

The morphological evolution of the Adephaga (Coleoptera)

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Abstract. The evolution of the coleopteran suborder Adephaga is discussed based on a robust phylogenetic background. Analyses of morphological characters yield results nearly identical to recent molecular phylogenies, with the highly specialized Gyrinidae placed as sister to the remaining families, which form two large, reciprocally monophyletic subunits, the aquatic Haliplidae + Dytiscoidea (Meruidae, Noteridae, Aspidytidae, Amphizoidae, Hygrobiidae, Dytiscidae) on one hand, and the terrestrial Geadephaga (Trachypachidae + Carabidae) on the other. The ancestral habitat of Adephaga, either terrestrial or aquatic, remains ambiguous. The former option would imply two or three independent invasions of aquatic habitats, with very different structural adaptations in larvae of Gyrinidae, Haliplidae and Dytiscoidea.

Introduction

Adephaga, the second largest suborder of the megadiverse Coleoptera, presently comprises >45 000 described species. The terrestrial Carabidae are one of the largest beetle families, comprising almost 90% of the extant adephagan diversity. By contrast, its equally terrestrial sister group, Trachypachidae, contains only two genera and six species. Eight out of 10 families of the suborder are aquatic, including hygropetric habitats. Four of them are taxa with a very low extant species diversity. The specific adaptations of the aquatic groups differ distinctly in the adults and strikingly in the immature stages (e.g. Larsén, 1966; Franciscolo, 1979; Ribera *et al.*, 2008; Balke & Hendrich, 2016; Beutel & Roughley, 2016; Dettner, 2016; Vondel, 2016). Whirligig beetles (Gyrinidae), the sister group of the remaining adephagan families according to some studies (e.g. Beutel & Roughley, 1988; Baca *et al.*, 2017a), have evolved highly specialized surface-swimming habits as adults, linked with numerous autapomorphic features (e.g. Larsén, 1966; Beutel, 1989a, 1989b; Beutel *et al.*, 2017, 2019a; Liu *et al.*, 2018).

Adephaga is traditionally a popular group among amateurs and researchers, with a large number of studies

dedicated to their taxonomy (examples for comprehensive studies are Sharp, 1882; Guignot, 1931–1933; Balfour-Browne & Balfour-Browne, 1940; Jeannel, 1941–1942; Brinck, 1955; Lindroth, 1961–1969; Franciscolo, 1979) and morphology. An outstanding contribution is the monograph on *Dytiscus marginalis* Linnaeus (Korschelt, 1923–1924), with a brilliant documentation of the anatomy of adults and immature stages, but also covering many other aspects. A comprehensive but often overlooked study on the thoracic locomotor apparatus of Gyrinidae was published by Larsén (1966), also providing rich data on the thoracic skeletomuscular apparatus of many other groups of beetles. Detailed studies on larval morphology were published by Noars (1956) and Jaboulet (1960). In the 1970s and following decades, a series of morphological studies emerged from G. Mickoleit's group at the institute of Zoology of the Universität Tübingen (e.g. Bils, 1976; Burmeister, 1976; Baehr, 1979; Ruhnau, 1985, 1986; Beutel, 1986a, 1986b; Belkaceme, 1991), explicitly aiming at phylogenetic reconstructions, by that time based on a traditional ('manual') Hennigian character evaluation. Since that time, the morphological knowledge of Adephaga has greatly increased, with studies dedicated to immature stages and adults (e.g. Beutel, 1989a,b, 1990a,b, 1991a,b, 1992a–e, 1993; Arndt, 1993; Alarie *et al.*, 1998, 2004, 2011; Miller, 2001; Beutel *et al.*, 2017, 2019).

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Roy A. Crowson, one of the most prominent coleopterists of the 20th century, postulated a terrestrial origin of Adephaga, and favoured a division into monophyletic Geadephaga and Hydradephaga in his review of ‘The phylogeny of Coleoptera’ (Crowson, 1960). He divided the latter group into three less advanced ‘lower’ types, i.e. Haliplidae, Amphizoidae and Hygrobiidae, and three ‘higher’ types with advanced swimming capacities, the families Gyrinidae, Noteridae and Dytiscidae. Crowson was aware of W. Hennig’s method of phylogenetic reconstruction (Hennig, 1950, 1966), but remained very sceptical (Crowson, 1991). His approach was based mainly on intuition and an encyclopaedic knowledge of Coleoptera. Hennigian evaluations of different morphological characters systems yielded different result. Characters of the ovipositor (Burmeister, 1976), larvae (Ruhnau, 1986) and prothorax (Baehr, 1979) suggested monophyletic Hydradephaga. Two clades [Gyrinidae + (Haliplidae + Noteridae)] + [Amphizoidae + (Hygrobiidae + Dytiscidae)] were proposed by Burmeister (1976) and Ruhnau (1986), whereas Baehr (1979) discussed a pattern Trachypachidae + (Gyrinidae + (Dytiscidae + (Amphizoidae + (Hygrobiidae + [Haliplidae + Noteridae])))). The discrepancies underline the difficulty of reconstructing the phylogeny based on single character systems. This also applies to Ward (1979), a study investigating metathoracic wing structures. An informal character evaluation suggested a pattern with monophyletic Hydradephaga ((Dytiscidae + Noteridae + Amphizoidae + Trachypachidae) + (Gyrinidae + Haliplidae + Hygrobiidae)) as sister group of Carabidae, including Rhysodinae and Cicindelinae as subordinate groups. Based on defensive components of the aquatic groups, Dettner (1979, 1987) emphasized the isolated position of Gyrinidae, which mainly produce sesquiterpenes. Hygrobiidae are characterized by α -hydrocarboxylic acids, which are unknown in the other groups. The other investigated groups, i.e. Haliplidae, Dytiscidae and Noteridae, almost exclusively produce aromatic substances, which are uncommon in Carabidae (Schildknecht *et al.*, 1968; Moore, 1979).

A sister-group relationship between Gyrinidae and the remaining adephagan families was suggested by Beutel & Roughley (1988) based on an informal evaluation of features of larvae and adults. The phylogenetic conclusions implied independent invasions of the aquatic environment, first by Gyrinidae, followed by Haliplidae, and then by an ancestor of Dytiscoidea, or alternatively by a common ancestor of the two latter groups (see also Beutel, 1995, 1997). The first formal cladistic parsimony analysis of morphological data was carried out by Beutel & Haas (1996), later followed by Beutel *et al.* (2006, 2013). The use of molecular data started in the late 1990s with analyses of 18S rRNA sequences (e.g. Maddison *et al.*, 1999; Shull *et al.*, 2001; Ribera *et al.*, 2002a; see also Tautz *et al.*, 2002). The size of the molecular datasets and taxon sampling increased rapidly (e.g. Balke *et al.*, 2005, 2008; López-López & Vogler, 2017; Zhang *et al.*, 2018; McKenna *et al.*, 2019). Baca *et al.* (2017a) analysed 305 ultra-conserved element loci for 18 representatives of all adephagan families except Aspidytidae, with a main focus on the aquatic groups.

Statements that the phylogeny of a large group is largely or completely clarified should always be taken with some

caution. However, in the case of some major groups of insects, this appears justified. The interordinal relationships of the entire Holometabola, for instance, seem to be very stable (Peters *et al.*, 2014). Largely congruent results were obtained with single protein-coding nuclear genes (Wiegmann *et al.*, 2009), morphology (Beutel *et al.*, 2011), genomes (Niehuis *et al.*, 2012) and transcriptomes (Peters *et al.*, 2014). Similarly, the relationships among families of Adephaga appear stable, with very similar results obtained with morphological (Beutel *et al.*, 2006, 2013) and molecular data (Baca *et al.*, 2017a; Vasilikopoulos *et al.*, 2019). This positive situation inspired us to carry out the present study, aiming at reconstructing the character evolution on the phenotypic level, based on a robust topology. We present the largest and most complete morphological character set ever compiled for Adephaga, based on previous (e.g. Beutel *et al.*, 2006) and newly acquired data. Based on the reconstructed character transformations, an evolutionary scenario for Adephaga is presented. Future research perspectives are discussed briefly.

Materials and methods

The results and interpretations in this contribution are, to a large extent, based on previous results (e.g. Beutel, 1986a,b, 1988, 1992a–e, 1993, 1997; Beutel & Roughley, 1987, 1988; Beutel *et al.*, 2006, 2013, 2019a). However, new semithin section series were prepared in the course of this study and specimens of many species were dissected (see details in the following sections).

List of examined species

Gyrinidae: *Heterogyrus milloti* Legros (adults, fixed in 97% ethanol, dissections, microtome sections); *Gyrinus argentinus* Steinheil [larva, formaldehyde-ethanol-acetic acid (FAE), dissections, microtome sections]; *Dineutus assimilis* Kirby (adults, FAE, microtome sections); *Orectogyrus* Regimbart sp. (adults, Duboscq-Brazil fixative, dissections); *Gyretes* Brullé sp. (adults, FAE, dissections, microtome sections).

Haliplidae: *Peltodytes caesus* (Duftschmid) (adults, FAE, dissections); *Brychius elevatus* (Panzer) (adults, FAE, microtome sections); *Haliplus (Liaphlus) laminatus* (Schaller) (adults, FAE, microtome sections); *Haliplus (Neohaliplus) lineatocollis* (Marshall) (adults, FAE, microtome sections).

Meruidae: *Meru phyllisae* Spangler & Steiner [larvae (poorly preserved, internal softparts decayed) and adults, 70% (?) ethanol, microtome sections].

Noteridae: *Notomicrus* Sharp sp. (adults, 70% ethanol, microtome sections), *Noterus laevis* Sturm (adults, FAE, microtome sections); *Hydrocanthus* Say sp. (adults, 70% ethanol, microtome sections); *Suphisellus bicolor* Say (70% adults, ethanol, microtome sections).

Aspidytidae: *Aspidytes niobe* Ribera, Beutel, Balke & Vogler (larvae and adults, 97% ethanol, microtome sections).

Hygrobiidae: *Hygrobia tarda* (Herbst) (adults and larvae, Duboscq-Brazil fixative, microtome sections).

Dytiscidae: *Batrachomatus daemeli* Sharp (larvae, ethanol, dissections); *Matus bicarinatus* (Say) (adults, ethanol, dissections); *Liopterus haemorrhoidalis* (Fabricius) (adults, FAE, microtome sections); *Hydrotrupes palpalis* Sharp (adults, FAE, microtome sections); *Agabus nebulosus* (Forster) (adults, FAE, dissections, microtome sections).

Trachypachidae: *Trachypachus holmbergi* Mannerheim (adults, FAE, microtome sections).

Carabidae: *Metrius contractus* Eschscholtz (adults, 70% ethanol, dissections); *Loricera pilicornis* (Fabricius) (adults, 75% ethanol, microtome sections) *Sphallomorpha uniformis* Baehr (adults, ethanol, dissections); *Brachinus* sp. (adult, FAE, microtome sections).

Leiodidae (outgroup): *Catops ventricosus* (Weise) (adults, 70% ethanol, microtome sections).

Additional information on the morphology of adults and immature stages was taken from the literature (e.g. Noars, 1956; Jaboulet, 1960; Larsén, 1966; Forsyth, 1968, 1969, 1972; Burmeister, 1976; Baehr, 1979; Belkaceme, 1986, 1991; Beutel, 1986a,b, 1988, 1989a,b, 1990a,b, 1991a,b, 1992a–e, 1993; Arndt, 1993; Alarie *et al.*, 2004, 2011; Alarie & Bilton, 2005; Beutel *et al.*, 2006, 2017, 2019a).

Microtome sectioning

Specimens were embedded in araldite CY 212® (Agar Scientific, Stansted, U.K.) and cut at 1 µm using a microtome HM 360 (Microm, Walldorf, Germany) equipped with a diamond knife. Sections were stained with toluidine blue and pyronin G (Waldeck GmbH and Co. KG/Division Chroma, Münster, Germany).

Parsimony analysis and analyses of character evolution

The data were entered in a matrix with WINCLADA (Nixon, 1999) and parsimony analyses were carried out with NONA (Goloboff, 1995) and TNT (Goloboff *et al.*, 2008). All characters had equal weight and were treated as unordered in the initial analyses. The *K* value was set as 3, 10 or 50 when the implied weighting option implied in TNT was used. Bremer support values (Bremer, 1988) were calculated with NONA. The character evolution with enforced topologies was reconstructed with MESQUITE (Maddison & Maddison, 2018) (stored tree, trace character history, parsimony ancestral states).

Results

The analyses of the morphological dataset with NONA (Goloboff, 1995) yielded 120 minimum length trees with 477 steps (Ci: 0.53, Ri: 0.85) (Fig. 1: strict consensus). Only 22 were obtained with TNT, and only one tree after applying the implied weighting option. The different *K*-values only affected the pattern within Dytiscidae, but *Liopterus* was always placed as sister to the other three included genera.

As in earlier studies based on morphology (e.g. Beutel & Roughley, 1988; Beutel *et al.*, 2006, 2013), Gyrinidae were placed as sister to all other families. Haliplidae + Dytiscoidea were placed as sister group of Geadephaga, with Trachypachidae as sister to a monophyletic Carabidae. Within Dytiscoidea, Meruidae + Noteridae form the sister group of a clade ((Aspidytidae + Amphizoidae) + (Hygrobiidae + Dytiscidae)). The internal topology of Gyrinidae is congruent with the phylogeny in Beutel *et al.* (2019a), and that of Noteridae is in agreement with Beutel & Roughley (1987), Belkaceme (1991) and Beutel *et al.* (2006), but differs in several points from a recent molecular study (Baca *et al.*, 2017b). The topology of Dytiscoidea also differs from Vasilikopoulos *et al.* (2019). These incongruences are discussed in the next section.

Discussion

The origin of Adephaga

The earliest undisputed fossils of Adephaga are from the Triassic (Ponomarenko, 1977), but an origin in the Permian is likely (Gustafson *et al.*, 2017). Possible early representatives of Gyrinidae from this period are the larva of *Permosialis* Sharov [Sharov, 1953 (originally interpreted as megalopteran larva); see Achtelig, 1981; Beutel & Roughley, 1988] and an adult of *Tunguskagyryus* Yan, Lawrence & Beutel (Yan *et al.*, 2018). Both were recently ascribed to an archostematan assemblage Schizophoroidea (Kirejtshuk & Prokin, 2018; Prokin *et al.*, 2019). However, this group was revealed as polyphyletic by Beutel *et al.* (2019b) and the taxonomic shift of *Tunguskagyryus* was rejected in the same study.

