THE ROYAL SOCIETY FirstCite® e-publishing

Received 24 May 2002
Accepted 7 August 2002
Published online

Discovery of Aspidytidae, a new family of aquatic Coleoptera

I. Ribera[1,2*], R. G. Beutel[3], M. Balke[1,4] and A. P. Vogler[1,2]

[1]*Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[2]*Department of Biology, Imperial College, Silwood Park, Ascot SL5 7PY, UK*
[3]*Institut für Spezielle Zoologie und Evolutionsbiologie, Erbertstrasse 1, 07743 Jena, Germany*
[4]*Zoologische Staatssammlung München, Münchhausenstrasse 21, München 81247, Germany*

The six extant aquatic families of Hydradephaga (Coleoptera) known so far represent a diverse group of beetles morphologically highly modified for life in the water. We report the discovery of a new genus with two species from South Africa and China, which differ greatly from all extant families, but resemble the Jurassic–Cretaceous †Liadytidae (the dagger symbol indicates that the taxa are known only as fossils). Based on a combined phylogenetic analysis of molecular and morphological data we erect a new family, Aspidytidae, which is the sister group of Dytiscidae plus Hygrobiidae. We propose a new scenario for the evolution of swimming behaviour in adephagan beetles, in which the transition into the aquatic environment is followed by complex and repeated changes in lifestyles, including the secondary complete loss of swimming ability in Aspidytidae.

Keywords: Coleoptera: Adephaga; Hydradephaga relationships; biodiversity; new species, genus and family; simultaneous phylogenetic analysis; evolution of swimming

1. INTRODUCTION

Over one-third of all described animal species are beetles, with estimates of the total number of species ranging from 1 to 30 million (Hammond 1994; Novotny *et al.* 2002). Although most of these remain undescribed, new high-level groups of Coleoptera are rarely discovered. In the suborder Adephaga (ground beetles, diving beetles and allies), representatives of almost all the currently accepted families (Lawrence & Newton 1995) had been described by the end of the 1700s, with only the Amphizoidae unknown until 1853.

Most adephagan species occur in terrestrial habitats, but *ca*. 5500 species in six extant families, generally referred to as Hydradephaga, live in aquatic environments (Guignot 1933; Crowson 1981). Hydradephagan beetles are usually characterized by a hydrodynamically shaped body and fringes of swimming hairs on their middle and hind legs, which facilitate locomotion in the aquatic medium. However, these traits differ widely between groups, reflecting the diversity of habitats, life strategies and swimming behaviours. The diversity of hydradephagan beetles ranges from groups that lack swimming ability (Amphizoidae), through poor (Haliplidae) and moderate (Hygrobiidae) swimmers, to the advanced swimming in Dytiscidae (diving beetles), Gyrinidae (whirligig beetles) and some Noteridae. These groups typically exhibit a streamlined body, flattened hind legs with swimming hairs, strong hind-leg muscles and synchronous leg movements (Ribera & Nilsson 1995). The Gyrinidae exhibit several spectacular adaptations to swimming on the water surface. The great diversity of swimming strategies has also brought into question the monophyly of the aquatic families, where morphological studies mostly support at least two, if not three (Beutel 1997), independent transitions to the aquatic medium. However, traditional taxonomy (Crowson 1981) and more recent molecular studies (Shull *et al.* 2001; Ribera *et al.* 2002) suggest the monophyly of all hydradephagan families and imply a single aquatic origin.

Whereas representatives of the larger families (such as Dytiscidae, with *ca*. 4000 species, or Gyrinidae, with *ca*. 1000 species) can be found in almost every running and standing water body worldwide, some families have very restricted distributions. There are only six species of Amphizoidae, three from China and three from western North America. Similarly, Hygrobiidae are species poor and widely scattered geographically, with four species in Australia, one in China and one in the western Palaearctic.

In addition, not all habitat types are equally abundant, nor have they been studied with equal intensity. In particular, hygropetric (rocks overflowing with water) habitats have only recently received more attention and this has led to the discovery of a set of uniquely adapted species from various aquatic families, among them Dytiscidae. They usually exhibit characteristic morphological features, including the loss of proper swimming abilities, reduction of swimming hairs on the legs, and shorter and more robust body appendages (Balke *et al.* 1997).

