

Book Reviews

Syst. Biol. 53(4):662–664, 2004
Copyright © Society of Systematic Biologists
ISSN: 1063-5157 print / 1076-836X online
DOI: 10.1080/10635150490472977

Invertebrates, Second Edition.—Richard C. Brusca and Gary J. Brusca. 2003. Sinauer Associates, Inc. Sunderland, Massachusetts. XV + 936 pp. 615 illustrations. ISBN 0-87893-097-3. \$109.95 (Instructor's CD available).

Invertebrate Zoology: A Functional Evolutionary Approach, Seventh Edition. Brooks/Cole Thompson Learning, Belmont, California. XVII + 962 + I-26 pp. ISBN 0-03-025982-7. \$106.95 (Online resources available).

The two leading invertebrate texts, Brusca and Brusca and Ruppert, Fox, and Barnes, recently published much anticipated updated editions. For both books, the new edition offers several improvements. Trying to cover all of invertebrate biology within a single volume is a daunting task, but both texts do a good job of offering a balanced approach to the many sides of invertebrate biology. Unfortunately both also have similar shortcomings, particularly in light of recent advances in animal phylogeny and the field of evo-devo (evolution of developmental mechanisms). As expected of invertebrate texts, both books spend most of their pages marching through taxa and provide critical chapters that unify themes throughout the text.

The most obvious improvements to both texts are aesthetic. Brusca and Brusca has gone from a drab monocolored text to a book rich with color plates, organismal photos, and improved illustrations (partly due to paper quality). Ruppert, Fox, and Barnes has benefited considerably from a change in publishers from Saunders College Press to Brooks/Cole (under Thompson Learning, Inc.). With this switch, several illustrations have been improved, but color plates are lacking despite the similar price between the books. Both have added companion resources for students and/or instructors. Brusca and Brusca offers a CD filled with photos (in jpeg and Powerpoint format) that are searchable by chapter or taxonomic group. Hopefully the CD will be upgraded in the future to include many of the illustrations in the text that would be useful for teaching. In contrast, Ruppert, Fox, and Barnes took an online approach (password protected) and posted over 300 photos and 300 illustrations from their text (searchable by chapter). The downloadable jpeg files have small file sizes allowing easy file transfer, but the quality of the photos clearly suffers on high-resolution monitors. All and all, a larger investment of companion material was given to the Ruppert, Fox, and Barnes book.

Another improvement to Ruppert, Fox, and Barnes is the addition of several chapters focused on evolu-

tionary concepts and functional morphology. In particular, the text includes information on the systematic methods and several figures of phylogenetic trees *à la* Brusca and Brusca, first addition. Both list relevant morphological apomorphies for nodes on the tree, which are easier to read in Brusca and Brusca, but Ruppert, Fox, and Barnes provide taxonomic labeling of interior nodes. In contrast, the layout of the second edition of Brusca and Brusca is almost identical to the first, the exception being rearrangement of five panarthropod chapters. In these chapters, considerable new material has been added and very useful text boxes have been employed for comparative purposes. Disappointingly, many other chapters were not similarly updated. For example, comparison between editions of the mollusk chapter reveals very limited revision except for the final section on evolution and phylogeny. Also in this vein, the diversity of panarthropods gets 239 well-deserved pages, but mollusks that are second in diversity only to arthropods receive 69 pages. In contrast, Ruppert, Fox, and Barnes have considerably reorganized their text to reflect a different understanding of animal relationships than in the sixth edition (which is still at odds with our current understanding—see below). They have also split up some chapters (e.g., cnidarians and ctenophores) to give a more appropriate treatment to these groups. The arthropod/mollusk balance in Ruppert, Fox, and Barnes seems more appropriate (247 pages on panarthropods in 7 chapters and 129 pages of mollusks in one chapter).

A head-to-head comparison between books of any given taxa-oriented chapter will quickly provide an idea of the slight differences in emphasis. Both provide useful synopses of taxonomic classification, phylogeny, functional morphology (e.g., feeding, gas exchange, nervous system, etc.), and reproduction. However, one noticeable difference is the emphasis of the “Bauplan” concept by Brusca and Brusca. Although this emphasis clearly has its advantages when trying to fit all invertebrate biology into a single-term course, it must be weighed against its implications about how we view animal diversity and evolution. Another difference is that Ruppert, Fox, and Barnes present a short outline at the beginning of each chapter that will be especially useful to students. Perhaps the most subtle difference, but with considerable conceptual ramifications, is the treatment of taxonomic ranks in the two texts. Brusca and Brusca present organismal groups as, for example, Phylum Annelida, Class Polychaeta, Order Phyllodocida. The same scheme in Ruppert, Fox and Barnes is presented as Annelida^p,

Polychaeta^c, Phyllococida^o. Although the superscripts still denote rank, they are much less obtrusive and I hope they are a step toward removing them in the next edition. These authors briefly discuss “downplaying the Linnean categories” in Chapter 1. Please note, however, both molecules and morphology show that “Polychaeta” is not a monophyletic clade (McHugh, 2000; Rouse and Pleijel, 2001). Clitellates, echuiran, and pogonophorans are derived polychaetes.

The texts treat higher-level phylogeny differently. Brusca and Brusca opt for the standard format of placing a single overview of metazoan phylogeny at the end of the book. In contrast, Ruppert, Fox, and Barnes, have split higher-level phylogeny up into several chunks spread throughout the text. Although this means searching for the tree of interest, it may have the beneficial aspect of keeping students more engaged in an evolutionary mindset. Specifically, it may help allow students to more thoroughly consider how all of the information they have learned for a given group bears on evolutionary history. Many invertebrate instructors have dealt with the problem of students have long forgotten what placozoans and ctenophores are by the time they get to the phylogeny chapter at the end of the book.

