Phylogeny of Megaloptera:
A review of present knowledge

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Abstract. Megaloptera is the second smallest order in the Holometabola. The phylogeny and evolution of Megaloptera is of high interest concerning the origin of aquatic life-style of their larvae, the evolution of remarkable sexually selected traits, and the formation of their modern disjunctive distribution pattern. The present review summarizes the research progress on the phylogeny of Megaloptera. The higher-level phylogeny of Megaloptera appears to be resolved owing to the recent phylogenomic studies based on genome-scale data. The intergeneric and interspecific phylogenies of Megaloptera were analyzed in a number of works mainly based on morphological data. Thus, phylogenetic analysis based on molecular data is essential for testing the previous morphology-based hypotheses in future studies.

Introduction

The order Megaloptera (dobsonflies, fishflies, and alderflies) belongs to the holometabolan superorder Neuropterida. Adults of Megaloptera are characterized by the prognathous head with well-developed gula and the broad hind wing anal area, while their larvae are exclusively aquatic, living in various freshwater habitats, and characterized by the presence of 7-8 pairs of lateral tracheal gills (New & Theischinger 1993). Currently, 373 valid species of Megaloptera are described worldwide (Oswald & Machado 2018). There are only two families in Megaloptera, *i.e.*, Sialidae (alderflies) and Corydalidae, which is divided into the subfamilies Corydalinae (dobsonflies) and Chauliodinae (fishflies). In light of their "archaic" appearance Megaloptera were often mentioned as a primitive group of Holometabola (Yang & Yang 1999; Grimaldi & Engel 2005). Therefore, the phylogeny and evolution of Megaloptera is of high interest, but the relevant studies have a long history of competing hypotheses.

Hitherto, the higher-level phylogeny of Megaloptera has been studied in a number of works for a long period, resulting in a monophyletic or paraphyletic Megaloptera, and controversial sister-group relationship of Megaloptera with either Raphidioptera or Neuroptera (reviewed in Aspöck et al. 2012). The phylogenetic relationships among genera and species within Megaloptera previously drew less attention than the higher-level phylogeny, although it is crucial for understanding the historical biogeography and character evolution of this group.

In this paper I provide an overview of the existing phylogenetic analyses on various groups of Megaloptera (Fig. 1). The following issues will be addressed: i) the higher-

level phylogeny of Megaloptera; ii) the intergeneric phylogeny within Corydalidae and Sialidae; and iii) the phylogenetic relationships among megalopteran species.
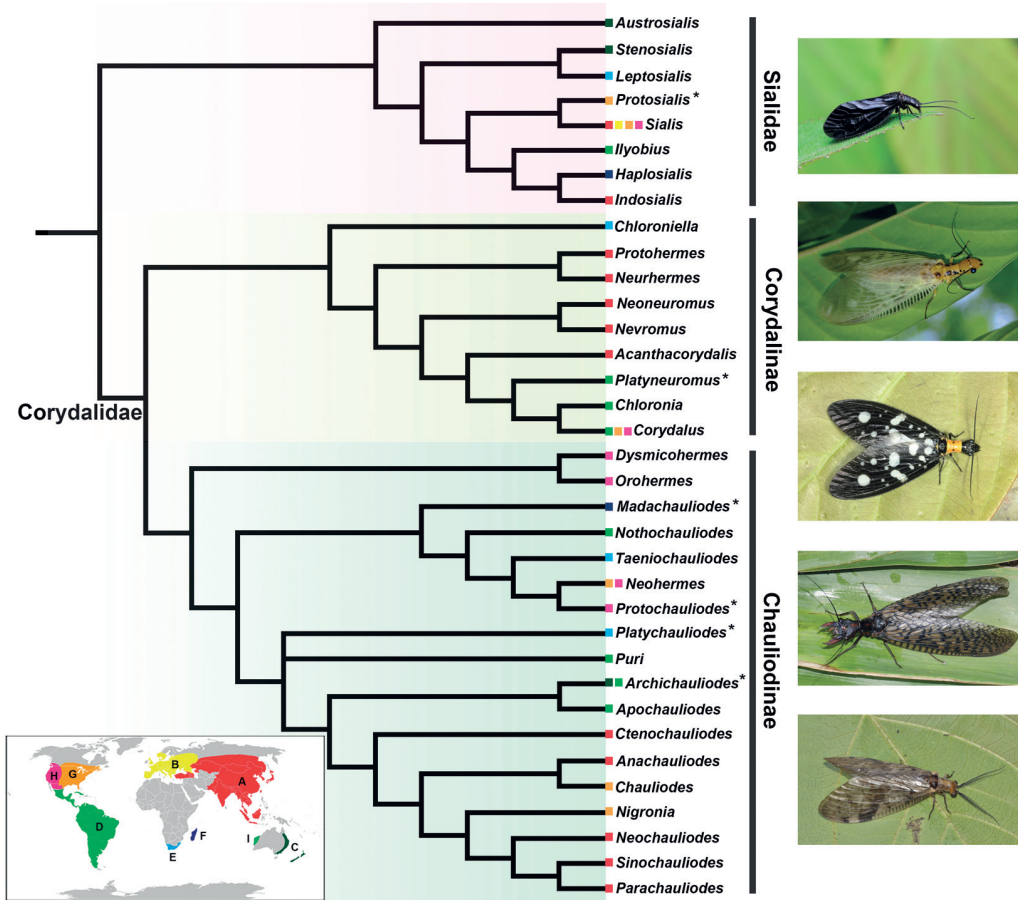

