracods to be 509 Ma, the age of the Burgess Shale). On the other hand, Ahyong (see above) appears to accept Harvey et al.’s (2012) identification and thus reports the earliest ostracods as “Late Cambrian” (more correctly, Furongian). Neither chapter mentions that this ostracod record was based on a single, damaged, 0.47-mm-long, isolated fossil mandible—a record that in my opinion clearly needs verification with additional material.

The Hegna et al. chapter would have benefited by adhering more strictly to accepted standards in naming geological time periods, and it would have been useful to have included a geological timescale in the front of the book for readers to refer to. The generally accepted standards are the International Union of Geological Science’s *International Chronostratigraphic Chart* (ICC) and the Geological Society of America’s *GSA Geologic Time Scale* (GSA). The two are nearly identical, although GSA prefers late, middle, and early for epochs, whereas ICC uses upper, middle, and lower. The ICC may be preferable because it is compiled by an international committee and updated annually.

Heather Bracken-Grissom and Joanna Wolfe (“The Pancrustacean Conundrum: A Conflicted Phylogeny with Emphasis on Crustacea”) review the history of ideas concerning Crustacea classification and pancrustacean relationships. They begin with brief synopses of the major groups, provide a current view of crustacean classification, and give a brief history of older classifications before getting to the good stuff—Dieter Walossek’s work. The history is mostly pre-Hennigian storytelling and will be of interest primarily to science historians or students curious about the history of research on this topic. Their brief review of molecular phylogenetics is quite useful, though not up to date with work since 2017.

In fact, arthropod phylogenetics has expanded and consolidated over the past decade, and there is now strong support for an overall framework of pancrustacean (= tetraconatan) evolution (e.g., Schwentner et al. 2018; Giribet and Edgecombe 2019; Lozano-Fernandez et al. 2019; Wolfe et al. 2019). We now know that Pancrustacea likely comprises three great clades: Oligostraca (Ostracoda, Mystacocarida, Branchiura, Pentastomida), Multicrustacea (Thecostraca, Copepoda, Malacostraca), and Allotriocarida (Cephalocarida, Branchiopoda, Remipedia, Hexapoda). Even within the large and megadiverse clade Malacostraca, phylogeny is beginning to stabilize. However, better resolution is still needed among the main Multicrustacea clades. Unfortunately, perhaps due to the lengthy production time of this volume, not all of this recent phylogenetic work was seen by all of the contributing authors, so this emergent phylogenetic framework is not included in most of the chapters. For example, the phylogeny presented in figure 3.1 (modified after Oakley et al. 2013) would have benefited from being updated with more recent phylogenomic work, as the

sister-group relationship between cephalocarids and brachiopods is questionable, as is the sister-group relationship between Thecostraca (“Cirripedia” of Ahyong) and Copepoda (the “new Maxillopoda” in Ahyong’s view).

Twelve chapters in the volume are dedicated to biogeographic reviews that are fairly comprehensive in scope, beginning with Claudia Halsband et al.’s overview of crustacean oceanic biogeography (“Biogeography of the Oceans”), which nicely summarizes biogeographic patterns in the major open ocean basins and polar regions, including patterns of species richness. They conclude that hydrographic features are the major structuring elements for pelagic species, while benthic species distributions are additionally influenced by continental barriers and submarine features (e.g., ridges, seamounts). Important biodiversity hot spots are the Indo-Australian archipelago (the “coral triangle”), Red Sea, and Mediterranean Sea. Note that this chapter is not an analysis of coastal or littoral biogeography.

Torben Riehl and colleagues tackle the origins of biodiversity in the deep sea (“Conquering the Ocean Depths over Three Geological Eras”), the largest habitat on Earth (which they define as everything below the continental shelf). They suggest that deep-sea and shallow-water faunas have been continuously and repeatedly exchanged, probably at least since the mid-Paleozoic. That is, species have moved not only from shallow waters to deeper waters (submergence) but likely also from deeper waters to shallow waters (emergence), in both cases initiating new radiations. Although focused strongly on the abyssal zone, the authors also discuss the hadal trenches, where it has long been known that isopods and tanaidaceans have notable deep-sea radiations. The authors challenge the idea of the abyss being inhabited predominantly by a fauna of at most late Mesozoic/early Cenozoic age (~68 Ma; phylogenetically younger than bathyal or littoral faunas). They also note that recent advances in molecular dating indicate that hydrothermal vent communities date only into the Cenozoic. Importantly, the authors note that most of the abyssal fauna still remains undescribed and unnamed; typically, more than 90% of the abyssal macrofaunal species sampled at sites in the Atlantic and Pacific are new to science.

