

**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**  
**(Coleoptera)**

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**Abstract**

A new family of adephagan Coleoptera, Aspidytidae, was discovered in China (Shaanxi) in 1995 and in South Africa in 2001. The formal description of the family was based on the South African species. In the present paper we describe the Chinese species, *Aspidytes wrasei* sp.n., provide a detailed account of the adult morphology of the family and include a key to fossil and extant adephagan families. Members of the family are characterised by a noterid- or dytiscid-like habitus in dorsal view, a short and laterally rounded, distinctly retracted head, a flat and broad prosternal process with straight transverse apical margin and rounded apicolateral edges, a small tuft of spines on the profemora, an exposed scutellum, a short, almost straight internal transverse ridge on the metaventrite, an almost completely lacking median discriminial line on the metaventrite, comparatively short metacoxae with distinct metacoxal plates, and slender hind legs without swimming hairs. The strongly shortened pedicellus is an autapomorphy of the genus and family. Assignment to Dytiscoidea is supported by the extensive median fusion of the metacoxae, i.e. the presence of a large midcoxal septum. The globular shape of the basal part of the scapus is similar to what is found in Noteridae, and the presence of a profemoral tuft of hairs is another feature shared with adults of this family, but also with adults of Dytiscidae (in part). The complex mesocoxal cavity is a character state shared with Amphizoidae, Dytiscidae (in part), Trachypachidae († Eodromeinae), and † Liadytidae.

**Key words:** Coleoptera, Aspidytidae, new family, new species, China.

**Introduction**

In 1995, David Wrase and Michael Schülke collected two females and a male of a strange dytiscoid adephagan beetle in Shaanxi (China). Eventually, these specimens were forwarded to Manfred A. Jäch (Naturhistorisches Museum Wien) and Anders N. Nilsson (Umeå), who suggested that these specimens might represent an undescribed genus of Noteridae. Six years later, in 2001, a second species of the same genus was discovered by Ignacio Ribera and Alexandra Cieslak in South Africa. The South African specimens were adequately preserved for molecular phylogenetic study and were described as *Aspidytes niobe* RIBERA et al., 2002. A combined morphological and molecular analysis of hydradephagan families suggested a sister group relation of *Aspidytes niobe* and Hygrobiidae plus Dytiscidae. Therefore, a new family, Aspidytidae, was erected (RIBERA et al. 2002). Herein, we describe the Chinese species and provide a detailed account of adult morphology for the genus and family, as well as a key to all extant and fossil families of Adephaga.

## Material and methods

The specimens of *A. wrasei* were examined either based on digital images, or with a Leitz MZ12 dissecting microscope and the drawings made with the help of ocular grids and a camera lucida attached to that microscope. In addition, the cleared and stained female genitalia were examined with a ZEISS Axioskop 2plus compound microscope.

Scanning electronic photographs were taken with a LEO 1430VP at the SEM unit of the Zoologische Staatssammlung München. The beetles were glued onto the targets with Elmer's Glue All ©. Beetles then were examined without previous sputter-coating, using low vacuum (~20 Pa) at 10-15 kv. Additional SEM photographs were taken with a FEI ESEM XL 30 at the Institut für Spezielle Zoologie und Evolutionsbiologie of the FSU Jena. Female genital tracts were prepared according to the following protocol: 1) relaxing the beetle in hot water and window cleaner for 30 minutes, 2) removing the abdomen with a pair of watchmaker's forceps, 3) transferring the abdomen to 10% cold KOH for 10 hours, 4) washing the abdomen in acetic acid, then in water, 5) transferring the material in water to a concave microscopic slide, 6) cleaning the female genitalia with a pair of watchmaker's forceps and a fine pin, 7) staining the genitalia in a light blue solution of Chlorazol Black in distilled water for ca. 10 minutes, 8) transferring the material to glycerine for inspection and illustration, 9) storage in glycerine in a microvial attached to the beetle, or embedding the parts in Euparal.

### *Aspidytes* RIBERA et al., 2002

TYPE SPECIES: *Aspidytes niobe* RIBERA et al., 2002.