Although both books will no doubt be useful, they both share some major pitfalls. Foremost the treatment of recent invertebrate phylogenetic research, especially in terms of relationships between major lineages, is wanting. Since the last of editions of these books (1990—Brusca and Brusca; 1994—Ruppert and Barnes), considerable advances have been made in our understanding of animal phylogeny, many of which are incorporated into introductory biology texts. Buyer beware!—Both texts are clearly promoted by their respective publishers as including up-to-date molecular phylogenetic results. However, both texts are clearly suspicious of molecular phylogenies. Whereas the Ruppert, Fox, Barnes present both morphological and molecular trees (e.g., Bilateria, Chapter 9), they often acquiesce by stating “current evidence is insufficient to choose between these two alternative phylogenies” (p. 221). In contrast, the Brusca and Brusca text pays lip service to new hypotheses such as Ecdyzoa and Lophotrochozoa, but does not even go as far as to present a figure of these hypotheses in the final chapter on phylogeny. Results from molecular data are explained away by stating that the “field of molecular phylogenetics is still in an emergent phase” (p. 822) among other statements. (It is troubling that such a viewpoint will reach so many students.) Both texts are steadfast in their placement of lophophorates and chaetognaths as deuterostomes even though abundant data show different. The Brusca and Brusca text does not consider the Ambulacraria (hemichordates and echinoderms), which changes our understanding deuterostome evolution, and Ruppert, Fox and Barnes recognize such a clade, but appear not to have been aware of the term Ambulacraria, which has gained popularity in the last several years. This lack of consideration of molecular findings extends to treatment within groups. For example, neither considers the only rigorous phylogenetic treatment for ctenophores, Podar et al.’s (2001) molec-

ular work. Unfortunately, invertebrate biology students may be deprived of understanding many recent molecular phylogenetic advances that have completely changed our views of animal evolution (reviewed in Adoutte et al., 2000; Halanych and Passamanek, 2001; Giribet, 2002; Halanych, 2004—obviously these later references were not available in time for these texts, but are given for the interested reader).

The molecular data notwithstanding, both texts fail to consider the morphological data appropriately. For example, in both texts the morphology is purported to support the Articulata concept (annelids and arthropods as sister taxa) and the Lophophorata concept (brachiopods, phoronids, and bryozoans as a monophyletic clade). However, at the time these texts were written, there were several morphological cladistic analyses that clearly demonstrated morphology did not support either of these two ideas (e.g., Eernisse et al., 1992; Zrzavy et al., 1998; Giribet et al., 2000; Peterson and Eernisse, 2001). Although these objections may sound trivial, they are not. Because phylogeny is the comparative framework upon which character evolution is based, several important concepts (e.g., segmentation, coelom formation, evolution of suspension feeding) are being incorrectly presented by these texts given our current understanding of animal evolution.

Major advances made on evolution of developmental mechanisms and in paleontology were not well represented in these texts. Brusca and Brusca does occasionally mention evo-devo findings, but given how the field has changed our understanding of “Bauplan” evolution, I expected more. Curiously, Ruppert, Fox, and Barnes provide a discussion of *Drosophila* segmentation in the annelid chapter (p. 422), and then conclude that *engrailed* is expressed similarly insects and leeches. They apparently did not consider that other annelids appear to be doing something different to insects (*engrailed*—Seaver et al., 2001; *hunchback*—Werbock et al., 2001). Because comparisons of body plans is a main component of invertebrate texts and embryogenesis has historically played a pivotal role in invertebrate evolutionary hypotheses, it would have been nice to see space given to explaining the formation of body plans from a molecular developmental perspective (e.g., deployment of Hox genes and determination of body axis polarity). Additionally, fossil discoveries from Lower Cambrian Chengjiang and Sirius Passet faunas have dramatically altered our views of early animal evolution (Knoll and Carroll, 1999). As such, invertebrate texts should take advantage of this exciting new information as a way to generate student interest. Even though an invertebrate text must by necessity be limited in scope, it would be worthwhile to expose students to these exciting finds.

In a field such as invertebrate biology, where a limited number of texts serve a large community, ideas presented can take hold rapidly, and falsities can be hard to eradicate. Surprisingly, both texts included new made-up taxonomic terms, or very obscure ones, that have no formal definition or are not found in the primary literature. In such cases, I fear that the texts will ultimately introduce confusion into the literature. For example, Brusca and

Brusca make up the term "Pogonophoridae" for the beard worms. However, according to the rules of nomenclature, this term is a junior synonym to Siboglinidae, a term espoused by McHugh (1997) and Rouse and Fauchald (1997), whose work both texts recognize in placing siboglinids within annelids. Brusca and Brusca also reintroduce the term "Blastocoelomates," which is basically just a reworking of psuedocoelomates or aschelminthes. This includes groups that appear to be widely dispersed on the tree given our current understanding. The argument that a psuedocoel is not a good character is valid, but the blastocoel is clearly not a synapomorphy for the taxa in question. Similarly, Ruppert, Fox, and Barnes use terms such as Pulvinifera (i.e., Sipuncula plus Articulata) and Lophodeuterostomia (i.e., Lophophorates plus Deuterostomes). Although I certainly have been accused of interjecting complicated novel terms into the literature, it is important that they are clearly defined, not redundant, and appropriately justified based on a rigorous phylogenetic analyses.

