

JOURNAL OF CRUSTACEAN BIOLOGY, 21(4): 1084–1086, 2001

Origin of the Hexapoda. *Annales de la Société entomologique de France*, Volume 37, Numbers 1–2, 304 pp. Thierry Deuve, editor.

This volume derives from a conference in Paris, 8–9 January 1999, sponsored by the Société entomologique and Société zoologique de France, two organizations with long and venerable histories. (The former was founded in 1832, under the presidency of Latreille; the latter was founded in 1876.) As noted by the volume's editor, the time seems ripe for reflection upon the vast amount of information that has accumulated on hexapod evolutionary relationships over just the past decade. Central to this emerging new body of data is the idea that hexapods (insects and their kin) may not be the sister group of the Myriapoda, as long thought, but of the Crustacea.

Orthodox views, codified by Robert Snod-

grass in the 1930s, have long classified the Hexapoda and Myriapoda together in a taxon known as the Atelocerata (or Tracheata, or Antennata). The name Atelocerata derives from the absence of the second antennae (*atelo* = imperfectly, *cerata* = horned). Tracheata, of course, derives from the presence of gas-exchange tracheae. The Atelocerata has been nested next to the Crustacea, in a larger group known as the Mandibulata (a term coined by Snodgrass). The idea that Crustacea and Hexapoda might be sister groups (exclusive of the Myriapoda) seems new to most of us. However, as Deuve notes, some excellent researchers made this proposal a century ago—E. R. Lankester; G. H. Carpenter; G. C. Crampton; and in the 1940s, A. Vandel.

Since 1990 an explosion of anatomical, paleontological, and molecular developmental and phylogenetic research on arthropods has

begun to change our views of arthropod evolution (see Brusca, 2000, for a summary of these data through 1999). On balance, recent research suggests that the hexapods might be more closely related to crustaceans than to myriapods—in fact, that the Hexapoda might have arisen from within the Crustacea. The implications of this hypothesis are profound. First, it demands that some long-standing characters shared between hexapods and myriapods be reinterpreted as convergences, rather than synapomorphies, including such things as the presence of anterior tentorial arms, a tracheal gas-exchange system, uniramous legs, Malpighian tubules, Tömösvary organs, absence of mandibular palps, and loss (or transformation) of the second antennae. Secondly, it implies that Crustacea are paraphyletic, the Hexapoda being a derived lineage emerging from deep within the crustacean clade, much as the birds arose from deep within the reptile line (i.e., insects would be flying crustaceans, in the same sense that birds are flying reptiles). Not all biologists agree with this new view, and the data, compelling as it is, is still preliminary. However, evidence is rapidly accumulating from a variety of disciplines, and the focus of this volume is to review the data for and against the idea of a Crustacea-Hexapod sister-group relationship.

The volume contains 13 papers, plus a Foreword by the editor. The scope of the papers runs from paleontology to molecular phylogenetics, developmental genetics, fine structure of the nervous system, and general morphology. Many papers are reviews of specific fields, whereas others are re-visits of previous work by the authors (e.g., Friedrich and Tautz on ribosomal DNA phylogenies of arthropods). It is worth noting that none of the papers in this volume really take a synthetic view of Crustacea-Hexapoda relationships—all focus on data from a single field. Also, some of the papers (e.g., Deuve) seem to present inaccurate interpretations of J. Kukalová-Peck's detailed work on insect anatomy (see end note).

Using a new generation of phylogenetic analysis tools, **Friedrich and Tautz** reanalyze the data from their important 1995 paper that used 18S and 28S sequences to generate trees that clustered crustaceans with insects rather than with myriapods, and they come to the same conclusions. **Deutsch** does a good job reviewing recent work on devel-

opmental genetics of arthropods, especially work on the derivation of the various appendages. **Simpson's** and **Dohle's** reviews of nervous system development are both excellent, packed with solid information and little fluff. However, Dohle's suggestion that the tetrapartite ommatidium is a synapomorphy of a Crustacea-Hexapoda sister group is unlikely, even though these kinds of compound eyes seem to be restricted to those two taxa. We don't yet know when the tetrapartite condition first appeared within the Crustacea, but it must have been well before the insects emerged (perhaps even in the arthropod stem line). Crustacea fossils from Cambrian *Lagerstätten* deposits have eyes strongly resembling those of modern Crustacea, at least superficially. Tetrapartite ommatidia must surely be a retained symplesiomorphy in both Hexapoda and crown Crustacea (their transformation in myriapods perhaps being a synapomorphy defining that clade).

**Koch's** detailed (46-page) overview of mandibular structure and articulation draws an unconventional conclusion—that the long-espoused dichotomy within the Hexapoda between “lower hexapods” (Entognatha + Archaeognatha) with monocondylic, rolling mandibles, and the “higher hexapods” (Dicondylia: Thysanura + Pterygota) with dicondylic, transversely biting mandibles should be abandoned. Koch argues that the capacity for transverse biting was a fundamental feature of the hexapod ground plan, probably inherited from a common ancestor of the Myriapoda-Hexapoda.