According to recent analyses of large molecular datasets, Adephaga are probably the sister group of a clade comprising the two small beetle suborders, Archostemata and Myxophaga (Misof *et al.*, 2014; McKenna *et al.*, 2015; Che *et al.*, 2017; Zhang *et al.*, 2018; McKenna *et al.*, 2019), which are associated with wood or with riparian or hygropetric habitats, respectively. Presently, the lifestyle of the last common ancestor of Adephaga is still equivocal. A preference for riparian habitats has been suggested (e.g. Crowson, 1981; Beutel, 1997), with pygidial glands [character state (char.) 106.1] possibly representing a defensive mechanism against microorganisms and fungi (Dettner, 1987), and also predaceous vertebrates. However, an aquatic origin cannot be ruled out, considering the position of Gyrinidae as sister to the remaining families (e.g. Beutel & Roughley, 1988; Beutel *et al.*, 2006, 2013; Baca *et al.*, 2017a). A single switch to aquatic habits achieved by a common ancestor of all adephagan groups and a secondary switch to terrestrial habits by Geadephaga (= Caraboidea) is as parsimonious as two independent invasions of the aquatic environments achieved by Gyrinidae and a common ancestor of Haliplidae + Dytiscoidea. The former option is tentatively supported by distinctly different adaptations of the aquatic larvae, especially very different breathing organs [characters (chars) 165–167] (e.g. Seeger, 1971a, 1971b; Bertrand, 1972; Beutel, 1997).

A profound transformation linked with the earliest evolution of Adephaga was certainly the switch to predaceous feeding

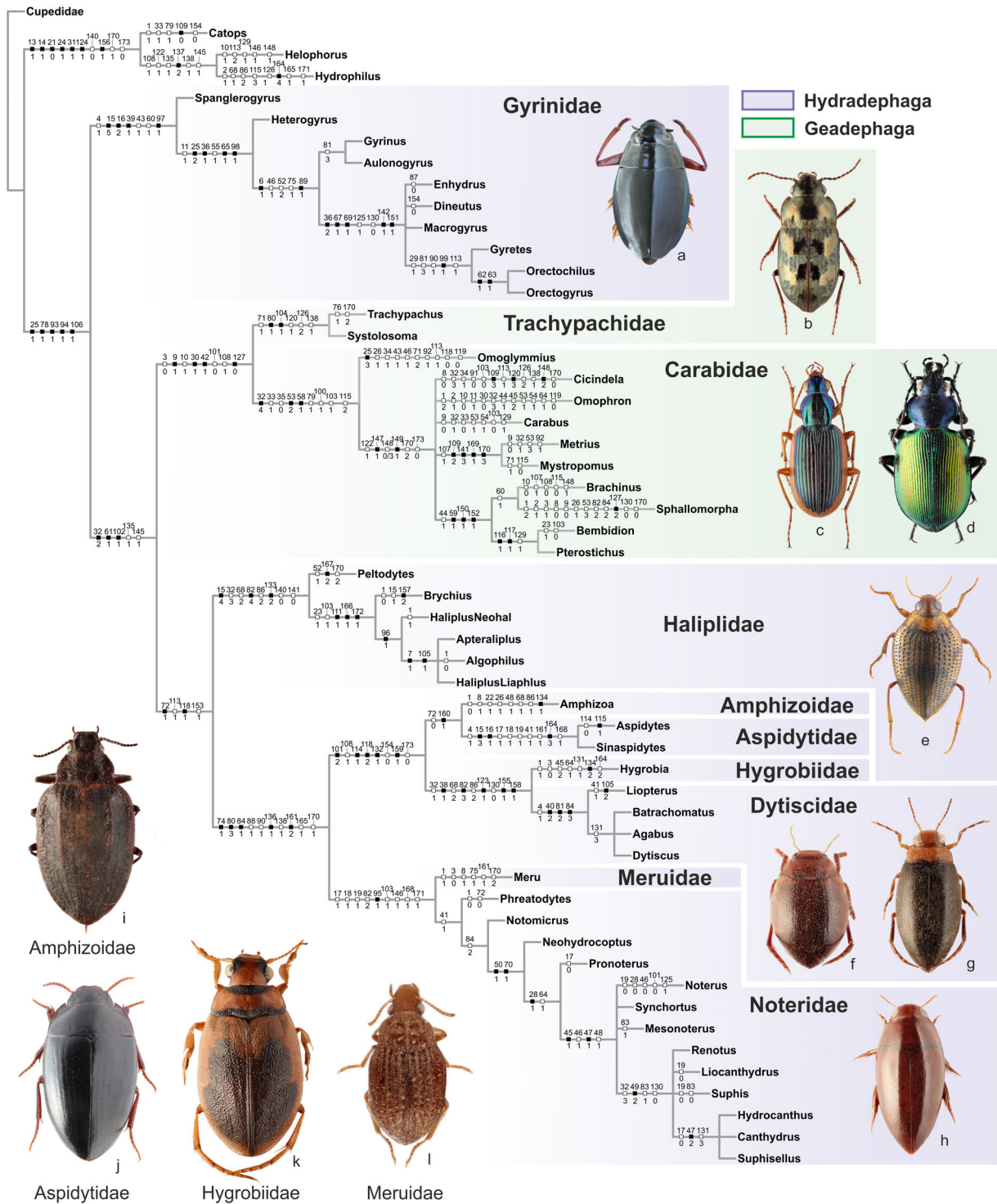


Fig. 1. Maximum parsimony analysis of the Adephaga dataset, strict consensus tree (NONA), without reweighting. Colour shading indicates aquatic (blue) and terrestrial (green) clades. Habitus photos: (a) *Dineutus indus* (Fabricius); (b) *Systolosoma breve* Solier; (c) *Chlaenius denticulatus* Dejean; (d) *Calosoma sycophanta* (L.); (e) *Haliplus regimbarti* Zaitzev; (f) *Hyphidrus ovatus* (L.); (g) *Derovatellus lentus* (Wehnke); (h) *Hydrocanthus waterhousei* Blackburn; (i) *Amphizoa lecontei* Matthews; (j) *Chinaspidytes wrasei* (Balke, Ribera & Beutel); (k) *Hygrobia tarda* (Herbst); (l) *Meru phyllisae* (Spangler & Steiner). For characters and character states, see text and Files S1, S2. [Colour figure can be viewed at wileyonlinelibrary.com].

habits. Feeding on soft materials or fine particles is very likely ancestral for Coleoptera s.s., with a complex feeding apparatus with mandibular molae and epipharyngeal and hypopharyngeal longitudinal processes with microtrichia in Myxophaga and different lineages of Polyphaga, especially Scirtoidea and Staphyliniformia (Anton *et al.*, 2016; Antunes-Carvalho *et al.*, 2017; Yavorskaya *et al.*, 2017, 2018). Adults of Adepnaga lack mandibular molae, and also the epi- and hypopharyngeal components (chars 13.1, 14.1, 21.1) of this ancestral feeding apparatus (e.g. Beutel, 1986a; Belkaceme, 1991; Dressler & Beutel, 2010; Beutel *et al.*, 2017). Likewise, the larvae are characterized by a feeding apparatus suitable for a carnivorous diet, with a clear tendency towards advanced liquid feeding, with mandibular sucking channels (char. 131.3) evolving four times independently in the aquatic groups [Gyrinidae, Haliplidae, Noteridae partim, Dytiscidae (with exceptions)] and once in Carabidae (*Graphipterus* Latreille; Brandmayr *et al.*, 1993).

Gyrinidae as sister to remaining Adepnaga

The phylogenetic split between Gyrinidae and the remaining families of Adepnaga (Fig. 1) was postulated by Beutel & Roughley (1988) for the first time, and since then was confirmed by numerical analyses of morphological characters (e.g. Beutel & Haas, 2000; Beutel *et al.*, 2006, 2013) and also recent phylogenomic studies (Baca *et al.*, 2017a; McKenna *et al.*, 2019). The monophyly of the aquatic families ('Hydradepnaga') was recovered only with analyses of the nuclear ribosomal and mitochondrial genes (Shull *et al.*, 2001; Hunt *et al.*, 2007; López-López & Vogler, 2017).

Character transformations in both the adult and larval stages are linked with the first split in Adepnaga. An apomorphic groundplan feature of Adepnaga excluding Gyrinidae is an elongated prosternal process articulating with a hexagonal groove of the strongly shortened mesoventrite (chars 32.1, 53.1) (Beutel, 1986a, 1992a). Anterior procoxal rests of the mesoventrite are present (char. 54.1) and the discrimen of this sclerite is absent (char. 55.1). The presence of metacoxal plates is a derived feature of the metathorax of Adepnaga excluding Gyrinidae (char. 82.1–4). Another complex apomorphy is the rotation of the aedeagus in the resting position (90°) and copulation (180°) (char. 102.1) (e.g. Jeannel & Paulian, 1944; Hieke, 1966; Beutel & Roughley, 1988). The ancestral mode in Adepnaga and Coleoptera (Crowson, 1981) is preserved in Gyrinidae, bending the tip of the abdomen downward and forward without torsion (Hatch, 1927; Ochs, 1969).

In the larval stages, the most important changes are linked with the maxillae. The maxillary grooves are largely or completely reduced (char. 133.1–3), resulting in increased degrees of freedom at the maxillary base in Dytiscoidea and Geadepnaga, with the maxillae acting like accessory antennae rather than grasping organs or structures involved in handling food particles in the preoral space. The lacinia is long, hook-shaped and movable in Gyrinidae (char. 139.0), with a typical *M. craniolacinalis* attached to the base by a tendon (char. 145.0). By contrast, it is

immobilized and usually shortened in the remaining groups. The long hook-shaped laciniae of larval Metriinae and Omophroninae (Beutel, 1991b, 1992c) are fixed and *M. craniolacinalis* is always transformed in a muscle attached to the dorsal stipital base (e.g. Beutel, 1991a, 1993). The palp is moved by two muscles in Gyrinidae (Noars, 1956; Beutel, 1993; Beutel & Roughley, 1993), but only one is present in the other groups (char. 143.1) (Beutel, 1991a,b, 1992b–e, 1993). A plesiomorphic character of the gyrinid egg is the presence of a distinctly sculptured honeycomb-like chorion, as it is also present in Archostemata (Saxod, 1964; Hinton, 1981). The chorion is very thin and lacking a recognizable surface sculpture (char. 174.1) in the other groups as far as is known (Hinton, 1981). The distinctly sculptured eggs of certain specialized representatives of Paussinae (Kaupp *et al.*, 2000) are probably due to an evolutionary reversal, considering the subordinate placement of this group in Carabidae.

Gyrinidae

Adults of Gyrinidae are highly adapted to a unique way of life in the surface film, with the dorsal side emergent and the middle and hind legs striking in the water and propelling them forward (Nachtigall, 1960; Larsén, 1966). They prey on arthropods caught in the surface film (e.g. Omer-Cooper, 1934: 'a world of the dead and the dying'), and dive when disturbed. A long list of adaptations and evolutionary novelties includes completely subdivided compound eyes (chars 5.1–2, 6.0–1) (e.g. Hatch, 1925, 1927; Honomichl, 1975; Beutel, 1989a; Beutel *et al.*, 2017), highly modified antennae (chars 15.5, 16.2) suitable to perceive slight disturbances of the surface film (Bendele, 1986), elongate grasping forelegs (char. 39.1) (e.g. Hatch, 1927; Beutel, 1990a), a unique prothoracic proprioceptive organ (char. 37.1–2), an extensive and flat mesoventrite (char. 53.4) (Larsén, 1966; Beutel, 1990a; Beutel *et al.*, 2019a), swimming middle and hind legs, and exposed gonocoxosterna (char. 97.1) (Burmeister, 1976, 1990; Beutel & Roughley, 1998).

Within Gyrinidae a sister-group relationship between *Spanglerogyrus albiventris* Folkerts (Folkerts, 1979) and the remaining genera (Fig. 1) is well supported by adult features of the head (Beutel, 1989a), thorax (Beutel, 1989b, 1990a) and abdomen (Burmeister, 1990). The upper and lower subunits of the compound eyes are separated by a relatively broad chitinous bridge, three rows of labral setae are present (char. 11.1), the palpigers are at least partly fused with the prementum (chars 27.1–2), the ventral procoxal joint is absent (char. 40.0), the procoxae are more or less triangular, the proprioceptive organ of the posterior side of the prothorax is formed by specialized sensilla (char. 37.2), excavations for the prolegs are present on the pronotal hypomeron and the elytral epipleura (char. 51.1), the metathoracic transverse ridge is absent (char. 71.2), and the primarily paired gonocoxosterna VIII are fused and form an undivided plate-like structure resembling a sternite VIII (char. 98.1). The most conspicuous and arguably most important character transformation in the common ancestor of *Heterogyrus milotti* Legros

and Gyrininae was the transformation of the middle and hind legs into short and flattened paddle-like structures with unique fringes of swimming lamellae (Larsén, 1966; Beutel, 1990a). According to detailed experimental investigations of Nachtigall (1961), this is the most efficient swimming apparatus in the entire animal kingdom.

The sister-group relationship between *Heterogyrus* and Gyrininae is also well established by apomorphies of different body regions. The upper unit of the compound eye of Gyrininae is reduced in size and shifted onto the dorsal side of the head (char. 6.1), the antennae entirely lack short setae, the palpigers are firmly fused with the prementum (char. 27.2), the galea is one-segmented (char. 22.1) (Beutel *et al.*, 2017), an opening between the mesanepisternum and the elytral epipleuron is present (char. 52.1), and the lateral metafurcal arms and the lateral component of *M. furcatrochanteralis* are reduced (char. 75.1) (Beutel *et al.*, 2019a).

Within Gyrininae, the tribe Gyrinini is placed as sister to the remaining genera, i.e. Dineutini and Orectochilini, in agreement with molecular data (Gustafson *et al.*, 2017). Dineutini are characterized by a tendency towards a larger and more flattened body. Their monophyly is not well supported. Orectochilini are arguably the most 'derived group of Gyrininae', with a row of setae on the elongated fused gonocoxosterna as a steering organ (char. 99.1), and a strongly simplified pterothoracic muscle system (Liu *et al.*, 2018), despite a functional flight apparatus.