Undoubtedly there are some issues with the new editions of both books, especially from the evolutionary prospective. Even so, all the authors should be soundly commended for accomplishing a task that many of us would loath. Both texts are still very valuable resources for the both students and researchers and will no doubt remain as the leading selling texts. As mentioned above, both also make considerable improvements over 7 previous additions due to contributions by both authors and publishers. Even though the Brusca and Brusca text appears at times to have a better grasp of the recent literature on metazoan phylogeny, the text is more skeptical and dismissive of recent findings. Ruppert, Fox, and Barnes integrated treatment of phylogeny I think is preferable and their online support will be a better teaching aid. Brusca and Brusca, however, will be appealing to students because of its superior aesthetic qualities. Having compared the two books, I prefer Ruppert, Fox, and Barnes. As a recommendation to those who may use either book, the texts will be useful for invertebrate organismal biology, but obtain a recent review of animal phylogeny as a supplement (e.g., Giribet et al., 2000; Peterson and Eernisse, 2001; Halanych, 2004).

Note: The fifth edition of Pechenik's invertebrate text (McGraw-Hill) hit shelves in Spring 2004. This text takes a more streamlined, less encyclopedic, approach to invertebrates. Although I have not seen the book yet,

from talking with the author, he appears to have made a considerable effort to incorporate the latest phylogenetic hypotheses. I encourage those interested to check it out.

REFERENCES

- Adoutte, A., G. Balavoine, N. Lartillot, O. Lespinet, B. Prud'homme, and R. de Rosa. 2000. The new animal phylogeny: Reliability and implications. *Proc. Natl. Acad. Sci., U.S.A.* 97:4453–4456.
- Eernisse, D. J., J. S. Albert, and F. E. Anderson. 1992. Annelida and Arthropoda are not sister taxa: A phylogenetic analysis of spiralian metazoan phylogeny. *Syst. Biol.* 41:305–330.
- Giribet, G. 2002. Current advances in the phylogenetic reconstruction of metazoan evolution. A new paradigm for the Cambrian explosion? *Mol. Phylogenet. Evol.* 24:345–357.
- Giribet, G., D. L. Distel, M. Polz, W. Sterrer, and W. C. Wheeler. 2000. Triploblastic relationships with emphasis on the acelomates and the position of Gnathostomulida, Cycliophora, Plathelminthes and Chaetognatha: A combined approach of 18S rDNA sequences and morphology. *Syst. Biol.* 49:539–562.
- Halanych, K. M. 2004. The new view of animal phylogeny. *Annu. Rev. Ecol. Evol. Syst.* 35:229–256.
- Halanych, K. M., and Y. Passamanek. 2001. A brief review of metazoan phylogeny and future prospects in Hox-research. *Am. Zoo.* 41:629–639.
- Knoll, A., and S. B. Carroll. 1999. Early animal evolution: Emerging views from comparative biology and geology. *Science* 284:2129–2137.
- McHugh, D. 1997. Molecular evidence that echiurans and pogonophorans are derived annelids. *Proc. Natl. Acad. Sci. U.S.A.* 94:8006–8009.
- McHugh, D. 2000. Molecular phylogeny of Annelida. *Can. J. Zool.* 78:1873–1884.
- Pechenik, J. A. 2004. *Biology of the invertebrates*, 5th edition. McGraw-Hill Higher Education, Boston.
- Peterson, K., R. Cameron, and E. Davidson. 2000. Bilaterian origins: Significance of new experimental observations. *Dev. Biol.* 219:1–17.
- Podar, M., S. H. Haddock, M. L. Sogin, and G. R. Harbison. 2001. A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. *Mol. Phylogenet. Evol.* 21:218–230.
- Rouse, G. W., and K. Fauchald. 1997. *Cladistics and polychaetes*. *Zool. Scripta* 26:139–204.
- Rouse, G. W., and F. Pleijel. 2001. *Polychaetes*. Oxford University Press, New York.
- Seaver, E. C., D. A. Paulson, S. Q. Irvine, and M. Q. Martindale. 2001. The spatial and temporal expression of Ch-en, the engrailed gene in the polychaete Chaetopterus, does not support a role in body axis segmentation. *Dev. Biol.* 236:195–209.
- Werbrock, A. H., D. A. Meiklejohn, A. Sainz, J. H. Iwasa, and R. M. Savage. 2001. A polychaete hunchback ortholog. *Dev. Biol.* 235:476–488.
- Zrzavy, J., S. Milhulka, P. Kepka, A. Bezdek, and D. F. Tietz. 1998. Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. *Cladistics* 14:249–285.

Kenneth M. Halanych, Department of Biological Sciences, Auburn University, Alabama, USA; E-mail: ken@auburn.edu

Invertebrates.—R. C. Brusca and G. J. Brusca. 2003. Sinauer Associates, Sunderland, Massachusetts. xix + 936 pp. ISBN 0-87893-097-3. \$109.95 (cloth).

For good reason, the release of the first edition of Brusca and Brusca's (1990) *Invertebrates* was a welcome

revolution in the content of textbooks designed for post-secondary education in comparative biology: included in most chapters were more than a dozen cladograms with explicit character and state argumentation, culminating with a composite Metazoan Tree of Life in the 24th

and final chapter devoted exclusively to "Perspectives on Invertebrate Phylogeny." In light of this revolutionary approach, and noting that at the time there were exceedingly few phylogenies concerning nonarthropod invertebrates, the Bruscas were easily forgiven the fact that few of the cladograms were more than 3- or 4-taxon statements with perfect consistency and with terminals presupposing large groups like "oligochaetes" to be monophyletic. The principal criticism of that first edition was its faith in bauplans and archetypes (Mooi, 1991; Calow, 1992).