**Bitsch's** summary of hexapod appendage morphology and evolution concludes that both hexapods and myriapods probably evolved from crustacean ancestors (independently) and that the legs of Protura and Collembola provide good working models of the hexapod leg groundplan, their undivided tarsus ending in a single claw being homologous to the propodus-dactyl of Crustacea. However, Bitsch's superficial dismissal of the huge body of detailed work by Kukalová-Peck (e.g., 1987, 1991, 1997) seems inappropriate, if not misleading. Personally, I find Kukalová-Peck's concept of an arthropod leg ground plan elegant, in that it provides a unified explanation for all fossil and recent arthropod appendages.

**Jarzembowski's** review of Paleozoic insects and paleocommunities is a bit anemic, falling

short of a thorough discussion of some critically important groups (e.g., Diaphanopteroidea). It devotes only three pages to an actual paleontological review, and four pages to a research case study and research protocols, concluding that, "At present, the fossil record can only provide some general pointers to the Palaeozoic adaptive radiation in which the evolution of insect flight undoubtedly had a key role"—to me, an uninspiring and imprecise view of the state of Paleozoic entomology.

**Kraus** presents a cladogram based on 94 rather traditional morphological characters, in support of the orthodox Hexapoda + Myriapoda relationship. His cladogram, however, appears to be hand-generated, and there are no clearly articulated methods or statistical values presented (Kraus notes that, ". . . polarity of character states are based on a priori judgements inferred from studies on comparative and/or functional morphology"). It is interesting to compare Kraus' characters and methods (?) to other recently published and well-documented phylogenies on these groups, such as Wills (1997), Wills *et al.* (1998), and Edgecombe *et al.* (2000)—the latter analysis being based on 211 non-sequence characters and two gene sequences (histone H3 and U2).

The inclusion of two detailed and useful indexes is testimony to the broad scope of the book's coverage. The index to taxonomic names is over five pages long (three columns), and the gene name index cites nearly six dozen genes. Unfortunately, these indexes appear to have been generated by a computer and not edited, as numerous duplicate entries occur: e.g., Tardigrada/tardigrades; *Distal-less (Dll)/Dll (Distal-less)*.

Overall, the case for a Hexapoda-Crustacea sister-group relationship looks very strong, but clearly more data are needed. This volume does a good job of shining a bright and critical light on the evidence for this relationship. It should be read cover-to-cover by anyone interested in arthropod evolution.

**END NOTE.**—For readers unfamiliar with Kukulová-Peck's hypothesis of limb evolution in the Arthropoda, it derives from 30 years of detailed comparative morphology of fossil and living arthropod limbs. In the Kukulová-Peck model, the arthropod ground-plan appendage comprised a series of 11 articles (4 protopodites, 7 telopodites), each of

which could theoretically bear an articulated endite or exite. Much has been said about this number of articles and its implications to limb homologization among arthropods. But, to me, the *number* of articles in her groundplan is not so important as her concept of a single series of articles, with endites and exites that, like a Swiss Army Knife, specialized to become the great diversity of structures seen in modern taxa (e.g., exites have evolved into a wide variety of epipods, gills, gill cleaners, and flattened paddles on "biramous" Crustacea; wings on insects; etc.). Over evolutionary time, various basal protopodites (especially the first two, the epicoxa and pre-coxa) fused with the pleural region in various arthropod lineages to form pleural sclerites. The epicoxa was incorporated into the pleural membrane early in the evolution of the Arthropoda. On the thoracic segments of insects, the epicoxa migrated dorsally, its exite giving rise to the wings. Viewing the arthropod-limb ground plan as a series of articles from which endites and exites were repeatedly modified in a variety of ways makes 100 years of arguing over the "primitive" nature of uniramous *versus* biramous *versus* polyramous limbs moot.—Richard C. Brusca, Arizona-Sonora Desert Museum, 2021 N. Kinney Road, Tucson, Arizona 85743, U.S.A. (e-mail: rbrusca@desertmuseum.org).

#### LITERATURE CITED

- Brusca, R. C. 2000. Unraveling the history of arthropod biodiversification.—*Annals of the Missouri Botanical Gardens* 87: 13–25.
- Edgecombe, G. D., G. D. F. Wilson, D. J. Colgan, M. R. Gray, and G. Cassis. 2000. Arthropod cladistics: combined analysis of histone H3 and U2 snRNA sequences and morphology.—*Cladistics* 16: 155–203.
- Kukulová-Peck, J. 1987. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta).—*Canadian Journal of Zoology* 65: 2327–2345.
- . 1991. Fossil history and the evolution of hexapod structures. Pp. 141–179 in I. D. Naumann, ed. *The Insects of Australia*. Cornell University Press, Ithaca.
- . 1997. Arthropod phylogeny and 'basal' morphological structures. Pp. 249–268 in R. A. Fortey and R. H. Thomas, eds. *Arthropod Relationships*. Chapman and Hall, London.
- Wills, M. A. 1997. A phylogeny of Recent and fossil Crustacea derived from morphological characters. Pp. 189–209 in R. A. Fortey and R. H. Thomas, eds. *Arthropod Relationships*. Chapman and Hall, London.
- , D. E. G. Briggs, R. A. Fortey, M. Wilkinson, and P. H. A. Sneath. 1998. An arthropod phylogeny based on fossil and Recent taxa. Pp. 33–105 in G. D. Edgecombe, ed. *Arthropod Fossils and Phylogeny*. Columbia University Press, New York.