Figure 1. Phylogenetic relationships within Megaloptera: summarizing tree combining previous studies. Topology of Sialidae follows Lɪᴜ et al. (2015a), topology of Corydalidae follows Lɪᴜ et al. (2015c), and topology of Chauliodinae follows Lɪᴜ et al. (2012) except for *Puri* with unresolved position. Geographical distribution of each genus is indicated by color square, which is linked to the global distribution map of Megaloptera: red (A), Asia; yellow (B), Europe; dark green (C), eastern Australia and New Zealand; pale green (D), Central and South America; blue (E), South Africa; dark blue (F), Madagascar; orange (G), eastern North America; pink (H), western North America; green (I), western Australia. Genus lacking any phylogenetic analysis on interspecific relationships is marked by an asterisk. Photos of living megalopterans: a – *Sialis jiyuni* Liu, Hayashi & Yang, 2015. Photo by Yun Ji; b – *Protohermes arunachalensis* Ghosh, 1991. Photo by Zhiliang Wang; c – *Neurhermes selysi* (van der Weele, 1909). Photo by Ross Piper; d – *Acanthacorydalis fruhstorferi* van der Weele, 1907. Photo by Feiyang Liang; e – *Neochauliodes fraternus* (McLachlan, 1869). Photo by Xingyue Liu

Higher-level phylogeny of Megaloptera

Due to morphological conservatism and consequent difficulties in identifying specific morphological apomorphies for the order in a phylogenetic context, the monophyly and higher phylogeny of Megaloptera have remained controversial. The monophyly of Megaloptera is supported in some morphology-based phylogenetic studies (Achtelig & Kristensen 1973; Aspöck et al. 2001; Aspöck & Aspöck 2008; Beutel & Friedrich 2008) by the larval head characters (*i.e.*, the presence of a special sensillum on the antepenultimate antennomere, a vestigial salivary duct, and a vertico-pharyngeal muscle with several subcomponents), by the presence of lateral tracheal gills in larval abdomen, and by the male genital characters (*i.e.*, the position of the male gonocoxite 9 close to the base of tergum 9, and the presence of eversible sacks of the male gonocoxites 11). However, a paraphyletic Megaloptera (*i.e.*, Sialidae as sister to Raphidioptera) had been proposed repeatedly based on the proximal fusion of fore wing MP and CuA veins and shared specialization of telotrophic ovarioles (Hennig 1953; Büning 1979; Afzelius & Dallai 1988; Štys & Biliński 1990). Besides, a molecular phylogenetic analysis based on four gene fragments (nuclear genes: CAD, 18S rRNA; mitochondrial genes: COI, 16S rRNA) did not recover a monophyletic Megaloptera (Winterton et al. 2010).

Traditional classifications place Megaloptera and Raphidioptera as sister groups (Hennig 1969), and in earlier studies Raphidioptera was even considered to be a family within Megaloptera (van der Weele 1910). The sister-group relationship between Megaloptera and Raphidioptera was also recovered in a recent comprehensive morphology-based study (Beutel et al. 2010) as well as in a molecular study (Wiegmann et al. 2009). In contrast, with a broader sampling of Neuropterida, Aspöck et al. (2001) first proposed a sister-group relationship between Megaloptera and Neuroptera, which was also subsequently supported by both morphological and molecular evidence (Kjer et al. 2006; Aspöck & Aspöck 2008; Cameron et al. 2009).

Owing to the recent progress of phylogenomics, with considerable increase of the genome-scale data of insects, we are getting close to resolving the above questions on the higher-level phylogeny of Megaloptera. In two phylogenomic studies of Neuropterida, respectively based on mitochondrial genome data and anchored hybrid enrichment data and both with comprehensive sampling, corroborated the monophyly of Megaloptera and recovered the sister-group relationship between Megaloptera and Neuroptera (Wang et al. 2017; Winterton et al. 2018). Moreover, in the milestone study on insect phylogeny based on transcriptome data, Megaloptera was also recovered to be the sister-group of Neuroptera (Misof et al. 2014). These recent studies (Wang et al. 2017; Winterton et al. 2018) suggested that the aquatic larval life-style of Megaloptera might either be a plesiomorphic condition in Neuropterida or have been independently evolved with respect to the aquatic Neuroptera (*i.e.*, Nevrorthidae and Sisyridae), but did not support the aquatic larval life-style as a synapomorphy of Megaloptera + Neuroptera, as proposed by Aspöck et al. (2001). The phylogenetic relationships among Corydalinae, Chauliodinae and Sialidae are also consistent in the above phylogenomic studies (Wang et al. 2017; Winterton et al. 2018), with Corydalinae + Chauliodinae as the sister-group of Sialidae.