DIAGNOSIS: Mesal walls of metacoxa extensively fused, thus forming a large midcoxal septum. This character assigns Aspdytidae to Dytiscoidea. *Aspidytes* differs from other dytiscoid adults in the absence of swimming hairs, presence of an indistinct, almost straight transverse suture of the metaventrite (Fig. 2) (externally not impressed in *A. niobe*) and a corresponding internal ridge, and in the pedicellus being distinctly shortened, appearing very closely connected with the scapus (Figs. 4, 5).

DESCRIPTION: Habitus (Figs. 1, 2). Body with distinct microreticulation (Figs. 8-12), still appearing moderately shiny; body noterid- or dytiscid-like in dorsal view, stream-lined, without pronoto-elytral angle. Flattened ventrally and convex dorsally. Pronotum broadest at base, lateral margins continuously curved towards anterior angles, strongly narrowing towards head. Scutellum partly exposed. Elytra smooth (i.e. not sulcate or costate), greatest width at level of anterior metacoxal margin, gradually narrowing towards abdominal apex. All legs slender and not flattened, carabid-like, without swimming hairs or any apparent modification for the aquatic life.

Head. Short, rounded laterally, posterior part retracted, without neck region. Compound eyes of moderate size, not protruding, emarginate in frontal view. Anterior labral margin concave. Antennae filiform, short, almost completely glabrous, with few minute spines. Length of flagellum (antennomeres III - XI) ~ 0.8 mm (*A. wrasei*). Antennomeres IV - IX very slightly expanded, somewhat globular or dilated. Scapus short with large basal articulatory part and globular distal part. Pedicellus extremely short, closely connected with scapus. Maxillary palp short. Submentomental suture distinct, mentum with long lateral lobes which enclose the prementum. Labial palp 3-segmented, inserting on distinct palpiger, about as long as maxillary palp. Apical palpomeres of maxilla and labium not broadened, truncate or emarginate. Gular suture not recognizable externally. Mid gular apodeme apparently absent. Posterior tentorial pits distinct.

Prothorax. Pronotum strongly narrowing anteriorly, evenly arcuate laterally, with broad lateral beads, which are connected by narrow bead along anterior margin. Ratio width pronotal base /

width between anterior angles = 1.85 (*A. wrasei*). Short, impressed median line present on disc. Sculpture similar to that of posterior head region, with moderately dense punctation. Inflected part broad, extending posteriorly, with semicircular impressed line posteromedially. Pleura with very distinct separate caudal part (erroneously interpreted as epimeron by some authors; see BAEHR 1979). Pleurosternal suture distinct. Prosternum (= Pleurosternum cf. BAEHR 1979) moderately long, with row of short hairs along anterior margin. Prosternal process well-developed, broadening posteriorly. Caudal margin transverse and with rounded posterolateral edges. Ventral side of prosternum and prosternal process on same plane. External postcoxal bridge absent. Protrochantin not visible externally. Coxa globular. Femur with two anterior edges and a tuft of spines at apical third of upper edge (profemoral antenna cleaner; cf. BELKACEME 1991). Two longer setae present at posterior margin. Tibia about as long as femur, not flattened, slender basally, moderately widening distally, with short spines on ventral side and along external margin. Apex with several short spines and two moderately long internal spurs, not rounded externally. Large burrowing spurs and/or flattened spines absent. Four basal tarsomeres short, not widened, without curved spines or ventral brushes. Ultimate tarsomere about two times as long as penultimate one, with long, equal claws.

Mesothorax. Slightly shorter than prothorax. Scutellum exposed. Elytra with lateral bead extending to apex. Epipleura broad anteriorly, strongly narrowing towards abdominal apex with polygonal meshes of different size and few punctures. Ventricle with distinct pentagonal groove, articulates with prosternal process when prothorax retracted and with metaventral process posteriorly. Faintly impressed pleural suture separates anepisternum from moderately broad epimeron. Mesocoxal cavity laterally bordered by mesal edge of epimeron and narrow apical part of metathoracic anepisternum (= complex type cf. BELL 1967). Middle legs similar to front legs, femur without tuft of spines, tibia and tarsus slightly longer, tibia only very slightly extended distally.

