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A Book Review of
The Biology of Wetas, King Crickets and their Allies Edited by L. H. Field

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REVIEWED BY DARRYL T. GWYNNE AND CLINT KELLY

There is little doubt that research on ensiferan Orthoptera is biased in favor of Tettigoniidae and Grylloidea. This is not surprising, given that the two are the most speciose ensiferan groups; they contain the bulk of the world's singing insects, and so have attracted much attention from behaviorists. *The Biology of Wetas, King Crickets and their Allies* is a solid start toward redressing the balance, by reviewing the current state of knowledge of some other ensiferan groups. This knowledge is delivered by 30 contributors, in a book that includes 22 chapters on the biology of the main group covered, the predominantly Southern Hemisphere Anostostomatidae (weta and king crickets). [Note that this family was split from Stenopelmatidae by Johns (1997).] As well, there are three chapters on 'Allies', the Gryllacrididae (raspy crickets) and Stenopelmatidae *sensu stricto* (Jerusalem crickets and relatives).

A key hope for a book such as this is that it encourages and directs future research. What new researcher would not be inspired by a group that includes some of the world's heaviest insects, with species that withstand freezing over several winters and others that sport elaborate male weaponry and common names such as 'parktown prawn' and 'wetapunga' (named after the 'Maori God of Ugly and Deformed Things'). A newcomer to any insect group would be aided immensely by a decent guide to taxonomy and phylogeny, by a thorough review of natural history and general biology and, of course, by a reasonable book price. Where the *Biology of Wetas…* succeeds well is in its presentation of biological reviews. We learn that amongst weta and their allies are behaviors and physiologies unique among insects and certainly every bit as fascinating as those of the more familiar ensiferans (and there are even surprises about diversity: D. Weissmann (Chapter 3) points to a threefold increase in the number of known stenopelmatids with 30 or more new species in California alone!). However, the book fails the newcomer with a poor introduction to taxonomy and relationships with other Ensifera. Another shortcoming is that sprinkled throughout the book are unsupported claims or conclusions lacking either data or references to literature. We feel this is important because it may mislead a new researcher to conclude that a particular idea has empirical support when in fact it remains a fertile area for study.

Relationships among the ensiferans covered in the book are dealt with in Chapter 1 (by A. V. Gorochov). 'The Higher Classification, Phylogeny and Evolution of the Superfamily Stenopelmatoidea' presents a novel systematic arrangement and phylogeny that includes three families: Anostostomatidae, Stenopelmatidae and Rhaphidophoridae. Thus the chapter is at odds taxonomically with others in the book in not recognizing the family Gryllacrididae (here reduced to a rhaphidophorid subfamily). Chapter 1 is also confusingly different than some other chapters in a number of taxonomic aspects, particularly in subfamilial and tribal arrangements. For example, it does not recognize the subfamily Henicinae ('henicine weta' is used for the genus *Hemiandrus* in some chapters, although to add to the confusion, Chapter 5 places the genus in Anostostomatinae).

Chapter 1 has two main problems. First, its statement that the "Phylogenetic relations of the three families of Stenopelmatoidea are more or less clear" (note that the chapter presents no formal character analysis) is not well supported and is contradicted by a summary figure (1.16) with an incomprehensible legend ("Vertical line, taxon represented: bold line; dependably; line from dots; problematically interrupted line; hypothetically; oblique interrupted line, hypothetical phylogenetic connection": the figure *per se* did not resolve our confusion). Second, the novel systematic arrangement is presented with virtually no reference or discussion of other published schemes, particularly thoughts on the flaws or virtues of other published phylogenies. A key omission is Flook & Fraser Rowell's work on the molecular phylogeny of Orthoptera (Flook & Rowell 1998, Flook *et al.* 1999), which suggests — as does Gorochov — that anostostomatids and rhaphidophorids form part of a monophyletic Stenopelmatoidea. A useful opportunity is missed by the author, a paleontologist, to compare his analysis based only on the characters of extinct orthopterans with hypotheses such as Flook *et al*. that are based upon modern taxa.