Benny Chan and colleagues provide an excellent overview of crustaceans that live with corals (“Biogeography and Host Usage of Coral-Associated Crustaceans: Barnacles, Copepods, and Gall Crabs as Model Organisms”), focusing on gall crabs (Brachyura, Cryptochiridae; females of which are obligate coral associates), copepods, and barnacles of the orders Acrothoracica and Thoracica. More than 635 crustacean species have been documented as coral associates. In the case of pyrgomatid coral barnacles, it has been shown that ammonium released from the barnacles is absorbed by the coral zooxanthellae, and organic matter produced by the coral-zooxanthellae partnership contributes to part of the barnacle’s carbon source. In the case of coral-specific copepods, some species live on the coral surface, while others live inside the gastrovascular cavities of the polyps, some of which form gall structures. The authors claim that copepod galls are created in a defensive reaction by the coral (deposition of a calcareous barrier), although they also note that the mechanism of gall formation remains unknown. An

exploration of the intriguing idea that gall/pit morphology among the gall crabs shows strong phylogenetic patterns (and is thus controlled by the crabs themselves) and that the galls can be considered an extension of the crabs’ phenotypes (Wei et al. 2013) would have been an interesting addition.

Joanna Legeżyńska and colleagues remind readers that Crustacea are a highly speciose taxon in the polar regions (“Invasion of the Poles”). Interestingly, despite profound differences in the evolutionary history and oceanography of the two polar regions, they seem to possess similar species richness of Crustacea. However, the longer period of isolation of Antarctica has resulted in a higher percentage of endemic species there than in the Arctic. The Arctic has been frigid (with sea ice) for only about 700,000 years, whereas the Antarctic has been so for more than 30 million years.

Joseph Staton and colleagues analyze global crustacean biodiversity patterns in coastal and estuarine environments (“Colonization of Coastal and Estuarine Environments”). They consider these to be ephemeral habitats, but I would disagree and suggest that they are simply dynamic habitats that change over time as a result of changes in river flow and sea level—but they rarely come or go altogether. Brief reviews of sandy beaches, mudflats, mangroves, salt marshes, and hard-bottom communities are given, emphasizing their crustacean faunas. The substantive contribution here is an analysis of shallow-water Crustacea (depth of ≤ 200 m; basically the continental shelves) based on OBIS data (the Ocean Biodiversity Information System, formerly known as the Ocean Biogeographic Information System). Staton et al. present an algorithm that allows for the frequency of observations of a taxon in a given area to influence the “estimated degree of endemism” of the taxon in that area (relative to other areas around the globe). However, I confess that the validity of viewing endemism as a “relative value” (not just presence/absence but somehow influenced by frequency of observation) eludes me. A summary of their data is presented graphically (fig. 10.5), but it is not an easily digested chart. Their analysis divides the world’s coastlines into 216 grids, delineated by 10° longitudinal windows. A surprising conclusion of their complex mathematical analyses is that the highest crustacean biodiversity in the world’s oceans, measured grid by grid (not by traditional biogeographic regions), is the Gulf of Mexico and western North Atlantic (even higher than in the Indo-West Pacific). However, their abstract states that the highest crustacean species richness and endemism occurs in the eastern temperate North Atlantic, western temperate North Atlantic, and western tropical South Pacific. Overall, the techniques, algorithms, conclusions, and relevance of this analysis could have been better explained.

Kristina von Rintelen and colleagues provide an excellent, succinct overview of the major higher crustacean taxa that inhabit freshwaters around the world (“Standing Waters, Especially Ancient Lakes”), walking the reader through the world’s dozen or so “ancient lakes” (at least 100,000 yr old and mostly more than 2 million yr old). All are characterized by notable species richness and endemism. Perhaps the most famous is Lake Baikal (in Siberia), with over 350 species of endemic amphipods (in 11 families), 200 endemic ostracods, and 120 largely endemic copepods. One

interesting pattern described is that the most diverse macroscopic taxon in tropical ancient lakes is decapods, whereas in temperate (and high-altitude tropical) lakes, it is amphipods.

