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100 years Zoraptera – a phantom in insect evolution and the history of its investigation

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Zoraptera are a cryptic and enigmatic group of insects. The species diversity is lower than in almost all other groups of Hexapoda, but may be distinctly higher than presently known. Several new species were described from different regions recently. The systematic placement was discussed controversially since the group was discovered 100 years ago. Affinities with Isoptera and Psocoptera were discussed in earlier studies. A sistergroup relationship with Acercaria (Psocodea, Thysanoptera, Hemiptera) was proposed by W. Hennig, for the first time based on a strictly phylogenetic argumentation. More recent studies consistently suggest a placement among the “lower neopteran orders” (Polyneoptera). Close affinities to Dictyoptera were proposed and alternatively a sistergroup relationship with Embioptera or with Embioptera + Phasmatodea (Eukinolabia), respectively. The precise placement is still controversial and the intraordinal relationships are largely unclear. Recent transcriptome analyses tentatively suggest a clade Zoraptera + Dermaptera as sistergroup of all other polyneopteran orders.

The oldest fossils are from Cretaceous amber. An extinct genus from this era may be the sistergroup of all the remaining zorapterans. The knowledge of the morphology, development and features related to the reproductive system greatly increased in recent years. The general body morphology is very uniform, whereas the genitalia differ strongly between species. This is likely due to different kinds of selection, i.e. sexual selection in the case of the genital organs. The mating pattern also differs profoundly within the order. A unique external sperm transfer occurs in *Zorotypus impolitus*. A species-level phylogeny and more investigations of the reproductive system should have high priority.

Introduction

Zoraptera, also known as groundlice or angel insects (e.g., Grimaldi & Engel 2005), are a cryptic, inconspicuous and still enigmatic group of insects. Weidner (1969) pessimistically pointed out that they are in an evolutionary dead end and can only lead a wretched life (“kümmerliches Dasein”) in a very limited habitat. The systematic placement has been controversial since the group was introduced as an order by Silvestri (1913) (e.g., Trautwein et al. 2012) (see Table 1). Consequently the term “the Zoraptera problem” was coined by Beutel & Weide (2005).

Zorapterans were characterized by Silvestri (1913) as „Insecta terrestria, parva, aptera, agila, praedantia“, which means „living in earth, small, apterous, agile and predacious insects” (Weidner 1969). The scientific name given to the order („purely apterous ones”, Greek: zoros = pure, strong; aptera = apterous) is a misnomer as zorapterans are primarily winged (Caudell 1920) and small and poorly sclerotized besides. The wing dimorphism is one of few autapomorphies of the order, correlated with the presence or absence of compound eyes and ocelli, and the presence or absence of a distinct pigmentation, with distinctly darker alate specimens.

Zoraptera currently comprise 39 extant species and nine species are known as fossils (Engel 2008; Mashimo et al. 2013). They were considered as the least known insect order by Kristensen (1995). The fact that the situation has changed profoundly in recent years (see Fig. 1) stimulated us to present this review. The aims are to summarize the current knowledge, to point out remaining problems, and to illuminate the history of the investigation of this small group of cryptic insects.

1. Distribution, diversity and taxonomy

Zoraptera are largely restricted to tropical and subtropical regions. They live under bark or inside galleries made in rotting wood by other insects. Only *Zorotypus hubbardi* has expanded its range as far north as Indiana, Iowa and Illinois. This species might survive in colder regions by hiding in sawdust (Riegel 1963). Zoraptera have not been recorded from Australia, but *Zorotypus novobritannicus* was recently described from New Britain (Terry & Whiting 2012) and the group was also recorded from New Zealand and Easter Island (Weidner 1969; Choe 1989, 1992; Grimaldi & Engel 2005).

Silvestri (1913) introduced the order and described the genus and three species (in Latin). He collected the type species *Zorotypus guineensis* himself in Ghana (“Costa d’Oro”), and specimens of *Zorotypus ceylonicus* (Sri Lanka) and *Zorotypus javanicus* (Java) were provided by other entomologists. Eight new species from different parts of the world were described in the next 15 years (e.g., Karny 1922, 1927), and four species including the North American *Z. hubbardi* were introduced in a study also containing a key and a discussion of possible relationships of the order (Caudell 1918). A catalog of the Order published by Hubbard (1990) contained 29 extant species and one from the Eocene. Two new species were described by Chao & Chen (2000) and Engel (2000). A distributional checklist of zorapteran species was published in Engel & Grimaldi (2002) and an updated checklist of "World Zoraptera" by Rafael & Engel (2006). In the latter, 34 extant and six fossil species were listed, and the authors provided information on sexes, winged forms, and nymphs of each species. The most recent account is given in Mashimo et al. (2013). This study contains the descriptions of three new species from Peninsular Malaysia, bringing the number of extant zorapterans to 39. Zoraptera have been regarded as rare and one of the least diverse group of hexapods. However, apparently their diversity remains underexplored (Rafael & Engel 2006; Mashimo et al. 2013).

In taxonomic studies the shape of the basal antennomeres, the chaetotaxy of the ventral metafemoral surface, the shape of the cerci, and the male genitalia are traditionally recognized as useful to define species. The male genitalia are highly variable and potentially suitable for classifying the group. It has been noted that closely related species with very similar external features can be clearly discriminated based on male genital structures (Paulian 1949, 1951; Hwang 1974, 1976; New, 1978; Rafael & Engel 2006; Rafael et al. 2008; Mashimo et al. 2013). Some species were described based solely on immature or female specimens (e.g., Silvestri 1913; Caudell 1923, 1927; New 1995), or the information on the male genitalia was insufficient (e.g., Choe 1989; Zompro 2005; Rafael & Engel 2006; Terry & Whiting 2012). In future taxonomic studies, a detailed investigation of both sexes or at least the male genitalia should be obligatory for an unambiguous circumscription of species (Mashimo et al. 2013).

2. Morphology

The illustrations provided by Silvestri (1913) were of high standard, displaying external and internal features, including the setation, the mouthparts, endoskeletal and pretarsal structures, and also internal organs such as the central nervous system, digestive tract, tracheal system and excretory organs (six free Malpighian tubules). A series of comparative studies were carried out by G.C. Crampton. They covered head structures, the neck region, the thorax, the wings, and wing base sclerites of Zoraptera and other groups of insects (Crampton 1918, 1920, 1921, 1926, 1927). Gurney (1938) provided more morphological information, mainly based on the North American species *Z. hubbardi*. Like Silvestri (1913) and Crampton (e.g., 1918, 1927) he used simple dissection techniques and light microscopy. He described and illustrated external body parts but also male and female internal genital organs, the digestive tract, Malpighian tubules and even eggs. Delamare-Deboutteville (1947) compared alate and wingless exemplars. The thoracic skeletomuscular system was described for the first time by Rasnitsyn (1998). The availability of only one damaged wingless exemplar and the application of simple preparation techniques led to incomplete and not fully satisfying results. Weidner (1970) summarized the available information in the "Handbuch der Zoologie" series.