Metathorax. Slightly longer than prothorax. Anepisternum triangular, with distinct bead along lateral and mesal margin. Epimeron covered by elytral epipleura. Ventricle composed of praeepisternum and katepisternum (cf. BAEHR 1975, BEUTEL 1986), moderately shortened, not reaching lateral metacoxal margin laterally, metaventral process well-developed, with rounded edges. Transverse suture present as faintly impressed line (Figs. 2, 3) (only present as internal ridge in *A. niobe*), about as long as width of internal lamina of metacoxa, separating posterior katepisternum from anterior praeepisternal<sup>1</sup> part of ventrite, corresponding with internal transverse ridge. Median longitudinal suture (= discriminial line or discrimen: BAEHR 1975, BELKACEME 1991: Fig. 50, BEUTEL & HAAS 2000: Fig. 1) very short, not surpassing posterior half of katepisternum (Figs. 2, 3). Metacoxa moderately extended, slightly longer than ventrite and lateral margin broadly contiguous with epipleural margin. Mesal walls extensively fused, thus forming a large midcoxal septum. Anterior paramedian angle absent (cf. BEUTEL & ROUGHLEY 1988: Figs. 1, 2). Inner lamina and coxal plates distinct, broadened posteriorly, distinctly curved outwards anteriorly (Fig. 3). Metatrochanter larger than pro- and mesotrochanter. Tibia and tarsus longer than those of middle leg, appearing thin and longish (*A. wrasei*: length of femur 0.80 mm, tibia 1.05 mm, tarsus 0.95 mm; ratio length of beetle / length of tibia + tarsus = 2.4; ratio in *Hygrotus impressopunctatus* (SCHALLER) 1.7; *Amphizoa lecontei* MATTHEWS 2.0; *Carabus auratus* L. 1.5). Wings well-developed.

Abdomen. Abdomen with six ventrites, which are equivalent to sternites II, III, IV, V, VI, VII (= last visible sternite), their length decreasing from III to VI. Sternite II only visible lateral to metacoxa. Sternites III and IV partly fused, but with a very distinct separating suture. All

<sup>1</sup> Lateral part of praeepisternum = 'metasternal wings' in the taxonomic literature.

sternites with lateral bead, which is most prominent along the lateral margin of sternite VII. The latter is roughly semicircular, evenly rounded posteriorly, and devoid of modifications (Fig. 6).

ETYMOLOGY: From the Greek *aspis* (shield) and *dytes* (diver). In reference to the shield like body shape and the systematic position of the species in Dytiscoidea.

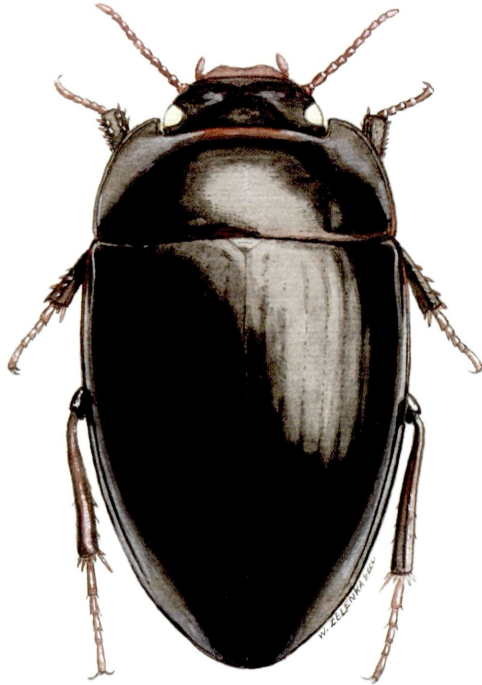


Fig. 1: Habitus of *Aspidytes wrasei*, dorsal view (© copyright NMW).

### *Aspidytes wrasei* sp.n.

TYPE LOCALITY (Fig. 18): Base of a vertical hygroscopic cliff, ca. 1200 – 1400 m a.s.l., below small hotel (situated at ca. 1600 m a.s.l.), Hua Shan, Qin Ling Shan, Shaanxi, China.

TYPE MATERIAL: **Holotype** ♂ (Naturhistorisches Museum Wien): "CHINA: Shaanxi, Qin Ling / 110°06'E / 34°27' N / 118 km E Xian / Hua Shan, N valley / 1200-1400m, sifted, 18.-20.8.1995 / leg. M. Schülke". **Paratypes**: 2 ♀♀ (Naturhistorisches Museum Wien; Naturkundemuseum Erfurt): "CHINA (Shaanxi) / Qin Ling Shan 110.06E / 34.27N, Hua Shan / 118 km E Xian, N valley / 1200-1400m, leafy wd. / 18./20.VIII.1995 Wrase".

