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REVIEW ARTICLE

Ice Crawlers (Grylloblattodea) – the history of the investigation of a highly unusual group of insects

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Abstract: Grylloblattodea are one of the most unusual groups of insects and the second smallest order. All known extant species are wingless and exhibit a remarkable preference for cold temperatures. Although their morphology was intensively investigated shortly after their discovery, the systematic position has been disputed for a long time. The placement of Grylloblattodea as sister-group to the recently described Mantophasmatodea is supported by morphological and molecular evidence. However, the relationships of this clade, Xenonomia, among the polyneopteran lineages is not clear. Transcriptome analyses, in addition to the study of winged grylloblattodean fossils, may help to clarify the position of Xenonomia and aid in the reconstruction of the "phylogenetic backbone" of Polyneoptera.

Key words: Grylloblattodea, history, diversity, habitats, morphology, phylogeny, fossils, reproduction, development.

Introduction

Grylloblattodea, also known as ice crawlers or rock crawlers, are a highly unusual group and – after Mantophasmatodea in 2002 – the second to last described order of insects. The first species was described as *Grylloblatta campodeiformis* by the Canadian entomologist E. M. Walker (Walker 1914). It occurs in the northwest of North America and is known colloquially as the Northern Rock Crawler. Grylloblattodea are a very atypical group of pterygote insects in several respects. They are secondarily wingless, which may be related to another unusual feature, the preference for cold temperatures. With 32 extant species, Grylloblattodea are- along with Zoraptera and Mantophasmatodea- among the smallest insect orders. However, the few species occurring in Japan, the northeastern Palaearctic and northwestern North America are probably only a relic of a formerly moderately successful group (e.g., Storozhenko 1997; Vrsansky *et al.* 2001).

The group has attracted the attention of insect systematists and morphologists since it was described. Shortly after its discovery, *Grylloblatta* was raised to ordinal status three times independently: by Crampton (1915) (as Notoptera), by Bruner (1915) (as Grylloblattaria) and by Brues & Melander (1915) (as Grylloblattoidea). The name of the first discovered species - *Grylloblatta campodeiformis* - underlines the ambiguous features of the group and reflects later phylogenetic statements, referring to assumed affinities to Orthoptera and Blattodea, respectively, and multisegmented cerci resembling those of campodeiform diplurans.

As pointed out by Hennig (1969), Kristensen (1975) and Wipfler *et al.* (2011, acc. for publ.) the systematic placement is impeded by the combination of a large number of apparently plesiomorphic features (e.g., filiform multi-segmented antennae, orthopteroid mouthparts, 5-segmented tarsi, multi-segmented cerci) with a complex of apomorphies linked to the complete loss of wings, and apparently highly derived asymmetric genitalia.

Recently the interest in the group was greatly stimulated by the discovery of Mantophasmatodea (Klass *et al.* 2002). Within few years a considerable number of studies have been published on Mantophasmatodea and Grylloblattodea (e.g., Dallai *et al.* 2005; Terry & Whiting 2005; Uchifune & Machida 2005; Jarvis & Whiting 2006; Bai *et al.* 2010; Schoville & Roderick 2010; Wipfler *et al.* 2011; Predel *et al.* 2012; Wipfler *et al.* acc.).

The upcoming 100th anniversary of the original description, and the tremendous rate of increasing knowledge, encouraged us to write this review article on Grylloblattodea.

Distribution and habitats

Presently 32 species are described in five genera (see Table 1). *Grylloblatta* occurs in northwestern North America and the other four genera are distributed in Japan, the Korean peninsula including northeastern China, the Russian Pacific coast, and the Altai and Sayan mountain ranges (Fig. 1). Grylloblattid species occur mostly in mountainous and high alpine regions, often at the edges of glaciers. However, species of *Galloisiana, Namkungia* and *Grylloblattina* live in dense forests and some are specialized cave dwellers.

All North American *Grylloblatta* are restricted to the west coast (Fig. 1A), where they are associated with environments characterized by low annual temperatures and extensive snowfall (Kamp 1963, 1979) (Fig. 2). In the United States, species are found in California, Oregon, Washington, Idaho, Montana, and Wyoming, and in Canada they are found in the provinces of Alberta, and British Columbia (Schoville & Graening 2013). In alpine habitats, ice crawlers are often found living in large talus fields (Fig. 2), in close proximity to lakes or streams (Schoville 2010). At low elevation localities, grylloblattids live near rock outcrops or in caves/lava tubes, where they are found under moist rocks or near ice formations (Kamp 1963; Jarvis & Whiting 2006).

Among the Asian Grylloblattidae, *Grylloblattella* is restricted to montane environments in southern Siberia, including Russia, China, and Kazakhstan. These species are found in rocky streams and talus fields, including low elevation sites where the

Table 1. Described species of Grylloblattodea with their type locality.

Species	Author	Year	Type locality
Galloisiana chujoi	Gurney	1961	Oninoiwaya Cave, Japan
Galloisiana kiyosawai	Asahina	1959	Hirayu-Onsen, Japan
Galloisiana kosuensis	Namkung	1974	Gosu Cave, South Korea
Galloisiana magnus	Namkung	1986	Balgudeok Cave, South Korea
Galloisiana nipponensis	Caudell & King	1924	Niko-Chuzenji, Japan
Galloisiana notabilis	Silvestri	1927	Nagasaki Prefecture, Japan
Galloisiana odaesanensis	Kim & Lee	2007	Mt. Odae, South Korea
Galloisiana olgae	Vrsansky & Storozhenko	2001	Mt. Olga, Russia
Galloisiana sinensis	Wang	1987	Mt. Jangpaik, PR China
Galloisiana sofiae	Szeptycki	1987	Mt. Myoyang, South Korea
Galloisiana ussuriensis	Storozhenko	1988	Primorje, Russia
Galloisiana yezoensis	Asahina	1961	Miyazaki-Toge
Galloisiana yuasai	Asahina	1959	Tokugo-Toge, Japan
Grylloblatta barberi	Caudell	1924	Sunny Side Mine, USA
Grylloblatta bifratrilecta	Gurney	1953	Sonora Pass, USA
Grylloblatta campodeiformis	Walker	1914	Suplhur Mountain, Canada
Grylloblatta chandleri	Kamp	1963	Eagle Lake, USA
Grylloblatta chirurgica	Gurney	1961	Ape Cave, USA
Grylloblatta gurneyi	Kamp	1963	Lava Beds National Monument, USA
Grylloblatta marmoreus	Schoville	2012	Marble Mountains, USA
Grylloblatta occidentalis	Silvestri	1931	Mt. Baker, USA
Grylloblatta oregonensis	Schoville	2012	Oregon Caves National Monument, USA
Grylloblatta rothi	Gurney	1953	Happy Valley, USA
Grylloblatta scudderi	Kamp	1979	Mt. Paul, Canada
Grylloblatta sculleni	Gurney	1937	Scott Camp, USA
Grylloblatta siskiyouensis	Schoville	2012	Oregon Caves National Monument, USA
Grylloblatta washoa	Gurney	1961	Echo Summit, USA
Grylloblattella cheni	Bai, Wang & Yang	2010	Kanas Nature Reserve, China
Grylloblattella pravdini	Storozhenko & Oliger	1984	Teletskoye Lake, Japan
Grylloblattella sayanensis	Storozhenko	1996	Sambyl Pass, Russia
Grylloblattina djakonovi	Bey-Bienko	1951	Yenhaeju, South Korea
Namkungia biryongensis	(Namkung	1974)	Biryong Cave, South Korea

microhabitat remains cold and humid (Fig. 2). *Grylloblattina* is restricted to far-eastern Russia, along stream banks in well-developed forest (Fig. 2). They are presently not known from montane sites. Species of *Galloisiana* and *Namkungia* are distributed from northeastern China through South Korea and Japan (Fig. 1B). Species in China and North Korea are only known from montane sites, whereas South Korean species inhabit montane sites and many low elevation caves. Several eyeless species in South Korea appear to be limited to cave environments. Japanese species of *Galloisiana* occur across the major islands of Kyushu, Shikoku, Honshu and Hokkaido, where they are most abundant in montane habitats in central Honshu (Schoville *et al.* 2013). Southern species of *Galloisiana* show evidence of adaptation to a cavernicolous or fossorial lifestyle, with reduced or missing eyes. Environmental features that are shared by all Japanese species include rocky substrates and cool, moist environments, with species frequently found near streams. Populations in montane habitats are easily found under rocks along small creeks or stream courses in healthy mixed forest (they are rare in secondary forest or plantation regrowth). Grylloblattids in both Asia and North America appear to have conserved microhabitat preferences focusing on temperature, precipitation and substrate conditions (Schoville 2010). In general, most grylloblattids are found in rocky habitats with cool temperatures and relatively high humidity, and they are noticeably more