Aside from an entire series of apomorphies linked with aquatic habits, larvae of Gyrinidae have preserved a number of plesiomorphies, especially of the maxillae. A relatively deep maxillary groove is preserved (char. 133.0), and in contrast to the other families the range of motion of the maxilla is therefore largely restricted to lateral movements. The lacinia is well developed, and hook-shaped, in contrast to all other families of Adephega movable by a typical *M. craniolacinalis* (*M.* 19) attached to its base with a thin tendon (chars 139.0, 145.0). In contrast to the larvae of the remaining families, two antagonistic muscles of the maxillary palp are present (char. 143.0) (Noars, 1956; Beutel, 1993). The larvae of *Spanglerogyrus* and *Heterogyrus* remain unknown, and the larval groundplan is therefore unclarified. Apomorphies of the known immature stages are the completely cleft prementum (char. 146.2), lateral abdominal gills (char. 167.1), which allow the larvae to stay at greater depths than most larvae of Dytiscidae (abdominal gills occur in *Coptotomus* Say), and terminal hooks on the pygopodium (char. 163.1) formed by abdominal segment X, probably providing anchorage in the substrate, as in larvae of Hydraenidae (Staphylinoidea), Trichoptera, Osmylidae (Neuroptera) and Chauliodinae (Megaloptera). Mandibular sucking channels are present in all known larvae of Gyrininae (Beutel & Roughley, 1993), relatively short in Gyrinini but elongated and with tightly connected mesal edges in Dineutini and Orectochilini (char. 131.3). A clade comprising both tribes is supported by several evolutionary novelties of larvae, a unique prepharyngeal filter apparatus formed by longitudinal lamellae (char. 151.1), and very slender antennae and maxillary palps (chars 124.1, 142.1).

Haliplidae

The phylogenetic placement of Haliplidae, a specialized and unusual group of Adephega, was controversial for a long time. The family was placed in a supposedly monophyletic group with Noteridae by Burmeister (1976) based on characters of the ovipositor, by Ruhnau (1986) using characters of larvae, and by Hunt *et al.* (2007) based on analyses of molecular data. A traditional Hennigian character evaluation was used in both morphological studies. A placement as second branch after Gyrinidae was suggested by Beutel & Roughley (1988) and Beutel (1993, 1997), implying a third independent invasion of the aquatic environment (assuming a terrestrial origin of Adephega). Currently, a sister-group relationship with Dytiscoidea (Fig. 1) is supported by cladistic analyses of large morphological datasets (Beutel *et al.*, 2006, 2013) as well as molecular data (McKenna *et al.*, 2015, 2019; Baca *et al.*, 2017a). This implies that maxillae inserted at the anteroventral margin of the head capsule and movable in all directions (char. 143.4) evolved independently in Dytiscoidea and Geadephega, respectively. Aquatic habits and immobilized metacoxae fused with the metaventre are potential synapomorphies of Haliplidae and Dytiscoidea. However, in contrast to the latter, adult haliplids have separate mesal metacoxal walls, a metafurca originating from the katepisternum, and a full set of furca-coxal muscles (chars 74.0, 80.0, 88.1, 90.1) (Belkaceme, 1986; Beutel & Belkaceme, 1986).

Haliplidae are characterized by numerous autapomorphies, mostly linked with their aquatic lifestyle. Adults use algae as a food source but also feed on aquatic animals (e.g. hydrozoans) (Seeger, 1971a). The larvae, which feed exclusively on Characeae or filamentous algae, have completely abandoned predacious habits in contrast to the other groups of Adephega (Seeger, 1971a). Their advanced mandibular sucking channels (char. 131.3) (Beutel, 1986b) allow them to suck the contents of single cells (Seeger, 1971a, 1971b). Specialized maxillary endite lobes (char. 139.4) have evolved in correlation with algophagous habits (Jaboulet, 1960; Seeger, 1971b; Beutel, 1986b), a prementum with short palps as a guiding device for filamentous algae, and clasping mechanisms of the legs, interestingly formed by different elements in *Pelodytes* Régimbart and *Haliphus* Latreille on the one hand, and species of *Brychius* Thomson on the other (char. 157.1, 2).

The legs of adults are adapted for swimming, slender and not flattened but with well-developed fringes of swimming hairs on all three pairs. The broadened and apically truncated prosternal process (char. 32.3) forms a specialized articulation with the mesoventrite and is adjacent with the anteromedian process of the metaventre posteriorly (e.g. Baehr, 1979). A conspicuous apomorphy of the family is seen in the greatly enlarged metacoxal plates, which cover a large part of the metafemora and abdominal ventrites (char. 82.4). The large duplicatures form an additional storage area for air connected with the subelytral space (Belkaceme, 1986). The function of this accessory breathing apparatus was described in detail by Beier (1929).

Within Haliplidae, a sister-group relationship between *Pelodytes* and the remaining genera (Fig. 1) is well established

(Beutel & Ruhnau, 1990; Baca *et al.*, 2017a; Vondel, 2019), including recently with an evaluation of the morphology of the pygidial glands (Dettner, 2019). *Peltodytes* displays autapomorphies such as a narrowed epistome and metacoxal plates which cover the abdominal venter almost completely.

The elongated filament-like dorsal gills of larvae (char. 167.2) (Jaboulet, 1960) are probably a groundplan feature of the family. Haliplidae excluding *Peltodytes* are characterized by a unique type of larval microtracheal gills (char. 166.1) (Jaboulet, 1960; Seeger, 1971b) and a subulate apical maxillary palpomere (Beutel & Ruhnau, 1990). The genera *Algophilus* Zimmermann and *Apteraliplus* Chandler were erected based on autapomorphies (Zimmermann, 1924; Chandler, 1943), a narrow parallel-sided prothorax in the former and reduced flight organs in the latter. As they are both closely related to and possibly subordinated within the subgenus *Liaphlus* Guignot of *Haliplus* (Beutel & Ruhnau, 1990), their generic status is not justified (Vondel, 2019; see also Komarek & Beutel, 2007). A shared derived feature of the *Algophilus*–*Apteraliplus*–*Liaphlus* complex is the presence of a digitiform appendage on one of the parameres.

Dytiscoidea

Dytiscoidea are strongly supported as monophyletic (Fig. 1), with medially fused mesal metacoxal walls forming a large intercoxal septum, the metafurca originating from this structure, and the loss of the Mm. furcaxialis anterior and posterior (Mm. 81, 83) as adult apomorphies (chars 74.1, 80.3, 88.1, 90.1). These features are probably linked to the presence of strongly developed coxo-trochanteral muscles (e.g. Beutel, 1986a; Belkaceme, 1991), probably adaptations to aquatic habits. This suggests that good swimming abilities belong to the groundplan of this adephagan clade (e.g. Nachtigall, 1960; Ribera *et al.*, 1997). The transverse ridge of the metaventricle is still distinct in Hygrobiidae and Amphizoidae (Beutel, 1986a, 1988), but shortened and not reaching the lateral edge of the sclerite. It is vestigial in Aspidytidae and absent in the other groups (chars 71.1, 2).

Within the Dytiscoidea, a clade Noteridae + Meruidae is the sister group of the remaining families, the latter supported by long caudal tentorial arms and an entire series of bundles of M. tentoriopharyngalis posterior (M. 52) originating from this structure (chars 120.2, 153.1), the latter feature also occurring in Haliplidae (Beutel, 1986b). Larval mandibular sucking channels (char. 131.3) have evolved twice in Dytiscoidea, closed only over a short distance in the noterid genera *Canthydrus* Sharp and *Hydrocanthus*, but elongated and closed by a groove and spring mechanism in Dytiscidae except for Copelatini and *Hydrotrupes* Sharp (De Marzo, 1979; Beutel, 1993, 1994b).

Meruidae

The single tiny species *Meru phyllisae* Spangler & Steiner (0.85–1 mm) was already discovered in 1985, but only described 20 years later by Spangler & Steiner (2005). It is one of the smallest adephagan species and only known from

a single site in southern Venezuela, El Tobogán de la Selva, a ‘waterslide’ and specific type of hygropetric habitat. The larvae were discovered in 2007 and described by Alarie *et al.* (2011). Smaller adephagan species are otherwise only known in the Carabidae (see later).

Despite the aberrant adult morphology, obviously affected by miniaturization, the placement as sister to Noteridae is firmly established by morphological (Beutel *et al.*, 2006) and molecular data (Balke *et al.*, 2008; Baca *et al.*, 2017a). The adults show hardly any structural affinities with Noteridae, but rather resemble miniaturized and light brown Amphizoidae. However, the larvae described by Alarie *et al.* (2011) are strikingly similar to those of Noteridae, including *Phreatodytes* Uéno (Uéno, 1957).

Noteridae

Noteridae are a relatively small group, with c. 270 described species. The phylogenetic relationships were analysed based on morphological characters (Beutel & Roughley, 1987; Belkaceme, 1991; Beutel *et al.*, 2006) and molecular data (Miller, 2009; Baca *et al.*, 2017b). In contrast to morphology-based analyses (e.g. Beutel *et al.*, 2006), including the one presented here, Baca *et al.* (2017b) combined the cave-dwelling *Phreatodytes* with Notomicrini, and placed *Noterus* Clairville as sister to *Neohydrocoptus* Satô. The molecular analyses suggested that *Pronoterus* Sharp and *Mesonoterus* Sharp are nested within *Suphisellus* Crotch and *Hydrocanthus*, respectively (see later). Both genera were synonymized in Baca *et al.* (2017b).

The Japanese *Phreatodytes* contains seven specialized groundwater species (Beutel & Roughley, 1987; Belkaceme, 1991; Uéno, 1996) and is either placed as sister to all remaining Noteridae genera (Belkaceme, 1991; Beutel *et al.*, 2006) or combined with Notomicrini as sister to Noterinae (Kato *et al.*, 2010; Baca *et al.*, 2017b). Presumptive autapomorphies of the genus are the strongly expanded metacoxae, the complete reduction of the eyes, and very long setae on the dorsal surface (Uéno, 1957: figs 1, 2), the latter features probably linked to subterranean habits. The larvae (Uéno, 1957: figs 14–21), which also lack visual organs, are otherwise very similar to the known immature stages of other noterid genera (see Dettner, 2016).

The larval biology of Noteridae is not well known and larvae of only a few genera are described (Dettner, 2016). In the case of *Noterus*, it is known that the immatures live in the mud at the bottom of ponds among roots of water plants and breathe using the plant aerenchyma (Balfour-Browne & Balfour-Browne, 1940; Ruhnau, 1985; Dettner, 2016), which explains the difficulty in collecting them (Bertrand, 1972). Pupation of *Noterus* also takes place in mud within the water body, which is a rare (or unique) exception in the aquatic groups of Adephaga (Ruhnau, 1985).

Adult Noteridae (with the exception of *Phreatodytes*; see Uéno, 1957, 1996) are characterized by metacoxae with a distinct anterior angle. The lateral edges of the well-developed metacoxal plates converge anteriorly and their posterolateral angle is distinct (Beutel & Roughley, 1987). Within the family,

a flattened median part of the metaventrite evolved, forming the ‘noterid platform’, together with the flat middle part of the hind coxa (Belkaceme, 1991: figs 67–69). A conspicuous character transformation of the forelegs takes place in Noterinae, with an increasing specialization as a burrowing structure, culminating in a derived condition in *Hydrocanthus* and related genera (Beutel & Roughley, 1987; Belkaceme, 1991: figs 70, 71). The phylogenetic pattern suggested by Baca *et al.* (2017b) implies several reversals in *Pronoterus* (now synonymized with *Suphisellus*) and *Mesonoterus* (now synonymized with *Hydrocanthus*). This includes the loss of the pouch of protarsomere I and a secondarily rounded prosternal process in both genera, and in the case of *Pronoterus*, the secondary absence of a specialized protibial burrowing spur, the loss of the protibial row of flattened spines, the secondary presence of a distinct angle at the external distal protibial edge, a secondarily elongated inner protibial spur, and the secondary absence of an angle formed by the posterior edges of the metacoxal plates (see Belkaceme, 1991: figs 61–70). A constrained tree with the topology of Baca *et al.* (2017b) and our data requires 18 additional steps.

Amphizoidae

Amphizoidae comprise only five species, three in western North America and two in China (one of which also occurs in North Korea). The group occurs only in running water, especially in fast-flowing streams (‘trout stream beetles’) (e.g. Kavanaugh, 1986; Dettner, 2016). The superficially carabid-like adults are quite frequently found under stones out of the water (Kavanaugh, 1986). The onisciform larvae are probably close to the dytiscoid groundplan in their character combination. Interestingly they are very similar to the larvae of the Chinese *Chinaspidytes niobe* (see the following section on Aspidytidae).

Adult Amphizoidae have slender legs with very sparse fringes of swimming hairs (Beutel, 1988; Dettner, 2016). They usually live among masses of twigs and leaves caught in the current and float on the surface when dislodged. Autapomorphies of adults are the reduced submento-mental suture (char. 25.1) (e.g. Lawrence & Newton, 1982; Dressler & Beutel, 2010), the one-segmented galea (char. 21.1), and possibly an unusually small metafurca (Beutel, 1988). The latter feature is probably linked with the lost capacity of active swimming. The flight apparatus of *Amphizoa lecontei* Matthews is well developed. However, the tissue of the large indirect flight muscles was degenerated in all specimens examined by Beutel (1988).