Here, we describe a new genus and species obtained from this kind of habitat in the Cape region of Southern Africa. We demonstrate, based on morphological and DNA characters, that this genus has no close extant relatives. It is therefore necessary to establish a new taxonomic group within the suborder Adephaga at the level of a family, for the first time since the Amphizoidae was described 150 years ago. This discovery adds significantly to our knowledge of biological diversity, and, because of the phylogenetic position of the new taxon, it also helps our understanding of the evolution of swimming behaviour in Hydradephaga.

* Author for correspondence (i.ribera@nhm.ac.uk).

02PB0426.1

2. MATERIAL AND METHODS

(a) *Morphology*

Scanning electron micrographs (SEMs) were taken with a LEO 1430VP and a FEI ESEM XL 30. We made drawings using a Leitz MZ12 dissecting microscope equipped with a camera lucida.

(b) *Phylogenetic analysis*

DNA was extracted non-destructively and used for PCR amplification. To determine phylogenetic relationships of the new taxon we obtained sequences of the complete 18S rRNA gene and partial 16S rRNA (*ca*. 510 bp) and cytochrome oxydase I (COI) (*ca*. 750 bp) genes for all families of aquatic Adephaga, with good representation of the basal lineages (Ribera *et al.* 2002). PCR amplification and DNA sequencing were as described in Shull *et al.* (2001) and Ribera *et al.* (2002). PCR primers for the 18S rRNA gene were from Shull *et al.* (2001), and primers for 16S rRNA and COI from Ribera *et al.* (2001). New sequences were deposited in GenBank under accession numbers AY071769–AY071818.

Phylogenetic analysis was performed using a one-step tree-alignment procedure (Sankoff 1975; Wheeler 1996), using Poy software (Gladstein & Wheeler 1997). Owing to the high variability, the hypervariable regions V4 and V6 (Tautz *et al.* 1988) of the 18S rRNA gene were excluded from the analyses. We assessed sensitivity to four different gap costs (1, 2, 5 and 10) and six weighting schemes (relative weights of 18S, 16S and COI genes 1 : 1 : 1, 5 : 1 : 1 and 5 : 5 : 1, respectively, including and excluding third positions in COI) (Wheeler 1995; Phillips *et al.* 2000). Within these 24 parameter combinations, the preferred settings were selected according to two criteria (Wheeler 1995): maximum congruence among genes (as measured with the incongruence–length difference test; Farris *et al.* 1995), and congruence with accepted independent (morphological) evidence, specifically the monophyly, respectively, of Gyrinidae, Haliplidae, Noteridae, Amphizoidae, Hygrobiidae and Dytiscidae. Molecular and morphological data were combined in a simultaneous analysis in Poy, using the preferred parameter combinations obtained in the above analysis. All searches were performed with Poy v. 2.0 on a multiprocessor computer running in parallel. Bootstrap and partitioned Bremer support values (Bremer 1994) were obtained for the combined molecular and morphology dataset in PAUP v. 4.0b8 (Swofford 1998) under the preferred parameter conditions, using a matrix generated with the 'impliedalignment' option in Poy.

3. RESULTS

(a) *Taxonomy*

(i) Aspidytes *gen. nov.*

Type species: *Aspidytes niobe* sp. nov. Western Cape Province, Republic of South Africa. An additional undescribed species is known from Shaanxi Province, China (Balke *et al.* 2002).

Diagnosis: mesal walls of metacoxae extensively fused; pedicellus very short and partly enclosed by scapus (figure 1*c*); legs without swimming hairs (figure 1*a*); transverse suture (very weakly impressed) and corresponding internal ridge of metaventrite present, median part of metacoxae elevated (figure 1*b*). *Aspidytes* can be readily separated from any genera of the other extant families of Dytiscoidea (Noteridae, Amphizoidae, Hygrobiidae, Dytiscidae (Lawrence & Newton 1995); table 1; see Balke *et al.* (2002) for a key and discussion of morphology; full character matrix and references available at http://www.bio.ic.ac.uk/research/apvogler/vogler.htm and upon request). Similarities exist to fossil †Liadytidae, a dytiscoid family recorded from the Jurassic (Toarcian, 187 Myr ago) to the Cretaceous (Albian, 97 Myr ago) (Ponomarenko 1977; Labandeira 1994). †*Liadytes* and *Aspidytes* share a broad lateral part of the metathoracic praeepisternum, a very similar metacoxal structure, a metathoracic anepisternum that reaches the midcoxal cavities, a transverse suture of the metaventrite (evident in *Aspidytes* mostly internally as the division of prae- and katepisternum III), and thin and longish metatibiae and tarsi. However, the inclusion of *Aspidytes* in the Liadytidae is not supported by any apomorphy shared only by these groups, and the shared characters are known to be present in other, unrelated, lineages. The character most clearly identifying *Aspidytes* (configuration of scapus and pedicellus) is not observable in the known specimens of †*Liadytes*.