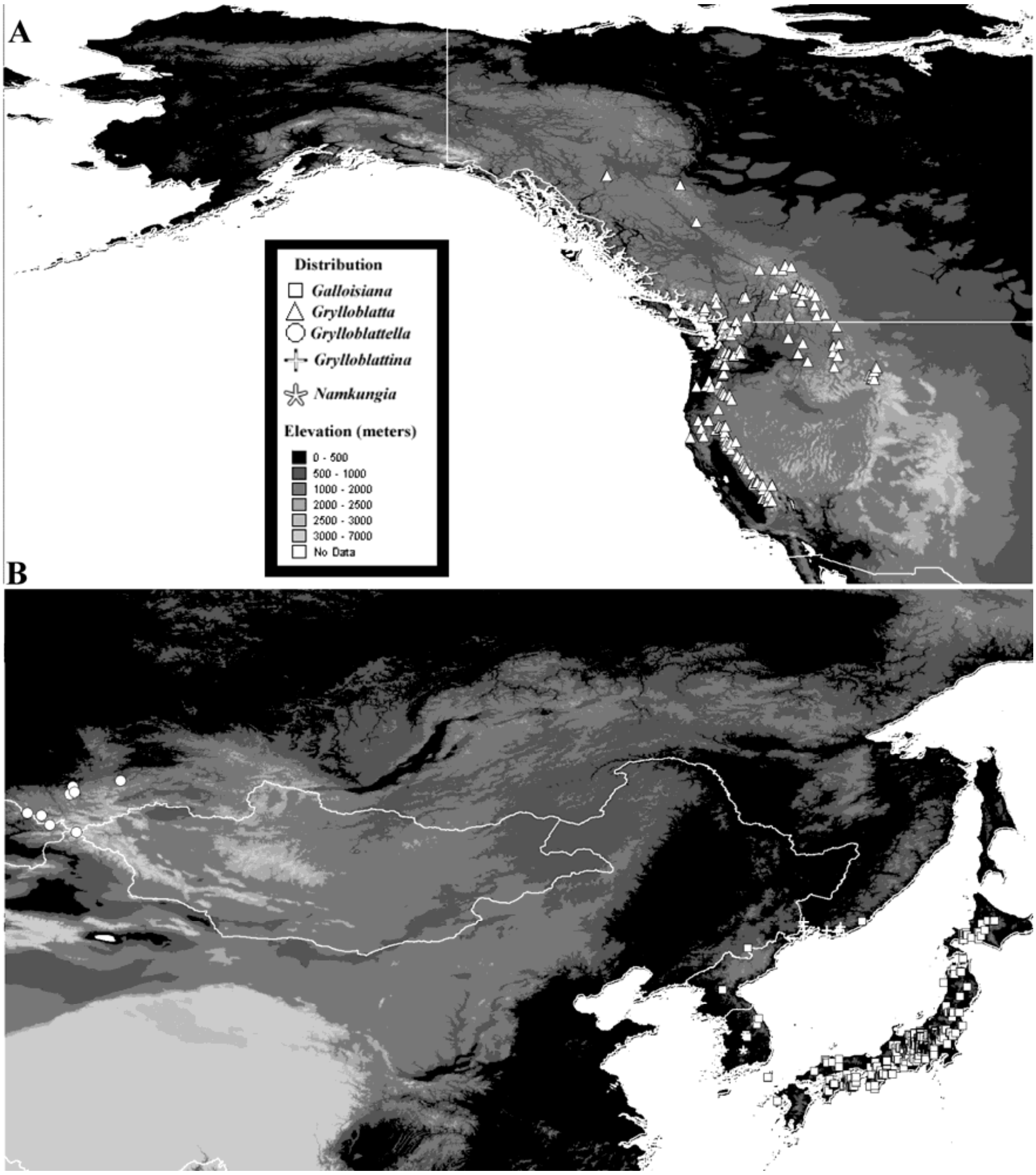

Figure 1. Geographical distribution of Grylloblattidae in **A,** North America and **B,** Asia.

abundant and widespread in montane habitats where annual snowfall is high. Grylloblattids prefer damp soil substrates that are composed of silty to sandy loam, rather than hard-packed soils. However, some populations occur at sites that experience warm, dry summers (e.g. Lava Beds National Monument, California, or Nagasaki, Japan). At these sites, grylloblattids modify microhabitat choice (i.e. populations in southern Japan are fossorial) and/or alter seasonal activity patterns (i.e. the Lava Beds population is found in ice caves predominately during the early summer, Table 2).

Some *Grylloblatta* populations are restricted to caves, morphological adaptations to the cave environment (troglomorphy) are not known, with the exception that cave-dwelling species lack pigmentation. Furthermore, several known species with cave affinities are found above ground during winter months (Schoville 2012).

Table 2. Microhabitat and seasonality. Examples of variation in microhabitat and seasonality across different species of Grylloblattidae.

	Habitat/Microhabitat	**Seasonality**
Grylloblatta bifratrilecta	Alpine/talus fields	May to late July
Grylloblatta gurneyi	Low elevation/lava tubes with ice formations	November to June
Grylloblatta siskiyouensis	Low elevation/caves and forested habitat	November to March
Grylloblattella pravdini	Low and high elevation/rocky stream banks and talus fields	April to late July
Galloisiana yuasai	Mid to high elevation/rocky stream banks	Late June to early November
Galloisiana notabilis	Low elevation/rocky stream banks	February to April