Aspidytidae

Like Meruidae, Amphizoidae and Hygrobiidae, Aspidytidae are probably a relict family, in this case with only two species with a highly disjunct distribution, *Chinaspidytes wrasei* (Balke, Ribera & Beutel) in China (Shaanxi) and *Aspidytes niobe* Ribera, Beutel Balke, & Vogler in South Africa (Cape Province). The family was recovered as monophyletic here, in agreement with recent phylogenomic data (Vasilikopoulos *et al.*, 2019),

and in contrast to a molecular phylogeny based on a Sanger sequencing dataset (Toussaint *et al.*, 2016). Both species are streamlined as adults but have lost swimming adaptations such as fringes of swimming hairs, and have alternate movements of the hind legs (e.g. Ribera *et al.*, 2002b; Beutel *et al.*, 2016). Both species live in hygropetric habitats, *S. wrasei* on steep seepages where they can be found under mats of grass, or creeping around on the wet rock surface (Balke *et al.*, 2003; Michat *et al.*, 2014), and *A. niobe* on permanent water seepages flowing over exposed, near-vertical rocks almost without vegetation (Ribera *et al.*, 2002b). An interesting feature of the family is that the larvae of the two species differ distinctly in their habitus and various specific features. The larva of *A. niobe* resembles noterid larvae in its cephalic features, with the head capsule reaching the maximum width in the posterior third, a narrow and distinctly prominent nasale separated from the adnasalia by deep incisions, a short coronal suture, an obsolete ventral gular suture (ventral ecdysial line), and posterior tentorial grooves relatively widely separated and slightly shifted towards the posterior head margin. As in Noteridae, tergal extensions of the thoracic segments are narrow, and they are indistinct or missing on the abdominal segments. By contrast, the larvae of *S. wrasei* are strikingly similar to those of species of *Amphizoa* (Beutel, 1991a; Dettner, 2016), with the greatest width of the head in the middle region, a broad and very slightly convex anterior clypeolabral margin with 16 short sensilla (lamellae clypealis), a dense vestiture of medium length setae, posterior tentorial grooves located on the anterior third of the ventral head capsule, and a very distinct median gular suture (Michat *et al.*, 2014). The entire larval body of *S. wrasei* is onisciform, as in Amphizoidae, with well-sclerotized and laterally expanded tergites.

Hygrobiidae

Hygrobiidae are another small family with a disjunct distribution pattern (Hawlitshchek *et al.*, 2012), with one species in Europe and North Africa, four species in Australia, and one in southeastern China (Jiangxi) (e.g. Dettner, 2016). The species typically live in stagnant water with rich vegetation and soft substrate. One of many autapomorphies of the family (see Beutel, 1986a) is the presence of double burrowing spurs on the protibiae (Beutel, 1986a: fig. 26), elongate and flattened structures which allow them to burrow very efficiently in mud and silt in ponds or other water bodies. In contrast to earlier observations, the adults swim exceptionally well (Beutel, 1986a), with alternative strokes of the legs. The presence of dense fringes of unusually long swimming hairs on all three pairs of legs is an additional autapomorphy of the family.

As is usually the case in Adephaga, both larvae and adults of *Hygrobia* are predacious (e.g. Franciscolo, 1979; Dettner, 2016). They may occasionally feed on aquatic larvae of Sialidae (Megaloptera) or Chironomidae (Diptera), but a far-reaching specialization on tubificid oligochaet worms is a characteristic of the group. The feeding apparatus of adults displays an entire series of derived features, such as mandibles completely lacking hairs, a bilobed distal galeomere, a deeply excavated

dorsal surface of the prelabium, and an exceptionally strongly developed *M. verticopharyngalis* with an entire series of lateral bundles (Beutel, 1986a). Apomorphies of the thorax are the elongated conical pro- and mesocoxae, and large and cup-shaped profurcae (Beutel, 1986a). An additional unusual apomorphy of adults is the stridulatory organ, enabling the beetles to produce loud screeching noises ('squeak beetles'; e.g. Balfour-Browne, 1922). A stridulatory file on the ventral side of the elytra interacts with the edge of abdominal sternite VII (Beutel, 1986a).

As in the adults, the larvae also display many autapomorphic features (e.g. Alarie *et al.*, 2004), frequently related to the specialized feeding habits. The elongate, falcate mandibles lack a second cutting edge (char. 131.1). Galea and lacinia are completely absent (chars 138.1). The maxillary base is retracted into a pouch (char. 143.2) and the cardo is also missing. The epipharynx is equipped with unusual lip-like lobes and gland tissue. The pharyngeal musculature is similar to that of the adults, with very strongly developed series of dorsal, lateral and ventral dilators. As in Dytiscidae the brain is shifted into the anterior third of the head (char 155). The legs of the later instars bear rather dense fringes of swimming hairs (Alarie *et al.*, 2004). Paired gill tufts inserted on the thorax and abdomen are a unique breathing specialization in Adephega and an autapomorphy of the family (e.g. Beutel, 1995). The reduction of the large terminal spiracles (char. 161.0) is apparently linked to this evolutionary novelty.

The position of Hygrobiidae within Dytiscoidea is not fully clarified as yet (e.g. Vasilikopoulos *et al.*, 2019). The presence of prothoracic defensive glands (char. 38.1) and the partial reduction of the metacoxal plates (char. 82.3) are potential synapomorphies with Dytiscidae, while molecular data tentatively suggest a closer relationship of Hygrobiidae with Amphizoidae and Aspidytidae (Toussaint *et al.*, 2016; Vasilikopoulos *et al.*, 2019). Both studies yielded a sister-group relationship between Hygrobiidae and a clade including Amphizoidae + Dytiscidae. However, as Aspidytidae was not included in the phylogenomic analyses of Baca *et al.* (2017a), this result should be taken with some caution.

Dytiscidae

A comprehensive treatment of the phylogeny, classification and evolution of Dytiscidae was presented by Miller & Bergsten (2014, 2016) (see also Balke & Hendrich, 2016). Consequently, the group will be treated only briefly here. Diving beetles are the most successful aquatic group of Adephega in terms of diversity, with about 4300 described species worldwide (Balke & Hendrich, 2016). With a few exceptions (e.g. subterranean species), diving beetles are characterized by excellent swimming abilities (Nachtigall, 1960; Ribera & Nilsson, 1995; Ribera *et al.*, 1997), with dense fringes of swimming hairs on the middle and hind legs, the latter distinctly flattened and moved synchronously. The extensively fused and plate-like metacoxae (char. 80.2) are greatly extended anteriorly, thus greatly narrowing the metaventrite and creating space for strongly developed coxo-trochanteral

muscles (Bauer, 1910; Larsén, 1966). The body is, in most species, streamlined (char. 1.2), having a shortened and rounded head (char.2.1) with compound eyes completely integrated into the lateral cephalic margin (char. 4.1), and a completely reduced pronoto-elytral angle (with some exceptions, e.g. Bidessini; Balke & Hendrich, 2016). In contrast to the other aquatic families of Adephega, a few small lineages of terrestrial species evolved in Dytiscidae (e.g. *Hydrotrupes palpalis* Sharp, *Geodessus* Brancucci; Balke & Hendrich, 1996, 2016), as well as subterranean adaptations (e.g. Uéno, 1957; Leys *et al.*, 2003).

The monophyly of the family has never been seriously questioned. Autapomorphies of adults include enlarged prothoracic glands (char. 38.1) not covered by muscular tissue (Miller, 2001), the vestigial ventral procoxal joint (char. 40.2) (Baehr, 1979), the complete loss of the transverse ridge of the metaventrite (char. 71.2), and strongly expanded metacoxae with rounded anterior margin.

The phylogeny of the group appears largely resolved with molecular data (Miller & Bergsten, 2014, 2016). A sister-group relationship between Matinae and the remaining Dytiscidae appears well established, and also monophyletic Lancetinae, Copelatinae, Agabinae + Colymbetinae, Coptotominae, Dytiscinae (including or excluding Cybistrinae), Hydaticinae and Hydroporinae (Ribera *et al.*, 2008; Miller & Bergsten, 2014, 2016).

A major trend in the evolution of the large subfamily Hydroporinae is size reduction, with species generally less than 5 mm long. A characteristic apomorphy of hydroporine larvae is a long nasal projection, correlated with a modified axis of movement of the mandibles (e.g. Bertrand, 1972; De Marzo, 1979; De Marzo & Nilsson, 1986). An unusual feature is the reduction of the mandibular sucking channel in *Liopterus* Dejean (De Marzo, 1979) and independently in the distantly related genus *Hydrotrupes* (Beutel, 1994b). The functional mouth opening, i.e. the anterior opening of the prepharyngeal tube, is usually hermetically closed in dytiscid larvae, but not in larvae with a missing sucking channel (Speyer, 1922; De Marzo, 1979; Beutel, 1994b). Dytiscidae are characterized by multiple independent trends towards large size, especially in the subfamilies Dytiscinae, Cybistrinae and Colymbetinae (Désamoré *et al.*, 2018). Large, specialized suction discs on the protarsomeres of males (e.g. Korschelt, 1923–1924; Balke & Hendrich, 2016) are potential synapomorphies of Dytiscinae and Cybistrinae, and have evolved independently in *Oreodytes* Seidlitz of Hydroporinae.

Caraboidea

The monophyly of Geadephaga (or Caraboidea) (Fig. 1) was long disputed (e.g. Burmeister, 1976; Baehr, 1979; Roughley, 1981). The position of the small family Trachypachidae as sister group of monophyletic Hydradephaga was suggested by Roughley (1981), Ruhnau (1986) and Beutel & Belkaceme (1986). Shared features are the lack of a dense antennal pubescence (char. 20.0), completely immobilized metacoxae reaching the elytral epipleura laterally (chars 78.1, 79.0), and a partly reduced

transverse ridge of the metaventrite (char. 71.1), similar to the condition found in Amphizoidae and Hygrobiidae (Lindroth, 1960, 1961–1969: fig. 10; Beutel, 1992a, 1994a; Beutel & Arndt, 2016). A clade comprising Trachypachidae and a monophyletic Carabidae including Cicindelinae and Rhysodinae is now widely accepted (e.g. Beutel *et al.*, 2006; McKenna *et al.*, 2015; Baca *et al.*, 2017a), although a sister-group relationship between Trachypachidae and tiger beetles was recently suggested based on analyses of mitochondrial genomes (López-López & Vogler, 2017). From a morphological perspective, this is highly unlikely and also in conflict with analyses of other molecular datasets (McKenna *et al.*, 2015, 2019; Baca *et al.*, 2017a; Zhang *et al.*, 2018).

Trachypachidae

The small relict family comprises only six extant species placed into two genera (e.g. Lindroth, 1961–1969; Beutel & Arndt, 2016). The extinct subfamily Eodromeinae is documented from Triassic deposits (Ponomarenko, 1977). The genus *Trachypachus* Motschulsky has a Holarctic range of distribution, whereas the two species of *Systolosoma* Solier are restricted to central and southern Chile (Arndt & Beutel, 1995; Beutel & Arndt, 2016). R.A. Crowson postulated a preference for ‘very wet habitats’ (Lindroth, 1960: p. 31), but in fact adults and larvae of *Trachypachus* are xerophilic, rather than preferring moist riparian environments (Lindroth, 1960).

A presumptive synapomorphy of Trachypachidae and Carabidae is the protibial antenna cleaner (char. 42.1) (Hlavac, 1971). However, the possibility cannot be excluded that this feature was secondarily lost in the remaining groups, linked to the absence of antennal setae (e.g. Franciscolo, 1979; Beutel, 1986a; Belkaceme, 1991; Dressler & Beutel, 2010; Beutel *et al.*, 2017) and aquatic habits. Another feature with ambivalent polarity is the presence of long tactile setae on the head and other body parts (chars 9.1, 10.1), depending on the aquatic or terrestrial origin of the suborder. The morphological support for Geodephaga is apparently weak. Larvae and adults of Trachypachidae are largely characterized by plesiomorphic features and arguably close to the groundplan of Adephaga (or Adephaga excluding Gyrinidae).

The list of larval plesiomorphies includes the lack of a dense preoral filter, a distinctly elevated and well-defined hypopharynx with a well-developed retractor (chars 149.0, 150.0) (M. tentoriopharyngalis anterior), antennae directed anterolaterally (char. 122.0), and a slender postcephalic body lacking specializations except for the fixed (*Trachypachus*) or reduced (*Systolosoma*) urogomphi. The head of adults is slightly longer than wide and lacks obvious specializations (Dressler & Beutel, 2010). Plesiomorphies of the thorax are the lack of an external postcoxal bridge in the prothorax, a mesoventrite with paired procoxal rests and an unpaired hexagonal groove (chars 53.1, 54.1), broad metacoxae reaching the elytral epipleura laterally (char. 79.0), and a triangular metepimeron (char. 58.0). The pro-mesothoracic configuration of Trachypachidae is largely identical with the ‘low grade ventral motility mechanism’

(Hlavac, 1975) found in ‘lower grade’ Carabidae, e.g. Opisthiini, Nebriini, Carabini and Hletini (Beutel, 1992a).

Carabidae

With more than 45 000 described species, the Carabidae are by far the largest family of the suborder. It contains the smallest known adephagan species [e.g. *Winklerites perpussilus* (Rottemberg), *Argiloborus* Jeannel and *Argilobius* Jeannel; each *c.* 0.8 mm long]. In contrast to the aquatic groups, published analyses of molecular datasets suffer from limited taxon sampling (e.g. Ober, 2002; Ribera *et al.*, 2005; Ober & Maddison, 2008; Maddison *et al.*, 2009, 2019; Gough *et al.*, 2019), and consequently different phylogenetic issues remain unclarified, such as the placement of the enigmatic monospecific Cicidini (Stork, 1982; Erwin & Aschero, 2004) and Nototylini (Deuve, 1994). Autapomorphies of the family are the characteristic fine pubescence on antennomeres four to 11 of adults (or three to 11 in Harpalini) (char. 20.1), metacoxae only as wide as the metaventrite (char. 79.1), a more or less parallel-sided metepimeron with a transverse orientation (Beutel, 1992a) (char. 58.1), and anteriorly directed antennae (char. 122.1) and a more or less dense preoral fringe of microtrichia in the larvae (char. 149.1) (e.g. Tröster, 1987). Retained plesiomorphies are a distinct pronoto-elytral angle (char. 1.0) (with some exceptions, e.g. Omophronini, Pseudomorphini), metacoxae with a retained limited movability (chars 78.1, 80.0) (Evans, 1977), and a full set of furca-coxal muscles in the metathorax (also retained in Haliplidae and Trachypachidae) (chars 88.0, 89.0, 90.0).