Etymology: from the Greek *aspis* (shield) and *dytes* (diver).

(ii) Aspidytes niobe *sp. nov.*

Material studied: holotype male (in Natural History Museum, London (NHM)) from 7 km southwest of Ceres and paratype male (Naturhistorisches Museum, Wien) and female (NHM) from Limiet Berge, 19 km northeast of Wellington. Both sites are in the Western Cape Province, South Africa, I. Ribera & A. Cieslak leg. 24.3.2001. DNA extractions of both males are stored in the tissue collection of the NHM (IR600, IR627).

Diagnosis: prosternal process widest caudally, subtriangular in shape; metacoxal plates with round apex, margin regularly curved; median lobe of aedeagus asymmetrical, parameters flat and wide (see Balke *et al.* (2002) for a detailed account of morphology).

Etymology: Níobe, queen of Tebas, was still covered in tears after being transformed to stone.

(b) *Phylogenetic relationships of* Aspidytes

The parameters for sequence alignment and character weighting for which the incongruence–length difference was minimized were: weight of 18S rRNA = 5, 16S rRNA and COI = 1; third codon positions excluded from COI; gap cost = 2. The final length of the aligned sequences was 2894 bp, of which 507 bp were parsimony informative. Under these conditions, two equally parsimonious trees of cost = 5824 were found (CI = 0.66, RI = 0.65, partition homogeneity test not significant, $p = 0.94$). *Aspidytes niobe* was placed within superfamily Dytiscoidea, as sister of Dytiscidae plus Hygrobiidae (figure 2). Trees obtained under the five next-best parameter combinations consistently placed *Aspidytes* sister to Hygrobiidae and Dytiscidae. An alternative position of *Aspidytes* was as sister to *Amphizoa*, which was obtained under the character combination that ranked ninth out of the 24 tested, whereas under the seventh and eighth highest scoring parameter settings Dytiscidae were paraphyletic with respect to two or more other families.

A morphological matrix including 49 adult and larval characters was compiled from Beutel (1990), Belkaceme

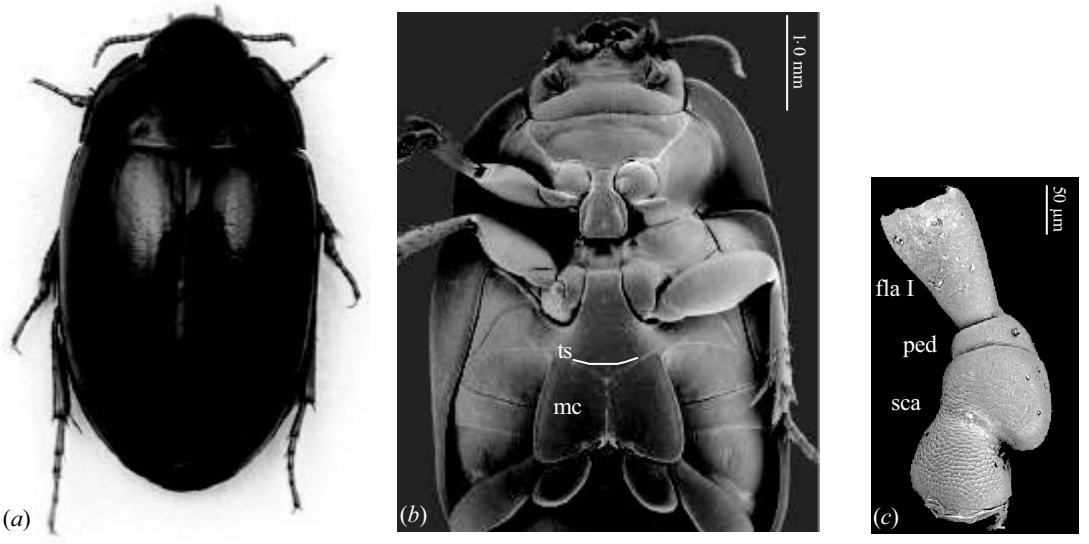

Figure 1. (*a*) *Aspidytes niobe*, new species, habitus of holotype. (*b*) *Aspidytes niobe*, new species, SEM of paratype male from Limiet Berge, South Africa, ventral view: mc, metacoxal plates; ts, position of the internal transverse suture of metaventrite, highlighted by white line. (*c*) *Aspidytes* sp. (undescribed Chinese species). SEM of female paratype: sca, configuration of scapus; ped, pedicellus; fla I, flagellomere I.