In the 21st century the study of Zoraptera accelerated. Beutel & Weide (2005) provided the first complete study of head structures (*Z. hubbardi*) using semithin microtome sections and SEM. Friedrich & Beutel (2008) described the thoracic anatomy of alate and wingless specimens of the same species and emphasized the highly conserved condition of the skeletomuscular apparatus, presumably close to the neopteran groundplan. Based on the results of this study the authors proposed a new consistent and extendable nomenclature for the thoracic muscle system of neopteran insects (Friedrich & Beutel 2008). Wing base structures of *Z. caudelli* were investigated by Yoshizawa (2007, 2011a). A computer-based 3D reconstruction of the male postabdomen of *Z. hubbardi* was presented by Hünefeld

(2007), based on microtome sections. Structures of the male postabdomen were described by Bolívar y Pieltain (1940), Hwang (1974), New (1978), Rafael & Engel (2006) and others. They are extremely variable, probably related to different mating patterns (e.g., Dallai et al. 2013).

Recently different aspects of Zoraptera were investigated by a collaborative group including entomologists from Japan (University of Tsukuba), Italy (University of Siena), and Germany (Friedrich-Schiller-Universität Jena), mainly specialized on development (R. Machida), ultrastructure (R. Dallai) and the skeletomuscular system (R.G. Beutel), respectively. Combined with collecting efforts in Malaysia (R. Machida and coworkers) and Ecuador (Y. Matsumura) (Fig. 2), several studies focused on the genital region were presented, using a broad array of techniques including transmission electron microscopy (TEM), confocal laser scanning microscopy (CLSM), and micro computed tomography (μCT) (Fig. 3). One result was the marked discrepancy between a far-reaching uniformity of the group in the general body morphology and conspicuous differences in the male genital structures (Dallai et al. 2011, 2012a, b; Y. Matsumura, pers. comm.).

Zorapteran eggs were described in earlier studies for several species (Caudell 1920; Gurney 1938; Silvestri 1946). SEM micrographs of eggs of *Zorotypus gurneyi* and *Zorotypus barberi* (Panama) were shown in Choe (1989). Mashimo et al. (2011) described eggs of *Z. caudelli* (Malaysia) with different approaches including TEM. The whitish egg is 0.6 mm long and 0.3 mm wide, the two-layered chorion shows a honeycomb pattern, and an operculum or a hatching line are missing. A pair of micropyles is present at the equator on the dorsal side, similar to the condition found in eggs of *Timema* (Phasmatodea) (Mashimo et al. 2011).

Spermatozoa were already observed by Silvestri (1913). The spermatogenesis and sperm ultrastructure was investigated by Dallai et al. (2011) using transmission electron microscopy. A common feature of Zoraptera is the great length of the spermatozoa. An unusual feature of *Z. caudelli* is a disconnection of sub-tubules A and B at the level of microtubule doublets 1 and 6 of the mature sperm cells (Dallai et al. 2011), whereas disproportionately large mitochondrial derivatives are characteristic for *Z. hubbardi* (Dallai et al. 2012b). Character combinations found in different species suggest that spermatozoa do not evolve as a unit, but that like in other body regions components can be modified independently from each other. A derived feature, dense laminae radiating in a cartwheel array between neighboring centriolar triplets, is shared with Phasmatodea and Embioptera. An apomorphy shared with Phasmatodea is the presence of 17 protofilaments in the tubular wall of the outer accessory microtubules (Dallai et al. 2011, 2012b; Gottardo et al. 2012).

3. The phylogenetic position of Zoraptera (Figs 4, 5)

3.1. Pre-Hennigian approaches

When Silvestri (1913) described the first zorapteran species and introduced the family Zorotypidae he assumed that they must be close relatives ("collocate vicino") of roaches ("Blattoidei") and Isoptera. He listed several differences separating Zoraptera from these polyneopteran groups, such as for instance the presence of a bundle of setae on the left mandible. He also mentioned similarities with Dermaptera, but explicitly referred to them as superficial. After Silvestri, affinities (not necessarily in a phylogenetic sense) with Isoptera were emphasized by Caudell (1918) and the "distinguished albeit eccentric" G.C. Crampton (1920) (Grimaldi & Engel 2005). Potential arguments for a closer relationship included a general resemblance in the habitus, certain structural details of the thorax and abdomen, colonial habits, and dehiscent wings. While recognizing these similarities, Crampton (1920) clearly pointed out affinities with the acercarian orders, for which he hypothesized an origin from "Prothorthopteroid ancestors in the common Prothorthopteran-Protoblattid stem". He explicitly suggested a very close relationship with Psocoptera ("Corrodentia"). A possible relationship with Psocoptera was also discussed in Gurney (1938), concluding that "affinities with Corrodentia are more noticeable than those with orthopteroid insects".

Weidner (1969) suggested "strong thoracic synapomorphies" of Zoraptera + Isoptera, but did not uphold this view in his Handbuch der Zoologie volume (Weidner 1970) where he explicitly rejected superficial arguments for such a hypothesis and emphasized the difficulty of placing Zoraptera. He rather vaguely referred to the order as a specialized, "today obsolete ("verkümmert") branch of Blattodea" (including roaches and termites).

3.2. Hennig's interpretation and follow up studies

W. Hennig revolutionized insect systematics with his classical work "Die Stammesgeschichte der Insekten" (Hennig 1969). In an earlier study he rather vaguely suggested monophyletic Paraneoptera[1] (Zoraptera + Acercaria [= Psocodea, Thysanoptera and Hemiptera]) with Zoraptera basal and definitely outside of Psocoptera (Hennig 1953). A similar hypothesis was proposed in a little-known study by Wille (1960: Fig. 1), who addressed Zoraptera as "the most primitive group of the hemipteroids [= Acercaria], at the base of their evolutionary branch and close to the orthopteroids". Hennig (1969) indicated a single "certain derived feature" supporting Paraneoptera, the greatly condensed condition of the abdominal ganglionic chain, with two separate ganglionic masses in zorapterans, and only one in the remaining groups (Hennig 1953, 1969). He considered the reduced number of three tarsomeres (groundplan) as an additional potential synapomorphy, but it is apparent that losses of tarsal segments occurred in many groups. The hypotheses suggested by Hennig (1953, 1969) and Wille (1960), were tentatively followed by Kristensen (e.g., 1975), Willmann (2005), and Beutel & Weide (2005). The presence of only six Malpighian tubules (four in Acercaria), a cercus composed of only one segment or entirely missing (Acercaria), a

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[1] The term Paraneoptera is presently often used for a group that does not include Zoraptera (e.g., Grimaldi & Engel 2005)

fork of the cubitus posterior (areola postica) (Willmann 2005), a strengthened cibarial sucking pump, and a blade-like lacinia lacking mesally directed spines (Beutel & Weide 2005) were considered as additional arguments. The last feature is likely an autapomorphy of *Zorotypus hubbardi*, the species examined by Beutel & Weide (2005). A largely unmodified lacinia is present in other species (e.g., Silvestri 1913). The strongly developed cibarial dilator is a rather unspecific feature which has also developed in other groups of insects (e.g., Antliophora; Beutel & Baum 2008). In his later review studies, Kristensen (e.g., 1995) questioned Hennig's Paraneoptera concept and treated acercarian and polyneopteran affinities of Zoraptera as competing working hypotheses.

Similarities of the antennae of Zoraptera and Isoptera (chemoreceptors, tactile setae, Johnston's organ) were described by Slifer & Sekhon (1978). However, it is evident that these features have evolved independently given the strong support for a subordinate placement of Isoptera within Blattodea (e.g., Deitz et al. 2003; Lo 2003; Klass 2009). A sistergroup relationship with Embioptera was first proposed by Minet & Bourgoin (1986), who suggested an entire series of potential synapomorphies including a reduced wing venation (groundplan), a hypertrophied metafemur and metathoracic tibial depressor, moniliform antennae, fusion of tarsomeres, loss of the arolium, reduction of the ovipositor, and gregarious habits. Even though some of these features are rather unspecific modifications or reductions, a close relationship with Embioptera gained further support by Engel & Grimaldi (2000) and Grimaldi (2001), like in Minet & Bourgoin (1986) based on informal character evaluations.