If the extent of the phylogenetic approach in the first edition made it revolutionary, its compass in the second is unfortunate. Although the authors state that the book still "takes evolution as its central theme" (p. 15), there has been scant revision of the phylogenetic perspectives that have so dramatically marked the last 10 years of invertebrate systematics. The change from "pseudocoelomates" to "blastocoelomates" is not a major retooling. Though the pogonophorans, tardigrades, and myxozoons may have found their way into chapters on annelids, arthropods, and cnidarians, respectively, there is little else reflecting the revisions that should be required by the 13 year long interval between editions. Chapters that lacked phylogenetic treatments in the first edition still lack them, even where considerable work has been accomplished (e.g., Giribet et al., 1999; Podar et al., 2001). Where they do occur, the majority of the cladograms are identical to those of the first edition and remain as 3- or 4-taxon statements. In several instances these contain even less information than was provided a dozen years earlier (e.g., chapters 11, 13, and 17). The extensive body of literature supporting the clade Ecdysozoa is dismissed in a paragraph (p. 883), in which we are reminded first that ecdysozoa has not been demonstrated for several members of the clade and second, that if it were, it wouldn't matter anyway. Similarly, the Bruscas still insist on an identity for annelidan and arthropodan metamerism, notwithstanding that for some time we have known the genetic control is distinct (Patel et al., 1989; Seaver and Shankland, 2001). As for the Trochozoa (Eu- or Lopho-), the very brief discussion (p. 883, there is no Index entry) denies its veracity on the grounds that not all of the listed phyla have both lophophores and trochophores (but wingless Hippoboscidae are listed with dipterans). The teleological, and now repudiated, progression from hemichordate through urochordate to cephalochordate and craniate remains intact in this edition, all but ignoring the convincing body of work in favor of a hemichordate-echinoderm clade (e.g., Cameron et al., 2000; Telford et al., 2000). In fact, the text remains replete with *scalae naturae* (the "evolutionary trees" illustrated distinct from cladograms) that will serve only to confuse students.

The reason given for the lack of protist phylogenies, for the monophyletic Porifera, for the assertion that "the evolutionary relationships of the Acanthocephala are particularly enigmatic" (p. 382), even though they have been repeatedly shown to group with rotifers (Garey et al., 1996; Welch, 2000), for dismissing the earnest endeav-

ors of several dozens of systematists over a dozen years, each of whom sought to tear away the obdurate shrouds of 19th century *Naturphilosophie* that have so long obscured invertebrate relationships, is that all of this is just "quirky and troublesome" and "still await rigorous testing" (p. XVIII).

Notwithstanding convincing arguments that bauplans cannot be reconciled with the inevitable realization that organisms are composites of plesiomorphic and apomorphic traits, this discredited posture is still central in the second edition. The authors appear to believe there is a single definable superencompassing plan (one presumes they do not intend to imply providential "design" on p. 41) governing all forms of "protists," including ciliates, diplomonads, microsporidians, and even kelp. The very "element of predictability" (p. 43) they trust *bauplâne* entails, belies a rigidity that renders relatedness opaque and leads them, for example, to ignore the fact that *Symbion* is a rotifer not worthy of a phylum unto itself.

Each chapter is equipped with "Selected References" that, though selective, are mostly not referred to in the body of the chapter. In these bibliographies, readers will find it very difficult to find evidence of work published in the last 5 years. Taking the Phylum Annelida as an example, it is hard to imagine how the extensive contributions by each of Erséus, Ferraguti, Pleijel, Purschke, Sawyer, and Weisblat could be completely overlooked. Under *Clitellata* one finds Brinkhurst and Gelder's (1989) "Did [*sic*] the lumbriculids provide the ancestors of the branchiobdellidans, acanthodbellidans and leeches?" but not the affirmative answer appearing a decade later. The Bruscas exculpate themselves from the "shocking and dangerous trend that encourages dilettantes" (p. XVIII) of which the rest of us are so guilty.

This is not to say the new edition is without improvements. There are color pictures for example. Others (Emler, 2003; Winston, 2003) have commented positively on the degree of taxonomic coverage and the attention to developmental details. But, this coverage was as good in the first edition, used copies of which can be found online for about a third of the price and which no student will be misled into believing is up-to-date.

REFERENCES

- Brinkhurst, R. O., and S. R. Gelder. 1989. Did the lumbriculids provide the ancestors of the branchiobdellidans, acanthodbellidans and leeches? *Hydrobiology* 180:7-15.
- Brusca, R. C., and G. J. Brusca. 1990. *Invertebrates*. Sinauer Associates, Sunderland, MA.
- Calow, P. 1992. Book Review—*Invertebrates*. Richard C. Brusca and Gary J. Brusca. *Quart. Rev. Biol.* 67:215-216.
- Cameron, C. B., J. R. Garey, and B. J. Swalla. 2000. Evolution of the chordate body plan: New insights from phylogenetic analyses of deuterostome phyla. *Proc. Natl. Acad. Sci. U.S.A.* 97:4469-4474.
- Emler, R. B. 2003. *Invertebrates*. Second Edition. Richard C. Brusca and Gary J. Brusca. *Limnol. Oceanogr. Bull.* 12:57-58.
- Garey, J. R., T. J. Near, M. R. Nonnemacher, and S. A. Nadler. 1996. Molecular evidence for Acanthocephala as a subtaxon of Rotifera. *J. Mol. Evol.* 43:287-292.