Table 1. Synoptic distribution of main morphological characters in hydradephagan families.
(Characters (C): 1, elongated head with protruding eyes (0), shortened and rounded laterally (1); 2, pedicellus not partly enclosed by scapus (0), partly enclosed by scapus (1); 3, prosternal process narrow and short (0), well developed (1); 4, pro- and metasternal process not in contact (0), in contact (1); 5, prothoracic defence glands absent (0), present (1); 6, mesoventrite large and flat (0), narrow with hexagonal groove (1); 7, mesocoxal cavity disjunct (0), complex (1); 8, mesocoxa triangular (0), globular or conical and sunk in deep cavities (1); 9, mesal metacoxal walls not fused or with small area of fusion (0), extensively fused (1); 10, metafurcal origin in metaventrite (0), intercoxal septum (1); 11, metasternal transverse ridge complete (0), partly reduced (1), absent (2); 12, cranial expansion of metacoxae absent (0), moderately expanded (1), strongly expanded (2); 13, metacoxal plates absent (0), moderately large (1), strongly enlarged (2), largely reduced (3); 14, swimming hairs absent (0), sparse fringes (1), dense fringes (2), feather-like (3), lamellae (4); 15, hind legs slender (0), broadened and flattened (1), with oar-like extension (2), short paddles (3). In parentheses, characters of *Spanglerogyrus* (Gyrinidae) and *Phreatodytes* (Noteridae). Some highly derived subterranean or terrestrial genera of Dytiscidae not scored.)

C	Gyrinidae	Haliplidae	Noteridae	Amphizoidae	Aspidytidae	†Liadytidae	Hygrobiidae	Dytiscidae
1	1	0	1	0	1	1	0	1
2	0	0	0	0	1	?	0	0
3	0	1	1	1	1	1	1	1
4	0	1	1(0)	0	0	0	1	1
5	0	0	0	0	0	?	1	1
6	0	1	1	1	1	1	1	1
7	0	0	0	1	1	1	0	0/1
8	0	1	1	1	1	1	1	1
9	0	0	1	1	1	1	1	1
10	0	0	1	1	1	1	1	1
11	2(0)	0	2	1	1	1	1	2
12	1/2(0)	0	2	1	1	1	1	2
13	0	2	1	1	1	1	3	3
14	4(3)	2	1/2(0)	1	0	2	2	2
15	3(2)	0	0/1	0	0	0	1	1

(1991), Beutel & Haas (1996) and original observations (full character matrix and references available at http://www.bio.ic.ac.uk/research/apvogler/vogler.htm). Parsimony analysis resulted in 226 trees of 89 steps (CI = 0.86, RI = 0.95), with the same topology as the preferred molecular tree, but with the node separating Amphizoidae, *Aspidytes* and Hygrobiidae plus Dytiscidae unresolved in the strict consensus. The internal topology of the families was either unresolved (Dytiscidae) or identical to that obtained with the molecular dataset (all other families).

Terminal taxa in the morphological study correspond to those used in the molecular analyses at the genus level. A simultaneous analysis of both datasets resulted in a single tree with the same topology as that obtained from molecular data. The tree from the simultaneous analysis was only one step longer than the sum of the separate analyses (partition homogeneity test not significant, $p = 0.98$), indi-