DESCRIPTION: Size: Length of beetle 4.80 – 5.10 mm (holotype 5.00 mm); length minus head 4.35 – 4.50 mm (holotype 4.40 mm); length of pronotum 0.90 – 1.00 mm (holotype 0.95 mm); width of pronotum at base 2.40 – 2.50 mm (holotype 2.40 mm); width of pronotum between anterior angles 1.30 – 1.40 mm (holotype 1.35 mm); greatest width of beetle 2.60 – 2.85 mm (holotype 2.70 mm); greatest height ~ 1.0 mm.

Colour. Posterior part of head black, anterior part paler, piceous to dark brown. Labrum orange. Pronotum blackish except ferruginous marginal area, base and fore margin appearing rufous. Elytra blackish, laterally ferruginous. Antennae and palpi orange, legs rufous. Colour of venter similar to colour of legs.

Surface sculpture (Leitz MZ12 at 50-80x). Posterodorsal part of head with large meshes with internal punctures; some meshes narrowed, chromosome-shaped (Figs. 8, 9); frontal area with a network of lines with larger punctures at intersections; punctuation coarser towards clypeus. Meshes of discal region with faint microreticulation or shagreenation; area around eyes with microreticulation of small, regular cells. Gena with microreticulation of slightly transverse cells, not deeply impressed. Mentum with microreticulation of transverse meshes, laterally with slightly diagonal meshes, these appearing more deeply impressed than on gena. Gula broad, with transverse microreticulation anteriorly, transverse cuts on middle part, and smooth surface structure posteriorly.

Elytron with eight rows of larger serial punctures obliterated posteriorly; marginal rows do not exceed middle of elytron; discal lines rather distinct, almost appearing like longitudinal lines. Microsculpture of larger, irregular polygonal meshes and a sparse, fine punctuation.

Head structures. Anterodistal area of penultimate labial palpomere with four sensilla of unusual type: with a short small sensorial hair inserted on a cupula, which is surrounded by a ring-shaped cuticular bulge (Fig. 7). Mentum medially only slightly concave.

Thoracic structures. Prosternal process with straight apical margin and with broadly rounded posterior angles; the prosternal process approximately of hexagonal shape in ventral view; lacking a lateral bead, ventral surface thus completely plane (Fig. 3). Metaventral process with very distinctly beaded margin (Fig. 3).

Male genitalia. Median lobe of aedeagus simply curved and with broadly rounded tip, without any conspicuous modifications (Fig. 17). Parameres symmetrical, triangular with basal portion broadly rounded, apically with long stylus that bears few, hardly visible setae on tip (Fig. 16).

Female genitalia. For ease of communication, the nomenclature applied here follows MILLER (2001).

Gonocoxa (= genital appendages IX, GH IX) (Fig. 14). In ventral view roughly rectangular, lateral margins very slightly curved, tip blunt; cranially with short external apodeme; laterally with rather long setae; distally with shorter setae. Proximal portion rather broad in lateral view (Fig. 13).

Laterotergite (= tergite IX; "Tergumhälften IX" or "Tergum IX" of BURMEISTER 1976); articulates with cranial tip of gonocoxa, extended caudally, shorter than gonocoxa (Fig. 13).

Gonocoxosternite (Coxosternum; = invaginated sternum VIII; "Gonocoxosternum" of BURMEISTER 1976): Somewhat rectangular, with short anterior lobe (= anteroexternal angle), a median anterior concavity, and anterointernal angle also forming a lobe that equals the anterior lobe in size. Posterior margin with a fringe of conspicuous long setae, comparable in length to height of gonocoxosternite (Fig. 15).

Ramen ("Vulvarklerite": BURMEISTER 1976; = GH VIII): short, triangular, rufous.

Vagina with a rather short and sac-like cranial expansion, probably representing a bursa copulatrix, and a conspicuous, slightly triangular dorsal pocket (Fig. 13: dp). Vagina and sac-like expansion not distinctly separated. Longish gland located in dorsomesal position ("dorsal gland", dg). Spermathecal duct (sd) comparably short and broad, originates very close to the insertion of the common oviduct (co) into the bursa or vaginal expansion. Spermatheca (sp) without any obvious modifications (50x). Without spermathecal gland. Narrow fertilization duct (fd) connects spermatheca and insertion of oviduct. Configuration and location of ducts entering bursa/vagina could not be reconstructed precisely with the material at hand and will be the subject of subsequent study when more specimens are available, especially for semithin microtome sectioning.