It is encouraging that recent phylogenetic studies based on wing-base character data and genital character data also corroborate the above higher-level phylogeny of Megaloptera (Zhao et al. 2014; Liu et al. 2016). In particular, Liu et al. (2016) proposed a series of autapomorpies of Megaloptera as well as the three major groups of the order based on genital character data. The autapomorphies of Megaloptera are the absence of male gonapophyses 9, the absence of the male hypandrium internum, and the paired female ectoprocts (Liu et al. 2016). Three autapomorphies of Corydalidae were proposed in Liu et al. (2016), including the reduced male gonocoxites 9, the female tergum 8 not enclosing spiracles, and the absence of female gonapophyses 8. Autapomorphies supporting the monophyly of Corydalinae are the presence of the male callus cerci between tergum 9 and ectoprocts and the arcuate male gonocoxites 10. Autapomorphies supporting the monophyly of Chauliodinae are the male tergum 9 with truncate anterior margin and the external position of male gonocoxites 10 with specialized lateral arms. The monophyly of Sialidae is supported by the reduced or obsolete male gonocoxites 10, the sub-oval female gonocoxites 9, and the reduced female ectoprocts.

Phylogenetic relationships among genera of Megaloptera

The extant Megaloptera include 35 genera worldwide (8 genera of Sialidae and 27 genera of Corydalidae; Oswald & Machado 2018). In addition, there are five fossil genera of Sialidae and five fossil genera of Corydalidae (Liu et al. 2012a, 2015a; Jepson & Heads 2016). The extant genera of Megaloptera are largely different between major zoogeographical regions and show a disjunct distribution pattern.

Herman Willem van der Weele may have been the first researcher dealing with the relationships among the megalopteran genera, and in his monograph of world Megaloptera (van der Weele 1910) some genera are considered to be »primitive« in Corydalinae as well as in Chauliodinae, while some of them are considered »derived« based on a few morphological characters. These hypotheses were proposed before the development of application of strict cladistic methods, but can be regarded as a starting point for later phylogenetic studies.

Corydalinae

The subfamily Corydalinae is the first group of which the intergeneric phylogeny was studied by modern cladistic analysis: in Glorioso (1981), 70 characters were used to infer the intergeneric phylogeny after a comprehensive comparative morphological study. This analysis that was performed manually recovered three assemblages of genera, *i.e.*, the *Protohermes* assemblage (*Protohermes* + *Neurhermes*), the *Nevromus* assemblage (*Nevrormus* + *Neoneuromus*), and the *Corydalus* assemblage {*Acanthacorydalis* + [*Platyneuromus* + (*Chloronia* + *Corydalus*)]}, with the latter two assemblages as each other's sister-group. Penny (1993) added the South African endemic genus *Chloroniella* Esben-Petersen that was not included by Glorioso (1981) and reanalyzed the matrix with a computer program. This analysis resulted in a mostly consistent phylogeny with that recovered in Glorioso (1981) but assigned *Chloroniella* as

the sister-group of the lineage comprising the *Nevromus* and *Corydalus* assemblages. Contreras-Ramos (1998) performed a phylogenetic analysis including all dobsonfly genera by adding and revising characters, although he deemed this analysis to be a test for the monophyly of *Corydalus* Latreille. In this work *Chloroniella* was recovered to be the sister-group of the lineage including all the other dobsonfly genera and *Acanthacorydalis* van der Weele was assigned to be the sister-group of *Nevromus* + *Neoneuromus*, which is incongruent with the results of Glorioso (1981) and Penny (1993). Contreras-Ramos (2011) presented a phylogenetic review of Corydalinae with re-analyses of all previous matrices in Glorioso (1981), Penny (1993) and Contreras-Ramos (1998). The resulting phylogeny of the dobsonfly genera was largely consistent with that in Contreras-Ramos (1998) except *Platyneuromus* van der Weele, which was assigned to be the sister-group of *Corydalus*. Liu et al. (2015c) reconstructed the phylogeny of Corydalinae based on a combined dataset of 71 morphological characters and multi-loci (16S rRNA+COI+ND2) sequences to investigate the evolutionary pattern of the sexually selected traits of male dobsonflies. This phylogeny is generally congruent with the morphology-based phylogeny in Contreras-Ramos (1998). However, *Acanthacorydalis* was assigned as sister group to the *Corydalus* assemblage. Moreover, *Protohermes* van der Weele was recovered to be paraphyletic with *Neurhermes* Navás included.

