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Systematic account and bibliography of the Notoptera (Insecta)

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Introduction

This report is a sequel to Bergdahl (2013a) and commemorates the 100th anniversary of the first description of a notopteran, the grylloblattid (Insecta, Notoptera, Grylloblattidae) *Grylloblatta campodeiformis* E. M. Walker, 1914, from the alpine zone near Banff (Alberta), Canada. This bibliography provides the most comprehensive list of references relating directly to Notoptera since Yamasaki (1982b). It includes references to published papers on grylloblattids (rock and ice crawlers) and the closely related species in the family Mantophasmatidae (gladiators and heelwalkers), an equally enigmatic group of flightless insects primarily from the winter rainfall regions of southern Africa that were first described in 2002 (see Predel et al. [2012] for a review). These two families form a well-documented monophyletic clade, Xenonomia, within Notoptera. There is also such a bewildering variety of winged "grylloblattodean" fossil taxa (many described only from wing venation patterns) that authors have erected many other families in Notoptera, but their evolutionary relationships are unclear, as are Notoptera's relationship with other Polyneoptera (Blattodea, Dermaptera, Embiodea, Isoptera, Mantodea, Orthoptera, Phasmatodea, Plecoptera, and Zoraptera). Grylloblattids get their name from their morphological similarity to crickets (gryllids) and cockroaches (blattids), whereas mantophasmatids resemble both mantises (mantids) and stick insects (phasmatids). A systematic account of the extant genera of Notoptera is provided below. Extant grylloblattids and mantophasmatids are unique among other closely related taxa in being apterous (flightless), and in having no ocelli (simple eyes; Grimaldi & Engel 2005). Grylloblattids are best described as omnivores, whereas mantophasmatids are predators.

Given the widespread (yet regionalized) occurrence of notopterans in southern Africa, eastern Asia and western North America, this bibliography is not totally complete since the literature is also widespread, and from many provinces and languages. For instance, it does not include all of the references listed by Yamasaki

(1982b), many of which are published in Japanese. There must be many articles on notopterans published in obscure places I have not discovered. Also, no attempt was made to include all the literature on the many fossil taxa; more of this literature may be accessed via Aristov & Storozhenko (2011), Aristov et al. (2013), Wipfler et al. (2012) and Wipfler et al. (2014a). A more complete account of the Asian and Russian grylloblattid literature may be accessed via Schoville & Kim (2011) and Schoville et al. (2013). Both Schoville (2014) and Wipfler et al. (2014a) provide an excellent summary of the fairly intensive search to better define the early history of the phylogeny of Polyneoptera and the role Notoptera has played in this quest. Many papers have now been published on this topic. Many of the old hypotheses are now obsolete given the many new techniques for more accurately defining evolutionary trees (phylograms), although it should be mentioned that there are still many unanswered questions and unresolved nodes given the deep history of time involved (>300 millions years?) since the apparent origination of proto-notopterans in the Late Carboniferous Period. The debate among phylogeneticists about such ancient evolutionary events will no doubt continue for many years since the many different morphological and molecular techniques for reconstructing phylograms may suggest conflicting relationships.

My academic training is primarily as an animal ecologist. As an undergraduate I was greatly influenced by Stephen F. MacLean (University of Alaska, Fairbanks) and John S. Edwards (University of Washington, Seattle) to focus on insects. Over the years I have worked on many fish and wildlife projects, but I have primarily focused on exploring factors influencing local species diversity in carabid beetles (Coleoptera, Carabidae) in the Pacific Northwest, including in cold arctic and alpine regions. Ecological adaptations of insects and their power of dispersal play a huge role in local diversity; this is especially apparent in grylloblattids. However the deeper paleo-biogeographic history of any group has greatly influenced the occurrence (e.g. speciation and extinction) of species on any landscape today due to its influence on the species pool from which local faunulas are assembled. There is a rich and fascinating, widely scattered literature on paleo-biogeography and climatology of the Asiamerica region that bears directly on the ecology, evolution and distribution of grylloblattids, and about southern Africa concerning the biogeography of mantophasmatids (e.g. Midgley et al. 2005).

The literature on insect taxa with disjunct intercontinental circum-North Pacific distributions, such as Grylloblattidae, is especially fascinating if one is interested in the deep history of Pacific Northwest insect biogeography since a number of unique groups occur only in these two regions. Unfortunately, this topic does not seem to have been comprehensively reviewed recently. Some examples I am familiar with in the Pacific Northwest Carabidae (Coleoptera) fauna are provided in item 11 at the end of this introduction.

Grylloblattid habitats are now fairly well defined in a general sense. Given the grylloblattids' close association with cool microclimates of caves, talus fields, small streams, ravines, and cold sub-alpine and alpine habitats, the literature on these environments should be consulted by students working on ice crawlers in the field. The addition of biogeographic and habitat references pertaining to notopterans would make this list much longer and the project much more complex.

The single largest gap in our understanding of grylloblattids at this time is their physiological, behavioral, phenological and other ecological adaptations to the environment, which is apparent from the comparatively few papers on these topics in this bibliography. For instance, we know very little about how long it takes individuals to complete their life cycle in the wild, and other aspects of reproduction that are so important to the management and conservation of local populations. Life history characteristics are best known for some of the Japanese and Korean species.