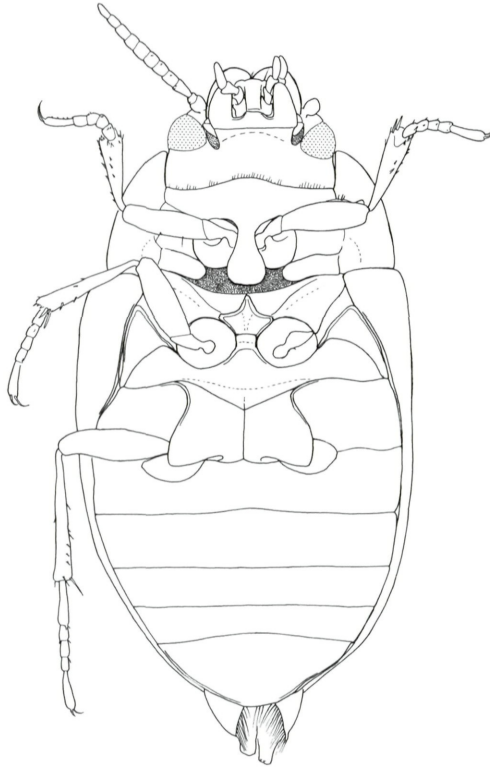


Fig. 2: Habitus of *Aspidytes wrasei*, ventral view.

**DISTRIBUTION:** Only known from the type locality.

**ECOLOGY:** Very little is known about the ecology of *Aspidytes wrasei*. It was collected from among stones and various plants at the base of a vertical hygroscopic cliff.

**ETYMOLOGY:** This remarkable and enigmatic new species is dedicated to one of its discoverers, our friend and colleague David Wrase.

**DIFFERENTIAL DIAGNOSIS:** This species can be identified by the following combination of characters: **1)** Size and habitus (Fig. 1). **2)** Prosternal process flat, not bordered, truncate posteriorly, with rounded posterolateral edges (Figs. 2, 3). **3)** Inner lamina and coxal plates distinct, broadened posteriorly, distinctly curved outwards anteriorly (Fig. 3). **4)** Gonocoxa and gonocoxosternum with extraordinarily long setae (Figs. 6, 14, 15).

The two species of the family differ as follows: **1)** Body length: 7.0 mm in *A. niobe* vs. less than 5.5 mm in *A. wrasei*. **2)** Prosternal process with a broad bead in *A. niobe*, metacoxal process unbeaded (vice-versa in *A. wrasei*). **3)** Mentum medially with a V-shaped emargination in *A. niobe* (slightly concave in *A. wrasei*). **4)** Ligula with long, thick setae in *A. niobe* (not in *A. wrasei*). **5)** Gonocoxa and gonocoxosternum without, or but a few short setae, respectively in *A. niobe* (with conspicuous long setae on both in *A. wrasei*). **6)** Vagina with a ventral gland in *A. niobe* (dorsal in *A. wrasei*). **7)** Median lobe of aedeagus with conspicuous membranous appendages in *A. niobe* (simple in *A. wrasei*).

## Discussion

A placement of Aspidytidae within Dytiscoidea is supported strongly by the extensively fused mesal walls of the metacoxae. This is congruent with molecular evidence presented lately (RIBERA et al. 2002), and it was shown that Aspidytidae are the sister group of a clade comprising Hygrobiidae and Dytiscidae. Amphizoidae are basal to this group, followed by Noteridae, Haliplidae and Gyrinidae (Geadephaga not included in the analysis). In the following, we present an account of our morphological findings. For a cladistic analysis see RIBERA et al. (2002).