In a study on the zorapteran wing venation Kukalová-Peck & Peck (1993) addressed the intraordinal relationships and also the placement of the order within neopteran insects. Based on an informal analysis of wing characters they suggested that Zoraptera "probably diverged from the Blattoneoptera (= Grylloblattodea, †Protelytroptera, Dermaptera and Dictyoptera), almost certainly before the (†Protelytroptera + Dermaptera) line, and much before the (Isoptera + (Blattodea + Mantodea)) line". The hypothesis was illustrated with a phylogenetic tree (Kukalová-Peck & Peck 1993: Fig. 23) showing Zoraptera as the second branch of Blattoneoptera after Grylloblattodea.

A sistergroup relationship with Holometabola ("Scarabaeiformes") was suggested by Rasnitsyn (1998) based on the alleged presence of a precursor of the medial mesocoxal articulation in *Z. hubbardi*. As pointed out above (2. Morphology), the morphological data were insufficient. Moreover, the phylogenetic argumentation was based on an ad hoc interpretation of a single vague character. Rasnitsyn (1998) provisionally placed Zoraptera in an otherwise extinct superorder Caloneurida, supposedly subordinate to a "Cohors Cimicoformes" (= Acercaria). He hypothesized Caloneurida "to be ancestral to other cimicoform superorders as well as to the Cohors Scarabaeiformia" (= Holometabola). This taxonomic treatment of Zoraptera is not compatible with the suggested phylogenetic position as sistergroup of Holometabola.

Kusnetsova et al. (2002) examined the karyotype (2n = 38, 36 + neo-XY) and genital structures of *Z. hubbardi*. Based on the presence of panoistic ovaries and holokinetic chromosomes they rather vaguely suggested that Zoraptera may "represent a group of Polyneoptera nearest to the origin of Paraneoptera".

Zompro (2005) suggested a position of Zoraptera in "Orthopteromorpha", supposedly comprising the polyneopteran orders excluding Plecoptera, Embioptera and Phasmatodea. This placement was based on elongate coxae and eggs without a strongly sclerotized egg capsule and also lacking an operculum. However, a stringent character discussion and analytical approach were lacking. Furthermore, the coxae of Zoraptera are not elongated (e.g., Friedrich & Beutel 2008) and the condition of the egg is obviously plesiomorphic (Mashimo et al. 2011).

A character system previously not explored with respect to the position of Zoraptera is the antennal heart and associated structures. The hitherto unknown antennal pulsatile organ of Zoraptera is characterized by a t-shaped configuration of muscles (pers. obs. B. Wipfler), with a fairly broad transverse muscle attached to the head capsule on both sides (assigned as "Mxy" in Beutel & Weide 2005) and a narrower vertical muscle. Such a configuration occurs in several groups of Polyneoptera but is completely unknown in Acercaria. This feature clearly supports a placement of Zoraptera among the polyneopteran lineages.

Recent detailed morphological studies related to the reproduction suggested a sistergroup relationship of Zoraptera with Embioptera or Eukinolabia (Embioptera + Phasmatodea), by Mashimo et al. (2011, in press) based on the egg structure and development of egg tooth and by Dallai et al. (2011, 2012b) based on the spermatozoan structures, i.e. 17 protofilaments comprising accessory tubules of axonomes and L-shaped electron-dense lamellae accompanying microtubular triplets in the centriole adjunct.

3.3. Cladistic approaches

The first morphology-based formal cladistics analysis including all hexapod orders were presented by Wheeler et al. (2001) and Beutel & Gorb (2001). Wheeler et al. (2001) was primarily based on molecular data but also presented an independent morphological analysis based on a matrix with 275 characters. The analysis of the morphological data yielded a sistergroup relationship between Acercaria and Zoraptera in agreement with Hennig (1969). Zoraptera were placed as sistergroup of Eumetabola (Acercaria + Holometabola) in the study of Beutel & Gorb (2001), which had a main focus on the evolution of attachment structures. The same result was obtained in a series of studies on the head morphology (Wipfler et al. 2011; Blanke et al. 2012; 2013; Wipfler 2012). However, it was pointed out by the authors that the unit Zoraptera + Eumetabola was not supported by convincing synapomorphies. In a follow-up study Beutel & Gorb (2006; expanded morphological data set, Mantophasmatodea included) retrieved Zoraptera as sister to Acercaria, essentially supported by the potential synapomorphies listed above (e.g., blade-like lacinia, condensed abdominal ganglionic chain).

Cladistic analyses of characters of the wing articulation (Yoshizawa 2007, 2011a) yielded a sistergroup relationship Zoraptera + Embioptera, like in Minet & Bourgoin (1986). This was also supported when additional characters from Beutel & Gorb (2001, 2006) were added to the matrix. The fusion between the first axillary sclerite and the posterior notal wing process was emphasized as a potential synapomorphy, as this modification also involves a modification of the wing hinge, which is extremely conservative throughout the winged insects (Yoshizawa & Ninomiya 2007; Ninomiya & Yoshizawa 2009).

3.4. Molecular phylogenetic and phylogenomic approach

Wheeler et al. (2001; 18S, 28S, morphology) and Terry &Whiting (2005; 18S, 28S, Histone 3, morphology) analyzed the relationships of the entire Hexapoda or of the polyneopteran orders, respectively. Very different placements of Zoraptera order resulted from separate analyses of 18S and 28S rRNA in Wheeler et al. (2001: Figs 13, 14) (see Table 1), and analyses of both genes combined suggested an unlikely unit comprising Zoraptera, Trichoptera and Lepidoptera. Terry & Whiting (2005) placed Zoraptera as sistergroup of Dermaptera and referred to this possible clade as Haplocecata. The analytical methods used in both studies (POY) have been criticized (Kjer et al. 2007; Ogden & Rosenberg 2007; Yoshizawa 2010). A contaminant of a dermapteran sequence in the zorapteran dataset (Yoshizawa 2010, 2011b) suggests that the clade Zoraptera + Dermaptera may be artificial.

Yoshizawa & Johnson (2005; 18S rRNA) aligned their data using a secondary structure model. Maximum likelihood and Bayesian analyses retrieved Zoraptera as sister to Dictyoptera. However, very unusual molecular evolutionary trends observed in Zoraptera (e.g., extremely accelerated substitution rates and modifications of secondary structures) made the placement of the order highly unstable. Wang et al. (2013; 28S rRNA) also employed secondary structure-based alignments and obtained the same result for Zoraptera. However, for both 18S and 28S rRNA an extreme acceleration of the substitution rate and modification of secondary structures is evident in Zoraptera, making the results unstable. Wang et al. (2013) identified unique features of the secondary structure of 28S rRNA shared by Zoraptera and Dictyoptera.

Misof et al. (2007; 18S rRNA) specifically addressed problems caused by character interdependence by employing secondary structure information and a Bayesian approach. A partly robust tree was obtained based on a hexapod consensus secondary structure model and mixed DNA/RNA substitution models. Zoraptera were placed as sistergroup of Dermaptera + Plecoptera, but with very low Bayesian support (0.45). This underlines that the frequently used 18S rRNA is apparently insufficient to fully resolve supraordinal insect interrelationships.