Transformation of thoracic sclerites have played a major role in the evolution of Carabidae. Externally and internally open procoxal cavities belong to the groundplan of the family, and also an elongated prosternal process, paired procoxal rests, and an unpaired hexagonal groove on the mesoventrite (chars 32.1, 53.1, 54.1) (Beutel, 1992a). This character combination, referred to as ‘low grade motility mechanism’ by Hlavac (1972, 1975), is also present in *Trachypachus* and aquatic groups (Beutel, 1986a, 1992a; Belkaceme, 1991), and consequently considered the plesiomorphic state. It stabilizes the postcephalic body but restricts the flexibility between the pro- and pterothorax. The corresponding derived condition is the ‘high grade motility mechanism’ (Hlavac, 1975) with externally closed procoxal cavities, a shortened and apically blunt prosternal process (chars 33.1, 32.4), an anterior smooth mesothoracic collar forming a ball-and-socket joint with the prothorax, reduced procoxal rests and hexagonal groove, and an anterior part of the mesoventrite horizontal in lateral view and a steeply descending posterior part (chars 53.2, 54.0) (Beutel, 1992a). This intersegmental connection guarantees a high flexibility between the pro- and mesothorax, arguably an adaptive novelty in the context of catching prey. Intermediate conditions are present in *Omophron* Latreille and *Metrius* Eschscholtz (Beutel, 1992a). As suggested by the phylogenetic pattern, the derived ‘high grade motility’ type of thorax has evolved several times independently, in Cicidini (Kavanaugh & Erwin, 1991), Nototylini (Deuve,

1994), Cicindelinae, Rhysodinae, Paussinae, and a large subunit of anisochaetous carabids [Loricinae, Scaritinae, Trechinae, Brachininae, Harpalinae (including Pseudomorphini)] (Beutel, 1992a). A tradeoff in the carabid locomotor apparatus was described in a comparative study of Evans & Forsythe (1984), with a wide range of compromises between speed and pushing force.

Extraoral digestion is a typical feature of Carabidae, which are primarily predators, but with a certain tendency towards herbivory (Acorn & Ball, 1991). The feeding apparatus of number of species was described by Forsythe (1983). A characteristic of the mandibles are fringes of microtrichia (Acorn & Ball, 1991), but these structures probably belong to the groundplan of Geadephaga (Dressler & Beutel, 2010). Interestingly, the elongate mandibles of Cicindini almost completely lack these fringes (Kavanaugh & Erwin, 1991).

The predacious larvae are characterized by dense preoral fringes of microtrichia (char. 149.1) (e.g. Tröster, 1987; Beutel, 1992b–d), which create capillary forces. They facilitate the uptake of food substrate liquefied in the preoral space and prevent solid particles from entering the narrow prepharyngeal tube. A prominent hypopharynx and a retractor muscle (*M. tentoriopharyngalis anterior*) are still present in basal grade carabids (e.g. Spence & Sutcliffe, 1982; Beutel, 1992c, 1992d) as in Trachypachidae (char. 150.0) and larvae of aquatic groups. By contrast, the floor of the prepharyngeal part of the digestive tract is completely flattened in Brachininae and Harpalinae, and *M. tentoriopharyngalis anterior* is generally absent (Tröster, 1987; Beutel, 1993).

The chemical compounds of the pygidial glands of Carabidae vary greatly (e.g. Giglio *et al.*, 2011). Explosive mechanisms for delivery of compounds have evolved independently in Metriinae and Paussinae on the one hand, and in Brachininae on the other.

A placement of the extremely rare (or extinct) Nototylini (only known from a single specimen from Espirito Santo; Deuve, 1994) and Cicindini (Stork, 1982; Kavanaugh & Erwin, 1991) will probably remain a great challenge. The larvae of both groups are unknown. Adults display the derived high-grade ventral motility mechanism of the pro- and mesothorax. Only a single female of *Nototylus fryi* (Schaum) is known (holotype), the only described species of Nototylini. It was collected in the state of Espirito Santo of Brazil. A remarkable feature is the lack of a protibial antenna cleaner (Deuve, 1994). Cicindini are represented by two species (Stork, 1982). One occurs in the Salinas Grandes in three western provinces of Argentina. It was observed and collected in numbers quite recently (Erwin & Aschero, 2004). The other species is recorded from tidal mudflats in Iran (Bushere) and Kuwait (Stork, 1982). Adults of *Cicindis* are similar to cincindelinae in their habitus (Erwin & Aschero, 2004). They possess well-developed fringes of swimming hairs on their legs and swim on the water surface or dive in alkaline ponds. Morphological features of adults will not be sufficient to clarify the position of both specialized groups. Material for DNA extraction is likely to be available from *Cicindis horni* (Bruch), but this is highly unlikely in the case of *Nototylus fryi*.

Rhysodinae

Rhysodinae (or Rhysodini; e.g. Bell & Bell, 1978) were traditionally treated as a separate family of Adephaga (e.g. Crowson, 1955; Lawrence & Newton, 1995; see also Bell & Bell, 1962), apparently isolated in terms of the larval and adult morphology and life habits (e.g. Bell & Bell, 1978; Beutel, 1992b, 2016). As is sometimes the case (Komarek & Beutel, 2007), this taxonomic rank was largely or exclusively based on autapomorphies, without evaluating the monophyly of Carabidae and a possible subordinate placement within this family. Later the group was considered as a carabid tribe closest to scaritine genus *Solenogenys* Westwood (Bell, 1998). Today, analyses of molecular data (e.g. McKenna *et al.*, 2015, 2019) suggest a position close to the root of Carabidae, and a rank as subfamily was adopted in recent studies (e.g. López-López & Vogler, 2017). The group has a close association with decaying wood in the larval and adult stages, and as a unique feature in Adephaga uses slime moulds (Myxomycetes) as a food source (Bell & Bell, 1991; Beutel, 2016). The adults have a strongly sclerotized nearly cylindrical and parallel-sided body, with a very broad prosternal process, a broad external prothoracic postcoxal bridge (char. 34.1), a greatly elongated metaventricle without transverse ridge (char. 71.2), and widely separated metacoxae. This configuration is apparently autapomorphic for the group (Beutel, 1990b) and advantageous for penetrating rotting wood (Bell & Bell, 1991). Head structures are also highly modified, with largely or completely reduced tactile setae, a condyliform constricted neck region, a frontal pit, median and temporal lobes, a small triangular or rounded labrum, and moniliform antennae with a very atypical pattern of setae.

Larvae, which live in short galleries in wood, are also characterized by a highly modified morphology. The head is strongly sclerotized and wedge-shaped, strongly widening posteriorly and equipped with a shovel-like nasal projection, apparently suitable for penetrating rotting wood. The postcephalic body is unsclerotized and grub-like, similar to the condition found in wood-boring larvae of Archostemata (Beutel & Hörnschemeyer, 2002a, 2002b). Additional autapomorphies (not included in the list of character in this study; see Beutel, 1990b, 1995; Bell, 1991) are the maxillolabial complex, a strongly modified galea, one-segmented labial palps, very short legs with a single claw, thoracic and abdominal terga with humps and rows of spinulae, and missing urogomphi (char. 170.0) (Beutel, 1995).

Cicindelinae

Like Rhysodinae, the popular and conspicuous tiger beetles were considered as a separate family of Adephaga (e.g. Shelford, 1908; Vogler & Pearson, 1996). A rank as a subfamily in Carabidae was widely accepted more recently, e.g. in Lindroth (1961–1969), Lawrence & Newton (1995) and Arndt *et al.* (2016) (see also Ball, 1979). The family rank was recently resurrected in a study based on mitochondrial genomes (López-López & Vogler, 2017), where a sister-group relationship with the remaining monophyletic Carabidae was supported.

However, results of this study, such as monophyletic ‘Hydrade-phaga’ or a clade Trachypachidae + ‘Cicindelidae’, are in conflict with recent phylogenies, e.g. Baca *et al.* (2017a) or Gough *et al.* (2019). Therefore, the information content of the data used, as well as the interpretations of the authors, should be taken with some caution.

The most conspicuous derived character complex in Cicindelinae is the transformation of larvae into highly specialized ambush predators, having a large hyperprognathous head (char. 109.3) with a flat upper surface and unusually large stemmata used for identifying prey (e.g. Shelford, 1908; Breyer, 1989). The larvae stay in vertical burrows in soil, with the opening covered by the lid-like head. The postcephalic body is largely unsclerotized and lacks urogomphi (char. 170.0). The posterior abdominal segments bear rows of spines stabilizing them in their tubes. Identified prey is caught with the mandibles accompanied by a very rapid movement of the head.

The genus *Amblycheila*, with large, black, flightless and strongly sclerotized species (Krell & Brookhart, 2012), belongs to Manticorini, which is probably the sister-group of the remaining Cicindelinae (Gough *et al.*, 2019). Interestingly, species of the genus *Omus* are also characterized by a distinctly modified pterothorax and obligatory flightlessness. This suggests that reduction of the flight apparatus occurred several times independently in the subfamily. In very clear contrast to Manticorini and *Omus*, ‘typical’ tiger beetles, such as species of the very species-rich genus *Cicindela*, are characterized by a light body with slender and elongate legs and a well-developed flight apparatus. Fast running (e.g. Evans, 1977; Evans & Forsythe, 1984) and excellent flying abilities are well-known characteristics of these very efficient predators of insects.

Concluding remarks

Based on extensive molecular data (Baca *et al.*, 2017a; McKenna *et al.*, 2019; Vasilikopoulos *et al.*, 2019) and large morphological character sets (e.g. Beutel *et al.*, 2006, 2013), including the one presented here, a stable pattern for the phylogenetic relationships of the families is reached, allowing a reliable reconstruction of character evolution. What is still pending but under way is a comprehensive molecular phylogeny of the megadiverse Carabidae. Other tasks for the future include the discovery of larvae of different important taxa, notably of the gyrinid genera *Spanglerogyrus* and *Heterogyrus*, several genera of Noteridae, and the mysterious carabid genus *Cicindis*. Another goal facilitated by modern technologies, especially microcomputed tomography, would be the documentation of anatomical data for a much more extensive sampling of immature stages and adults.

Fossils played only a marginal role in this study. However, it is evident that their detailed study and robust placement are very important tasks, not only for calibrating molecular trees (e.g. Gustafson *et al.*, 2017), but also for improving our understanding of evolutionary transformations and communities of beetles and other organisms of the past. The phylogenetic placement of Mesozoic aedeophagan taxa was addressed in Beutel

et al. (2013), but since that time a considerable number of relevant studies was published (e.g. Prokin *et al.*, 2013a, 2013b; Kirejtshuk & Prokin, 2018; Volkov, 2013; Yan *et al.*, 2018; see also Ponomarenko & Prokin, 2015). A time-calibrated phylogeny with reliably placed fossils and an extensive sampling of genes and ‘hydradephagan’ and geadephagan taxa should be the goal for the near future.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1. List of characters (Aedeophaga List of characters.doc)

File S2. Character state matrix (Aedeophaga_Evolution_Supplementum 2.nex)

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References

- Achtelig, M. (1981) Neuropteroidea. Revisionary notes. *Insect Phylogeny* (ed. by W. Hennig), pp. 286–287, 290, 293–295, 299–300, 387–388. Wiley, Chichester.
- Acorn, J.H. & Ball, G.E. (1991) The mandibles of some adult ground beetles: structure, function, and the evolution of herbivory (Coleoptera: Carabidae). *Canadian Journal of Zoology*, **69**, 638–650.
- Alarie, Y., Beutel, R.G. & Watts, C.H.S. (2004) Larval morphology of the Hygrobiidae (Coleoptera: Aedeophaga: Dytiscoidea) with phylogenetic considerations. *European Journal of Entomology*, **101**, 293–311.
- Alarie, Y. & Bilton, D. (2005) Larval morphology of Aspidytidae (Coleoptera: Aedeophaga) and its phylogenetic implications. *Annals of the Entomological Society of America*, **98**, 417–430.
- Alarie, Y., Short, A.E., Garcia, M. & Joly, L. (2011) Larval morphology of Meruidae (Coleoptera: Aedeophaga) and its phylogenetic implications. *Annals of the Entomological Society of America*, **104**, 25–36.
- Alarie, Y., Spangler, P.J. & Perkins, P.D. (1998) Study of the larvae of *Hydrotrupes palpalis* Sharp (Coleoptera: Aedeophaga, Dytiscidae). *The Coleopterist's Bulletin*, **51**, 120–139.