Chauliodinae

Using the fore wing anal veins as the basis for a phylogenetic scheme, Munroe (1951) considered *Protochauliodes* van der Weele and *Neohermes* Banks being primitive or ancestral fishflies, while *Archichauliodes* van der Weele, *Chauliodes* Latreille, *Parachauliodes* van der Weele, *Neochauliodes* van der Weele and *Nigronia* Banks are derived genera. Evans (1972) in his doctoral thesis proposed a scheme of intergeneric relationships of the world Chauliodinae based mainly on wing venation supplemented by distributions, but lacking rigorous phylogenetic analysis. Notably, the phylogenetic position of *Dysmicohermes* + *Orohermes* as the sister-group of the other fishfly genera as well as the monophylum comprising all Asian genera plus *Archichauliodes*, *Platychauliodes* Esben-Petersen, *Chauliodes* and *Nigronia*, hypothesized in Evans (1972), were also recovered in recent phylogenetic analyses (see Liu et al. 2012a, 2016). Liu & Yang (2006a) first performed a phylogenetic analysis based on morphological characters to infer the relationships among the fishfly genera. A monophyletic group comprising all Asian fishfly genera and two eastern North American genera (*i.e.*, *Chauliodes* and *Nigronia*) was recovered in this study. However, the phylogenetic positions of the other fishfly genera were poorly resolved due to incomplete sampling. By adding more genera, Liu et al. (2012a) again reconstructed a morphology-based intergeneric phylogeny of Chauliodinae including all extant and fossil genera worldwide. The phylogeny shows that the extant fishfly genera respectively belong to three main clades, *i.e.*, the *Dysmicohermes* clade, the *Protochauliodes* clade, and the *Archichauliodes* clade. A group of genera, referred to as the *Protochauliodes* lineage, formed a monophylum based on the unique

fusion between stem of 1A and anterior branch of 2A in the fore wing. All Asian genera plus *Chauliodes* and *Nigronia* were also recovered to be monophyletic, supported by the pectinate or subserrate antennae.

By using ancestral area reconstruction, Liu et al. (2012a) fully discussed the historical biogeography of Chauliodinae. The result indicated a Pangaean distribution of fishflies before the Middle Jurassic and suggested the Gondwanan origin of most fishfly genera whose diversification might be affected by the subsequent breakup of Pangaea. It also demonstrated that the modern fauna of Asian fishflies is probably derived from Gondwanan ancestors, rather than directly descended from Mesozoic fossil genera from Asia.

Sialidae

The phylogeny of Sialidae was completely untreated for a long period. Nel et al. (2002) first attempted to reconstruct a phylogeny of the alderfly genera based on wing characters in order to reveal the systematic position of the Baltic amber genus *Eosialis* Nel et al. that was described in that study. Unfortunately, the wing character data is too limited to resolve the intergeneric phylogeny of Sialidae. Liu et al. (2015a) reconstructed the first phylogeny for Sialidae worldwide based on the most comprehensive sampling and broadest morphological data ever presented. Within extant Sialidae, *Austrosialis* Tillyard was recovered to be the sister-group of the monophylum including the remaining genera. The latter monophyletic group consists of three lineages, namely the *Stenosialis* lineage (*Leptosialis* + *Stenosialis*), the *Ilyobius* lineage [(*Haplosialis* + *Indosialis*) + *Ilyobius*], and the *Sialis* lineage (*Protosialis* + *Sialis*). According to the phylogenetic scheme of Sialidae, Liu et al. (2015a) clarified that *Ilyobius* Enderlein and *Protosialis* van der Weele are valid genera, while *Nipponosialis* Kuwayama was treated as a junior synonym of *Sialis* Latreille. The ancestral area reconstruction performed in Liu et al. (2015a) suggested a Pangaean distribution of ancestral alderflies and suggested that the deep divergence of several lineages might have also occurred before the breakup of the supercontinent Pangaea during the Jurassic and Cretaceous.