Ishiwata et al. (2011; DPD1, RPB1, RPB2) retrieved Polyneoptera incl. Zoraptera with good support, and a sistergroup relationship Zoraptera + Dictyoptera in some of the trees with low support. Consequently, Zoraptera were shown in an unresolved polyneopteran polytomy in a summary tree (Ishiwata et al. 2011).

Simon et al. (2012) placed Zoraptera as sister to all other polyneopteran terminals in a preliminary phylogenomic study. The support values were extremely low and several orders (Embioptera, Phasmatodea, Mantophasmatodea, Grylloblattodea) were not included. In a follow-up study (Letsch & Simon 2013) Embioptera and Phasmatodea were added. The analyses also supported a sistergroup relationship between Zoraptera and the remaining polyneopteran lineages. Recent unpublished results from the 1KITE project (ca. 100 hexapod terminals representing all orders) suggest a sistergroup relationship between a unit Zoraptera + Dermaptera (confirming the Haplocercata s. Terry & Whiting 2005) and a clade comprising all other polyneopteran orders. However, this pattern is not strongly supported statistically.

4. Intraordinal phylogeny

Kukalová-Peck & Peck (1993) suggested a classification based on an informal evaluation of wing characters. They recognized two families of Zoraptera and several genera. A new genus *Formosozoros* (from Taiwan) was described by Chao & Chen (2000). However, like the genera introduced by Kukalová-Peck & Peck (1993) it was not considered as valid in recent studies, and all extant species are currently classified into a single genus *Zorotypus* (e.g., Engel & Grimaldi 2002; Grimaldi & Engel 2005).

No molecular approach explicitly addressing the intraordinal phylogeny has been made to date. Yoshizawa & Johnson (2005; 18S rRNA) included four representatives of Zoraptera in their study (Old World and New World samples) and Yoshizawa (2010, 2011b; 18S rRNA) six. A deep divergence between the Old World and New World species was demonstrated. This is seemingly in conflict with evidence from male genitalia. The New World *Zorotypus snyderi* shares an elongated and coiled intromittent organ with the Old World species (Gurney 1938; Dallai et al. 2011; Mashimo et al. 2013), but molecular data suggest that it is closely related with *Z. hubbardi* (also New World) which lacks this unusual structure. Therefore it is conceivable that the coil was present in the groundplan of Zoraptera (or a large subgroup) and was secondarily lost in the majority of species. It cannot be fully excluded that it was acquired independently in several lineages, but independent gain of such a complex structure appears less likely.

5. Fossils

Grimaldi & Engel (2005) suggested a possible origin of Zoraptera in the lower Mesozoic. The first described extinct species was an apterous female of †*Zorotypus palaeus* from Dominican amber (Middle Miocene; Poinar 1988; Iturralde-Vinent & MacPhee 1996). The first winged specimen was described by Engel & Grimaldi (2000) from the same formation. Four species were identified in Burmese Cretaceous amber (Engel & Grimaldi, 2002). Three of them were very similar to extant zorapterans and consequently assigned to the genus *Zorotypus*. A basal position of two of them (†*Zorotypus anathothorax*, †*Zorotypus nascimbenei*) was tentatively suggested by Engel (2003), and both were placed in a subgenus †*Octozoros* based on a reduced number of eight antennomeres and the presence of jugate setae along a part of the posterior forewing border (Engel, 2003). One of the four species was placed in a separate genus †*Xenozorotypus* (Engel & Grimaldi, 2002) and considered as sister to all other zorapterans. †*Palaeospinosus hudae* was described from Jordanian amber by Kaddumi (2005), but the genus has been synonymized with *Zorotypus* (Engel 2008).

6. General biology

Zorapterans are omnivorous scavengers and feed on fungal hyphae and spores and on very small arthropods like mites and collembolans (Choe 1992; Grimaldi & Engel 2005). They are usually found in colonies under bark of decaying logs. As social behavior has not been reported yet and is probably missing in all species, zorapterans should be referred to as gregarious. The individuals spend much time grooming various body parts (Valentin 1986). In *Zorotypus barberi* some parts that cannot be reached are groomed by conspecifics (Choe 1992). Some species emit a slight but characteristic odor, reminiscent of a fragrance produced by the osmeterium of some swallowtail butterfly (Shetlar 1978; pers. obs. Y. Mashimo). Little is known about the life cycle of Zoraptera. The length of the nymphal period is about 1-2 months and adult lifespan is a few months, as reported by Gurney (1938) and Shetlar (1978). While Shetlar (1974) estimated five nymphal instars by measuring morphological features, Riegel & Eytalis (1974) suggested four instars based on different head widths. However, these descriptions are insufficient and the conclusions largely speculative. The specific wing dimorphism, a potential autapomorphy of the order, is also insufficiently investigated. According to observations mentioned in a review by Choe (1992) crowding and heredity seem to affect the production of the winged morphs. However, relevant details are unknown. Further intensive observations and investigations of the biology of Zoraptera are required.

7. Embryonic development

The embryonic development of Zoraptera was described recently by Mashimo et al, (in press). The embryo is formed by a fusion of paired blastoderm regions with higher cellular density extends along the egg surface. After reaching its full length, it migrates into the yolk and finally moves to take its position on the ventral surface of the egg accompanied by a reversion of its anteroposterior axis. These embryological features are widely known in Polyneoptera, and strongly suggest a placement of Zoraptera in this lineage (Mashimo et al. in press).

8. Mating behavior

Several studies on the mating behaviour were carried out by Choe (1994a, b, 1995, 1997), focused on the precopulatory courtship and copulation of *Z. gurneyi* and *Z. barberi* from Panama. The two sympatric species display a distinctly different mating behaviour. In *Z. gurneyi* a linear dominance hierarchy is established by mutual antennation and females were fertilized only once with very few exceptions. Dominant males performed 72% of the copulations, while the others were able to mate only occasionally. *Z. barberi* males lack this hierarchy. They are characterized by a highly unusual courtship ritual including nuptial feeding on a secretion of a cephalic gland (Choe 1997).

The mating behaviour of several Asian species was documented by Dallai et al. (2013) (Fig. 3). Mating sequences were recorded for many hours and observations were compared to earlier findings of Choe (1994a, b, 1995, 1997). An unusual case of external sperm transfer was described for *Z. impolitus*, a feature unknown in other pterygote insects. The high variability not only of the genital structures but also of the mating behaviour and reproductive strategies was underlined by Dallai et al. (2013).

9. Discussion

Despite of their small size, inconspicuous appearance, cryptic habits and very low diversity it would be misleading to consider Zoraptera as “unsuccessful” in their evolution. An origin in the early Mesozoic was suggested by Grimaldi & Engel (2005). Considering a possible placement as sistergroup of a large polyneopteran subunit (possibly together with Dermaptera), an origin in the Carboniferous appears likely. In any case the group has survived for a period of at least 200 Mya. Very small size and cryptic habits, which have prevented discovery by insect collectors until the early 20th century, may have contributed to the long survival. Recently collected and described species from different regions (e.g., Mashimo et al. 2013) indicate that the true diversity of the order is likely distinctly higher than known at present.