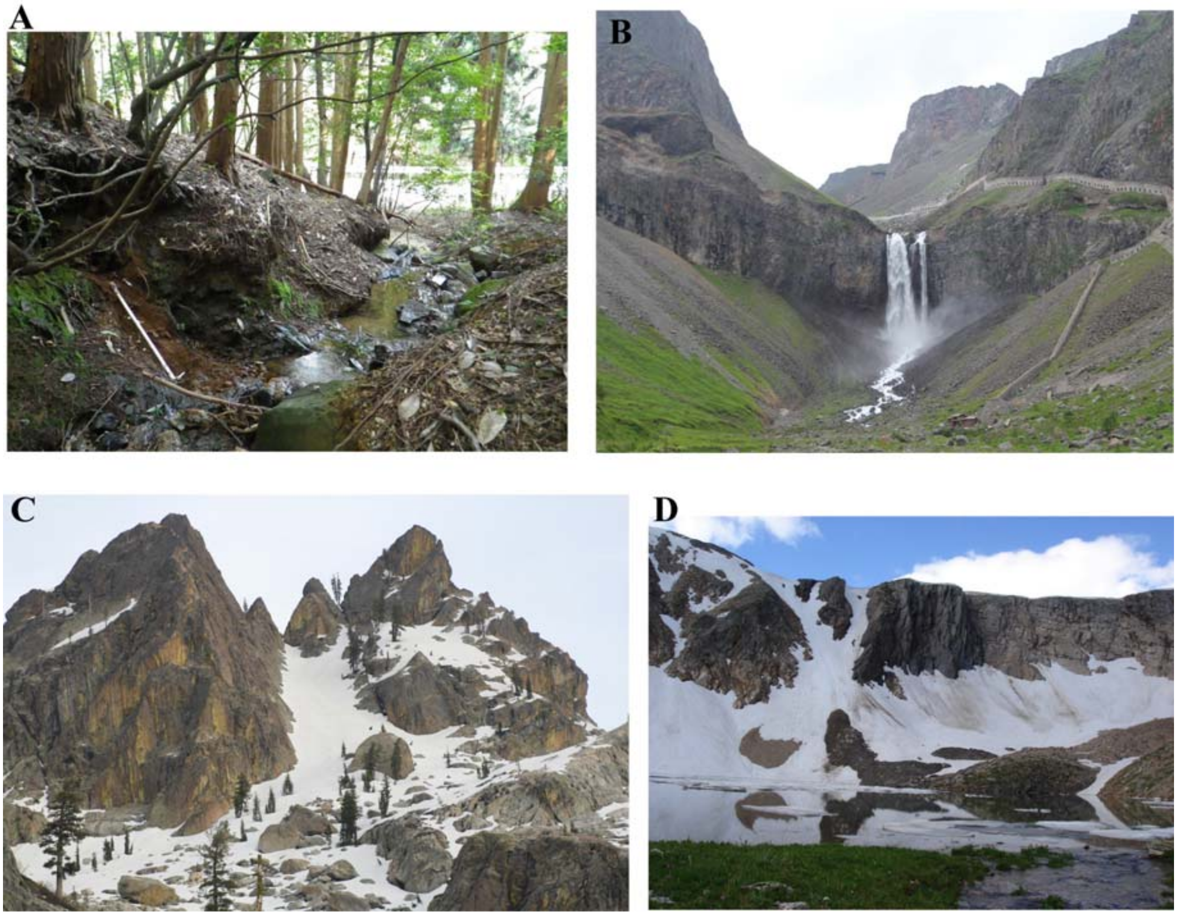

Figure 2. Photos of typical Grylloblattidae habitat. **A,** Rocky stream bank in southwestern Japan. **B,** Alpine waterfall and talus field at Changbaishan, China. **C,** A snow-covered talus field at Sierra Buttes, California, United States of America. **D,** A snow-covered talus field in the Holzun Mountains, Russia.

As temperature is the main barrier to dispersing grylloblattids, the distribution area of each species is very limited. Migration among populations is almost certainly severely limited or non-existent in current conditions due to grylloblattids' habitat specificity, limited geographic range of populations, and winglessness (Kamp 1979). Grylloblattids' dependence on glacial margin habitats suggests that global warming could be a direct threat to their future.

Another potentially significant threat to grylloblattids is alteration of their habitat. Most localities (Fig. 1) are in very remote areas, and have thus far been protected from expanding human populations. However, many of these areas are seeing increased human activity and landscape transformation, which could negatively impact grylloblattid habitats (Bai *et al.* 2010).

Behavior and species interactions

North American *Grylloblatta* are nocturnally active on snowfields and most frequently observed when conditions near 0°C, although their acute temperature tolerance ranges from -8.5 – 20.5°C (Henson 1957; Edwards 1982). Anecdotal evidence suggests that they are less active following summer storms, thus avoiding sub-zero freezing conditions on snowfields triggered by high humidity and dropping temperatures (S. Schoville pers. obs.). *Grylloblatta* species retreat to rocky habitats during the day and are notably photophobic, suggesting that they may limit their feeding to nocturnal periods. They are scavengers that feed on wind-blown plant and animal detritus, usually small insects frozen on the snow and/or debris that falls into rock-retreats (Edwards 1987). Few arthropod species are found in association with *Grylloblatta*, but the alpine snowfield community includes species of ground beetles (Carabidae: *Nebria* and *Bembidion*), staphylinid beetles (*Phlaeopterus*), harvestman (Opiliones: Phalangoidea), and snow scorpionflies (Boreidae: *Boreus*). *Grylloblatta* co-occur with a different assemblage of arthropod species in cave habitats, including arachnids, beetles, diplurans, and collembolans. Direct interspecific interactions may be rare and grylloblattids rapidly retreat when they encounter living arthropods, including other *Grylloblatta* individuals. They quickly succumb to the defensive chemistry of *Nebria* and do not appear to employ their own chemical deterrents.

The Asian rock-crawlers appear to differ behaviorally from *Grylloblatta* in several respects. In Siberia, *Grylloblattella* forage on snowfields at night, but are frequently collected in rocky habitats where they may remain active diurnally. Japanese *Galloisiana* are not known to forage on snow and are most often associated with rocky habitats near small streams (Schoville 2010). *Galloisiana* species are considered generalist scavengers, eating both plant and animal material, and are thought to be active both diurnally and nocturnally (Nagashima *et al.* 1982). They are frequently found in association with a diverse arthropod community in the following major groups: Coleoptera (especially Carabidae), Diplura, Dermaptera, Arachnida, Chilopoda, and Diplopoda. It is unclear whether rock crawlers are preyed upon, but it is notable that Japanese *Galloisiana* excrete volatile chemicals upon handling that may represent deterrents to other arthropods.

Longevity, age structure and sex ratio

Relatively little is known about the life history of grylloblattids, though a few studies have been undertaken and some details can be gleaned from field observations. It is clear from collecting data that nymphs and adults are frequently collected at the same time and therefore species of *Grylloblatta*, *Galloisiana*, and *Grylloblattella* have overlapping generations (Schoville & Graening acc. for publ.; S. Schoville unpubl. data). Laboratory experiments have shown that Japanese *Galloisiana nipponensis* (Nagashima *et al.* 1982) live at least five years. *Grylloblatta* lives between 6-10 years, based on the number of instars and the slow molting rate observed in the laboratory (Walker 1937; Visscher *et al.* 1982). Similarly, some information can be taken on the sex ratio based on field collections, where there is a notable bias towards late-stage nymphs and adult females (Schoville & Graening acc. for publ.). Even in populations with hundreds of individuals, the scarcity of males is so apparent that it would seem to suggest a highly-skewed sex ratio. Edwards (1982) suggests that *Grylloblatta* females are more active foragers due to energy demands from developing ovules, and therefore the sex ratio simply appears unequal. But because a skewed sex ratio is evident in collections across genera and over different seasons (Schoville & Graening acc. for publ.; S. Schoville unpubl. data), it would seem that some factor other than activity rate might account for the biased sex ratio in Grylloblattidae.

Morphology

The description of *Grylloblatta campodeiformis* (Walker, 1914) and its subsequent elevation to ordinal status caused great interest in the new taxon. In the following decades, a long series of morphological studies was dedicated to the group (see Table 3). This is similar to the investigation of Mantophasmatodea with a considerable number of studies (e.g., Klass *et al.* 2003; Baum *et al.* 2007; Beutel & Gorb 2008) published in the years after the description (Klass *et al.* 2002). The great interest in structural features of Grylloblattodea stands in distinct contrast to Zoraptera, which were discovered one year earlier (Silvestri 1913) and were long neglected by morphologists (Mashimo *et al.* acc.).

Shortly after the description of *Grylloblatta campodeiformis* (Walker, 1914), the highly productive but controversial G. C. Crampton published a series of articles dealing with the morphology of the group: he studied the antenna (Crampton 1917a), the lateral head, neck and prothorax (Crampton 1917b), the external terminal segments and appendages of the female abdomen (Crampton 1917c), the maxilla (Crampton 1923), the neck and prothoracic sclerites (Crampton 1926a), the abdominal morphology (Crampton 1927), the female abdomen (Crampton 1929), the posterior metathoracic region (Crampton 1931), and the head capsule (Crampton 1926b, 1932). At the same time a remarkable series of detailed studies was launched by E. M. Walker, covering immature stages (Walker 1919), the skeleton-muscular system of the head (Walker 1931, 1933), thorax (Walker 1938) and abdomen (Walker 1943), and also the alimentary tract (Walker 1949). Even though he used only conventional dissection techniques, Walker provided an outstanding documentation of the external and internal structures of the species. Additionally the cephalic morphology was studied by Ferris (1942), Nagashima (1982) and Wipfler *et al.* (2011). Beutel & Gorb (2006, 2008) studied the tarsal attachment structures, Ford (1923) the abdominal musculature, and Scudder (1961) and Klass (2005) the ovipositor. The nervous and sensory system was investigated by Nessbit (1958), Rae & O´Farrell (1959), Slifer (1976), Pritchard & Scholefield (1978), Edwards & Ball (1980), Edwards & Mann (1981), Gokan *et al.* (1982), McIver & Sutcliffe (1982) and Gäde & Simek (2010). Nutting (1951) described the heart and accessory elements of the circulatory system and Judd (1948) the proventriculus. Bai *et al.* (2010) applied geometric morphometrics to the pronotum of both recent and extinct species. Finally several studies addressed the embryonic development, sperm ultrastructure, nymphal morphology, and oocytes and follicular cells (Matsuzaki *et al.* 1979, 1982; Ando & Nagashima 1982; Baccetti 1982; Yamasaki 1982; Dallai *et al.* 2005; Uchifune & Machida 2005).