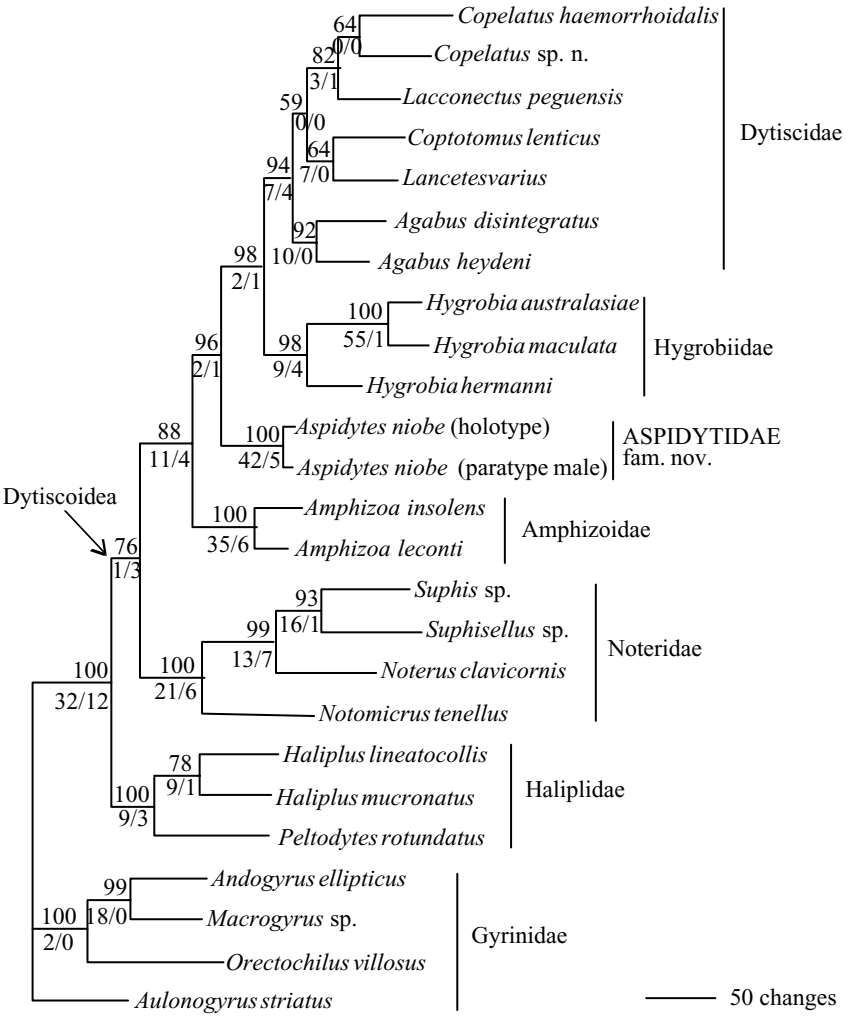

Figure 2. Single tree obtained in the simultaneous analysis of the molecular and morphological dataset, with the optimal parameter combination obtained in the molecular analysis (weight of 18S rRNA = 5, 16S rRNA, COI and morphology = 1; third codon positions excluded from COI; gap cost = 2). The tree is rooted on Gyrinidae, which are clearly basal to Dytiscoidea (Beutel 1997; Ribera *et al.* 2002). Branch lengths refer to molecular data only. Numbers above branches, bootstrap support values; below branches, partitioned Bremer support values (combined molecular/morphology).

cating minimal conflict between the two datasets. Most nodes had high Bremer and bootstrap support, including a 96% support value for the node determining the position of *Aspidytes* (figure 2).

(i) *Aspidytidae fam. nov.*

According to the morphological and phylogenetic evidence provided above, we classified our discovery as follows: Insecta; Coleoptera; Suborder Adephaga; Superfamily Dytiscoidea; Aspidytidae fam. nov. ('cliff water beetles'). This is a monogeneric family, erected for the South African *Aspidytes niobe* and an undescribed Chinese species (Balke *et al.* 2002). The diagnosis of the new family is the same as that of the genus *Aspidytes*.

4. DISCUSSION

(a) *Systematics*

Based on its morphology, the placement of *Aspidytes* within Dytiscoidea is strongly supported by the extensively fused mesal walls of the metacoxae. The inclusion in any of the extant families of Dytiscoidea is, however, not possible. The presence of a metasternal transverse ridge excludes it from Dytiscidae and Noteridae. The absence of prothoracic glands also excludes it from Dytiscidae and Hygrobiidae, and the absence of spermathecal glands excludes it from Noteridae. The configuration of the pedicellus and scapus is unique, despite the superficial resemblance to the shortened scapus of Noteridae. Other characters of the meso- and metacoxae also exclude *Aspidytes* from any of the known Dytiscoidea families (table 1; Kavanaugh 1986; Balke *et al.* 2002).