Shane Ahyong and Chao Huang offer an informative discussion of the epigeal (freshwater) taxa and discuss their possible modes of colonization from the sea/land to epigeal waters (“Colonization, Adaptation, Radiation, and Diversity in Fresh Water”). In a complementary paper to Ahyong and Huang, Renée Bishop and colleagues (“Subterranean and Anchialine Waters”) review Crustacea of subterranean and anchialine waters. They provide brief discussions of geology, hydrology, and water chemistry of subterranean habitats and very brief summaries of adaptations to subterranean existence. Oddly, the authors consider mystacocarids as stygobionts, even though since their original discovery near Woods Hole (Pennak and Zinn 1943), they have consistently been shown to be a marine meiofaunal group and their specific intertidal/shallow subtidal requirements are well known (e.g., Dahl 1952; Delamare-Deboutteville 1953, 1960; Hessler 1971).

Spyros Sfenthourakis and colleagues (“Terrestrial Environments”) analyze the only two crustacean groups “fully adapted to live on land”—the amphipod family Talitridae (with ~117 terrestrial species) and the isopod suborder Oniscidea (with ~3,710 species). Talitrids are most diverse in New Zealand, Tasmania, and Japan/Taiwan, although some species also occur in the Caribbean and Central America; and they are absent from North and South America except as introduced taxa. The authors provide elegant reviews of adaptations to terrestrial life (e.g., enlarged gills and osmoregulatory structures, complex water-conducting systems that rely on capillarity and grooves/scales on the body surface, closed marsupia to house the developing embryos, behavioral adaptations such as aggregation and deep burrowing) in these two groups, and intriguingly, they ascribe low diversity of terrestrial talitrids in the Northern Hemisphere to the KT boundary bolide impact (although there are talitrid species in the Caribbean and Central America).

Marcelo Rivadeneira and Gary Poore’s analyses of latitudinal biodiversity gradients in several major crustacean clades reveal some intriguing patterns (“Latitudinal Gradient of Diversity of Marine Crustaceans: Toward a Synthesis”). For example, higher taxa show bimodal patterns of species richness, either with both peaks occurring in or near the tropics (e.g., calanoid copepods, decapods, acorn barnacles) or with the peaks occurring outside the tropics, in north and south temperate zones ~30°–50°N and ~30°–50°S (e.g., amphipods, isopods). They suggest that ultimate causes of broadscale latitudinal diversity gradients may be tied to greater rates of species origin and lower rates of extinction in the tropics than in higher latitudes (combined with “strong tropical niche conservatism”).

Anna McCallum and Torben Riehl (“Intertidal to Abyss: Crustaceans and Depth”) provide a well-written review of patterns of crustacean abundance, species richness, and size across depths, from the continental shelf to hadal depths (>6,500 m). They argue that aside from the expected decrease in macrofaunal biomass and abundance with depth (due to food limitations),

crustaceans exhibit a decrease in body size with depth (with some notable exceptions of gigantism), limited species depth ranges, and taxon-dependent diversity patterns. Meiofaunal species, however, tend to show increasing abundance and density as depths increase. Overall, deep-sea crustaceans tend to have broad latitudinal ranges and narrow depth ranges.

Christine Ewers-Saucedo and John Wares (“Population Connectivity and Phylogeography of Crustaceans”) discuss major past vicariance events that affected multiple lineages to establish broad-scale biogeographic patterns (e.g., uplift of the Isthmus of Panama, the trans-Arctic interchange, flooding of the Mediterranean Sea, historical climate shifts that led to amphitropical distributions, oceanic rafting). They conclude that future work would benefit from greater reliance on nuclear genes (not just single mitochondrial markers) and should give greater consideration to anthropogenic drivers of changing biogeographic patterns.

The volume ends with a chapter by Karolina Bacela-Spychalska and colleagues (“Outlook: Crustaceans in the Anthropocene”), who give a succinct overview of anthropogenically driven factors that threaten crustaceans (or that facilitate crustaceans threatening nonnative habitats). These concerns include habitat destruction, climate change, aquatic acidification, eutrophication, and biological translocation. They conclude with the rather depressing, yet accurate, conclusion that growing human pressure will likely continue to accelerate the nonnatural dispersal and extinction rates of crustaceans and other living organisms.

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