- Giribet, G., S. Carranza, M. Riutort, J. Baguna, and C. Ribera. 1999. Internal phylogeny of the Chilopoda (Myriapoda, Arthropoda) using complete 18S rDNA and partial 28S rDNA sequences. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* 354:215–222.
- Mooi, R. 1991. Book Review—Invertebrates. Richard C. Brusca and Gary J. Brusca. *Syst. Zool.* 40:245–247.
- Patel, N. H., E. Martin-Blanco, K. G. Coleman, S. J. Poole, M. C. Ellis, T. B. Kornberg, and C. S. Goodman. 1989. Expression of engrailed proteins in arthropods, annelids, and chordates. *Cell* 58:955–968.
- Podar, M., S. H. D. Haddock, M. L. Sogin, and G. R. Harbison. 2001. A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. *Mol. Biol. Evol.* 21:218–230.
- Seaver, E., and M. Shankland. 2001. Establishment of segment polarity in the ectoderm of the leech *Helobdella*. *Development* 128:1629–1641.
- Telford, M. J., E. A. Herniou, R. B. Russell, and D. T. Littlewood. 2000. Changes in mitochondrial genetic codes as phylogenetic characters: Two examples from the flatworms. *Proc. Natl. Acad. Sci. U.S.A.* 97:11359–11364.
- Welch, M. 2000. Evidence from a protein-coding gene that acanthocephalans are rotifers. *Invert. Biol.* 119:17–26.
- Winston, J. E. 2003. *Invertebrates*. Second Edition. Richard C. Brusca and Gary J. Brusca. *J. Crustacean Biol.* 23:974–976.
- Mark E. Siddall, *Invertebrate Zoology, American Museum of Natural History, New York, NY 10024.*

Syst. Biol. 53(4):666–668, 2004
 Copyright © Society of Systematic Biologists
 ISSN: 1063-5157 print / 1076-836X online
 DOI: 10.1080/10635150490468521

Lousy Lists

The Chewing Lice: World Checklist and Biological Overview.—R. D. Price, R. A. Hellenenthal, R. L. Palma, K. P. Johnson, D. H. Clayton. 2003. Illinois Natural History Survey Special Publication 24. x + 501 pp. ISBN 1-882932-08-0. \$35.00 (hard cover).

“The student of the Mallophaga . . . can be compared to the palaeontologist. He delves into the past, not by quarrying into the rocks for fragments of bones, but by studying the morphology and distribution of these living fossils. As he pieces together the story of their evolution, he likewise unfolds the story of the evolution of the birds.”

(Rothschild and Clay, 1952: p. 146)

Arguably no insect has played a more prominent role in the study of cospeciation than that of the parasitic louse. From the formulation of the rules of parasitism by Fahrenholz (1913) and Eichler (1948), through to the seminal gopher louse studies of Mark Hafner and colleagues (Hafner et al., 1994), the study of parasitic lice is as intertwined with the study of cospeciation, as lice are with the evolution of their hosts. Passed like genetic heirlooms from one host generation to the next, lice track their hosts' evolutionary histories with varying degrees of fidelity. The study of this association has spawned a cottage industry of empirical research aimed at building and comparing host and louse phylogenies. Evidence of host-lice cospeciation provides an opportunity to test hypotheses of coadaptation, and calibrate rates of evolution in biologically disparate taxa. Lice have even been the subject of a recent conference (Smith, 2003) and formed the prevailing empirical examples in two recent symposia on cophylogeny (Johnson and Clayton, 2004; Page, 2002). Intense methodological debate surrounds the best method of reconciling host and parasite trees, and louse datasets form the basis for the development of many of these methods. Despite this interest, obtaining the evidence for cospeciation, particularly host-lice cospeciation is fraught with difficulties; perhaps the most fundamental of these is the necessity to understand the basic diversity and distribution of lice.

Until recently, these data have largely sat unpublished in patchy card catalogues of the world's major natural history museums, or in obscure publications written in many different languages. Price, Palma, and Hellenenthal unite this information in a new checklist of chewing lice, a landmark publication that provides an unparalleled opportunity to study the global diversification of this large parasite fauna across its avian and mammalian hosts. This book represents the fourth published checklist of world chewing lice, and almost doubles the number of chewing louse taxa recognised since the last checklist, printed some 50 years ago (Hopkins and Clay, 1952). It documents a staggering 9311 associations between 4464 chewing lice, parasitizing 3248 bird and 422 mammal species—not counting a further 1880 species and subspecies considered in synonymy. Given this breathtaking scope, it is not surprising that it has taken the three principal authors almost 20 years to compile. Taxonomic coverage is restricted to “Mallophaga,” a large paraphyletic group that, together with the Anoplura or ‘sucking lice,’ form the insect order Phthiraptera. This division reflects the specialisation of the authors and will appeal to entomologists that traditionally consider these insect groups separately (Durden and Musser, 1994). The checklist is accompanied by keys for every host order, illustrations of all 253 chewing louse genera, and through the collaboration of Kevin Johnson and Dale Clayton, includes an extensive review of chewing louse biology, ecology and evolution.

The book's introduction charts the rise and fall of louse taxonomy from the late 18th century to the present day, encompassing a so-called “Golden Era,” between 1953 and 1972 that saw the description of almost 30% of all chewing louse taxa. Although some aspects of louse research have undergone a minor renaissance of late, the same cannot be said of louse taxonomy, and this takes on a special significance when one considers issues of host specificity. Price et al. vividly portray this in their

introduction, taking the unusual approach of tabulating the number of louse taxa described by each of the worlds leading louse systematists, and what proportion of these taxa they consider valid in the new checklist. Respectfully, the authors only include deceased workers, but the results are nonetheless revealing, implying that either many early louse taxonomists were poor morphologists, or more likely, were somewhat seduced by host associations as an indicator of louse specificity. The latter assumption is born out by subsequent tables that chart louse specificity among each bird and mammal order. Any expectation of strict host specificity is quickly dismissed. Nevertheless, the tables reveal six bird and mammal orders where each known louse species is restricted to a single host species, and several other host orders where the level of louse specificity lies tantalizingly close to this mark. Although it is naïve to suggest that these data alone provide an indication of the extent of louse cospeciation or coevolution within a host clade, the temptation to make this link is strong and the tables do provide a starting place for those seeking groups of hosts where we might expect to see evidence of cophylogeny.