The phylogenetic position of *Aspidytes* as sister to Hygrobiidae plus Dytiscidae has strong support from both the combined molecular and the morphological datasets, with very little conflict between the two. Accepting the convention of taxonomic classification on the basis of monophyly (Hennig 1966), the only alternative to establishing a new family would be the inclusion of Dytiscidae, Hygrobiidae and Aspidytidae in a single family. We consider this possibility to be less desirable, both because of the deep morphological and genetic differences between the three groups, and for reasons of stability, as Hygrobiidae and Dytiscidae have been considered as separate families for more than a century (Franciscolo 1979; Kavanaugh 1986).

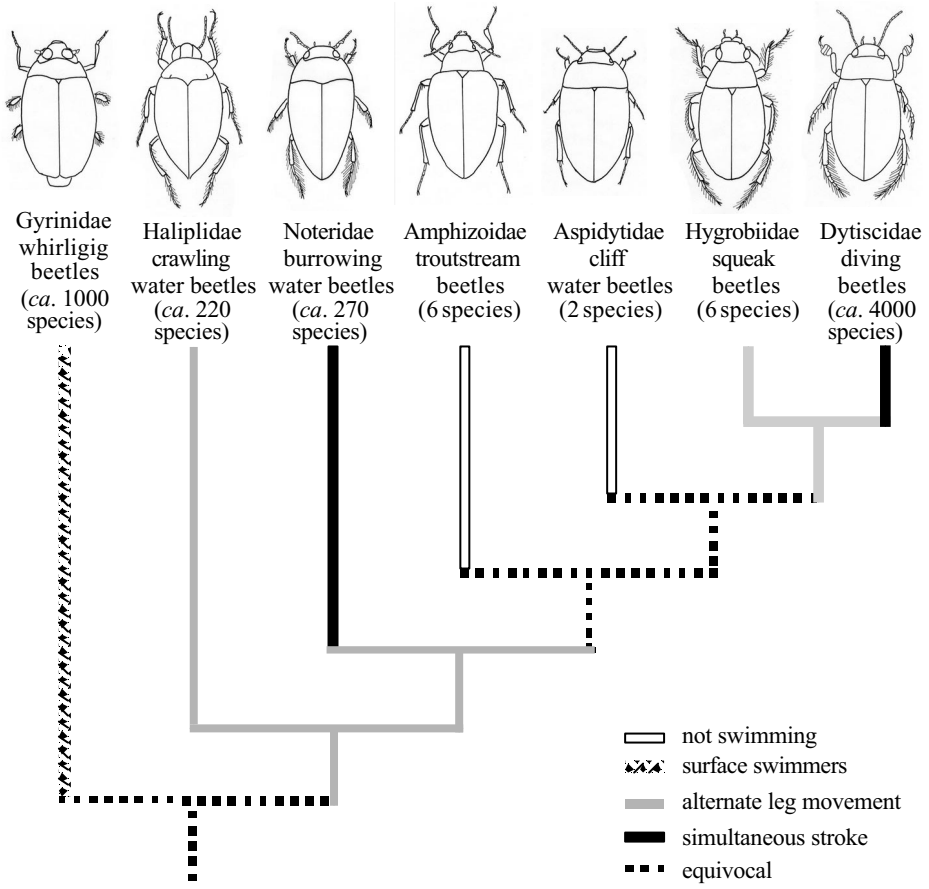

Figure 3. Evolution of swimming behaviour in the aquatic families of Hydradephaga, according to the phylogenetic hypothesis of figure 2. All families have well-developed swimming hairs except Amphizoidae (reduced) and Aspidytidae (absent). Modifications of the legs are different in Haliplidae (very slender, well-developed metacoxal plates, middle legs providing the main thrust) and Hygrobiidae (more robust, metacoxal plates reduced, hind legs providing the main thrust). Higher Noteridae have front legs modified for burrowing.

(b) *Evolution of the swimming behaviour in adephagan beetles*

The cladogram was used to evaluate scenarios for the evolution of swimming behaviour and associated morphological traits in Hydradephaga (figure 3). Once the transition to the aquatic medium had occurred in the stem species of Hydradephaga (Shull *et al.* 2001; Ribera *et al.* 2002), possibly excluding Gyrinidae (Beutel 1990; Beutel & Haas 1996), traditional views support a linear progression within Dytiscoidea from non-swimming forms (Amphizoidae) to imperfect swimming in Hygrobiidae and full swimming in Noteridae and Dytiscidae (Guignot 1933; Franciscolo 1979; also compatible with the phylogeny in Miller (2001); although see Beutel (1997) for an alternative view). We reveal a more complex situation, where idiosyncratic swimming morphologies and behaviours arose independently in various groups, but were constrained by functional requirements leading to convergence.