The morphological investigation of the group mainly profited from three factors. The availability of innovative techniques greatly facilitated detailed anatomical and ultrastructural studies (Fig. 1; e.g., Friedrich & Beutel 2008; Dallai et al. 2012a, b). The coordinated effort of researchers with different specialized skills also led to a markedly improved knowledge of the group. Moreover, improved collecting and fixation yielded more and better conserved material for anatomical investigations.

Unlike in Strepsiptera (“the Strepsiptera problem”; e.g., Kristensen 1991, 1995; Beutel & Pohl 2006; Beutel et al. 2011) the systematic position of Zoraptera is not obscured by numerous autapomorphies, but rather by many preserved plesiomorphic features, combined with far-reaching reductions in some body regions (e.g., attachment structures, ovipositor). Friedrich & Beutel (2008) showed that the thoracic skeleto-muscular system of winged morphs is probably close to the groundplan of Neoptera. Whereas Strepsiptera have been recently placed as the sistergroup of Coleoptera with strong support (Niehuis et al. 2012; Pohl & Beutel 2013), the “Zoraptera problem” is still not completely resolved.

Widely divergent placements were suggested for Zoraptera (Figs 4, 5) and Strepsiptera and in both cases early attempts were impeded by the lack of a sound phylogenetic methodology (Pohl & Beutel 2013). That the spectrum of proposed positions is somewhat narrower in the case of Zoraptera may be partly due to its later discovery, about 120 years after the description of the first strepsipteran species (Rossius 1793; see Pohl & Beutel 2013). The placement of Zoraptera as close relatives of termites (e.g., Weidner 1969) was based on superficial similarities (see Weidner 1970) and an insufficient character evaluation. The structural affinities with Psocoptera emphasized by Crampton (e.g., 1921) and others are either plesiomorphic, superficial, or due to homoplasy. The placement of barklice (paraphyletic with respect to Liposcelididae) within a clade Psocodea is undisputed (e.g., Yoshizawa & Saigusa 2001; Yoshizawa & Johnson 2006, 2010; Friedemann et al. in press). The sistergroup relationship with Holometabola suggested by Rasnitsyn (1998) was based on an insufficient evaluation of very incomplete morphological data. A clade Zoraptera + Eumetabola (Beutel & Gorb 2001) is an artifact mainly caused by parallel reductions (e.g., ocelli in immature stages, number of Malpighian tubules).

The hypothesized sistergroup relationship between Zoraptera and Acercaria (Hennig 1953, 1969; Wille 1960; Kristensen 1975; Willmann 2003, 2005; Beutel & Weide 2005; Beutel & Gorb 2006) is presently largely refuted (Figs 4, 5). Most characters suggesting monophyletic Paraneoptera (incl. Zoraptera) are reductions (e.g., number of tarsomeres, cercomeres, and abdominal ganglia) and polyneopteran affinities (e.g., Yoshizawa 2007, 2011a; Ishiwata et al. 2011) imply that these structural modifications evolved independently.

A placement of Zoraptera within Polyneoptera is gaining more and more support (Fig. 5). However, the monophyly of this unit is not sufficiently supported yet (e.g., Whitfield & Kjer 2008; Trautwein et al. 2012) and the precise placement of Zoraptera is still controversial. A close relationship with Dictyoptera (Boudreaux 1979; Wheeler et al. 2001: p. 148 [“based on the discussion”]; Yoshizawa & Johnson 2005; Wang et al. 2013) is a possible option, but convincing synapomorphies are missing. Boudreaux’ (1979) arguments were not based on a formal character analyses and the features are unspecific or widespread in Insecta (e.g., "backwardly directed hind coxae"). The conclusion presented by Wheeler et al. (2001) in a summary tree is weakened by conflicting results obtained with the different data sets (morphology, 18S rRNA, 28S rRNA, 18S + 28S rRNA) (see Table 1). It is conceivable that the results based on molecular data were negatively affected by the use of POY (e.g., Yoshizawa 2010, 2011b). Kukalová-Peck & Peck (1993) provided useful data, but the hypothesized placement of Zoraptera in a clade Blattoneoptera is weakened by the lack of a formal analysis and the exclusive use of wing characters. Wing base characters and morphological features linked to reproduction suggest a placement as sistergroup Embioptera (Yoshizawa 2007, 2011a) or Eukinolabia (Embioptera + Phasmatodea) (Mashimo et al. 2011, in press; egg and embryonic development; Dallai et al. 2011, 2012b; spermatozoa), respectively. Results of single gene analyses of single genes did not yield congruent results yet (e.g., Yoshizawa & Johnson 2005; Misof et al. 2007). Likewise, presently available transcriptome-based studies are not fully convincing. The basal placement within Polyneoptera suggested by Simon et al. (2012) and Letsch & Simon (2013) is weakened by the incomplete ordinal taxon sampling. As the pattern in the recent 1KITE-tree ((Zoraptera + Dermaptera) + (remaining Polyneoptera) is not is not strongly supported statistically, the precise placement of Zoraptera remains a challenge.

Despite a considerable progress in zorapteran studies it is apparent that important problems remain to be solved, not only concerning the systematic position. To understand the phenomenon of different forms of selective pressure shaping different body parts (natural selection [ecological]/sexual selection) detailed information on genital structures of more species is required. Moreover, a species level phylogeny based on morphological *and* molecular data should have high priority in future studies. A solid intraordinal phylogeny is an essential basis for reconstructing the evolution of the group and to understand evolutionary processes.

It is probably safe to assume that zorapterans will remain one of the smallest hexapod orders and only few entomologists would address them as attractive insects. Nevertheless the group is intriguing in different aspects, phylogenetically, as a model case in evolutionary biology, and as cryptic survivors with a hidden diversity still to explore.

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Table 1. Systematic placements of Zoraptera with different approaches and character sets.

Systematic approach/ Study	**Characters**	**Systematic placement**
Pre-Hennigian concepts		
Silvestri (1913)	morphology	closely related with **roaches** and **termites** (Blattodea)
Caudell (1918)	morphology	affinities with **Isoptera**
Crampton (1920, 1921, 1926)	different morphological character systems	affinities with **Psocoptera** ("Corrodentia")
Weber (1933)	morphology	tentatively in a superorder **Blattoidea** (Mantodea, Zoraptera, Blattaria, Isoptera)
Gurney (1938)	morphology	affinities with **Psocoptera** ("Corrodentia")
Hennigian concepts		
Hennig (1953)	morphological characters	tentatively as basal lineage of **Paraneoptera**, outside of Psocoptera
Hennig (1969)	morphological characters, abdominal ganglionic chain, number of tarsomeres	sistergroup of **Acercaria** (**Paraneoptera** concept)
Weidner (1969)	mainly thoracic characters	tentatively as sistergroup of **Isoptera**
Weidner (1970)	mainly thoracic characters	obsolete branch of **Blattodea**
Kristensen (1975)	different morphological	**Paraneoptera concept** as

	characters	working hypothesis, polyneopteran affinities tentatively refuted
Boudreaux (1979)	wing venation, metacoxae	sistergroup of **Dictyoptera** („Cursorida = Zorapterida + Blattarida“
Minet et Bourgoin (1986)	wing venation, thoracic and abdominal morphology	sistergroup of **Embioptera**
Kristensen (1995)	different morphological characters	either acercarian or polyneopteran affinities
Kukalová-Peck & Peck (1997)	wing base and venation	sistergroup of †Protelytroptera, Dermaptera and Dictyoptera (**Blattoneoptera** excl. Grylloblattodea)
Kusnetsova et al. (2002)	chromosome structure and genitalia	"in **Polyneoptera** close to the origin of Paraneoptera"
Zompro (2005)	morphology and egg structure	**"Orthopteromorpha"** (=Polyneoptera excl. Plecoptera, Embioptera and Phasmatodea)
Dallai et al. (2011)	sperm ultrastructure	In a clade with **Embioptera** and **Phasmatodea**
Mashimo et al. (2011, in press)	egg structure and development	In a clade with **Embioptera** and **Phasmatodea**