The last set of comprehensive generic keys and illustrations for chewing lice was published in 1908. Price et al. produce a much-needed update with a complete set of illustrated keys for all genera. The literature on louse morphology is replete with conflicting interpretations and synonyms, making the compilation and use of keys for chewing lice exceedingly difficult. Price et al. avoid much of this nomenclatural jargon by arranging the key by host order. This has the effect of dramatically simplifying each couplet, making it much more widely accessible than would otherwise have been possible. It does mean that at least some knowledge of the host taxon is required before the key can be useful. However, the number of instances when the host order of a louse is unknown are thankfully few. This key, coupled with the illustrations, make this a valuable resource that alone is worth the cover price of the book.

The *pièce de résistance* comprising the bulk of this book is the checklist, divided into two sections arranged by louse and by host. Host classification follows Howard and Moore (1991) for birds, and Wilson and Reeder (1993) for mammals. The authors have been ultraconservative in their classification of the lice, accepting fewer familial names than were considered valid in the last louse checklist published 50 years ago. Furthermore, the decision to arrange the louse portion of the checklist alphabetically by family is surprising given recent efforts to identify and resolve the phylogeny of the major chewing louse clades. This arrangement could either be seen as prescient given the transient nature of some recent phylogenetic hypotheses for lice, or at best rather "traditional." I reserve judgement, but failure to divide this section up by the principal louse suborders whose monophyly has been generally accepted for at least 50 years seems odd—at least it is an improvement on the 1952 checklist, which was entirely arranged alphabetically by genus. Within both portions of the checklist each entry

is arranged in the form of an indented list. Authorities, synonyms, hosts, and type hosts are indicated, and the checklist is completed by an extensive bibliography that includes references to every alpha taxonomic publication ever published on chewing lice.

Navigating the checklist is difficult, hindered by headers that provide little more than the briefest indication of context. Within the host section, anyone with a good working knowledge of bird or mammal classification is unlikely to be too impeded by this, but I can think of fewer than 10 individuals worldwide that would be equivalently familiar with louse taxonomy. I regularly found myself getting lost amongst the myriad of pages devoted to speciose louse genera, amongst whose pages there is no indication of the louse genus and only the family name is indicated by the header. The situation is worse in the host list, where the header is limited to distinguishing between mammals and birds. Separate indices to genus are provided for louse and host taxa, alongside another index for host common names. However, in such a large and unwieldy book I found myself spending more time trying to locate the right index and find the appropriate entry than I did when I actually arrived at the relevant page. These niggles are unlikely to deter a casual user, interested in the host distribution of a particular louse species, or the louse fauna present on a particular bird or mammal. As such, amateur entomologists, ornithologists, and veterinarians will doubtless find the checklist a valuable addition to their bookshelves. However, as a resource for wider scientific research, such niggles become an insurmountable barrier to unlocking the true potential of the data contained within these pages.

From the perspective of an evolutionary parasitologist, biogeographer, or comparative biologist, this checklist offers the raw material to study the forces driving the radiation and diversification of a major lineage of insects of worldwide distribution. Estimates of host specificity and species diversification are directly available from data within the checklist. If these were coupled with host geographic ranges, and a growing forest of known phylogenies for both the hosts and their parasites, the checklist would offer an unparalleled tool for addressing many fundamental questions concerning host-parasite evolution. Only an electronic release of the checklist would make this meta-analysis possible, and it is unfortunate that the checklist authors did not have the vision to present their data in a more accessible format to accompany the published book. Inclusion of a CD-ROM, or development of an accompanying website would enable the book to reach an audience far broader than the relatively narrow band of systematists it doubtless will otherwise attract. The inevitable additions and corrections necessary for a checklist of this scale would also be much easier to administer and release in electronic form. It is particularly frustrating that the authors are clearly aware of some of the issues surrounding electronic release of data, as a portion of the introduction is devoted to describing the relational data model in which

the checklist data was stored prior to publication. A lack of digitized taxonomic records frustrates efforts to compile lists of the world's living species, and development of the next generation of tools and data repositories that can be woven using web services into GenBank, PubMed, or the fledgling Global Biodiversity Information Facility (GBIF) (Agosti, 2003). GBIF recently announced a major funding initiative designed to digitize old taxonomic catalogues and checklists in an attempt to speed up the electronic capture of taxonomic names. It borderlines on madness that while some members of the systematic community are busy digitizing taxonomic works produced before the dawn of the personal computer, others are using electronic techniques to publishing new paper-based catalogues that will at some future point need to be redigitized!

Publication of this checklist was aided by the PEET initiative (Partnerships for Enhancing Expertise in Taxonomy) funded by the US National Science Foundation (Rodman and Cody, 2003). This funding was intended to bridge the gap between an aging population of taxonomic specialists and a new generation of phylogeneticists and ecologists, and enabled the hardbound checklist to be published by Illinois Natural History Survey at the reduced price of \$35. It also brought with it the collaboration of Kevin Johnson and Dale Clayton who contributed the final chapter on chewing louse biology, ecology, and evolution. The position of this chapter reflects this change in authorship but is perhaps unfortunate, as this section is arguably more accessible to the casual reader than much of the preceding text. Parasitic lice dominate methodological and empirical debates on cospeciation and form a useful 'model system' to address a range of questions associated with the evolution of host-parasite faunas. Johnson and Clayton seek to explain the unique characteristics of these parasites that have enabled them to acquire 'model' status, and in doing so provide a detailed account of chewing louse natural history. This authoritative account gathers data on all aspects of chewing louse biology, and succeeds where similar accounts in entomological textbooks have failed by placing these data in a broader research context. Anyone interested in the evolutionary ecology or cophylogeny of parasites is encouraged to read this chapter, which makes valuable addition to the book.