Basal to all other aquatic families, and possibly unrelated (Beutel 1997), is Gyrinidae, with unique and highly derived specializations for locomotion in the water surface film. Species of Haliplidae retain primitive swimming abilities, with slender legs that are moved alternately, similar to basal groups of Noteridae. Derived genera of Noteridae have advanced swimming abilities, with simultaneous movements of the middle and hind legs (Belkaceme 1991), and front legs adapted for burrowing. An independent origin of simultaneous leg movements is inferred in the Dytiscidae, which, together with gyrinids, have the most advanced swimming abilities (Nachtigall 1961; Balke 2003).

Hygrobiidae, as sister of Dytiscidae, retain alternate leg movements and exhibit dense fringes of long swimming hairs on all legs, with the forelegs developed for burrowing, similarly to 'higher' Noteridae. Finally, Amphizoidae and Aspidytidae live in fast-flowing rivers and on hygropetric surfaces, respectively, but are entirely unable to swim. Amphizoids exhibit very sparse fringes of swimming hairs, which are entirely absent in Aspidytidae. The phylogenetic placement of Amphizoidae and Aspidytidae amidst a clade of moderate ('basal' Noteridae, Hygrobiidae) and good swimmers indicates that swimming abilities and some associated morphological traits have been lost secondarily, possibly independently in each of the two groups.

Transitions into novel life zones produce opportunities for diversification (Simpson 1953). The spectacular ecological and morphological diversity of hydradephagan beetles was enhanced by independent and convergent diversification of aquatic life forms, rather than progressive refinement in a single lineage. However, the adaptive radiation of Hydradephaga, with 5500 species compared with over 24 000 species in their terrestrial counterpart

(Geadephaga), can hardly be considered an evolutionary success with regard to their taxonomic diversity. Aspidytidae remains a small apparently relictual group, but the finding of two species of *Aspidytes* in different parts of the globe highlights our ignorance of biological diversity in extreme or rare habitats and these habitats' importance for understanding the evolution and diversification process of extant lineages.

Alexandra Cieslak found the male paratype of *A. niobe*. Manfred A. Jäch trusted us with the Chinese species for study and helped in many ways. We thank Peter Forey, Peter Hammond and John Lawrence for comments on the manuscript. Konrad Dettner helped with the dissection of the prothorax. Kosmas Theodorides helped to compose the genus name. This work was supported by the Leverhulme Trust, FAZIT Foundation, Marie Curie fellowships of the EU, NERC and British Airways.

REFERENCES

Balke, M. 2003 Dytiscidae. In *Handbook of zoology*, vol. 3 (ed. R. G. Beutel & R. A. B. Leschen). Berlin: De Gruyter (In the press.)

Balke, M., Dettner, K. & Hendrich, L. 1997 *Agabus 'Metronectes' aubei* Perris: habitat, morphological adaptations, systematics, evolution and notes on the phanaerofluicolous fauna (Coleoptera: Dytiscidae). *Aquat. Insects* **19**, 75–90.

Balke, M., Ribera, I. & Beutel, R. G. 2002 Aspidytidae: on the discovery of a new family of beetles and a key to fossil and extant adephagan families. In *Water beetles of China*, vol. 3 (ed. M. A. Jäch & L. Ji). Vienna: Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein (In the press.)

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 Beitr. Naturk. Ser. A* **462**, 1–94.

Beutel, R. G. 1990 Phylogenetic analysis of the family Gyrinidae (Coleoptera) based on meso- and metathoracic characters. *Quaest. Entomol.* **26**, 163–191.

Beutel, R. G. 1997 Über Phylogenese und evolution der Coleoptera (Insecta), insbesondere der Adephaga. *Abh. Natur. Ver. Hamburg* **31**, 1–164.

Beutel, R. G. & Haas, A. 1996 Phylogenetic analysis of larval and adult characters of Adephaga (Coleoptera) using cladistic computer programs. *Entomol. Scand.* **27**, 197–205.