All of the aforementioned phylogenetic studies concern one of the three major groups of Megaloptera. Based on a comprehensive study of the homology of the genital sclerites, Liu et al. (2016) first reconstructed the intergeneric phylogenetic relationships including all extant genera of Megaloptera. The recovered relationships among dobsonfly genera are congruent with the result in Liu et al. (2015c). In Chauliodinae the monophyly of the *Dysmicohermes* clade, the *Protochauliodes* clade, and the *Archichauliodes* clade was respectively corroborated in Liu et al. (2016), and the sister-group relationship of the *Dysmicohermes* clade to the *Protochauliodes* clade + the *Archichauliodes* clade, as recovered in Liu et al. (2012a), was supported again. However, the Oriental endemic genus *Ctenochauliodes* van der Weele was grouped with *Archichauliodes* and *Platychauliodes* in the analysis using genital characters, and the phylogenetic position of the enigmatic genus *Puri* Cardoso-Costa, Azevedo & Ferreira-Jr, recently discovered from Brazil, remains unresolved. With respect to Sialidae, the sister-group relationship

of *Protosialis* + *Sialis*, as well as that of *Haplosialis* + *Indosialis*, are consistent with the morphology-based phylogeny of Sialidae (Liu et al. 2015a). Moreover, the monophyletic group including *Ilyobius*, *Protosialis*, *Sialis*, *Haplosialis* Navás and *Indosialis* Banks was also recovered in Liu et al. (2016), while the phylogenetic positions of the remaining genera, especially *Leptosialis* Esben-Petersen and *Stenosialis* Tillyard, were not resolved.

So far, the molecular phylogenetic studies focusing on the intergeneric phylogeny of Megaloptera are limited. Besides the phylogenetic analysis of Corydalinae based on multi-loci data (Liu et al. 2015c), there are a few works on mitochondrial phylogenomics of Corydalidae (Wang et al. 2014; Jiang et al. 2015, 2016; Yang et al. 2017). Considering Corydalinae, *Acanthacorydalis* was repeatedly recovered to be the sister group of the clade including the American dobsonfly genera but not the sister-group of *Neoneuromus* + *Nevromus*, and *Protohermes* was assigned to be the sister-group of the clade including *Neoneuromus* + *Nevromus*, *Acanthacorydalis*, and the American dobsonfly genera (Wang et al. 2014; Jiang et al. 2015, 2016). In Yang et al. (2017) the relationship among the three major clades of Chauliodinae was recovered as the *Dysmicohermes* clade + (the *Protochauliodes* clade + the *Archichauliodes* clade). These results corroborate the previous results from the morphological evidence (*e.g.*, Liu et al. 2012a, 2016). However, broader sampling is needed for further testing of the intergeneric phylogeny including all world genera of Megaloptera.

Although fossils of Megaloptera are scarce, revealing their phylogenetic positions is important for better understanding the evolutionary history of the order. However, it is usually difficult to clearly resolve this question because the morphological characters preserved in fossils are incomplete and thus provide limited information for phylogenetic reconstruction. Liu et al. (2012a) attempted a morphology-based phylogenetic analysis including fossil and extant genera of Chauliodinae and found that the hitherto oldest fishflies (*Jurochauliodes* Wang and *Eochauliodes* Liu et al.) have distant positions with *Eochauliodes* assigned to be in the crown group of the subfamily. Liu et al. (2015a) also investigated the phylogenetic positions of fossil genera of Sialidae following the method used in Liu et al. (2012a). Unfortunately, the resulted phylogeny including all fossil and extant alderfly genera is poorly resolved largely due to data deficiency. Nevertheless, Liu et al. (2015a) recovered a sister group relationship between the fossil genus *Sharasialis* Ponomarenko from the Upper Jurassic of Mongolia (Ponomarenko 2012) and the clade including all Cenozoic alderfly genera. The larva of *Sharasialis* has a pair of short lateral tracheal gills on the abdominal segment 8 (similar to Corydalidae), while all Cenozoic Sialidae lack the 8th pair of larval lateral tracheal gills. Accordingly, Liu et al. (2015a) established a new alderfly subfamily, namely Sharasialinae Liu, Hayashi & Yang. Besides Sharasialinae, there are other fossil megalopterans which are neither typical Sialidae nor Corydalidae. For example, the genus *Chauliosialis* Ponomarenko from the Upper Cretaceous of Russia lacks the lateral filaments of larval abdominal segments 7 and 8, while there is a pair of ventral prolegs that are similar to Corydalidae as well as a short and thick terminal appendage that is similar to Sialidae (Ponomarenko 1976). Jepson & Heads (2016) described two corydalid genera, *i.e.*, *Cratocorydalopsis* Jepson

& Heads and *Lithocorydalus* Jepson & Heads from the Lower Cretaceous of Brazil, both of which have fishfly-like wing venation but possess a very short and relatively wide pronotum that is similar to Sialidae. Therefore, the early divergence of Megaloptera appears to be much more complicated than could be expected in the light of findings of putative transitional lineages of Corydalidae and Sialidae.

Phylogeny of Megaloptera at species-level

Corydalinae

Of the nine dobsonfly genera, seven were subject to phylogenetic analyses, but mostly based solely on morphological data. The Neotropical genus *Chloronia* Banks was the first genus with the interspecific phylogeny studied (Penny & Flint 1982). Penny & Flint (1982) proposed the phylogenetic relationships among the ten species recorded at that time primarily based on male genital characters, *e.g.*, the shape of sternum 9, ectoprocts and gonostyli 10. However, no rigorous phylogenetic analysis was applied in this study, and no updated work has been presented with the subsequent discoveries of species in this genus (Contreras-Ramos 1995, 2000, 2002).