To some (probably not the readers of this review), checklists epitomize traditional taxonomy—dry lists of species diversity with few redeeming qualities. Indeed it is fair to say that most checklists don't make exciting reading, are hard to fund, almost impossible to publish, and require years of expertise to compile. With the exception of a handful of taxonomists working on high profile taxa, the majority of taxonomists compiling checklists are close to or over retirement age and un-

paid for their efforts. Yet these lists represent the foundation stone for understanding biological diversity. Making sense of this data requires releasing it to the widest possible audience and in the case of taxonomic data, this can only mean an electronic release to accompany traditional methods of publication. This checklist of chewing lice is far more than a list of names. It represents the collective efforts of three taxonomists that between them have more than 100 years of experience in insect systematics. Their description of that diversity is a magnificent achievement that will doubtless form the cornerstone of chewing louse biology for many years to come. Yet this description is just a first step towards understanding that diversity, and it is vital that taxonomists recognise this role for their data. Taxonomy is a tool—like any other it serves a wider purpose. Only by embracing this fact and releasing taxonomic data to the widest possible audience will this role be realized. In doing so perhaps the profile of taxonomists will be raised in the process.

REFERENCES

- Agosti, D. 2003. The last of its kind? *Nature* 424:727.
- Durden, L. A., and G. G. Musser. 1994. The sucking lice (Insecta, Anoplura) of the world: A taxonomic checklist with records of mammalian hosts and geographic distributions. *Bull. Am. Mus. Nat. Hist.* 218:1–90.
- Eichler, W. D. 1948. Some rules in ectoparasitism. *Ann. Mag. Nat. Hist. (Series 12)* 1:588–598.
- Hafner, M. S., P. D. Sudman, F. X. Villablanca, T. A. Spradling, J. W. Demastes, and S. A. Nadler. 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science* 265:1087–1090.
- Hopkins, G. H. E., and T. Clay. 1952. A checklist of the genera and species of Mallophaga. British Museum of Natural History, London.
- Howard, R., and A. Moore. 1991. A complete checklist of birds of the world, 2nd edition. Academic Press, London.
- Johnson, K. P., and D. H. Clayton. 2004. Untangling coevolutionary history. *Syst. Biol.* 53:92–94.
- Page, R. D. M. (ed.) 2002. *Tangled Trees: Phylogeny, cospeciation and coevolution*. University of Chicago, Chicago.
- Rodman, J. E., and J. H. Cody. 2003. The taxonomic impediment overcome: NSF's partnerships for enhancing expertise in taxonomy (PEET) as a model. *Syst. Biol.* 52:428–453.
- Rothschild, M., and T. Clay. 1952. *Fleas, flukes and cuckoos: A study of bird parasites*. Collins, London.
- Smith, V. S. 2003. The Second International Congress on Phthiraptera (lice), held 8–12 July 2002 at the University of Queensland, Brisbane, Australia. *N. Z. J. Zool.* 30:327–331.
- Wilson, D. E., and D. M. Reeder. 1993. *Mammal species of the world: A taxonomic and geographic reference*, 2nd edition. Smithsonian Institution Press, Washington and London.

Vincent S. Smith, *Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, United Kingdom; E-mail: v.smith@bio.gla.ac.uk*

Syst. Biol. 53(4):669–670, 2004
 Copyright © Society of Systematic Biologists
 ISSN: 1063-5157 print / 1076-836X online
 DOI: 10.1080/10635150490468530

Phylogeny in the Comfort Zone

Inferring Phylogenies.—Joseph Felsenstein. 2003. Sinauer Associates, Sunderland, Massachusetts.

This is the book we have been waiting for—occasionally a book is a classic by the time it is published and this is it. We have needed this for a long time; phylogenetics has grown enormously over the last two decades and it is almost impossible to keep a proper overview. By my estimate (not ML, I'm afraid) this book has around 1000 references. There is no way that ordinary mortals can keep up with such a literature on methodology alone, let alone work back through it to find sources of ideas, or possible alternative approaches that need developing.

The breadth is very wide with all the main expected topics. Numbers of trees, parsimony algorithms, distance calculations, Markov models for sequence evolution, likelihood and Bayesian methods, bootstraps, likelihood ratio and other tests, consensus, and coalescents. Such a full treatment requires over 600 pages, which is not surprising given that many less common approaches are also covered including compatibility, invariants, Hadamard transforms, restriction site data, quantitative characters, tree shapes, and even to ways of drawing trees. A strength of the book is that it presents the theory behind the methods in a clear manner. A lot of thought has gone into presenting the equations in ways that quantitative biologists can gather the key points without being lost in additional mathematics and proofs. Okay, perhaps the others can skip over the equations and follow the text, but that would miss a lot of the benefit.

The book has clearly been put together over a long time period, it is of mature vintage. There has been time to fine-tune the wording, to look over how the equations and diagrams are presented. The extra time has helped get things right, sentences reworked, an obscure reference found, a gentle joke included. It turns out that Joe is the founder of the "It-Doesn't-Matter-Very-Much" school—get the tree right and shut up—with a healthy scepticism towards the importance of a formal classification. Overall the book has that comfortable mature feeling, no, not quite like mulled wine, more a really good mellow single-malt whisky with just a bit of bite—the Laphroig of the phylogenetics market.

One theme that becomes apparent is that many ideas have been discovered or reinvented several times. This is not really surprising, estimating evolutionary trees accurately is a major problem in mathematical inference with the relevant theory coming from mathematics (graph theory, combinatorics, and Markov chains), statistics (likelihood, resampling, Bayesian), operations research (optimization, search heuristics), and computer science (complexity theory). No one (including mathematicians!) are expert in all those fields. Consequently

anyone with a new idea to try out will especially gain from the book; there is just so much in it that will help get a quick start on how similar ideas have worked.