- Anton, E., Yavorskaya, M.I. & Beutel, R.G. (2016) The head morphology of adults of Clambidae (Coleoptera: Polyphaga: Scirtoidea). *Journal of Morphology*, **277**, 615–633.
- Antunes-Carvalho, C., Yavorskaya, M., Gnaspini, P., Ribera, I. & Beutel, R.G. (2017) Cephalic anatomy and three-dimensional reconstruction of the head of *Catops ventricosus* (Weise, 1877) (Coleoptera: Leiodidae: Cholevinae). *Organisms Diversity and Evolution*, **17**, 199–212.
- Arndt, E. (1993) Phylogenetische Untersuchungen larvalmorphologischer Merkmale der Carabidae (Insecta: Coleoptera). *Stuttgarter Beiträge zur Naturkunde*, **488**, 1–56.
- Arndt, E. & Beutel, R.G. (1995) Larval morphology of *Systolosoma* Solier and *Trachypachus* Motschulsky (Coleoptera: Trachypachidae) with phylogenetic considerations. *Entomologica Scandinivica*, **26**, 439–446.
- Arndt, E., Beutel, R.G. & Will, K. (2016) 7.8. Carabidae Latreille, 1802. *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adephaga, Myxophaga, Polyphaga (partim). Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd edn (ed. by N.P. Kristensen and R.G. Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 89–98. Walter De Gruyter, Berlin, New York.
- Baca, S.M., Alexander, A., Gustafson, G.T. & Short, A.E. (2017a) Ultraconserved elements show utility in phylogenetic inference of Adephaga (Coleoptera) and suggest paraphyly of ‘Hydradephaga’. *Systematic Entomology*, **42**, 786–795.
- Baca, S.M., Toussaint, E.F.A., Miller, K.B. & Short, A.E.Z. (2017b) Molecular phylogeny of the aquatic beetle family Noteridae (Coleoptera: Adephaga) with an emphasis on data partitioning strategies. *Molecular Phylogenetics and Evolution*, **107**, 282–292.
- Baehr, M. (1979) Vergleichende Untersuchungen am Skelett und an der Coxalmuskulatur des Prothorax der Coleoptera. Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera, Insecta). *Zoologica*, **44**, 1–76.
- Balfour-Browne, F. (1922) 5. The life-history of the water-beetle *Pelobius tardus* Herbst. *Proceedings of the Zoological Society of London*, **92**, 79–97.
- Balfour-Browne, F. & Balfour-Browne, J. (1940) An outline of the habits of the water-beetle *Noterus capricornis* Herbst (Coleopt.). *Proceedings of the Royal Entomological Society of London*, **15**, 105–112.
- Balke, M. & Hendrich, L. (1996) A new species of the terrestrial water beetle genus *Geodessus* Brancucci (Coleoptera: Dytiscidae), sieved from leaf litter in southern India. *Aquatic Insects*, **18**, 91–99.
- Balke, M. & Hendrich, L. (2016) 7.6. Dytiscidae Leach 1915. *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adephaga, Myxophaga, Polyphaga (partim). Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd edn (ed. by N.P. Kristensen and R.G. Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 89–98. Walter De Gruyter, Berlin, New York.
- Balke, M., Ribera, I. & Beutel, R.G. (2003) Aspidytidae: on the discovery of a new beetle family: detailed morphological analysis, description of a second species, and key to fossil and extant adephagan families. *Water Beetles of China*, Vol. **3** (ed. by M.A. Jäch and L. Ji), pp. 53–66. Zoologisch-Botanische Gesellschaft in Österreich und Wiener Coleopterologenverein, Wien.
- Balke, M., Ribera, I. & Beutel, R.G. (2005) The systematic position of Aspidytidae, the diversification of Dytiscoidea (Coleoptera, Adephaga) and the phylogenetic signal of third codon positions. *Journal of Zoological Systematics and Evolutionary Research*, **43**, 223–242.
- Balke, M., Ribera, I., Beutel, R., Vilorio, A., Garcia, M. & Vogler, A.P. (2008) Systematic placement of the recently discovered beetle family Meruidae (Coleoptera: Dytiscoidea) based on molecular data. *Zoologica Scripta*, **37**, 647–650.
- Ball, G.E. (1979) Conspectus of carabid classification: history, homology, and higher taxa. *Carabid Beetles: Their Evolution, Natural History, and Classification* (ed. by T.L. Erwin, G.E. Ball, G.E. Whitehead and A.L. Halpern), pp. 63–111. W. Junk, The Hague.
- Bauer, A. (1910) Die Muskulatur von *Dytiscus marginalis* L. Ein Beitrag zur Morphologie des Insektenkörpers. *Zeitschrift für Wissenschaftliche Zoologie*, **95**, 594–646.
- Beier, M. (1929) Zur Kenntnis der Lebensweise von *Haliplus wehnckei* Gerh. *Zeitschrift für Morphologie und Ökologie der Tiere*, **14**, 191–233.
- Belkaceme, T. (1986) Skelet und Muskulatur der Hinterhüfte von *Haliplus lineatocollis* Mrsh. (Haliplidae, Coleoptera). *Stuttgarter Beiträge zur Naturkunde*, **393**, 1–12.
- Belkaceme, T. (1991) Skelet und Muskulatur des Kopfes und Thorax von *Noterus laevis* Sturm. Ein Beitrag zur Morphologie und Phylogenie der Noteridae (Coleoptera: Adephaga). *Stuttgarter Beiträge zur Naturkunde*, **462**, 1–94.
- Bell, R.T. (1991) Rhysodidae (Adephaga). *Immature Insects, Vol. 2* (ed. by F. Stehr), pp. 304–305. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Bell, R.T. (1998) Where do the Rhysodini (Coleoptera) belong? *Phylogeny and Classification of Caraboidea. XX. I.C.E. (1996, Firenze, Italy)* (ed. by G.E. Ball, A. Casale and A. Vigna Taglianti), pp. 261–272. Museo Regionale di Scienze Naturali, Torino.
- Bell, R.T. & Bell, J.R. (1962) The taxonomic position of the Rhysodidae (Coleoptera). *The Coleopterist's Bulletin*, **16**, 99–106.
- Bell, R.T. & Bell, J.R. (1978) Rhysodini of the world part I. a new classification of the tribe, and a synopsis of *Omoglymmius* subgenus *Nitiglymmius* new subgenus (Coleoptera: Carabidae or Rhysodidae). *Quaestiones Entomologicae*, **14**, 43–88.
- Bell, R.T. & Bell, J.R. (1991) The Rhysodini of Australia (Insecta: Coleoptera). *Annals of the Carnegie Museum*, **60**, 179–210.
- Bendele, H. (1986) Mechanosensory cues control chasing behaviour of whirligig beetles (Coleoptera, Gyrinidae). *Journal of Comparative Physiology*, **158**, 405–411.
- Bertrand, H. (1972) *Larves et Nymphes des Coléoptères Aquatiques du Globe*. F. Paillart, Abbeville.
- Beutel, R.G. (1986a) Skelet und Muskulatur des Kopfes und Thorax von *Hygrobia tarda* (Herbst). Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Hydradephaga (Insecta: Coleoptera). *Stuttgarter Beiträge zur Naturkunde*, **388**, 1–54.
- Beutel, R.G. (1986b) Skelet und Muskulatur des Kopfes der Larve von *Haliplus lineatocollis* Mrsh. (Coleoptera). *Stuttgarter Beiträge zur Naturkunde*, **390**, 1–15.
- Beutel, R.G. (1988) Studies on the metathorax of the trout-stream beetle, *Amphizoa lecontei* Matthews (Coleoptera: Amphizoidae): contribution towards clarification of the systematic position of Amphizoidae. *International Journal of Insect Morphology and Embryology*, **17**, 63–81.
- Beutel, R.G. (1989a) The head of *Spanglerogyrus albiventris* Folkerts (Coleoptera: Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae and Adephaga. *Zoologische Jahrbücher für Anatomie*, **118**, 431–461.
- Beutel, R.G. (1989b) The prothorax of *Spanglerogyrus albiventris* Folkerts 1979 (Coleoptera, Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae. *Entomologica Basiliensia*, **13**, 151–173.
- Beutel, R.G. (1990a) Phylogenetic analysis of the family Gyrinidae (Coleoptera) based on meso- and metathoracic characters. *Quaestiones Entomologicae*, **26**, 163–191.
- Beutel, R.G. (1990b) Metathoracic features of *Omoglymmius hamatus* and their significance for classification of Rhysodini (Coleoptera: Adephaga). *Entomologia generalis*, **15**, 185–201.

- Beutel, R.G. (1991a) Internal and external structures of the head of 3rd instar larvae of *Amphizoa lecontei* Matthews (Coleoptera: Amphizoidae). A contribution towards the clarification of the systematic position of Amphizoidae. *Stuttgarter Beiträge zur Naturkunde*, **469**, 1–24.
- Beutel, R.G. (1991b) Larval head structures of *Omophron* and their implications for the relationships of Omophronini (Coleoptera: Carabidae). *Entomologica Scandinavica*, **22**, 55–67.
- Beutel, R.G. (1992a) Phylogenetic analysis of thoracic structures of Carabidae (Coleoptera). *Journal of Zoological Systematics and Evolutionary Research*, **30**, 53–74.
- Beutel, R.G. (1992b) On the morphology of the head of the larva of *Omoglymmius hamatus* (LeConte) and the systematic position of Rhysodidae (Coleoptera, Adepaga). *Entomologica Scandinavica*, **23**, 169–184.
- Beutel, R.G. (1992c) Study on the systematic position of Metriini (Coleoptera, Carabidae) based on characters of the larval head. *Systematic Entomology*, **17**, 207–218.
- Beutel, R.G. (1992d) External and internal structures of the head of 3rd instar larvae of *Carabus coriaceus* F. (Adepaga: Carabidae). *Entomologica Basiliensia*, **15**, 147–168.
- Beutel, R.G. (1992e) Larval head structures of *Licinus silphoides* Rossi (Coleoptera: Carabidae) and their phylogenetic implications. *Entomologica Basiliensia*, **15**, 169–194.
- Beutel, R.G. (1993) Phylogenetic analysis of Adepaga (Coleoptera) based on characters of the larval head. *Systematic Entomology*, **18**, 127–147.
- Beutel, R.G. (1994a) Study on the systematic position of *Systolosoma breve* Solier (Adepaga: Trachypachidae) based on characters of the thorax. *Studies on the Neotropical Fauna and Environment*, **29**, 161–167.
- Beutel, R.G. (1994b) On the systematic position of *Hydrotrupes palpalis* Sharp (Coleoptera: Dytiscidae). *Aquatic Insects*, **16**, 157–164.
- Beutel, R.G. (1995) The Adepaga (Coleoptera): phylogenetic analysis and thoughts on the evolutionary history. *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson* (ed. by J. Pakaluk and S.A. Ślipiński), pp. 173–217. Muzeum i Instytut Zoologii PAN, Warszawa.
- Beutel, R.G. (1997) Über Phylogenese und evolution der Coleoptera (Insecta). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)*, **31**, 1–164.
- Beutel, R.G. (2016) 7.11. Rhysodidae Laporte, 1840 (=Rhysodini s. Bell). *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adepaga, Myxophaga, Polyphaga (partim). Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd edn (ed. by N.P. Kristensen and R.G. Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 190–197. Walter De Gruyter, Berlin, New York.
- Beutel, R.G. & Arndt, E. (2016) 7.9. Trachypachidae C.G. Thomson, 1857. *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adepaga, Myxophaga, Polyphaga (partim). Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd edn (ed. by N.P. Kristensen and R.G., Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 159–162. Walter De Gruyter, Berlin, New York.
- Beutel, R.G. & Belkaceme, T. (1986) Comparative studies on the metathorax of Hydradephaga and Trachypachidae. *Entomologica Basiliensia*, **11**, 221–229.
- Beutel, R.G. & Haas, A. (1996) Phylogenetic analysis of larval and adult characters of Adepaga (Coleoptera) using cladistic computer programs. *Entomologica Scandinavica*, **27**, 197–205.
- Beutel, R.G. & Haas, F. (2000) Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics*, **16**, 103–141.
- Beutel, R.G. & Hörnschemeyer, T. (2002a) Larval morphology and phylogenetic position of *Micromalthus debilis* LeConte (Coleoptera: Micromalthidae). *Systematic Entomology*, **27**, 169–190.
- Beutel, R.G. & Hörnschemeyer, T. (2002b) Description of the larva of *Rhysodidigma raffrayi* (Coleoptera, Archostemata), with phylogenetic and functional implications. *European Journal of Entomology*, **99**, 53–66.
- Beutel, R.G. & Roughley, R.E. (1987) On the systematic position of the genus *Notomicrus* Sharp (Hydradephaga, Coleoptera). *Canadian Journal of Zoology*, **65**, 1898–1905.
- Beutel, R.G. & Roughley, R.E. (1988) On the systematic position of the family Gyrinidae (Coleoptera: Adepaga). *Journal of Zoological Systematics and Evolutionary Research*, **26**, 380–400.
- Beutel, R.G. & Roughley, R.E. (1993) Phylogenetic analysis of Gyrinidae based on characters of the larval head (Coleoptera: Adepaga). *Entomologica Scandinavica*, **24**, 459–468.
- Beutel, R.G. & Roughley, R.E. (2016) 7.1. Gyrinidae Latreille, 1830. *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adepaga, Myxophaga, Polyphaga (partim). Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd edn (ed. by N.P. Kristensen and R.G. Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 80–89. Walter De Gruyter, Berlin, New York.
- Beutel, R.G. & Ruhnau, S. (1990) Phylogenetic analysis of the genera of Halplidae (Coleoptera) based on characters of adults. *Aquatic Insects*, **12**, 1–17.
- Beutel, R.G., Balke, M. & Ribera, I. (2016) 7.7 Aspidytidae Ribera, Beutel, Balke & Vogler, 2002. *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adepaga, Myxophaga, Polyphaga (partim) Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd ed. (ed. by N.P. Kristensen and R.G. Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 141–149. Walter De Gruyter, Berlin, New York.
- Beutel, R.G., Balke, M. & Steiner, W.E. (2006) On the systematic position of Meruidae (Coleoptera, Adepaga) and the phylogeny of the smaller hydradephagan families. *Cladistics*, **22**, 102–131.
- Beutel, R.G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Vilhelmsen, L. et al. (2011) Morphological and molecular evidence converging upon a robust phylogeny of the megadiverse Holometabola. *Cladistics*, **26**, 1–15.
- Beutel, R.G., Wang, B., Tan, J.J., Ge, S.Q., Ren, D. & Yang, X.K. (2013) On the phylogeny and evolution of Mesozoic and extant lineages of Adepaga (Coleoptera, Insecta). *Cladistics*, **29**, 47–65.
- Beutel, R.G., Yan, E., Richter, A., Büsse, S., Miller, K.B., Yavorskaya, M. & Wipfler, B. (2017) The head of *Heterogyrus milloti* (Coleoptera: Gyrinidae) and its phylogenetic implications. *Arthropod Systematics and Phylogeny*, **75**, 261–280.
- Beutel, R.G., Yan, E., Yavorskaya, M., Büsse, S., Gorb, S.N. & Wipfler, B. (2019a) On the thoracic anatomy of the Madagascan *Heterogyrus milloti* and the phylogeny of Gyrinidae (Coleoptera). *Systematic Entomology*, **44**, 336–360.
- Beutel, R.G., Yan, E.V. & Lawrence, J.F. (2019b) Phylogenetic methods applied to extinct beetles – the case of †*Tunguskagyris* (Gyrinidae or †Triaplidae). *Palaeoentomology*. <https://doi.org/10.11646/palaeoentomology.2.4.11>.
- Bils, W. (1976) Das Abdomenende weiblicher, terrestrisch lebender Adepaga (Coleoptera) und seine Bedeutung für die Phylogenie. *Zoomorphologie*, **84**, 113–193.
- Brandmayr, T.Z., Brandmayr, P., Marano, I. & Paarmann, W. (1993) The larva of *Graphipterus serrator* (Forskäl 1775) (Coleoptera Carabidae Graphipterini): description and functional morphology. *Tropical Zoology*, **6**, 299–312.
- Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, **42**, 795–803.
- Breyer, S. (1989) Skelet und Muskulatur des Kopfes der Larve von *Cicindela campestris* L. (Coleoptera: Cicindelidae). *Stuttgarter Beiträge zur Naturkunde*, **438**, 1–60.