Bremer, K. 1994 Branch support and tree stability. *Cladistics* **10**, 295–304.

Crowson, R. A. 1981 *The biology of the Coleoptera*. London: Academic Press.

Farris, J. S., Käallersjö, M., Kluge, A. G. & Bult, C. 1995 Testing significance of incongruence. *Cladistics* **10**, 315–319.

Franciscolo, M. E. 1979 *Fauna d'Italia, vol. XIV: Coleoptera Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae*. Bologna, Italy: Edizioni Calderini.

Gladstein, D. S. & Wheeler, W. C. 1997 *POY: the optimization of alignment characters*. New York: American Museum of Natural History.

Guignot, F. 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*. Toulouse, France: Miscellanea Entomologica.

Hammond, P. M. 1994 Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Phil. Trans. R. Soc. Lond.* B **345**, 119–136.

Hennig, W. 1966 *Phylogenetic systematics*. Urbana, IL: University of Illinois Press.

Kavanaugh, D. H. 1986 A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. *Proc. Calif. Acad. Sci.* **44**, 67–109.

Labandeira, C. C. 1994 A compendium of fossil insect families. *Milwaukee Public Mus. Contrib. Biol. Geol.* **88**, 1–71.

Lawrence, J. F. & Newton Jr, A. F. 1995 Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In *Biology, phylogeny, and classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson* (ed. J. Pakaluk & S. A. Slipinski), pp. 779–1006. Warsaw, Poland: Museum I Instytut Zoologii PAN.

Miller, K. B. 2001 On the phylogeny of the Dytiscidae (Insecta: Coleoptera) with emphasis on the morphology of the female reproductive system. *Insect Syst. Evol.* **32**, 45–92.

Nachtigall, W. 1961 Funktionelle Morphologie, Kinematik und Hydromechanik des Ruderapparates von *Gyrinus*. *Z. vergl. Phys.* **45**, 193–226.

Novotny, V., Basset, Y., Miller, S. E., Weiblen, G. D., Bremer, B. & Drozd, P. 2002 Low host specificity of herbivorous insects in a tropical forest. *Nature* **416**, 841–844.

Phillips, A., Janies, D. & Wheeler, W. C. 2000 Multiple sequence alignment in phylogenetic analysis. *Mol. Phylogenet. Evol.* **16**, 317–330.

Ponomarenko, A. G. 1977 Suborder Adephaga, etc. In *Mesozoic Coleoptera* (ed. L. V. Arnoldy, V. V. Jerikin, L. M. Nikritin & A. G. Ponomarenko), pp. 3–104. Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR [in Russian.] 161.

Ribera, I. & Nilsson, A. N. 1995 Morphometric patterns among diving beetles (Coleoptera: Noteridae, Hygrobiidae, Dytiscidae). *Can. J. Zool.* **73**, 2343–2360.

Ribera, I., Hernando, C. & Aguilera, P. 2001 *Agabus alexandrae* sp.n. from Morocco, with a molecular phylogeny of the western Mediterranean species of the *A. guttatus* group (Coleoptera: Dytiscidae). *Insect Syst. Evol.* **32**, 253–262.

Ribera, I., Hogan, J. H. & Vogler, A. P. 2002 Phylogeny of Hydradephagan water beetles inferred from 18S rDNA sequences. *Mol. Phyl. Evol.* **23**, 43–62.

Sankoff, D. 1975 Minimal mutation trees of sequences. *SIAM J. Appl. Math.* **28**, 35–42.

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. *Syst. Biol.* **50**, 945–969.

Simpson, G. G. 1953 *The major features of evolution*. New York: Columbia University Press.

Swofford, D. L. 1998 *PAUP*, phylogenetic analysis using parsimony (*and other methods)*, v. 4. Sunderland, MA: Sinauer.

Tautz, D., Hancock, J. M., Webb, D. A., Tautz, C. & Dover, A. 1988 Complete sequence of the rRNA genes of *Drosophila melanogaster*. *Mol. Biol. Evol.* **5**, 366–376.

Wheeler, W. C. 1995 Sequence alignment, parameter sensitivity and the phylogenetic analysis of molecular data. *Syst. Biol.* **44**, 321–331.

Wheeler, W. C. 1996 Optimization alignment: the end of multiple sequence alignment in phylogenetics? *Cladistics* **12**, 1–9.