Contreras-Ramos (1998) performed a comprehensive phylogenetic analysis to infer the relationships among the 30 species of the American endemic genus *Corydalus* based on 120 morphological characters. By adding four species described in Contreras-Ramos (2002), Contreras-Ramos (2011) again reconstructed the interspecific phylogeny of *Corydalus* based on updated morphological data. Accordingly, 19 species are placed into five species-groups of *Corydalus*, namely, the *Corydalus arpi* group, the *Corydalus nubilus* group, the *Corydalus armatus* group, the *Corydalus cornutus* group, and the *Corydalus batesii* group. However, the topology received only moderate or low nodal supports, so the phylogenetic positions of some species were not resolved. The historical biogeography of *Corydalus* was also constructed in Contreras-Ramos (1998), in which *Corydalus* was considered to have originated during the Late Jurassic and subsequent speciation generally lasted from the Early Cretaceous to the early Miocene due to some geographical isolation (*e.g.*, the uplifting of the Andes) as well as land connection (*e.g.*, the connection between North and South America).

The remaining published studies on the interspecific phylogeny of Corydalinae are a series of works done by Xingyue Liu and colleagues on the Asian endemic dobsonflies. Liu et al. (2005) presented a phylogenetic review of the genus *Acanthacorydalis* (giant dobsonflies) from China, in which, however, the interspecific relationships were poorly resolved due to the limited number of morphological characters used. Yang & Liu (2010) revised the character matrix and added *Acanthacorydalis asiatica* in an updated analysis, which yielded a better resolved topology. Biogeography of *Acanthacorydalis* was also discussed based on the resulting phylogeny, but no clear pattern of speciation was found to correlate with their distributions.

Liu et al. (2012b) reconstructed an interspecific phylogeny of the genus *Nevromus* Rambur based on morphological data, resulting in two main clades within the genus,

i.e., the mainland clade (*Nevromus austroindicus*, *Nevromus aspoeck*, *Nevromus exterior*, and *Nevromus intimus*) and the insular clade (*Nevromus gloriosoi* and *Nevromus testaceus*). An Indian origin and a historically widespread distribution in southern Eurasia were proposed for *Nevromus*, while the deep divergence between the mainland and insular clades was postulated to have taken place during the separation of Sundaland from Eurasia (Liu et al. 2012b).

Concerning the genus *Neoneuromus* van der Weele, which is the sister-group of *Nevromus*, the interspecific phylogeny is difficult to infer based on morphological data, because the genitalia of *Neoneuromus* are conserved in morphology with very limited number of phylogenetically informative characters, and because the other diagnostic characters, *e.g.*, body coloration and wing patterns, are highly variable not only among species but also among conspecific individuals (Yang et al. 2018). Therefore, Yang et al. (2018) reconstructed the interspecific phylogeny of *Neoneuromus* based on multi-loci sequence data. The molecular data appears to be efficient to resolve the species delimitation and interspecific relationships of *Neoneuromus*, and five new species were found by using this method (Yang et al. 2018). The dated phylogeny with reconstructed ancestral areas indicates an initial divergence of *Neoneuromus* during the mid-Eocene and that a broad area including northeastern India and northern Indochina could be the center for early divergence of the genus (Yang et al. 2018).

The genus *Protohermes* is the most speciose group of Megaloptera. Currently, there are 76 species and the genus is divided into 13 species-groups that comprise most of these species (Yang & Liu 2010; Liu et al. 2013b). So far there is no study to infer the phylogenetic relationships among all species of *Protohermes*. Nevertheless, there are some works with phylogenetic analyses on the interspecific relationships within certain species-groups. Based on morphological data, these works inferred the interspecific phylogeny of the *Protohermes changninganus* group (Liu & Yang 2005), the *Protohermes costalis* group (Liu et al. 2007), the *Protohermes davidi* group (Liu & Yang 2006c; Liu et al. 2010a), the *Protohermes parcus* group (Liu et al. 2009), and the *Protohermes xanthodes* group (Liu et al. 2006). The aim of future works should be to reconstruct the relationships among these species-groups or even among all *Protohermes* species, which will be helpful for understanding the evolutionary pattern of their diverse wing patterns and genital sclerites as well as the historical biogeography.

The genus *Neurhermes* is one of the most impressive dobsonflies on account of striking coloration and patterns that probably imitate some diurnal toxic moths (Hayashi 1995). The systematic position of *Neurhermes* is probably within *Protohermes* (see Liu et al. 2015b), while no taxonomic treatment/change has been made. The phylogenetic relationship among the seven species of *Neurhermes* was reconstructed based on the morphological data in Liu et al. (2015b) and the historical biogeography of *Neurhermes* was also discussed. Origin and a historically widespread distribution in southern Eurasia at least during Eocene were proposed, and the speciation within the genus was suggested to be correlated with the Tertiary orogenic events after the collision between the Indian subcontinent and Eurasia (Liu et al. 2015b).