The phylogenetic placement of Grylloblattodea

The systematic position of Grylloblattodea has been discussed controversially over the last hundred years and several distinct relationships have been proposed (Table 4).

Pre-Hennigian

In the original description, Walker (1914) pointed out similarities with Isoptera and especially nymphs of Plecoptera. He concluded that they are “genuine Orthoptera, but of a very generalized type", and that they therefore cannot be placed in any of the extant families of the order. Consequently he introduced the family Grylloblattidae within Orthoptera for the new species and genus.

Table 3. Morphological data available for Grylloblattodea.

Character system	**Species**	**Source**
Head		
Antenna	*Grylloblatta campodeiformis*	Crampton 1917a
Maxilla	*G. campodeiformis*	Crampton 1923
Frontal view of head	*G. barberi*	Crampton 1932
Exterior head capsule	*G. campodeiformis*	Cramtpon 1926b
Exterior head capsule	*G. barberi*	Cramtpon 1926b
Exterior head capsule	*Grylloblatta* sp.	Ferris 1942
Exoskeleton and musculature of the head	*Galloisiana nipponensis*	Nagashima 1982
Exoskeleton and musculature of the head	*G. campodeiformis*	Walker 1931, 1933
Exoskeleton and musculature of the head	*Galloisiana yuasai*	Wipfler *et al.* 2011
Thorax		
Attachment structures	*Grylloblatta* sp.	Beutel & Gorb 2006
Lateral head, neck and prothorax	*G. campodeiformis*	Crampton 1917b
Neck and prothoracic sclerites only	*G. campodeiformis*	Crampton 1926a
Posterior metathoracic region	*G. campodeiformis*	Crampton 1931
Exoskeleton and musculature of the thorax and neck	*G. campodeiformis*	Walker 1938
Abdomen		
External terminal segments and appendages of female abdomen	*Grylloblatta* sp.	Crampton 1917c
General abdominal morphology	*G. campodeiformis*	Crampton 1927
Female abdomen	*G. campodeiformis*	Crampton 1929
Abdominal musculature	*Grylloblatta* sp.	Ford 1923
Ovipositor	*G. campodeiformis*	Scudder 1961
Ovipositor	*G. campodeiformis*	Klass 2005
Exoskeleton and abdominal muscles	*G. campodeiformis*	Walker 1943
Nervous and sensory system		
Cerebral sensory system and ventral nerve cord	*Grylloblatta* sp.	Edwards & Mann 1981
Cephalic sense organs	*G. campodeiformis*	Pritchard & Scholefield 1978
Neuropeptides	*Galloisiana yuasai*	Gäde & Simek 2010
Fine structure of the eye	*Galloisiana nipponensis*	Gokan *et al.* 1982
Cercal sensory projections	*Grylloblatta* sp.	Edwards & Ball 1980
Sensilla	*Grylloblatta campodeiformis*	McIver & Sutcliffe 1982
Nervous system	*Grylloblatta campodeiformis*	Nesbitt 1958
Retrocerebral complex and ventral glands	*Grylloblatta campodeiformis*	Rae & O´Farrell 1959
Circulatory system		
Heart and accesorry structures	*Grylloblatta campodeiformis*	Nutting 1951
Digestive system		
Proventriculus	*Grylloblatta* sp.	Judd 1948
Digestive system	*Grylloblatta campodeiformis*	Walker 1949
Development		
Embryogenesis	*Galloisiana nipponensis*	Ando & Nagashima 1982
Sperm ultrastructure	*Galloisiana nipponensis*	Baccetti 1982
Sperm ultrastructure	*Galloisiana yuasai*	Dallai *et al.* 2005
Oocyte and folicular cells	*Galloisiana nipponensis*	Matsuzaki *et al.* 1979
Oocyte and folicular cells	*Galloisiana nipponensis*	Matsuzaki *et al.* 1982
Embryonic development	*Galloisiana yuasai*	Uchifune & Machida 2005
Nymphal morphology	*Galloisiana nipponensis*	Yamasaki 1982

Table 4. Different systematic placements of Grylloblattodea with different approaches and character sets.

Systematic approach / study	**Characters**	**Systematic placement**
Pre-Hennigian concepts		
Crampton (1927)	abdominal morphology	closely related to **Ensifera**
Walker (1933, 1938, 1943)	morphology	Closely related to **Orthoptera**
Hennigian concepts		
Giles 1962	numerical analysis, morphology characters	sistergroup to **Dermaptera**
Hennig 1969	morphology	sistergroup to **Dictyopera + Dermaptera**
Kamp 1973	numerical analysis, morphology	sistergroup to **Dermaptera**
Grimaldi & Engel 2005	morphology and palaeontology	sistergroup to **Mantophasmatodea**
Cladistic approach based on morphology		
Kuperus & Chapco 1996	analysis of data of Giles (1962) and Kamps (1973)	sistergroup to **Dermaptera**
Beutel & Gorb 2001	morphological characters	unresolved at the **neopteran base**
Beutel & Gorb 2006	morphological characters	sistergroup to **Mantophasmatodea**
Yoshizawa 2011	wing joint characters + characters of Beutel & Gorb 2006	sistergroup to **Mantophasmatodea**
Wipfler *et al.* 2011	head morphology	sistergroup to **Mantophasmatodea**
Friedemann *et al.* 2012	head morphology	sistergroup to **Mantophasmatodea**
Blanke *et al.* 2012	head morphology	sistergroup to **Mantophasmatodea**
Wipfler 2012	head morphology	sistergroup to **Mantophasmatodea**
Blanke *et al.* 2013	head morphology	sistergroup to **Mantophasmatodea**
Wipfler *et al.* subm.	thoracic morphology	sistergroup to **Mantophasmatodea**
Analyses of molecular data		
Wheeler *et al.* 2001	18S rDNA, 28S rDNA & morphology	**unresolved node** at the neopteran base
Kjer 2004	18S rDNA	**unresolved node** with Dictyoptera, Embioptera and Phasmatodea + (Orthoptera + Eumetabola)
Yoshizawa & Johnson 2005	18S rDNA	sistergroup to the phasmatodea **Timema**
Terry & Whiting 2005	18S rDNA, 28S rDNA, Histone 3 & morphology	sistergroup to **Mantophasmatodea**
Kjer *et al.* 2006	18S rDNA	sistergroup to **Mantophasmatodea**
Misof *et al.* 2007	18S rDNA	sistergroup to **Orthoptera + Phasmatodea**
Ma *et al.* 2009	complete mitochondrial genome	sistergroup to **Mantophasmatodea + Phasmatodea**
Simon *et al.* 2010	EF-1α	sistergroup to **(Dermaptera + Plecoptera) + Mantophasmatodea**
Ishwata *et al.* 2011	DPD1, RPB1, RPB2	sistergroup to **Mantophasmatodea**
Wan *et al.* 2012	complete mitochondrial genome	sistergroup to **Mantophasmatodea + Phasmatodea**
Plazzi *et al.* 2011	complete mitochondrial genome	sistergroup to **Mantophasmatodea + Phasmatodea**
Tomita *et al.* 2011	complete mitochondrial genome	sistergroup to **Mantophasmatodea + Phasmatodea**
Komoto *et al.* 2012	complete mitochondrial genome	sistergroup to **Mantophasmatodea + Phasmatodea**
Djernaes *et al.* 2012	CO1 + CO2 + 16S + 18S + 28S	sistergroup to **Mantophasmatodea**
Wang *et al.* 2013	18SrDNA + 28SrDNA	sistergroup to **Mantophasmatodea**