Cladistic approach based on morphology		
Kukalová-Peck & Peck (1993)	wing base and venation	sistergroup of †Protelytroptera, Dermaptera and Dictyoptera (**Blattoneoptera**)
Wheeler et al. (2001)	morphological matrix with 275 characters, extracted from literature	sistergroup of **Acercaria**
Beutel & Gorb (2001)	characters of adults and larvae including attachment structures	sistergroup of **Eumetabola** (Acercaria + Holometabola)
Beutel & Gorb (2006)	characters of adults and larvae including attachment structures, Mantophasmatodea and some developmental features added	sistergroup of **Acercaria**
Yoshizawa (2011)	wing base	**Embioptera**
Single gene analyses		
Wheeler et al. (2001)	18S rRNA (analyzed with POY)	Sistergroup of **Psocodea**
	28S rRNA (POY)	sistergroup of a clade comprising all pterygote

		groups except for Strepsiptera and two ephemeropteran terminals
	18S + 28S rRNA	sistergroup of **Amphiesmenoptera** (trichopteran and lepidopteran terminals)
	18S, 28S rRNA + morphological data extracted from literature ("total evidence")	sistergroup of **Dictyoptera**
Yoshizawa & Johnson (2005)	18S rRNA	**Dictyoptera**
Misof et al. (2007)	18S rRNA, special focus on character interdepedence	sistergroup of **Plecoptera + Dermaptera**
Ishiwata et al. (2011)	3 nuclear protein-coding genes	In **Polyneoptera**, possibly sistergroup of **Dictyoptera**
Wang et al. (2013)	28S rRNA	Dictyoptera
Phylogenomic approach		
Simon et al. (2012)	Transcriptomes, Embioptera, Phasmstodea, Grylloblattodea, and Mantophasmatodea not included	sistergroup of remaining polyneopteran terminals with low support
Letsch & Simon (2013)	Transcriptomes,	sistergroup of remaining

	Grylloblattodea and Mantophasmatodea not included	polyneopteran terminals

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Fig. 1. Histogram showing number of publications on Zoraptera under different aspects.

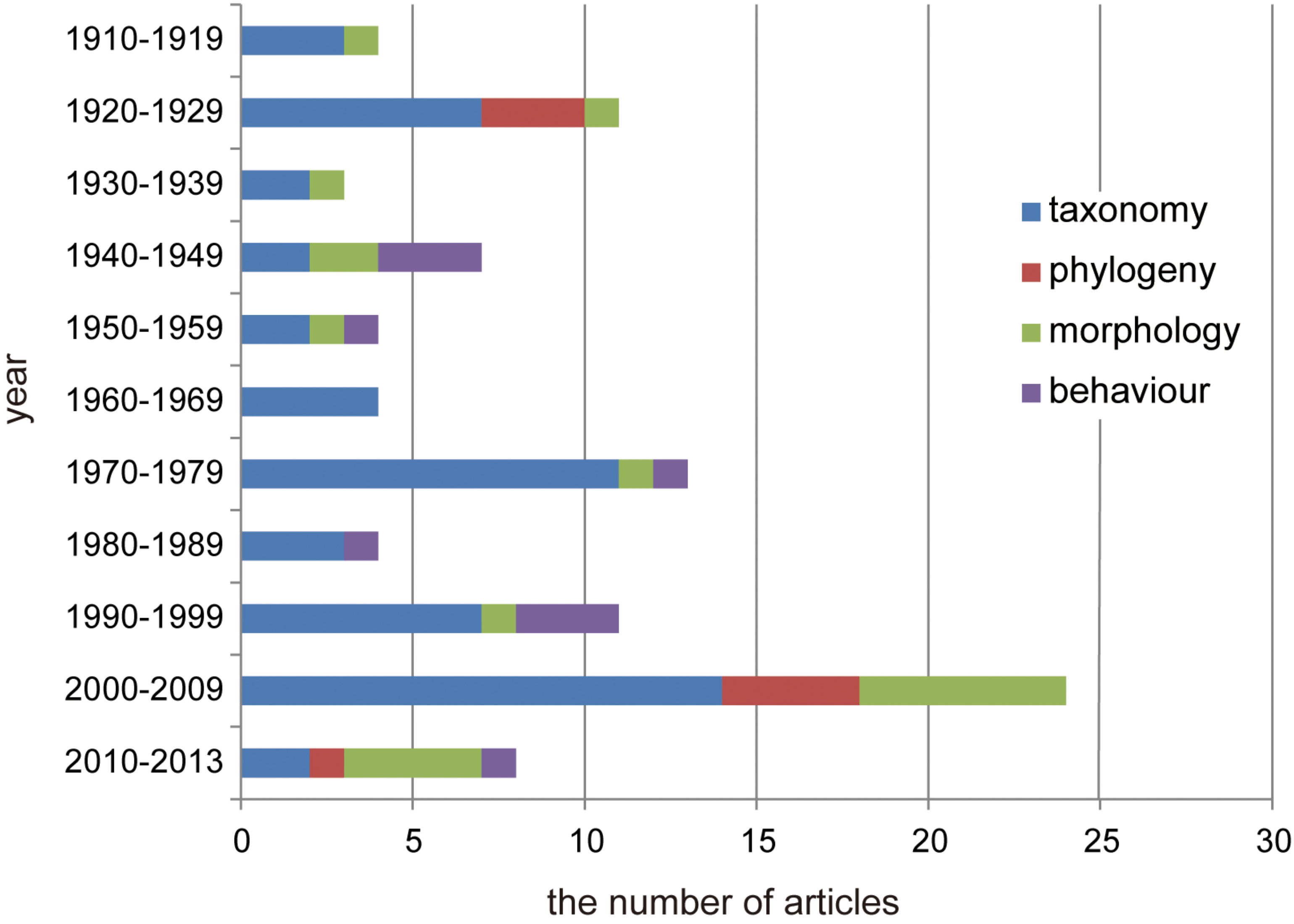
Fig. 2. Collecting site of different *Zorotypus* species in Ecuador, Zamora-Chinchipe, Copalinga Lodge Reserve Rainforest, with nymph (lower right).

Fig. 3. Copula of *Zorotypus caudelli*, volume render of μ-Ct image stacks.

Fig. 4. Cladograms showing different placements of Zoraptera.

Fig. 5. Cladograms from recent studies showing different placements of Zoraptera.