Chauliodinae

Without performing phylogenetic analyses, Evans (1972) proposed relationships among the fishfly species of *Dysmicohermes* Munroe, *Orohermes* Evans, *Neohermes* and *Protochauliodes* from the Pacific Coastal Region of the USA based on wing venation, male genital characters, larval habitats and distribution. Subsequently, most works on the interspecific phylogeny of fishflies were done by Xingyue Liu and colleagues. Most of these works refer to the Asian fishflies.

In the first morphology-based phylogenetic analysis of fishfly genera (Liu & Yang 2006a), the interspecific relationships of *Sinochauliodes* Liu & Yang, that was simultaneously described, were recovered. However, the result is very preliminary with limited characters to support the relationships. Furthermore, the generic status of *Sinochauliodes* with respect to *Parachauliodes* van der Weele is questioned based on our unpublished molecular data, and there are also some undescribed species of *Sinochauliodes*. Thus, the phylogeny of *Sinochauliodes* requires further analysis.

By using morphological data, Liu & Yang (2006b) also reconstructed the phylogenetic relationships among the species of *Ctenochauliodes*. Under a revised classification of *Ctenochauliodes*, Liu et al. (2011) re-analyzed the interspecific phylogeny of *Ctenochauliodes* based on morphological characters. The results between these two studies were mostly consistent. *Ctenochauliodes* splits into two main clades, each of which contains nearly a half of the species of the genus, supported by the shape of ectoproct and male gonocoxites 10.

The interspecific phylogeny of *Parachauliodes*, which mainly ranges along Taiwan, Japan, and Korea, was reconstructed based on morphological data by Liu et al. (2008). Two main clades within the genus were recovered, with one including *Parachauliodes asahinai* and *Parachauliodes continentalis* and another one including the remaining four species. By combining the phylogenetic scheme and distribution pattern, the dispersal track of *Parachauliodes* was considered leading from Taiwan via the Ryukyu Arc to the Japanese archipelago, and the speciation was thought to be correlated with the isolations of several islands in its distribution range (Liu et al. 2008).

Regarding *Neochauliodes*, the largest genus of Chauliodinae, the interspecific phylogeny is poorly known. The only published work (Liu et al. 2010b) refers to a species-group of *Neochauliodes*, viz. the *N. sundaicus* species-group with six species endemic to Indo-Malaysia. The morphology-based phylogeny of the *N. sundaicus* species-group suggested that the speciation of this group might be correlated to the formation of Borneo, Java, Sumatra and some other islands in the Cenozoic.

Yue et al. (2015) presented a phylogeny of *Anachauliodes* Kimmins based on the DNA sequence data from three mitochondrial genes. This work confirmed that the two known species of *Anachauliodes* are the same. Accordingly, a taxonomic revision of *Anachauliodes* was provided.

Liu et al. (2013) inferred the interspecific phylogeny of *Taeniochauliodes* Esben-Petersen, a genus endemic to South Africa, based on adult morphological data. This represents the only published phylogenetic analysis on the African Megaloptera. *Taenio-*

chauliodes natalensis was recovered to be the sister of the clade including the remaining species, which suggested an early vicariance event occurring between KwaZulu-Natal and western South Africa. Speciation of the remaining *Taeniochauliodes* species was hypothesized to be correlated with fragmentation of their forest habitats during the Plio-Pleistocene (Liu et al. 2013a).

With the surprising discovery of new species of the endemic North American genus *Neohermes*, Liu & Winterton (2016) performed a phylogenetic analysis using adult morphological data to recover the interspecific relationships of this genus. *Neohermes inexpectatus* was recovered as the sister to the remaining *Neohermes*, which splits into two clades, one including two species from western North America and the other including three species from eastern North America. The ancestral areas reconstruction suggested that the initial divergence within *Neohermes* might have taken place in western North America with a subsequent eastward dispersal, and the uplift of the Cordilleran System probably accounted for the divergence between the eastern and western *Neohermes* species (Liu & Winterton 2016).