I would like to mention a few of my favorite papers that pertain *indirectly* to North American grylloblattid habitat, life cycle characteristics, evolution and biogeography, which will give students a portal to other papers on these topics:

1. subterranean environment within talus fields (Huber & Molenda 2004),
2. cave invertebrates in western North America (Peck 1973),
3. montane "sky islands" in the western North America (DeBano et al. 1995; Volker & MacKinnon 2000),
4. alpine aeolian habitats (Pruitt 1970; Edwards & Banko 1976; Papp 1978; Edwards 1987),
5. ecological adaptations of insects to cold environments (Mani 1968; MacLean 1975, 1980; Danks 2006),
6. local adaptation and genetic differentiation of populations (Schoville et al. 2012a),
7. taxon cycles and species pumps (Howden 1985; Ricklefs & Bermingham 2002; Knowles 2001; Schoville et al. 2012b; Rovito et al. 2012; Jockusch et al. 2012),
8. speciation in periglacial environments (Brochman et al. 2003; Weir & Schluter 2004; Brunsfeld & Sullivan 2006; Carstens & Knowles 2007; Marr et al. 2008; Shafer et al. 2010),
9. phylogeography of northwestern North America (Brunsfeld et al. 2001; Carstens et al. 2005),
10. phylogeography of southern Africa (Midgley et al. 2005), and
11. taxa with Asiamerican distributions: 1) the odd, large-bodied, flightless paussine carabid beetles in the tribe Metriini, *Sinometrius* (1 species in China) and *Metrius* (2 species in Pacific Northwest) (Wrase & Schmidt 2006; Bergdahl 2013b), and 2) the large-bodied, winged nebriines *Nippononebria* (3 spp. in Japan; 1 sp. in China) and *Vancouveria* (3 species in Pacific Northwest) (Kavanaugh 1995; Kavanaugh & Liang 2010).

To the best of my knowledge most of the publications listed below specifically mention notopterans in one way or another.

Systematic Account of Extant Genera of Notoptera

Phylum Arthropoda
  Subphylum Hexapoda
    Class Insecta
      Subclass Pterygota
        Supercohort Polyneoptera
          Order Notoptera
            Clade Xenonomia
              Suborder Grylloblattodea
                Family Grylloblattidae Walker, 1914 (32 species in 5 genera)

Galloisiana Caudell & King, 1924 (12 spp.; Japan, South Korea, North Korea, Russia, China)
Grylloblattella Storozhenko & Oliger, 1984 (3 spp.; Russia, China)
Grylloblattina Bey-Bienko, 1951 (2 spp.; Russia)
Namkungia (Namkung, 1974)(2 spp.; South Korea)
Grylloblatta Walker, 1914 (13 spp.; PNW of USA & Canada)

Suborder Mantophasmatodea Zompro et al., 2002^
Family Mantophasmatidae Zompro et al., 2002^
Subfamily Mantophasmatinae Zompro et al., 2002^
Tribe Mantophasmatini Zompro et al., 2002^
Mantophasma Zompro et al., 2002^ (many spp.; Namibia, Angola?)
Pachyphasma Wipfler et al., 2012 (1 sp.; Namibia)
Sclerophasma Klass et al., 2003 (1 sp.; Namibia)
Tribe Tyrannophasmatini Zompro, 2005
Tyrannophasma Zompro, 2003 (1 sp.; Namibia)
Praedatophasma Zompro & Adis, 2002 (1 sp.; Namibia)
Tribe Austrophasmatini*
Austrophasma Klass et al., 2003 (2 spp.; South Africa)
Hemilobophasma Klass et al., 2003 (1 sp.; South Africa)
Karoophasma Klass et al., 2003 (2 spp.; South Africa)
Lobatophasma Klass et al., 2003 (1 sp.; South Africa)
Namaquaphasma Klass et al., 2003 (1 sp.; South Africa)
Viridiphasma Eberhard et al., 2011 (1 sp.; South Africa)
Striatophasma Wipfler et al., 2012 (1 sp.; Namibia)
Gen. & Sp. nov. “RV” in Predel et al., 2012 (1 sp.; Namibia)
Subfamily Tanzaniophasmatinae
Tanzaniophasma Klass et al., 2003 (1 sp.; south Tanzania)**

^ Described in Klass et al. (2002).
* According to Predel et al. (2012) the group includes 13 putative species, some undescribed, and possibly fewer genera since so many of them in the tribe are monospecific.
** Apparently known from a single museum specimen (Predel et al., 2012). This species is considered a *Mantophasma* by Zompro (2005: 101) and Zompro & Adis (2006: 22).

The notopteran lineages that eventually evolved into grylloblattids and mantophasmatids probably became isolated (split) when Pangaea began to break up forming Gondwana and Laurasia, during the Triassic Period of the early Mesozoic Era, when the first dinosaurs and mammals enter the fossil record (Predel et al. 2012). The region of maximum diversity of a taxon is probably the single best indicator of its province of origin; therefore grylloblattids may have originated in the eastern Asia region, and subsequently migrated overland via Beringia to the Pacific Northwest, perhaps in the Tertiary Period during one of the many long periods of time the continent Asiamerica was intact (Sampson 2009). Transoceanic rafting (e.g. in log debris) across the North Pacific is another option. Although the probabilty of a successful colonization by trans-Pacific rafting many be very small, an enormous amount of time has lapsed for such an unlikely event to have occurred. No similar long distance, intercontinental dispersal event is required to explain the known distribution of extant mantophasmatids since they are all found in southern Africa.

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