Crampton addressed the systematic position of Grylloblattodea in a series of studies (e.g. Crampton 1915, 1917abc, 1923, 1926b). In Crampton (1917c) he placed the group in a superorder Panorthoptera comprising “Orthopteroid and Phasmoid Grylloblattoid, insects” and pointed out closer affinities with crickets (Gryllidae, especially *Oecanthus*) based on the elongated cerci. He clearly excluded a closer relationship with “Blattoid insects”

(Dictyoptera) and basically considered Grylloblattodea as “primitive” orthopterans. In other studies (Crampton 1917bc) he emphasized great structural affinities with Embioptera. Later he considered a position within Orthoptera, with closer affinities with “Tettigoniods” (Crampton 1926b) or stenopelmatids (Crampton 1933). A statement in a study related to the subject (Crampton 1926b) reflects his phylogenetic concept, which was somewhat blurred but not unusual for pre-Hennigian studies: “I believe that *Grylloblatta* is practically a living Protorthopteran very closely related to the common stock from which sprang the Tettigonioid and Grylloid Orthoptera, and the closest affinities of *Grylloblatta* are with the Tettigonioids. Outside of the true Orthoptera, the next of kin of the Grylloblattids are the Dermaptera, and the Phasmids are somewhat more remotely related to them.”

The first review of the Grylloblattodea phylogenetic position was published by Imms (1927). In his “Lehrbuch der Entomologie”, Weber (1933) treated Grylloblattodea as a subfamily of Saltatoria (= Orthoptera).

Hennig’s hypothesis and other Hennigian approaches

In an important but often overlooked study, Wille (1960) placed Grylloblattodea in a “line” Panorthoptera, together with Phasmatodea (as Phasmida) and Orthoptera (as Saltatoria). However, none of the seven characters he presented was a synapomorphy (e.g., ovipositor usually well developed, eggs not laid in an ootheca) and Grylloblattodea deviated in two cases (male genitalia asymmetrical, segmented cerci).

In a study focused on Dermaptera, Giles (1963) evaluated a total of 283 features and postulated a common ancestry with Grylloblattodea. He identified two potential synapomorphies, the absence of the mesosternellum, and the almost horizontal orientation of the metepisternum and metepimeron. Giles study was later enhanced by Kamp (1973). Kuperus & Chapco (1996) analyzed their data cladistically and came to the same result, a sistergroup relationship with Dermaptera.

In contrast to Crampton (e.g., 1938) and Wille (1960), Hennig (1969) assumed that Grylloblattodea (as Notoptera) are more closely related to Blattopteroidea (=Dictyoptera) than to Orthopteroidea (Orthoptera + Phasmatodea. He considered enlarged coxae as a potential argument for this concept. In a tree (“Stammbaum der Paurometabola”) he placed Grylloblattodea as sistergroup of a clade comprising Dermaptera and Dictyoptera (Hennig 1969: fig. 40), without suggesting apomorphies supporting specific branches. He emphasized the problem of a large number of preserved plesiomorphies in the order and predicted that paleontological data will probably never help to solve the problem as wings are missing in all extant species. Interestingly, he criticized Giles’ (1963) approach as too statistical (“… zu statistische Methode”) and implicitly also the large number of characters he used.

Kristensen (1970) largely followed Hennig (1969) in his interpretation of enlarged coxae, also assuming a closer relationship with Blattoneoptera. In Kristensen (1975) he pointed out the unclear phylogenetic significance of coxal size. He emphasized a potential synapomorphy of Grylloblattodea and Orthoptera, the presence of “peculiar open-ended chambers (formed by the development of secondary segments of dorsal diaphragm) enclosing the paired excurrent ostia”. Within Orthoptera, this feature described by Nutting (1951) occurs at least in some members of Ensifera.

Boudreaux (1979), partly in agreement with Hennig (1969), also assumed a close relationship with Dictyoptera. He placed Grylloblattodea in a polyneopteran “Cohort” Blattiformia including †Protelytroptera, Dermaptera, and a Subcohort Dictyopterida, the latter subdivided into †Protoblattaria, Grylloblattaria (=Grylloblattodea), and an “Infracohort”

Cursorida comprising Zoraptera (as “Infracohort” Zorapterida) and Dictyoptera. The arguments presented for his Blattiformia (e.g., disk-like pronotum, loss of action of tergosternal muscles for indirect wing elevation and dorsal longitudinal wing depression) are far from convincing (e.g., Friedrich & Beutel 2008). Moreover the introduction of many categories is confusing and lacking scientific rationale.

In a study mainly based on “modern cladistics literature”, Minet & Bourgoin (1986) placed Grylloblattodea in an almost completely unresolved polytomy in monophyletic Polyneoptera.

In a study with a main focus on Dermaptera and their hind wings, but also aiming at a reconstruction of superordinal relationships of Neoptera, Haas & Kukalová-Peck (2001) placed Grylloblattodea in one of three major “lower neopteran” lineages, Blattoneoptera, with a branching pattern Grylloblattodea + (Dermaptera + Dictyoptera). But since this study was based on hindwing features, the placement of the wingless Grylloblattodea obviously required additional arguments. Haas & Kukalová-Peck (2001) cited characters suggested earlier by Bourdreaux (1979) in support of monophyletic Blattoneoptera (incl. Grylloblattodea) (see above).

A sistergroup relationship between Mantophasmatodea and Grylloblattodea was proposed in the non-cladistic analysis of Klass *et al.* (2003) based on proventricular structures as well as by Uchifune & Machida (2005) on composition of the egg membrane and blastokinesis.

Cladistic approaches

Sizeable morphological data sets coded for all hexapod orders were analyzed cladistically (numerically) for the first time by Wheeler *et al.* (2001) and Beutel & Gorb (2001). In the tree based on 275 morphological characters, Wheeler *et al.* (2001) confirmed a clade Grylloblattodea + (Dermaptera + Dictyoptera) as suggested by Boudreaux (1979) and Haas & Kukalová-Peck (2001). Beutel & Gorb (2001) later analyzed 10 features of attachment structures and 105 additional morphological characters placing Grylloblattodea as the sistergroup of a clade Phasmatodea + Dictyoptera, but with weak support. Mantophasmatodea + Grylloblattodea (=Xenonomia) was supported in a subsequent study with a slightly modified data set (Beutel & Gorb 2006).

In a cladistic evaluation of characters of the wing articulation, Yoshizawa (2011) included the wingless Grylloblattodea and Mantophasmatodea in some of the analyses, which were based on matrices also containing the data set used by Beutel & Gorb (2006). The results suggested a placement of monophyletic Xenonomia either as sistergroup of Dermaptera or of Orthopterida (Orthoptera + Phasmatodea). Xenonomia was also supported by a study of the thoracic morphology (Wipfler *et al.* acc.) and a whole series of works focusing on head morphology (Wipfler *et al.* 2011; Friedemann *et al.* 2012; Blanke *et al.* 2012; Blanke *et al.* 2013).

Molecular phylogenetic and phylogenomic approach

In an often cited study, published shortly before the discovery of Mantophasmatodea, Wheeler *et al.* (2001) (18S, 28S and morphology) placed Grylloblattodea in an unresolved polytomy with Dermaptera, Zoraptera and Dictyoptera in a summary tree based on a conflicting data set. This was largely in agreement with Boudreaux’ hypothesis (Boudreaux 1979). The entire combined data set (morphology, 18S, 28 S rRNA) yielded a sistergroup relationship between *Grylloblatta* and Dermaptera, while the sequences of both genes pointed to a sistergroup relationship between *Grylloblatta* and the neuropteran genus *Hemerobia* (Hemebrobiidae), the 18S rRNA a clade *Grylloblatta* + Neuroptera, and 28S a sistergroup relationship with an assemblage containing the apterygote *Lepisma* (Zygentoma), odonatans, and members of different polyneopteran lineages. It was pointed out earlier (e.g., Pohl & Beutel 2013) that the apparent problems are partly due to POY (direct optimization: synchronous alignment and parsimony analysis), an analytical approach which was identified as unreliable in an empirical study (e.g., Ogden & Rosenberg 2007; see also Kjer *et al.* 2007).