The phylogeny of the Australian species of Chauliodinae is the most poorly known. The latest classification of Australian Chauliodinae was proposed by Theischinger (1999) based on adult and larval morphological characters. Following this classification, *Archichauliodes* and *Apochauliodes* Theischinger are closely related; *Archichauliodes* includes two subgenera; the subgenus *Riekochauliodes* splits into three species-groups, the *Archichauliodes* (*R.*) *guttiferus* group, the *Archichauliodes* (*R.*) *deceptor* group and the *Archichauliodes* (*R.*) *polypastus* group. However, no phylogenetic analysis has been made to test this classification. Baker & Theischinger (2004) attempted to use DNA sequence data for a test of the classification based on morphology, and they deemed that the morphological classification is concordant with the result from molecular data. Nevertheless, the sampling of this study was insufficient, with only three species of *Archichauliodes* and *Protochauliodes* included. It is notable that *Archichauliodes* and *Protochauliodes* are not endemic to the Australian region. Both genera comprise some species in South America, while there are some species of *Protochauliodes* distributed in western North America. The phylogenetic relationships among congeneric species from disjunct areas of different zoogeographical regions are of high interest and in need of resolution.

Sialidae

Among the eight extant genera of Sialidae, only four genera comprise three or more species, namely *Indosialis*, *Ilyobius*, *Protosialis*, and *Sialis*. Most studies have focused on the interspecific phylogeny of *Sialis*. In a taxonomic revision of the North American *Sialis*, Ross (1937) divided the genus into four species-groups, *i.e.*, the *S. californica* group, the *S. americana* group (currently regarded as genus *Protosialis*; see Liu et al. 2015a), the *S. infumata* group, and the *S. aequalis* group. This hypothesis is based on a few male genital characters but lacks a test of phylogenetic analysis. Evans (1972) followed the above classification and proposed an evolutionary scheme for the *Sialis*

species from the Pacific Coastal Region of USA based on geographical distribution. The first phylogenetic analysis on *Sialis* was made by Whiting (1994). This study provided a fine comparison of the male genital sclerites of *Sialis* and presented an interspecific phylogeny including all North American species based on a matrix with 35 morphological characters. The species-group division of Ross (1937) was largely corroborated by Whiting (1994), while the relationships among these species-groups were not recovered. In a comprehensive phylogenetic study on Sialidae based on morphological data (Liu et al. 2015a), the interspecific phylogeny of world *Sialis* was recovered. The Nearctic species, *Sialis americana* and *S. glabella*, were revised to be placed in *Protosialis*. The species previously placed in *Nipponosialis*, *i.e.*, *Sialis kumejimae*, *S. jezoensis*, and *S. kuwayamai*, were found to have diverged relatively earlier. All North American and European species as well as a few Asian species form the crown-group of *Sialis*, which is supported by the male mandible without additional distal tooth. This group splits into three main lineages, namely the *S. lutaria* lineage (monophyly supported by the lingulate male sternum 9), the *S. infumata* lineage (monophyly supported by the male ectoproct entirely sclerotized ventrally and the male gonocoxite 11 with rather elongate and arcuately curved median processes), and the *S. sinensis* lineage (monophyly supported by the transversely band-like male sternum 9), and the latter two lineages were recovered to be sister-groups. The three species-groups of the North American *Sialis* were also supported in Liu et al. (2015a), while four other species-groups were also proposed, *i.e.*, the *S. lutaria* group, the *S. longidens* group, the *S. sinensis* group, and the *S. melania* group. It is notable that the *Sialis* species respectively endemic to Asia, Europe, and North America do not form three monophyletic groups as hypothesized by Evans (1972). The sister-group relationship, *e.g.*, between the European *S. nigripes* and the North American *S. infumata* group, suggests faunal exchange of ancestral *Sialis* via intercontinental dispersal.

Considering the Neotropical genus *Ilyobius*, two species-groups were proposed based on the phylogenetic scheme of Liu et al. (2015a), namely the *Ilyobius chilensis* group and the *Ilyobius mexicana* group. However, the phylogenetic analysis of Liu et al. (2015a) did not include all known species of *Ilyobius*, particularly the fossil species recorded from Eocene Baltic amber. It would be of value to figure out the phylogenetic relationships between the extant *Ilyobius* and their fossil counterparts from the Northern Hemisphere.

The interspecific phylogeny within the Oriental endemic genus *Indosialis* was recovered in Liu et al. (2015a). *Indosialis bannaensis* and *I. indicus* are sisters, while *I. minora* is the sister of the former two species. However, the systematic position of the fossil *Indosialis* species is still unclear.

Conclusion

The aforementioned recent works considerably increased our knowledge on the phylogeny of Megaloptera at different taxonomic levels. Future works may focus on the following issues. First and most importantly, phylogenetic analyses based on molecular

data needs to be done for many groups of Megaloptera, which will provide an opportunity to critically test the previous results from the morphological data as well as the hypotheses concerning the historical biogeography. Second, exploration of more morphological characters for phylogenetic analysis is desirable using modern techniques of morphology, such as the micro-CT and 3D tomography. Last, as a group of aquatic insects that are sensitive to the quality of the freshwater environment, the population genetics of some widespread species of Megaloptera need more attention and will be valuable for our understanding on the global change and conservation of insect biodiversity.

Acknowledgements

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