Figure



1910-1919
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1930-1939
1940-1949
1950-1959
1960-1969
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1980-1989
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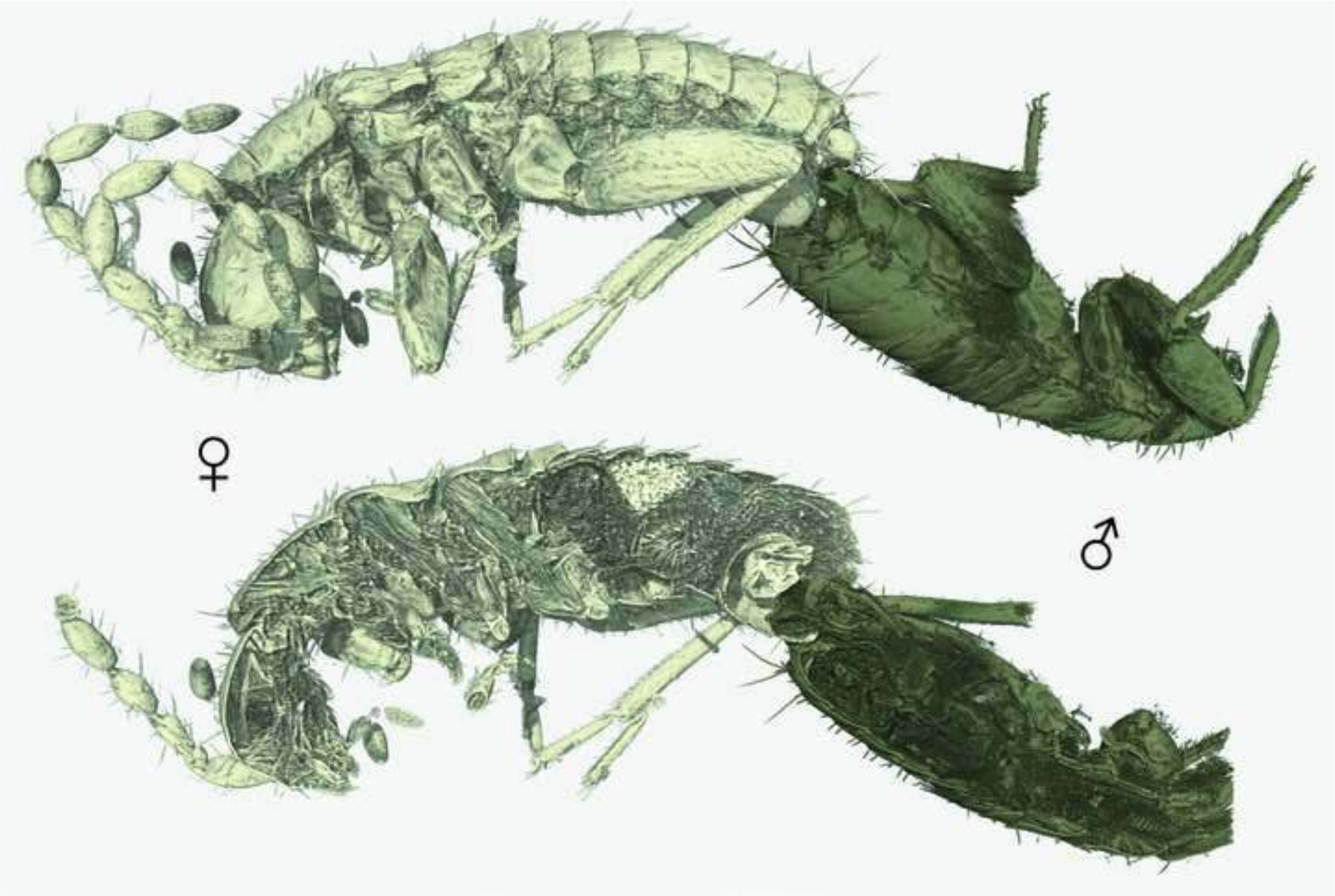
taxonomy
phylogeny
morphology
behaviour