Somehow a reviewer feels duty bound to find some reference missed, a factlet wrong, or similar minor misdemeanour. I definitely would have included Hartigan (1973) as a brilliant early piece of work; he proved that the Fitch algorithm for the length of a specified tree would always give the minimum length. On the surface it looked as if that calculation had to increase exponentially with the number of taxa—just look at the number of ways you could label the internal nodes of Figure 1A as the number of taxa grew. Then find your way though all possible paths to get the shortest. Surely, the calculation had to be exponential. To prove an algorithm that increased linearly with the number of species was amazing. So having found one reference missed I could feel pleased with myself, relax, and enjoy the book. However, I was soon deflated by a (favorable) reference to my own work that I had completely forgotten about! The moral of the story is not to try and catch Joe out, just enjoy the amazing resource he has assembled. (You still should check the list of corrections at <http://evolution.gs.washington.edu/book/typos.html>.)

Perhaps the only change in emphasis I would like is to see more attention given to properties of the data—and therefore when method X might therefore be preferred over method Y. For example, there is still a strong tendency to say that maximum likelihood on sequences is 'statistical' whereas parsimony on morphological data is not. This seems wrong; both examples are ML estimators for different classes of data (see Fig. 1). An important

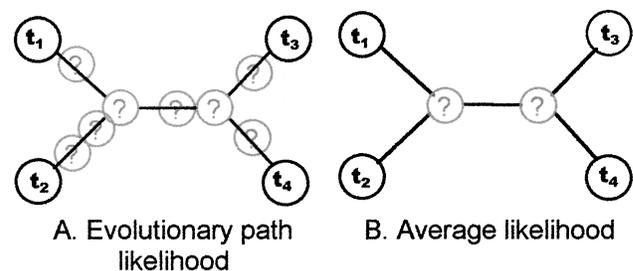


FIGURE 1. Averaging over missing data for (A) morphological data and (B) for molecular data. For molecular data (B) maximum likelihood need only average over all codes at the internal points, the Markov model handles the ways the data may have changed along each branch, this is ML_{average} of Steel and Penny (2000). For morphological data (A), on current implementations without an easy justification for a Markov model, maximum likelihood has to consider what the data might have been at all points along each branch, and gives $ML_{\text{evolutionary path}}$, which is parsimony. Will still could do better, but the maximum likelihood estimator depends on the properties of the data.

difference is how we handle missing data for sequences and for morphology. We have information about the leaves (terminal nodes) of the tree, but not about the changes along the branches or internal nodes (see Fig. 1A). The brilliant thing about molecular data is that in treating it as a Markov model we do not have to estimate the character-state at all points along the branch. Integrating the rate matrix does this for us (Fig. 1B); all we need do is sum likelihood values over all character states at the internal nodes, giving maximum average likelihood (Steel and Penny, 2000).

With morphological data a Markov model does not seem relevant. It's the data that are different, not the maths. We still have further to go here; Paul Lewis (2001) has a brave attempt at a new ML method for morphological data. Both approaches—parsimony and likelihood—are 'statistical'; it is the data that's different. Myself, I'm a fan for using molecular data in phylogeny; then using morphological data to trace the real biological questions—morphological, ecological and physiological changes and adaptations during evolution. Speaking of properties of the data, we really also needed more on the importance of among site rate variation, and the consequences of not considering it. The properties of the data are as important as how the methods actually work. Okay, stop whinging.

What of the future; we now have an outstanding summary of where we have been over the last 25 years. Perhaps it is foolish to try and be 'wise before the event,' but that is what fools are for. Take just one example, for the last 20 years phylogenetics has been dominated by sampling error—we have bootstrapping, convergence tests, Templeton, Shimodaira–Hasegawa tests, and on and on. In the past the universal problem seemed to be short sequences—not enough data. Suddenly we are getting much longer sequences (for example, Rokas et al., 2003), so why do we keep getting some particular trees wrong?

We increasingly understand that, according to the current models we love and trust, sequences must run out of phylogenetic information after a few hundred million years (see Mossel, 2003). There is a comfort zone where

sequences work well. Graduate students please their advisors by running simulations in this zone, and cunningly leave the time-scale as the proportion of mutations per site (not as the product of mutation rate and time, that would upset our belief in the infallibility of sequences).

Our models are still incomplete by a long way, and there can be strong systematic biases in many data sets. Bootstrapping or Bayesian support values are no help if we are converging to the wrong tree. Is Bayesian support the art of being wrong—with confidence? How well does the best model fit the data, how much of the variability is explained by the model? Yes, there is a lot to do. But if Joe had stopped to write a chapter on possible future directions we would have had to wait much longer for this book—perhaps forever. The rest of the field keeps expanding and would then require more writing; we needed this book now!

The advertisements suggest that *Inferring Phylogenies* could be used as a textbook. I doubt it—that's really publisher mis-talk. The book is a resource. It is absolutely essential for any laboratory. I am keeping mine at home so that I can always find it—keeps the fingers of grad students and postdocs off my copy. No, I am not being mean; we have bought two copies for the lab. It is hard to imagine how any lab could function without this book.

REFERENCES

- Hartigan, J. A. 1973. Minimum mutation fits to a given tree. *Biometrics* 29:53–65.
- Lewis, P. P. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* 50:913–925.
- Mossel, E. 2003. On the impossibility of reconstructing ancestral data and phylogenies. *J. Comp. Biol.* 10:669–676.
- Rokas, A., B. L. Williams, N. King, and S. B. Carroll. 2003. Genome-scale approaches to resolving incongruence in molecular phylogenies. *Nature* 425:798–804.
- Steel, M. A. and D. Penny. 2000. Parsimony, likelihood and the role of models in molecular phylogenetics. *Mol. Biol. Evol.* 17:839–885.

David Penny, Allan Wilson Center for Molecular Ecology and Evolution, Massey University, Palmerston North, PO Box 11–222, New Zealand.