The book has no review of phylogenetic relationships within the main subjects, the anostostomatids. In part this is because there has been little work in this area. Morgan-Richards & Gibbs do provide information on relationships among a few tree weta species (*Hemideina*) in a clearly-written chapter (7) on the evolutionary genetics of this New Zealand genus. The chapter reviews evidence of genetic differentiation (mainly in mtDNA) between two color morphs of the mountain stone weta (*H. maori*), the possible result of past isolation due to mountain building. The chapter also describes a surprisingly large number of chromosomal races within the tokoriro, or Auckland tree weta (*H. thoracica*) that probably evolved through the isolation of populations on islands during the Pliocene. A useful extension of this evolutionary theme

would have been the inclusion of a phylogenetic hypothesis for all tree weta (*Hemideina*) and giant weta (*Deinacrida*), the two genera in the subfamily Deinacridinae (the phylogeny is mentioned by G. W. Gibbs in Chapter 2 but apparently was not available in time for the book, but now see Morgan-Richards & Gibbs, 2001). Such a hypothesis could have served as a guide in understanding the evolution of traits like sound-producing mechanisms (Chapter 15 by L. Field). Implied in this chapter is that New Zealand's anostostomatids evolved from a single ancestral stock in these islands. For example, Chapter 15 implies that social stridulation in tree weta evolved from defensive stridulation (such as in ground weta *Hemiandrus*) 'during the early stages of radiation in New Zealand'. The evidence suggests, however, that each group of New Zealand's anostostomatids (deinacridines, ground weta and tusked weta) has its closest relatives on other land masses (see Chapter 2 by G. Gibbs).

Stridulation and aspects of social and reproductive biology, as well as associated morphology are major themes in the book, covered in detail in seven chapters by L. H. Field and coauthors, and in one chapter by I. Stringer. Front and center in these chapters are the tree weta (*Hemideina*), an intriguing genus in which males with massive jaws compete to cohabit with groups of adult females in tree holes. One wishes for fewer chapters on these topics (for example, reviewing all defense behavior and sound production in Chapter 15, already entitled 'Stridulatory Mechanisms and Associated Behaviour in New Zealand Wetas'); this would have allowed both additional coverage of other burgeoning areas of anostostomatid research, such as evolutionary genetics, and in reducing some redundancy. In their favor, however, the chapters on behavior and bionomics pull together a surprisingly large amount of the knowledge of New Zealand weta from unpublished documents and other sources that are difficult to access, such as B.Sc. and M.Sc. theses and government reports.

Some of the book's coverage of reproductive behavior illustrates one of our main quibbles: there are some strikingly firm conclusions not backed up with data or referenced work. Some examples: from Chapter 17 "(in tree weta) mate choice is controlled by females which allow a relatively low percentage of successful matings by males" (no study has examined mate choice and its relation to mating success); "(previous work) showed that tree weta males fight vigorously for and defend harems of females", and a few lines later an apparent contradiction, "Sandlant (1981) showed that the mating system of tree wetas conforms to a resource defence polygyny". Our point here is that there are alternative, and as yet untested, hypotheses for what males defend in order to obtain matings: either the tree-hole resource or the females themselves. Finally, there is the very pressing question of how the sexes of any anastostomatid, gryllacridid or stenopelmatid species get together for mating, a process well understood in grylloids and tettigoniids where typically females are attracted to male 'calling' song. With no data or reference support, D. Weissman (Chapter 19) concludes that "individual (Jerusalem crickets) respond only to drumming similar to their own calling song" and refers to "sex clarification drums" that "besides telling females there is a male nearby may also give an indication of his size." Moreover, in Chapter 17 L. H. Field reports that there "is a volatile substance produced by female giant wetas, which attracts males as females wander about" and "a much less volatile (or non-volatile) substance present on female cuticle of *all* species of *Hemideina*" (the emphasis is ours). The fact is, however, that no experimental studies have supported these conclusions about chemical communication. The chapter does report experimental data for one *Hemideina* species showing that more males attempt copulation with dead females than with dead females washed in ether. However, there were no reported data on how confounding effects of an ether bath (other than in removing carcass chemicals) may have affected the response of males.