- Brinck, P. (1955) A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. I. *Lunds Universitets Arsskrift N.F.* **2**, 51, 1–141.
- Burmeister, E.G. (1976) Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. *Zoomorphologie*, **85**, 165–257.
- Burmeister, E.G. (1990) The female genital structures of *Spanglerogyrus albiventris* Folkerts 1979. A contribution to the systematic position of the Gyrinidae. *Spixiana*, **13**, 253–265.
- Chandler, H.P. (1943) A new genus of Haliplidae (Coleoptera) from California. *Pan-Pacific Entomologist*, **24**, 154–158.
- Che, L.H., Zhang, S.Q., Li, Y., Liang, D., Pang, H., Ślipiński, A. & Zhang, P. (2017) Genome-wide survey of nuclear protein-coding markers for beetle phylogenetics and their application in resolving both deep and shallow-level divergences. *Molecular Ecology Resources*, **17**, 1342–1358.
- Crowson, R.A. (1955) *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd, London.
- Crowson, R.A. (1960) The phylogeny of Coleoptera. *Annual Review of Entomology*, **5**, 111–415.
- Crowson, R.A. (1981) *The Biology of the Coleoptera*. John Murray, London.
- Crowson, R.A. (1991) A critique of current cladistics. *Journal of Natural History*, **25**, 3–5.
- De Marzo, L. (1979) Studi sulle larve dei Coleotteri Ditiscidi. X. Anatomia e funzionamento dell' apparato succhiante cibario-faringeo in alcune forme larvali delle subff. Dytiscinae, Colymbetinae, Lacophilinae e Hydroporinae. *Entomologica, Bari*, **15**, 5–72.
- De Marzo, L. & Nilsson, A.N. (1986) Morphological variation and fine structure of some head structures in larvae of Dytiscidae (Coleoptera). *Entomologica Basiliensis*, **11**, 29–42.
- Désamoré, A., Laenen, B., Miller, K.B. & Bergsten, J. (2018) Early burst in body size evolution is uncoupled from species diversification in diving beetles (Dytiscidae). *Molecular Ecology*, **27**, 979–993. <https://doi.org/10.1111/mec.14492>.
- Dettner, K. (1979) Chemotaxonomy of water beetles based on their pygidial gland constituents. *Biochemical Systematics and Ecology*, **7**, 129–140.
- Dettner, K. (1987) Chemosystematics and evolution of beetle chemical defenses. *Annual Review of Entomology*, **32**, 17–48.
- Dettner, K. (2016) 7.3. Noteridae Thomson, 1857. 7.4. Amphizoidae LeConte, 1853. 7.5. Hygrobiidae Régimbart 1879. *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adephaga, Myxophaga, Polyphaga (partim). Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd edn (ed. by N.P. Kristensen and R.G. Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 98–118. Walter De Gruyter, Berlin, New York.
- Dettner, K. (2019) Defenses of Water Insects. *Aquatic Insects* (ed. by K. del-Claro and R. Guillermo), pp. 191–262. Springer, Cham.
- Deuve, T. (1994) Les Nototylidae, une famille énigmatique de Coléoptères Adephaga. *Annales de la Société entomologique de France*, **30**, 133–144.
- Dressler, C. & Beutel, R.G. (2010) The morphology and evolution of the adult head of Adephaga (Insecta: Coleoptera). *Arthropod Systematics and Phylogeny*, **68**, 239–287.
- Erwin, T.L. & Aschero, V. (2004) *Cicindis horni* Bruch (Coleoptera: Carabidae, Cicindini): the fairy shrimp hunting beetle, its way of life on the Salinas Grandes of Argentina. *Zootaxa*, **553**, 16.
- Evans, M.E.G. (1977) Locomotion in the Coleoptera Adephaga, especially Carabidae. *Journal of Zoology*, **181**, 189–226.
- Evans, M.E.G. & Forsythe, T.G. (1984) A comparison of adaptations to running, pushing and burrowing in some adult Coleoptera: especially Carabidae. *Journal of Zoology*, **202**, 513–534.
- Folkerts, G.W. (1979) *Spanglerogyrus albiventris*, a primitive new genus and species of Gyrinidae (Coleoptera) from Alabama. *The Coleopterist's Bulletin*, **33**, 1–8.
- Forsyth, D.J. (1968) The structure of the defence glands in the Dytiscidae, Noteridae, Haliplidae and Gyrinidae (Coleoptera). *Transactions of the Royal Entomological Society of London*, **120**, 159–182.
- Forsyth, D.J. (1969) The structure of the defence glands of the Cincindelidae, Amphizoidae and Hygrobiidae (Insecta: Coleoptera). *Journal of Zoology*, **160**, 51–69.
- Forsyth, D.J. (1972) The structure of the pygidial defence glands of Carabidae (Coleoptera). *Transactions of the Zoological Society of London*, **32**, 249–309.
- Forsythe, T.G. (1983) Mouthparts and feeding of certain ground beetles (Coleoptera: Carabidae). *Zoological Journal of the Linnean Society*, **79**, 319–376.
- Franciscolo, M.E. (1979) Coleoptera. Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae. *Fauna d'Italia*. Calderini, Bologna.
- Giglio, A., Brandmayr, P., Talarico, F. & Brandmayr, T.Z. (2011) Current knowledge on exocrine glands in carabid beetles: structure, function and chemical compounds. *ZooKeys*, **100**, 193–201.
- Goloboff, P. (1995) *NONA Version 1.5*. Fundación e Instituto Miguel Lillo, Tucuman.
- Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.
- Gough, H.M., Duran, D.P., Kawahara, A.Y. & Toussaint, E.F.A. (2019) A comprehensive molecular phylogeny of tiger beetles (Coleoptera, Carabidae, Cicindelinae). *Systematic Entomology*, **44**, 305–321.
- Guignot, F. (1931–1933) Les Hydrocanthares de France. Hygrobiidae, Haliplidae, Dytiscidae et Gyrinidae de la France continentale, avec notes sur les espèces de la Corse et de l'Afrique du Nord française. *Miscellanea Entomologica*, 1057 pp. Toulouse.
- Gustafson, G.T., Prokin, A.A., Bukontaite, R., Bergsten, J. & Miller, K.B. (2017) Tip-dated phylogeny of whirligig beetles reveals ancient lineage surviving on Madagascar. *Scientific Reports*, **7**, 8619.
- Hatch, M.H. (1925) An outline of the ecology of Gyrinidae. *Bulletin of the Brooklyn Entomological Society*, **20**, 101–114.
- Hatch, M.H. (1927) The morphology of Gyrinidae. *Papers of the Michigan Academy of Science, Arts and Letters*, **7**, 311–350.
- Hawlitsek, O., Hendrich, L. & Balke, M. (2012) Molecular phylogeny of the squeak beetles, a family with disjunct Palearctic-Australian range. *Molecular Phylogenetics and Evolution*, **62**, 550–554.
- Hennig, W. (1950) *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.
- Hennig, W. (1966) *Phylogenetic Systematics*, p. 263. University of Illinois Press, Champaign, IL.
- Hieke, F. (1966) Vergleichend funktionelle Anatomie der Abdominalmuskulatur einiger männlicher Coleopteren unter besonderer Berücksichtigung des Genitoanalkomplexes. *Deutsche entomologische Zeitschrift*, **13**, 1–68.
- Hinton, H.E. (1981) *Biology of Insect Eggs*. Pergamon Press, Oxford, New York, Toronto, Sydney Paris, Frankfurt.
- Hlavac, T.F. (1971) Differentiation of the carabid antenna cleaner. *Psyche*, **78**, 51–66.
- Hlavac, T.F. (1972) The prothorax of Coleoptera: origin, major features of variation. *Psyche*, **79**, 123–149.
- Hlavac, T.F. (1975) The prothorax of Coleoptera (except Bostrichiformia-Cucujiformia). *Bulletin of the Museum of Comparative Zoology*, **147**, 137–183.
- Honomichl, K. (1975) Beitrag zur Morphologie des Kopfes der Imago von *Gyrinus substriatus* Stephens, 1829 (Coleoptera, Insecta). *Zoologische Jahrbücher für Anatomie*, **94**, 218–295.
- Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., John, O.S., Vogler, A.P. *et al.* (2007) A comprehensive phylogeny of beetles

- reveals the evolutionary origins of a super-radiation. *Science*, **318**, 1913–1916.
- Jaboulet, M.C. (1960) Contribution à l'étude des larves d'Haliplides. *Travaux du Laboratoire de Zoologie et de la Station Aquicole Grimaldi de la Faculté des Sciences de Dijon*, **31**, 1–17.
- Jeannel, R. (1941–1942) *Coléoptères Carabiques. Faune de France*, 39–40, 1173 pp. Librairie de la Faculté des Sciences, Paris.
- Jeannel, R. & Paulian, R. (1944) Morphologie abdominale des Coléoptères et systématique de l'ordre. *Revue française d'Entomologie*, **9**, 65–109.
- Kato, M., Kawakita, A. & Kato, T. (2010) Colonization to aquifers and adaptations to subterranean interstitial life by a water beetle clade (Noteridae) with description of a new *Phreatodytes* species. *Zoological Science*, **27**, 717–723.
- Kaupp, A., Guggenheim, R. & Nagel, P. (2000) Egg-shell structure of Paussinae and other Carabidae, with notes on its phylogenetic relevance (Coleoptera). *Natural History and Applied Ecology of Carabid Beetles* (ed. by P. Brandmayr), pp. 111–122. Pensoft Publishers, Sofia, Moscow.
- Kavanaugh, D.H. (1986) A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. *Proceedings of the California Academy of Sciences*, **44**, 67–109.
- Kavanaugh, D.H. & Erwin, T.L. (1991) The tribe Cicindini Bänninger (Coleoptera: Carabidae): comparative morphology, classification, natural history, and evolution. *Proceedings of the Entomological Society of Washington*, **93**, 356–389.
- Kirejtshuk, A.G. & Prokin, A.A. (2018) The position of the Palaeozoic genus *Tunguskagyris* Yan, Beutel et Lawrence in the family Triaplidae sensu n. (Coleoptera, Archostemata: Schizophoroidea). *Entomological Review*, **98**, 872–882.
- Komarek, A. & Beutel, R.G. (2007) Problems in taxonomy and suggestions for a standardized description of new insect taxa. *Entomological Problems*, **36**, 55–70.
- Korschelt, E. (1923–1924) *Bearbeitung einheimischer Tiere. Erste Monographie: Der Gelbrand Dytiscus marginalis L. Bd. 1 (1923), Bd. 2 (1924)*. W. Engelmann, Leipzig.
- Krell, F.T. & Brookhart, J.O. (2012) The plateau giant tiger beetle, *Amblycheila picolomini* Reiche, 1839, in Utah: new state record (Coleoptera: Carabidae: Cicindelinae). *Western North American Naturalist*, **72**, 110–111.
- Larsén, O. (1966) On the morphology and function of locomotor organs of the Gyrinidae and other Coleoptera. *Opuscula Entomologica Supplementum*, **30**, 1–241.
- Lawrence, J.F. & Newton, A.F.J. (1982) Evolution and classification of beetles. *Annual Review of Ecology and Systematics*, **13**, 261–290.
- Lawrence, J.F. & Newton, A.F. Jr (1995) Families and subfamilies of Coleoptera (with Selected genera, notes, references and data on family-group names). *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson* (ed. by J. Pakaluk and S.A. Ślipiński), pp. 634–797. Muzeum i Instytut Zoologii PAN, Warszawa.
- Leys, R., Watts, C.H.S., Cooper, S.J.B. & Humphreys, W.F. (2003) Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. *Evolution*, **57**, 2819–2834.
- Lindroth, C.H. (1960) The larva of *Trachypachus* Mtsch., *Gehringia* Darl., and *Opisthius* Kirby (Col. Carabidae). *Opuscula Entomologica*, **25**, 30–42.
- Lindroth, C.H. (1961–1969) The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Parts 1–6. *Opuscula Entomologica* XIVIII + 1192 pp. 1961, Part 2, Suppl. 20: 1–20; 1963, Part 3, Suppl. 24: 201–408; 1966, Part 4, Suppl. 29: 409–648; 1968, Part 5, Suppl. 33: 649–944; 1969 Part 6, Suppl. 34: 945–1192; 1969 Part 1, Suppl. 35 I + XIVIII.
- Liu, S.P., Wipfler, B. & Beutel, R.G. (2018) The unique locomotor apparatus of whirligig beetles of the tribe Orectochilini (Gyrinidae, Coleoptera). *Journal of Zoological Systematics and Evolutionary Research*, **56**, 196–208.
- López-López, A. & Vogler, A.P. (2017) The mitogenome phylogeny of Adephaga (Coleoptera). *Molecular Phylogenetics and Evolution*, **114**, 166–174.
- Maddison, D.R., Baker, M.D. & Ober, K.A. (1999) Phylogeny of carabid beetles as inferred from 18S ribosomal DNA (Coleoptera: Carabidae). *Systematic Entomology*, **24**, 103–138.
- Maddison, D.R., Kanda, K., Boyd, O.F., Faille, A., Porch, N., Erwin, T.L. & Roig-Juñent, S. (2019) Phylogeny of the beetle supertribe Trechitae (Coleoptera: Carabidae): unexpected clades, isolated lineages, and morphological convergence. *Molecular Phylogenetics and Evolution*, **132**, 151–176.
- Maddison, W.P. & Maddison D.R. (2018) Mesquite: a modular system for evolutionary analysis. Version 3.51. <http://www.mesquiteproject.org>
- Maddison, D.R., Moore, W., Baker, M.D., Ellis, T.M., Ober, K.A., Cannone, J.J. & Gutell, R.R. (2009) Monophyly of terrestrial adepghan beetles as indicated by three nuclear genes (Coleoptera: Carabidae and Trachypachidae). *Zoologica Scripta*, **38**, 43–62.
- McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Farrell, B.D. et al. (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, **40**, 835–880.
- McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Beutel, R.G. et al. (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences*.
- Michat, M.C., Alarie, Y., Jia, F., Xu, S., Hajek, J. & Balke, M. (2014) Description of the second and third instars of *Aspidytes wraesei* Balke, Ribera & Beutel, 2003, with comments on the identification of larvae of *Aspidytes* Ribera, Beutel, Balke & Vogler, 2002 (Coleoptera: Aspidytidae), and phylogenetic considerations. *Zootaxa*, **3881**, 362–372.
- Miller, K.B. (2001) On the phylogeny of the Dytiscidae (Insecta: Coleoptera) with emphasis on the morphology of the female reproductive system. *Insect Systematics and Evolution*, **32**, 45–92.
- Miller, K.B. (2009) On the systematics of Noteridae (Coleoptera: Adephaga: Hydradephaga): phylogeny, description of a new tribe, genus and species, and survey of female genital morphology. *Systematics and Biodiversity*, **7**, 191–214.
- Miller, K.B. & Bergsten, J. (2014) The phylogeny and classification of predaceous diving beetles. *Ecology, Systematics, and the Natural History of Predaceous Diving Beetles (Coleoptera: Dytiscidae)* (ed. by D. Yee), pp. 49–172. Springer, Dordrecht.
- Miller, K.B. & Bergsten, J. (2016) *Diving Beetles of the World: Systematics and Biology of the Dytiscidae*. John Hopkins University Press, Baltimore.
- Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Zhou, X. et al. (2014) Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.
- Moore, B.P. (1979) Chemical defense in carabids and its bearing on phylogeny. *Carabid Beetles: Their Evolution, Natural History, and Classification* (ed. by T.L. Erwin, G.E. Ball, G.E. Whitehead and A.L. Halpern), pp. 193–203. Dr. W. Junk, The Hague.
- Nachtigall, W. (1960) Über Kinematik, Dynamik und Energetik des Schwimmens einheimischer Dytisciden. *Journal of Comparative Physiology A*, **43**, 48–118.