Figure



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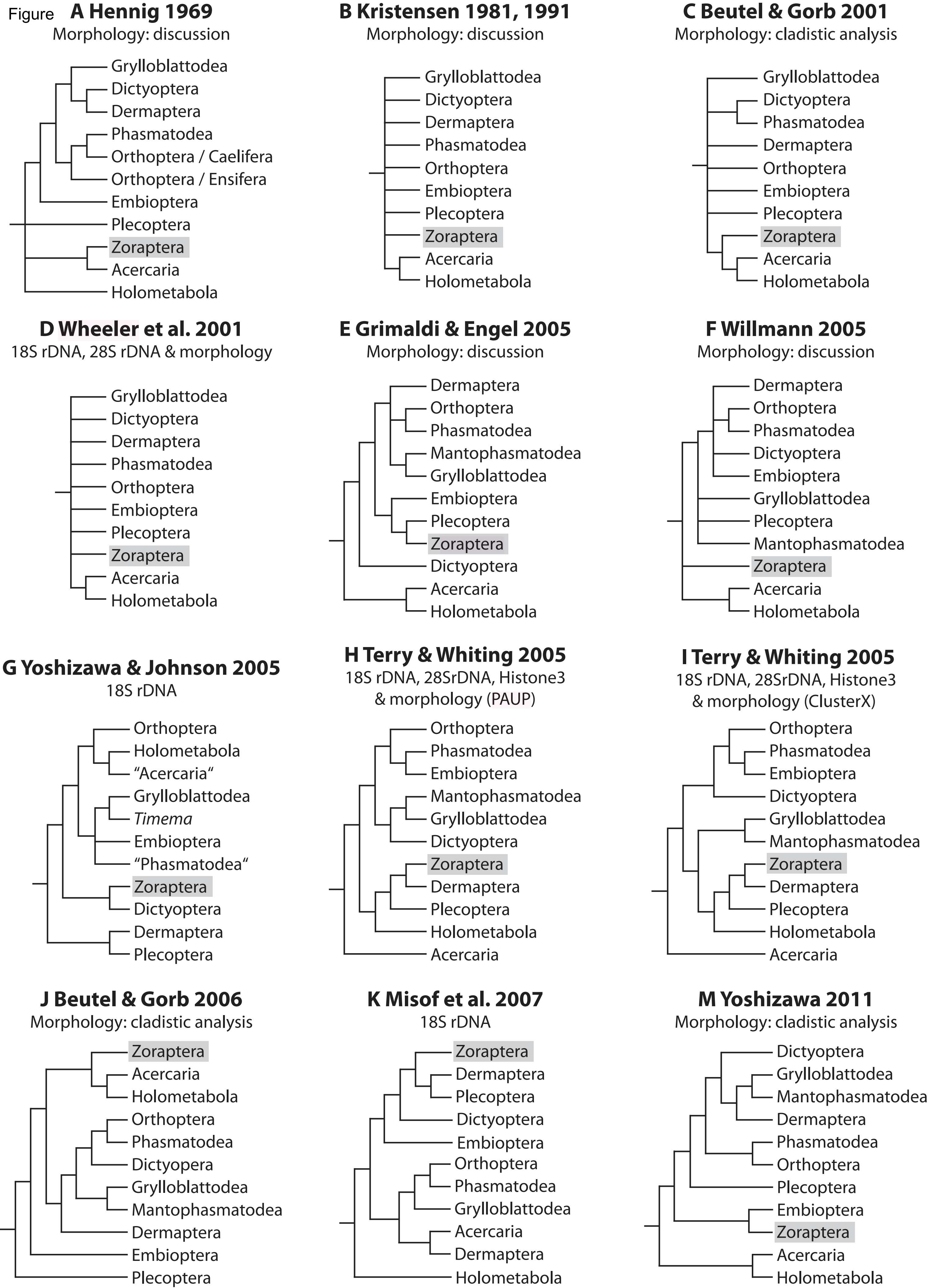
A Hennig 1969
Morphology: discussion
Grylloblattodea
Dictyoptera
Dermaptera
Phasmatodea
Orthoptera / Caelifera
Orthoptera / Ensifera
Embioptera
Plecoptera
Zoraptera
Acercaria
Holometabola
B Kristensen 1981, 1991
Morphology: discussion
Grylloblattodea
Dictyoptera
Dermaptera
Phasmatodea
Orthoptera
Embioptera
Plecoptera
Zoraptera
Acercaria
Holometabola
C Beutel & Gorb 2001
Morphology: cladistic analysis
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Dermaptera
Orthoptera
Embioptera
Plecoptera
Zoraptera
Acercaria
Holometabola
D Wheeler et al. 2001
18S rDNA, 28S rDNA & morphology
Grylloblattodea
Dictyoptera
Dermaptera
Phasmatodea
Orthoptera
Embioptera
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Zoraptera
Acercaria
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E Grimaldi & Engel 2005
Morphology: discussion
Dermaptera
Orthoptera
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Mantophasmatodea
Grylloblattodea
Embioptera
Plecoptera
Zoraptera
Dictyoptera
Acercaria
Holometabola
F Willmann 2005
Morphology: discussion
Dermaptera
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Plecoptera
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Zoraptera
Acercaria
Holometabola
G Yoshizawa & Johnson 2005
18S rDNA
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"Acercaria"
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Embioptera
"Phasmatodea"
Zoraptera
Dictyoptera
Dermaptera
Plecoptera
H Terry & Whiting 2005
18S rDNA, 28SrDNA, Histone3
& morphology (PAUP)
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Plecoptera
Holometabola
Acercaria
I Terry & Whiting 2005
18S rDNA, 28SrDNA, Histone3
& morphology (ClusterX)
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Dictyoptera
Grylloblattodea
Mantophasmatodea
Zoraptera
Dermaptera
Plecoptera
Holometabola
Acercaria
J Beutel & Gorb 2006
Morphology: cladistic analysis
Zoraptera
Acercaria
Holometabola
Orthoptera
Phasmatodea
Dictyopera
Grylloblattodea
Mantophasmatodea
Dermaptera
Embioptera
Plecoptera
K Misof et al. 2007
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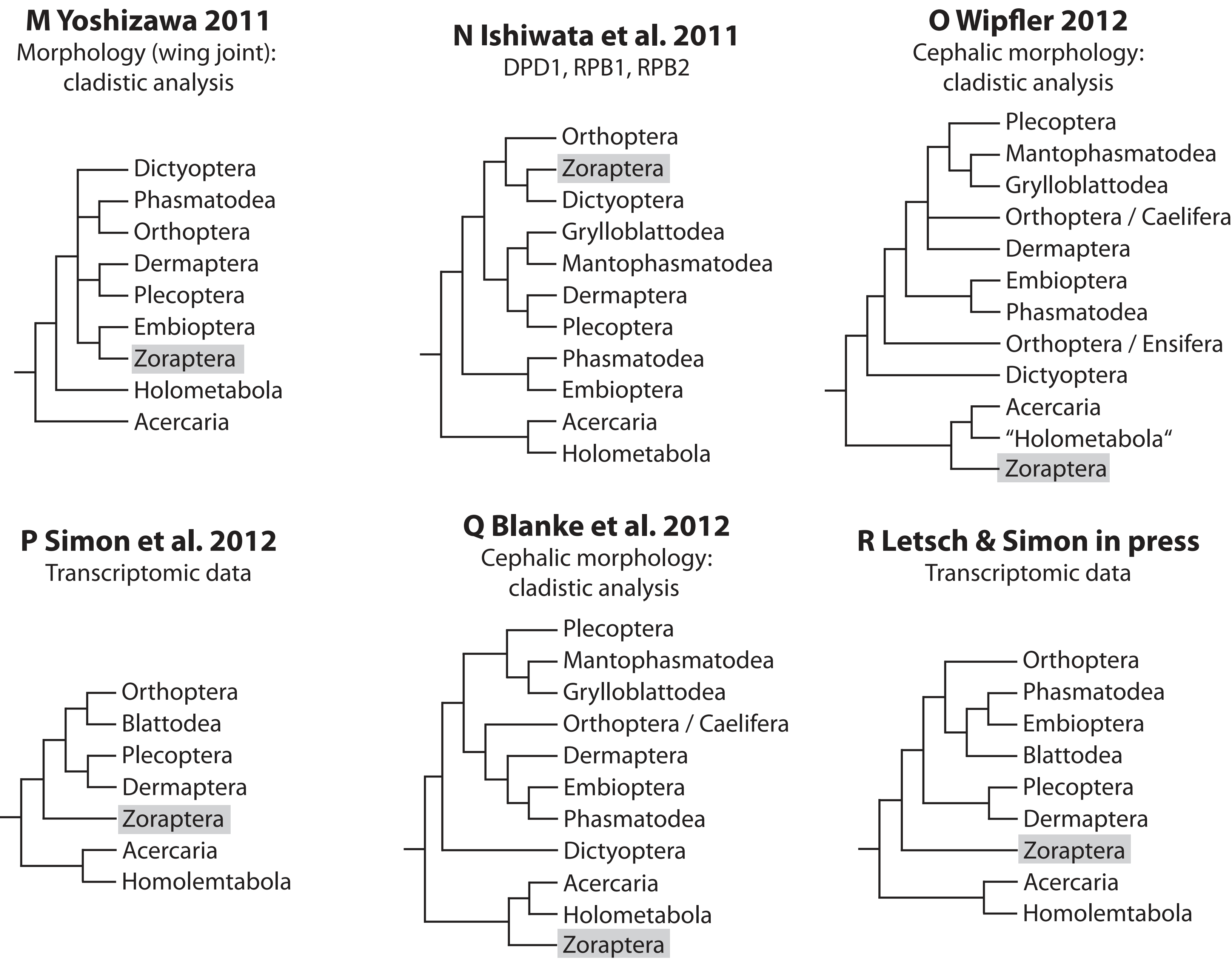
Dermaptera
Plecoptera
Dictyoptera
Embioptera
Orthoptera
Phasmatodea
Grylloblattodea
Acercaria
Dermaptera
Holometabola
M Yoshizawa 2011
Morphology: cladistic analysis
Dictyoptera
Grylloblattodea
Mantophasmatodea
Dermaptera
Phasmatodea
Orthoptera
Plecoptera
Embioptera
Zoraptera
Acercaria
Holometabola

Figure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Dictyoptera
Phasmatodea
Orthoptera
Dermaptera
Plecoptera
Embioptera
Zoraptera
Holometabola
Acercaria
N Ishiwata et al. 2011
DPD1, RPB1, RPB2
Orthoptera
Zoraptera
Dictyoptera
Grylloblattodea
Mantophasmatodea
Dermaptera
Plecoptera
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Plecoptera
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Grylloblattodea
Orthoptera / Caelifera
Dermaptera
Embioptera
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Orthoptera / Ensifera
Dictyoptera
Acercaria
"Holometabola"
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P Simon et al. 2012
Transcriptomic data
Orthoptera
Blattodea
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Dermaptera
Zoraptera
Acercaria
Homolemtabola
Q Blanke et al. 2012
Cephalic morphology: cladistic analysis
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Dermaptera
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Phasmatodea
Dictyoptera
Acercaria
Holometabola
Zoraptera
R Letsch & Simon in press
Transcriptomic data
Orthoptera
Phasmatodea
Embioptera
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Plecoptera
Dermaptera
Zoraptera
Acercaria
Homolemtabola