Following the major portions of the book on behavior, bionomics, and morphology are four chapters on physiology. Again the New Zealand genus *Hemideina* is the main subject, in part because species of tree weta have some fascinating and unique physiological adaptations. Chapter 22 by L. Field includes a discussion of the sensory physiology of the intriguing deinacridine ear, a structure whose adaptive significance is almost unknown. Males of most *Hemideina* species stridulate near their tree-hole retreats and so may attract females (Chapter 15). However, ear function of other deinacridines is unknown, and this includes the 45-gm behemoths such as wetapunga (*Deinacrida heteracantha*). (Chapter 12 by M. McIntyre reviews the ecology of wetapunga and other giant weta, including studies of females fitted with radio transmitters!). Tree weta also have unique components of neuromuscular control (Chapter 23) and Chapter 25 presents the fascinating evidence that *H. maori*, the largest insect known to survive freezing, copes with subzero temperatures not by supercooling, but by the use of proteins that allow the nucleation of ice crystals in the haemolymph. These insects probably freeze not only several times per winter (due to the temperature fluctuations in New Zealand's alpine habitat) but, given their longevity, suffer bouts of freezing through several winters (mark recapture studies by I. Jamieson, pers. comm.).

The last chapter (26), G. Sherley's on conservation of weta in New Zealand, is in one respect, the most important one, because there are threatened species of weta. Most of the largest of the giant weta species (*Deinacrida*) and one enormous tusked weta (*Motuweta isolata*) are now found only on offshore islands, apparently as a result of predation on the mainland by introduced mammals (reports as early as the 1800s described Norway rats devastating populations of wetapunga in the forests north of Auckland (Gibbs, 1998, see reference above)). Almost all giant weta species are now protected under New Zealand law. *D. mahoenui* is the focus of this chapter in which G. Sherley reviews in detail the methods used by conservation biologists to translocate giant weta to safer havens. *D. mahoenui* is the only North Island species that has managed to hang on in two small populations on the mainland. Ironically, it appears to be thanks to two other aliens that the species survives in the relict mainland populations. These weta live in spiny thickets of European gorse, bushes that

are kept thick enough to apparently repel rats as a result of the pruning action of goats (Gibbs, 1998, see reference above). Perhaps a significant future direction for research on the conservation biology of weta will be to use tools and information from population genetics to aid in the conservation effort. For example, monitoring programs incorporating molecular techniques could function to assess gene flow between endangered populations and to preserve genetic diversity.

In closing, we must comment on the excessive cost of this book. In 1997 CABI's The *Bionomics of Grasshoppers, Katydids and their Kin* was expensive enough at $US160. However, "wetas and allies" is a record holder at $US175 (for this price some color plates, for example depicting *Hemideina* colour patterns (Chapter 9), would have been most welcome). One of us shelled out $315 Canadian for the book and in the Southern hemisphere (where, given the Gondwanaland distribution of anostostomatids, there is surely to be a lot of interest) entomologists will be spending (by early Feb 2002 exchange rates), $344 in Australia, $420 in New Zealand (the home of weta) and a whopping 2,031 rand in South Africa.

For less than the cost of the (Canadian) Goods and Services tax on *The Biology of Wetas* we acquired the colorfully illustrated *New Zealand Weta* by George Gibbs [1998. Reed Publishing, Auckland, New Zealand, 71 pages. $NZ19.95] providing a concise introduction to the New Zealand weta fauna. This 71-page field guide is written with the layperson in mind and is replete with excellent color photographs, distribution maps, pictorial keys, sections on biology (diet, natural enemies etc), conservation and even a section on keeping and studying weta. There is useful information here for both the amateur and professional entomologist. The distribution maps are particularly helpful; the only maps not included are those for ground weta and some distribution maps for ground weta species were recently published by Johns (2001).

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[1]Both 'wetas' and 'weta' are used as plural forms in this book. The latter is probably more correct as this is a maori word. (for additional details see the Introduction to *The Biology of Wetas* . .).