As was the case with morphological studies, the situation changed profoundly after the discovery of Mantophasmatodea (Klass *et al.* 2002). Terry & Whiting (2005) analysed complete 18S rDNA, 28S rDNA, Histone 3 DNA sequences, and a previously published morphology matrix coded at the ordinal level (see also Terry 2003). The analyses with different approaches (e.g., POY, MP analysis with ClustalX alignement, Bayesian inference) supported unambiguously a clade comprising Grylloblattodea and Mantophasmatodea, which was named Xenonomia. This clade is also supported by a study of 18S rDNA by Kjer *et al.* (2006).

Cameron *et al.* (2006a) evaluated the potential of mitochondrial genomics for resolving the interordinal relationships of Hexapoda, and Cameron *et al.* (2006b) was specifically focused on Mantophasmatodea, also using mitochondrial genomics, but with a relatively limited taxon sampling (e.g., compared to Terry & Whiting 2005). The analyses were carried out with different approaches (MP and Bayesian inference) and coding schemes. They yielded different results with respect to Mantophasmatodea and Grylloblattodea. Parsimony analyses grouped Mantophasmatodea (*Sclerophasma*) with either Grylloblattodea (*Grylloblatta*), Phasmatodea (*Timema*) or Orthoptera (*Locusta*). However, significant bootstrap values (›70%) were lacking for any resolution of relationships within Polyneoptera. In Bayesian analyses, Mantophasmatodea consistently grouped with Phasmatodea in five of the six coding schemes. Using reductive coding approaches, Mantophasmatodea + Phasmatodea was the only significantly supported clade with both analytical approaches (MP and BI). Ma *et al.* (2009), Plazzi *et al.* (2011), Tomita *et al.* (2011), Wan *et al.* (2012) and Komoto *et al.* (2012) also analysed complete mitochondrial genomes. Like Cameron *et al.* (2006b) they obtained a clade Mantophasmatodea + Phasmatodea, with Grylloblattodea as sistergroup of both. However all these studies contain only a limited sampling of lower neopteran insects and no sufficient outgroup.

Gäde & Simek (2010) support Xenonomia based on neuropeptides. Three nuclear protein coding genes were analysed by Ishiwata *et al.* (2011), unequivocally supporting a clade Grylloblattodea + Mantophasmatodea. Although his maximum likelihood and Bayesian analyses supported monophyletic Polyneoptera, a robust phylogenetic backbone of this lineage was not obtained. Wang *et al.* (2013) analysed regions of complete 18S and 28S rRNA sequences, focusing on highly conserved segments (ML and BI). Xenonomia and Eukinolabia were well-supported, and a clade comprising both lineages was moderately supported.

The value of the elongation factor-1α was evaluated by Simon *et al.* (2010). The Bayesian analysis yielded a rather unorthodox placement of Grylloblattodea as sistergroup of a clade Mantophasmatodae + (Plecoptera + Dermaptera). A comparative analysis of complete hexapod mitochondrial genomes was carried out by Simon & Hadrys (2013). The tree (Simon & Hadrys. 2013: fig. 2) contained many unconventional groupings (e.g., Ephemeroptera + (Tettigonoidea + Plecoptera)). Grylloblattodea were not included. Due to a limited taxon sampling, the results for Polyneoptera were inconclusive. So far no phylogenomic tree contains Grylloblattodea or Mantophasmatodea. However, a preliminary analysis of transcriptomes from circa 100 representatives of all hexapod orders including Grylloblattodea has been carried out by the 1KITE project (unpublished data). They consistently yield a pattern with Xenonomia as the sistergroup of Eukinolabia (Phasmatodea + Embioptera), with both as sistergroup of Dictyoptera.

Intraordinal phylogeny

Jarvis & Whiting (2006) provided the first genetic analysis of relationships within Grylloblattidae. Their data suggested *Grylloblatta* was monophyletic and sister to *Grylloblattina* from far-eastern Russia, with Japanese *Galloisiana* as the sister group to their combined lineage. Perhaps most notably, the inclusion of unidentified specimens sampled across a broad geographic range revealed substantial phylogenetic diversity within *Grylloblatta* (Jarvis & Whiting 2006). This result suggested that unidentified cryptic species were present in North America and even occurred in sympatry. More recent genetic work has expanded genetic sampling within North America (Schoville & Roderick 2010; Schoville 2012), South Korea (Schoville & Kim 2011) and Japan (Schoville *et al.* 2013). The number of cryptic lineages has increased in each of these studies, suggesting the diversity of Grylloblattidae has been grossly underestimated and that substantial taxonomic work remains. Furthermore, several taxonomic problems emerged, including the paraphyletic relationship of *Namkungia* and *Galloisiana* (Schoville & Kim 2011), as well as extreme genetic subdivision within Japanese *Galloisiana* (Schoville *et al.* 2013). In the most recent study, Schoville *et al.* (2013) found evidence for a polytomy among *Galloisiana* from Hokkaido, *Grylloblatta* and *Grylloblattina*, raising uncertainty in the sister-group relationship of *Grylloblatta*. At present, six major species complexes can be identified (Fig. 3), one within far-eastern Russia, three within Japan-South Korea, and two within North America. On-going investigations of the Grylloblattidae phylogeny are focusing on including *Grylloblattella* from southern Siberia, *Galloisiana sinensis* from northeastern China, and also expanding the sampling of genetic markers to resolve phylogenetic relationships among genera.

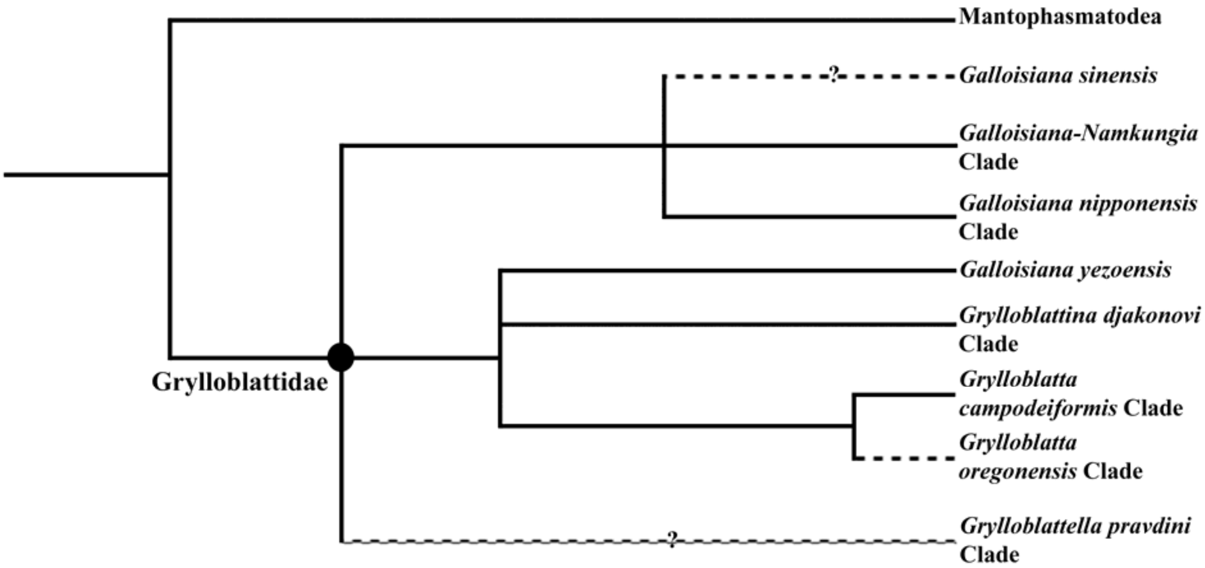

Figure 3. A phylogeny of the major species groups in Grylloblattidae (sensu Schoville *et al.* 2013), based on genetic data. Branch lengths are not to scale.