- Nachtigall, W. (1961) Funktionelle Morphologie, Kinematik und Hydromechanik des Ruderapparates von *Gyrinus*. *Zeitschrift für Vergleichende Physiologie*, **45**, 193–226.
- Niehuis, O., Hartig, G., Grath, S., Pohl, H., Lehmann, J., Misof, B. *et al.* (2012) Genomic and morphological evidence converge to resolve the enigma of Strepsiptera. *Current Biology*, **22**, 1309–1313.
- Nixon, K.C. (1999) Winclada (BETA) ver. 0.9.9 Published by the author, Ithaca, N.Y.
- Noars, R. (1956) Contribution à la connaissance de la larve d'*Orectochilus villosus* Müll. Coléoptères Gyrinides. *Travaux du Laboratoire de Zoologie et de la Station Aquicole Grimaldi de la Faculté des Sciences de Dijon*, **17**, 1–32.
- Ober, K.A. (2002) Phylogenetic relationships of the carabid subfamily Harpalinae (Coleoptera) based on molecular sequence data. *Molecular Phylogenetics and Evolution*, **24**, 228–248.
- Ober, K.A. & Maddison, D.R. (2008) Phylogenetic relationships of tribes within Harpalinae (Coleoptera: Carabidae) as inferred from 28S ribosomal DNA and the wingless gene. *Journal of Insect Science*, **8**, 1–32.
- Ochs, G. (1969) Zur Ethökologie der Taumelkäfer (Col., Gyrinoidea). *Archiv für Hydrobiologie Supplementum XXXV*, **4**, 373–410.
- Omer-Cooper, J. (1934) Notes on the Gyrinidae. *Odbitka Archiwum Hydrobiologii i Rybactwa*, **8**, 1–26.
- Peters, R.S., Meusemann, K., Petersen, M., Wilbrandt, J., Ziesmann, J., Misof, B. *et al.* (2014) The evolutionary history of holometabolous insects inferred from transcriptome-based phylogeny and comprehensive morphological data. *BMC Evolutionary Biology*, **14**, 52.
- Ponomarenko, A.G. (1977) Suborder Adephaga, etc., pp. 1–158. *Mesozoic Coleoptera (in Russian)*, Vol. **161** (ed. by L.V. Arnoldi, V.V. Zherikin, L.M. Nikritin and A.G. Ponomarenko), pp. 1–204. Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, Moscow.
- Ponomarenko, A.G. & Prokin, A.A. (2015) Review of paleontological data on the evolution of aquatic Coleoptera. *Paleontological Journal*, **49**, 1383–1412.
- Prokin, A.A., Makarov, K.V., Ponomarenko, A.G. & Bashkuev, A.S. (2013a) New beetle larvae (Coleoptera: Coptoclauidae, Carabidae, Polyphaga) from the upper Triassic of Germany. *Russian Entomological Journal*, **22**, 259–274.
- Prokin, A.A., Petrov, P.N., Wang, B. & Ponomarenko, A.G. (2013b) New fossil taxa and notes on the Mesozoic evolution of Liadytidae and Dytiscidae (Coleoptera). *Zootaxa*, **3666**, 137–159.
- Prokin, A.A., Ponomarenko, A.G. & Kirejtshuk, A.G. (2019) Description of a larva of *Kargalarva permiosialis* gen. et. sp. nov. (Coleoptera: Schizophoromorpha) from the Kargala fossil site. *Paleontological Journal*, **53**, 282–286.
- Ribera, I. & Nilsson, A.N. (1995) Morphometric patterns among diving beetles (Coleoptera: Noteridae, Hygrobiidae, Dytiscidae). *Canadian Journal of Zoology*, **73**, 2343–2360.
- Ribera, I., Beutel, R.G., Balke, M. & Vogler, A.P. (2002b) Discovery of Aspidytidae, a new family of aquatic Coleoptera. *Proceedings of the Royal Society, London*, **269**, 2351–2356.
- Ribera, I., Foster, G.N. & Holt, W.V. (1997) Functional types of diving beetle (Coleoptera: Hygrobiidae and Dytiscidae), as identified by comparative swimming behaviour. *Biological Journal of the Linnean Society*, **61**, 537–558.
- Ribera, I., Hogan, J.E. & Vogler, A.P. (2002a) Phylogeny of Hydradephagan water beetles inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution*, **23**, 43–62.
- Ribera, I., Mateu, J. & Bellés, X. (2005) Phylogenetic relationships of *Dalyat mirabilis* Mateu, 2002, with a revised molecular phylogeny of ground beetles (Coleoptera, Carabidae). *Journal of Zoological Systematics and Evolutionary Research*, **43**, 284–296.
- Ribera, I., Vogler, A.P. & Balke, M. (2008) Phylogeny and diversification of diving beetles (Coleoptera: Dytiscidae). *Cladistics*, **24**, 563–590.
- Roughley, R.E. (1981) Trachypachidae and Hydradephaga (Coleoptera): a monophyletic unit? *Pan-Pacific Entomologist*, **57**, 273–285.
- Ruhnau, S. (1985) Zur Morphologie und Biologie der praeimaginellen Stadien des Wasserkäfers *Noterus crassicornis* (Müller, 1776) (Coleoptera, Hydradephaga, Noteridae). 99 pp., unpubl. Diplomarbeit, Fakultät für Biologie, Universität Tübingen.
- Ruhnau, S. (1986) Phylogenetic relations within the Hydradephaga (Coleoptera) using larval and pupal characters. *Entomologica Basiliensia*, **11**, 231–272.
- Saxod, R. (1964) L'oeuf, l'éclosion, la cuticule embryonnaire et la larve néonate de *Gyrinus substriatus* Steph. *Travaux du Laboratoire d'Hydrobiologie et de Pisciculture de l'Université de Grenoble*, **56**, 17–28.
- Schildknecht, H., Winkler, H. & Maschwitz, U. (1968) Vergleichend chemische Untersuchungen der Inhaltsstoffe der Pygidialwehrblasen von Carabiden. *Zeitschrift für Naturforschung B*, **23**, 637–644.
- Seeger, W. (1971a) Autökologische Laboruntersuchungen an Halipliden mit zoogeographischen Anmerkungen (Haliplidae: Coleoptera). *Archiv für Hydrobiologie*, **68**, 528–574.
- Seeger, W. (1971b) Morphologie, Bionomie und Ethologie von Halipliden, unter besonderer Berücksichtigung funktionsmorphologischer Gesichtspunkte (Haliplidae: Coleoptera). *Archiv für Hydrobiologie*, **68**, 400–435.
- Sharov, A.G. (1953) The discovery of Permian larvae of alderflies (Megaloptera) from Kargala. *Doklady Akademii Nauk SSSR*, **89**, 731–732.
- Sharp, D. (1882) On aquatic carnivorous Coleoptera or Dytiscidae. *The Scientific Transactions of the Royal Dublin Society*, **2**, 178–1003 + pls. 6–14.
- Shelford, V.E. (1908) Life histories and larval habits of the tiger beetle (Cicindelidae). *Zoological Journal of the Linnean Society of London*, **30**, 157–184.
- Shull, V.L., Vogler, A.P., Baker, M.D., Maddison, D.R. & Hammond, P.M. (2001) Sequence alignment of 18S ribosomal RNA and the basal relationships of adephagan beetles: evidence for monophyly of aquatic families and the placement of Trachypachidae. *Systematic Biology*, **50**, 945–969.
- Spangler, P.J. & Steiner, W.E. (2005) A new aquatic beetle family, Meruidae from Venezuela. *Systematic Entomology*, **30**, 339–357.
- Spence, J.R. & Sutcliffe, J.F. (1982) Structure and function of feeding in larvae of *Nebria* (Coleoptera: Carabidae). *Canadian Journal of Zoology*, **60**, 2382–2394.
- Speyer, W. (1922) Die Muskulatur der Larve von *Dytiscus marginalis* L. *Zeitschrift für Wissenschaftliche Zoologie*, **119**, 423–492.
- Stork, N.E. (1982) Discovery of *Cicindis*, a remarkable carabid beetle, in Kuwait. *Journal of Natural History*, **16**, 883–885.
- Tautz, D., Arctander, P., Minelli, A., Thomas, R.H. & Vogler, A.P. (2002) DNA points the way ahead in taxonomy. *Nature*, **418**, 479.
- Toussaint, E.F.A., Beutel, R.G., Morinière, J., Jia, F., Xu, S., Balke, M. *et al.* (2016) Molecular phylogeny of the highly disjunct cliff water beetles (Coleoptera, Aspidytidae) and description of *Sinaspidytes* gen nov. for the Chinese lineage. *Zoological Journal of the Linnean Society*, **176**, 537–546.
- Tröster, G. (1987) Skelett und Muskulatur des Kopfes der Larve von *Pterostichus nigrita* (Paykull) (Coleoptera: Carabidae). *Stuttgarter Beiträge zur Naturkunde*, **399**, 1–23.
- Uéno, S.I. (1957) Blind aquatic beetles of Japan, with some accounts of the fauna of Japanese subterranean waters. *Archiv für Hydrobiologie*, **53**, 250–296.

- Uéno, S.I. (1996) New phreatobiotic beetles (Coleoptera, Phreatodytidae and Dytiscidae) from Japan. *Journal of the Speleological Society of Japan*, **21**, 1–50.
- Vasilikopoulos, A., Balke, M., Beutel, R.G., Donath, A., Podsiadlowski, L., Misof, B. *et al.* (2019) Phylogenomics of the superfamily Dytiscoidea (Coleoptera: Adephaga) with an evaluation of phylogenetic conflict and systematic error. *Molecular Phylogenetics and Evolution*, **135**, 270–285.
- Vogler, A.P. & Pearson, D.L. (1996) A molecular phylogeny of the tiger beetles (Cicindelidae): congruence of mitochondrial and nuclear rDNA data sets. *Molecular Phylogenetics and Evolution*, **6**, 321–338.
- Volkov, A.N. (2013) New species of Triaplidae from the Babii Kamen locality (Kuznetsk Basin). *Paleontological Journal*, **47**, 94–97.
- Vondel, B. v. (2016) 7.2. Haliplidae Aubé, 1836. *Coleoptera, Vol. 1: Morphology and Systematics Archostemata, Adephaga, Myxophaga, Polyphaga (partim) Handbook of Zoology Vol. IV, Arthropoda: Insecta*, 2nd ed. (ed. by N.P. Kristensen and R.G. Beutel, vol. eds. R.G. Beutel and R.A.B. Leschen), pp. 89–98. Walter De Gruyter, Berlin, New York.
- Vondel, B. v. (2019) Features of the metacoxal airstorage space as additional characters for reconstructing the phylogeny of Haliplidae (Coleoptera). *Tijdschrift voor Entomologie*, **162**, 13–32.
- Ward, R.D. (1979) Metathoracic wing structures as phylogenetic indicators in the Adephaga (Coleoptera). *Carabid Beetles: Their Evolution, Natural History, and Classification* (ed. by T.L. Erwin, G.E. Ball, G.E. Whitehead and A.L. Halpern), pp. 181–191. W. Junk, The Hague.
- Wiegmann, B.M., Trautwein, M.D., Kim, J.W., Cassel, B.K., Bertone, M.A., Winterton, S.L. & Yeates, D.K. (2009) Single-copy nuclear genes resolve the phylogeny of the holometabolous insects. *BMC Biology*, **7**, 34.
- Yan, E.V., Beutel, R.G. & Lawrence, J.F. (2018) Whirling in the late Permian: ancestral Gyrinidae show early radiation of beetles before Permian-Triassic mass extinction. *BMC Evolutionary Biology*, **18**, 33.
- Yavorskaya, M., Beutel, R.G. & Polilov, A. (2017) Head morphology of the smallest beetles (Coleoptera: Ptiliidae) and the evolution of sporophagy within Staphyliniformia. *Arthropod Systematics and Phylogeny*, **75**, 417–434.
- Yavorskaya, M.I., Anton, E., Jałoszyński, P., Polilov, A. & Beutel, R.G. (2018) Cephalic anatomy of Sphaeriusidae and a morphology-based phylogeny of the suborder Myxophaga (Coleoptera). *Systematic Entomology*, **43**, 777–797.
- Zhang, S.Q., Che, L.H., Li, Y., Liang, D., Pang, H., Ślipiński, A. & Zhang, P. (2018) Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications*, **9**, 205.
- Zimmermann, A. (1924) Die Halipliden der Welt. Bestimmungstabellen der Haliplidae mit gleichzeitig beigefügten Detailbeschreibungen der einzelnen Arten. *Entomologische Blätter*, **20**, 1–16, 65–80, 129–144 193–213.

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