Fossils

The systematic interpretation of Palaeozoic and Mesozoic fossils linked with extant Grylloblattodea (Rasnitsyn 1976; Storozhenko 1998, 2002; Huang & Nel 2007; Huang *et al.* 2008; Cui *et al.* 2011; Cui 2012) is presently still problematic (e.g., Grimaldi & Engel 2005; Huang *et al.* 2008). Formal character evaluations have not been presented due to a severe lack of data. Consequently, we present only a brief treatment of extinct taxa possibly related to modern ice crawlers.

In contrast to the very limited extant diversity (32 sp.), it was hypothesized that Grylloblattodea including its stem group has an abundant fossil record from the Late Palaeozoic and the Mesozoic (Storozhenko 1998, 2002). About 50 extinct families were assigned to an "order" Grylloblattida (Aristov 2009; Storozhenko 1998, 2002). The interpretation of numerous fossilized wings is problematic as all extant grylloblattean species are completely wingless, and this may have already been the case in the common ancestor shared with Mantophasmatodea (see also Grimaldi & Engel 2005). Recently well preserved fossil species with nearly complete bodies were described from the Late Carboniferous (Cui *et al.* 2011) and the Middle Jurassic (Huang & Nel 2007; Huang *et al.* 2008). Head structures suggesting grylloblattodean affinities of the very large *Plesioblattogryllus magnificus* (Plesioblattogryllidae) were pointed out by Huang *et al.* (2008). However, most of these features are either plesiomorphic (5-segmented maxillary palps, 3-segmented labial palps, labrum developed, features of the ovipositor) or commonly found in other groups (large scapus, small pedicellus, presence of euplantulae, tiny setae on the cuticular surface). Surprisingly the distinctly prognathous head, which is very likely an apomorphic condition (Wipfler *et al.* 2011), was not mentioned. Prognathism, predaceous habits suggested by features of the mouthparts (Huang *et al.* 2008), and the large size tentatively support the hypothesized relationship with modern Grylloblattodea. Well-established relationships between winged extinct species with preserved body and extant grylloblattodeans will make it possible to evaluate the phylogenetic affinities of other fossils preserved only as wings.

In the late Carboniferous, fossils assigned to Grylloblattida (e.g., Storozhenko 1998) are still rare (Béthoux & Nel 2010). Less than 10 species are known, recovered from the famous localities of Mazon Creek (USA), and Commentry (France), among other localities in Europe, and also in Tunguska Basin (Russia) and Ningxia (China). The "order" reaches its peak in species-richness and abundance in the Permian (see e.g., Beckemeyer & Hall 2007). The actual diversity at the species and genus level in particular localities may be overestimated. However, a remarkable diversity and wide distribution is documented, with more than 30 families and nearly 200 species from Lodève (France), Obora (Czech Republic), Elmo & Midco (USA), and multiple localities in Germany and Russia.

During the Mesozoic the diversity of grylloblattidan groups declines. Less than 60 species are known from the Triassic. One of them was found in the Kemerovo region (Russia) and one at Cerro Cacheuta (Argentina). The bulk of the species is from a rich assemblage in Central Asia, the Madygen Formation. The diversity at the species and genus levels is also possibly over-estimated. Other records are from South Africa and the northeast of Australia.

The diversity in the Jurassic is presently intensively investigated. Up to now, about 40 species placed in six families are described. The detailed description of specimens with well-preserved body parts is crucial in a phylogenetic context (see above). Very important and well-preserved specimens were recently discovered at the famous Chinese Dahugou locality (Huang et al 2008; Huang & Nel 2008; Cui *et al.* 2012; Cui 2012).

No fossils are known later than the Early Cretaceous. In this period only three species are recorded (Vrsansky *et al.* 2001).

Reproduction and evolution of genital organs and mating

Eggs

The female reproductive system and oogenesis of Grylloblattodea were studied by Matsuzaki *et al.* (1982). The typical panoistic ovaries consist of about 14 ovarioles. The eggs of *Galloisiana* were described in detail by Matsuzaki *et al.* (1982), Ando & Nagashima (1982) and Uchifune & Machida (2005). They are coal black and ellipsoidal, with a length of ca. 1.6 mm and a width of ca. 0.75 mm. Micropyles (eight to ten in *G. nipponensis* and two to six in *G. yuasai*) are irregularly arranged in a circle on the anterior pole of the egg. The egg membrane consists of the chorion and vitelline membrane. The chorion is composed of two layers, an outer exochorion and an inner endochorion, 0.5-1.0 µm and 0.1-0.2 µm thick, respectively. Numerous fine aeropyles are present on the endochorion. The vitelline membrane is only ca. 0.1-0.2 µm thick.

Spermiogenesis and sperm ultrastructure

Sperm of *Galloisiana yuasai* were described in detail by Dallai *et al.* (2005). A brief description and hitherto unpublished images (Fig. 4) are presented here. The spermatozoa are about 200 µm long. They are linked in the seminal vesicle, thus forming a compact sperm bundle. Within this unit the spermatozoa beat synchronously in a helical fashion when placed in a proper buffer. The individual sperm cells are connected in their apical region, with closely adhering plasma membranes. Apically, a simple mono-layered acrosome is present, filled with dense material. A perforatorium is missing. The nucleus is elongated and elliptic in a cross section and contains compact chromatin material. The posterior nuclear region is embedded in centriole adjunct material. The derived centriole, consisting of microtubular doublets, is located in this region. The flagellar axoneme has the conventional 9+9+2 pattern, with accessory microtubules consisting of 16 protofilaments in their tubular wall. Intertubular material is also visible. Two pear-shaped mitochondrial derivatives with cristae are present, with two small cisternae adhering to them. A band of granular material is present in the space between the flagellar axoneme and the two mitochondrial derivatives.

Chromosomes

The chromosomes of a species of Grylloblattodea (unidentified species of *Galloisiana* from Japan) was described by Nakamura & Kitada (1955). The spermatogonial equatorial plate contains 30 chromosomes. Three of them are distinctly larger than the others and metacentric. The two largest form a pair and the somewhat smaller third one is an odd chromosome, which apparently forms a male XY pair with one of the remaining 27 short ones. These are either rod-shaped or appear like dots of various sizes. The largest rod-shaped chromosome is almost as long as the shorter arms of the three large metacentric chromosomes. In the largest pair, the longer arm is about twice as long as the shorter arm and 1.5 times longer than the odd chromosome. An XX-apparatus is present in the female.

Embryology

The embryonic development was described for *Galloisiana nipponensis* by Ando & Nagashima (1982) and Ando & Machida (1987), and studied in detail in *G. yuasai* by

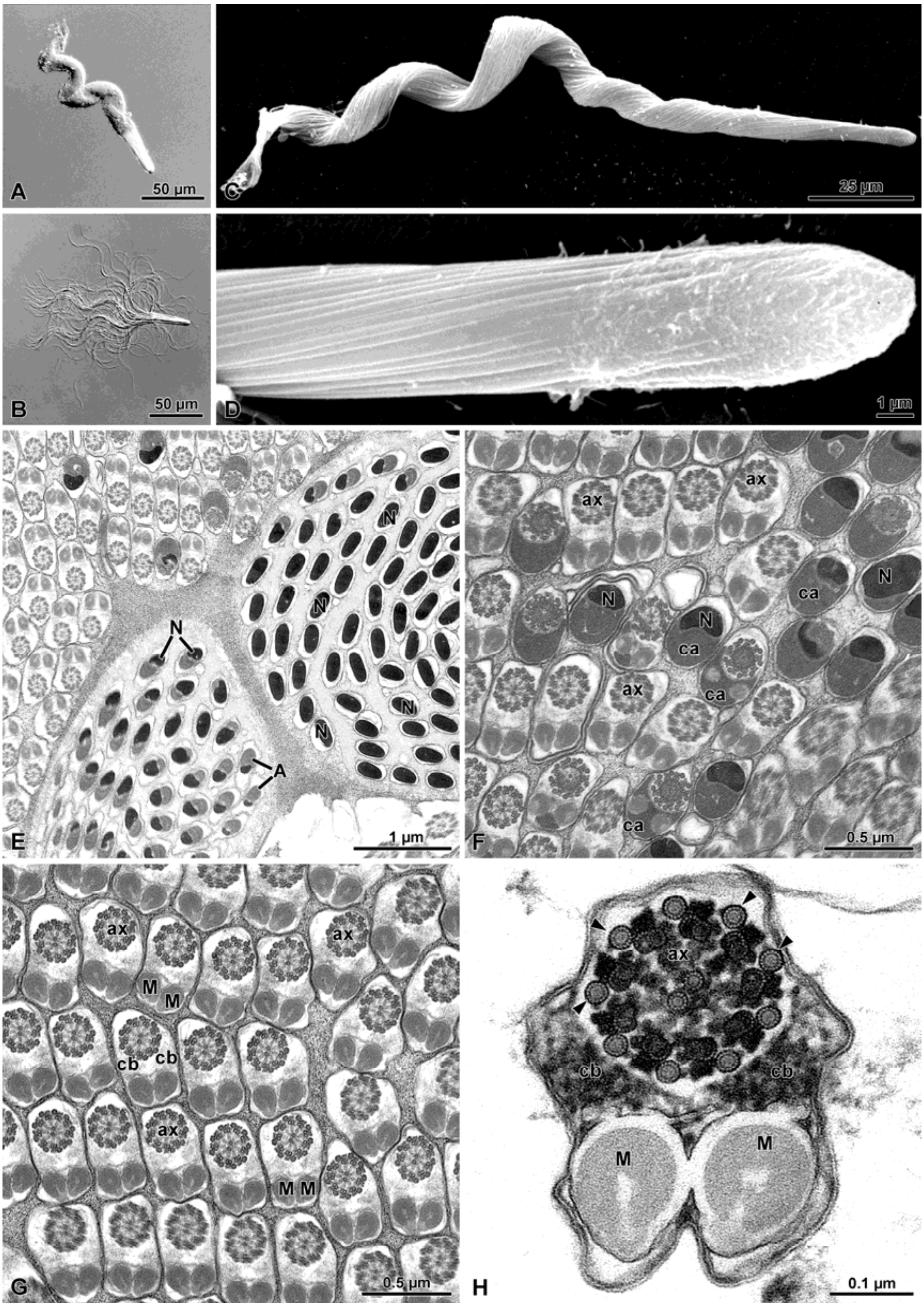

Figure 4. Sperms of *Galloisiana yuasai*, A, B: light microscopic photographs; C-H: SEM microghraphs. **A,** view of spermatodesm; **B,** view of spermatodesm; **C,** spermatodesm showing the helicoidal array of the sperm bundle; **D,** apical cap of the sperm bundle; **E,** cross section through sperm cysts at different levels; **F,** cross section through the centriolar region; **G,** cross section of the sperm flagella; **H,** cross section of a flagellum with the two mitochondrial derivatives. Abbreviations: ax: axoneme, ca: centriole adjunct material, cb: pale connective bands, M: mitochondrial derivatives, N: nucleus.

Uchifune & Machida (2005). The earliest embryonic stage is horseshoe-shaped and forms a small germ disc around the posterior egg pole. The following development is of a typical short germ type. The blastokinesis of the immersion type does not occur until the full elongation and segmentation on the egg surface are completed. Eleven abdominal segments are formed in the intertrepsis stage, and segmental appendages develop as paired swellings in each of the first nine segments and segment XI. The first abdominal appendages are embryonic organs or the pleuropodia, the second to eighth are degenerate, and the ninth and 11th develop into styli and cerci, respectively. The eversible sac, which is a potential autapomorphy of Grylloblattodea, arises at the mid-posterior margin of the first abdominal segment as an unpaired apodeme, possible homologous of the spinae in the thorax. The embryonic membrane, which consists of the amnion and serosa, forms the amnioserosal fold during anatrepsis. The thickened serosal part of the amnioserosal fold forms a disc-shaped structure (hydropylar cells) at the posterior egg pole, which function as a water absorber. Uchifune & Machida (2005) investigated the development of pleural and sternal sclerites, following the development of ectodermal invaginations, i.e., the sternal apophyses, spinae, tracheae etc., with a focus on the subcoxal theory. Based on close resemblances in the egg membranes (see above) and blastokinesis, they suggested a close affinity between Grylloblattodea and Mantophasmatodea.

Discussion

Since its discovery in the early 20th century, Grylloblattodea has fascinated entomologists, particularly in its unusual preference for remote mountainous areas and cold temperatures. Shortly after the description and the assignment of ordinal rank, a whole series of studies was published covering different aspects of their biology. In contrast to the small and cryptic Zoraptera, which were discovered in 1913 (e.g., Grimaldi & Engel 2005), the morphology of the order was investigated intensively within a few years, mainly aiming to clarify their systematic placement. Grylloblattodea were expected to play a crucial role in the understanding of the relationships of the lower neopteran insects: they were considered to be “living fossils” (Walker 1937) or “living protorthoperans” (Crampton 1926) and Crampton (1933) referred to the group as “among the most important of living insects”. However, the data did not reveal a clear picture. The main problem was the lack of an appropriate phylogenetic approach, i.e. a strict character analysis distinguishing between plesiomorphic and apomorphic features, and the use of apomorphies for establishing relationships in a strictly phylogenetic sense, i.e. monophyletic units. This inadequacy is strongly reflected in Crampton’s studies (e.g., Crampton 1915), who was a dedicated morphologist but struggled to interpret his findings in a consistent manner. As a result, he proposed different phylogenetic placements of the group in subsequent studies. Due to the difficulties in ascertaining deeper relationships among neopteran insects, the morphological and systematic interest in Grylloblattodea declined by the late 1950s. Species-level taxonomists, however, continued their work and today a total of 32 species in five genera have been described.

The remarkable volume “Biology of the Notoptera” edited by Hiroshi Ando (Ando 1982) revitalized morphological, behavioural and ecological investigations on Grylloblattodea. The volume is important in that it reviewed the available knowledge of Grylloblattodea at that time, including a complete literature survey, and presented a number of original studies covering a broad spectrum of research topics.

The third phase of intensified grylloblattodean studies was initiated by the description of Mantophasmatodea, a small relict group distributed in Southern Africa (Klass *et al.* 2002). This discovery greatly stimulated the interest in lower neopteran insects and specifically in

Grylloblattodea. In the following years a remarkable series of articles was dedicated to Mantophasmatodea. This included treatments of the ovipositor (Klass 2005), sperm ultrastructure (Dallai *et al.* 2005), embryology (Uchifune & Machida 2005), attachment structures (Beutel & Gorb 2006), neuropeptides (Gäde & Simek 2010) and cephalic morphology (Baum *et al.* 2007; Wipfler *et al.* 2011), and also an entire series of molecular studies. Only shortly after the description, a sistergroup relationship between Mantophasmatodea and Grylloblattodea was suggested by several authors, referring to this supraordinal unit either as “Lathonomeria” (Terry 2003), “Xenonomia” (Terry & Whiting 2005) or “Chimaeraptera” (Uchifune & Machida 2005). Reinforced by cephalic and thoracic morphology, embryology, and analyses of molecular data including neuropeptides, this clade is now considered very well supported.

Today Grylloblattodea have become one of the most intensively studied insect orders, especially with respect to the morphology and phylogeny. However, the available information on the lifestyle and ecology of these cryptic and fascinating insects is still insufficient. Considering the potential threats to grylloblattid habitats and populations, intensified investigation by ecologists is highly desirable.

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