Aspidytidae do not share apomorphies with other families. It is remarkable that Aspidytidae show certain affinities with Liadytidae (genus *Liadytes* PONOMARENKO) a family of Dytiscoidea recorded since the Jurassic (Toarcian, 187 million years ago) and which became extinct in the Cretaceous (Albian, 97 million years ago) (PONOMARENKO 1977, 1985, LABANDEIRA 1994). *Liadytes* species and *A. wrasei* share a stream-lined body without pronoto-elytral angle, a distinctly retracted, laterally rounded head, an exposed scutellum, a metathoracic anepisternum, which reaches the midcoxal cavities, an almost straight transverse suture of the metaventricle, thin and longish metatibiae and tarsi, and clearly separated abdominal sternites III and IV. Despite these similarities, a close relationship with Liadytidae cannot be established with current available information. Most of these features are probably plesiomorphies, and we did not find a synapomorphy for *Liadytes* + *Aspidytes*. The absence of swimming hairs distinguishes *Aspidytes* from *Liadytes* species described by PONOMARENKO (1977, 1985) (see also CARPENTER 1992).

A close sistergroup relationship between Liadytidae and Noteridae was considered by PONOMARENKO (1977). Even though this possibility cannot be ruled out, the presumptive synapomorphy presented by this author, the presence of a median platform of the metaventricle (absent in *Aspidytes*) is not very convincing. It was pointed out by BEUTEL & ROUGHLEY (1997) and BELKACEME (1991) that this probably is not a groundplan feature of Noteridae. Besides that, this median platform is recognizable only in *Liadytes longus* (PONOMARENKO 1977: Fig. 14) but not in *L. crassus* (PONOMARENKO 1977: Fig. 15) and *L. avus* (PONOMARENKO 1985: Fig. 7). Its actual structure in *L. longus* also cannot be reconstructed in much detail.

A feature which suggests a closer relationship between Aspidytidae and Noteridae is the shortened scapus with a large, globular articular portion. However, the remaining configuration of the scapus is different in both taxa. The distal part of the scapus is narrower than the basal part in adults of Noteridae (BEUTEL & ROUGHLEY 1987: Figs. 4, 5, 14; BELKACEME 1991: Fig. 59), whereas it is globular and larger than the articular part in Aspidytidae (Figs. 4, 5). Besides that, the pedicellus is connected very closely with the distal part of the scapus and strongly shortened. This condition is found only in *Aspidytes* and thus is considered as an autapomorphy here. Aspidytidae and Noteridae share the presence of a tuft of spines at the anterior margin of the profemur, i.e. a profemoral cleaning device (BELKACEME 1991). However a very similar condition also occurs in adults of some Dytiscidae (e.g. *Copelatus*, *Rhantus*, *Laccophilus*; Balke pers. obs., BELKACEME 1991).

Character states which clearly are in contrast to a placement within Noteridae (BELKACEME 1991) are the presence of a transverse suture of the metaventricle, the contact of the metathoracic anepisternum with the mesocoxal cavities (complex type cf. BELL 1987), the absence of a paramedian angle of the anterior metacoxal wall (BEUTEL & ROUGHLEY 1987: Figs. 1, 2: "pma"), the absence of a completely separate median lamina of the metacoxae (= metacoxal "noterid platform"; BELKACEME 1991), and the distinct suture separating abdominal sternites III and IV (i.e. there are six easily recognizable ventrites in Aspidytidae vs. five in Noteridae).

Derived features which support the monophyly of noterid subgroups (e.g. Noterinae, Noterinae excl. *Notomicrus*, *Eunoterinae* cf. BELKACEME 1991) are absent in Aspidytidae: strong protibial

burrowing spurs, protibial rows of flattened spines, loss of external protibial spur, rounded outer edge of protibia, curved spines of protarsomeres I - III, broadened and elongated pro- and mesotarsomeres, broadened apical labial palpomere, flattened median portion of the metaventre (praecoxal "noterid platform"), and presence of swimming hairs.

In Aspidytidae, the laterotergite articulates with the cranial portion of the gonocoxa; it has a strictly caudal orientation (in resting position). This state is present in females of all other groups of Dytiscoidea except for Noteridae, where the laterotergite has either a short apodeme which is extended cranially while the rest has a more or less caudal orientation (*Notomicrus*), or the laterotergite is much longer than the gonocoxa and completely orientated cranially (see BURMEISTER 1976: 227, read: Fig. 41a = *Noterus* not *Notomicrus*!; DETTNER 1997: 112; MILLER 2001: 53). Aspidytidae lack a spermathecal gland, the presence of which is an apomorphy for Noteridae (MILLER 2001).

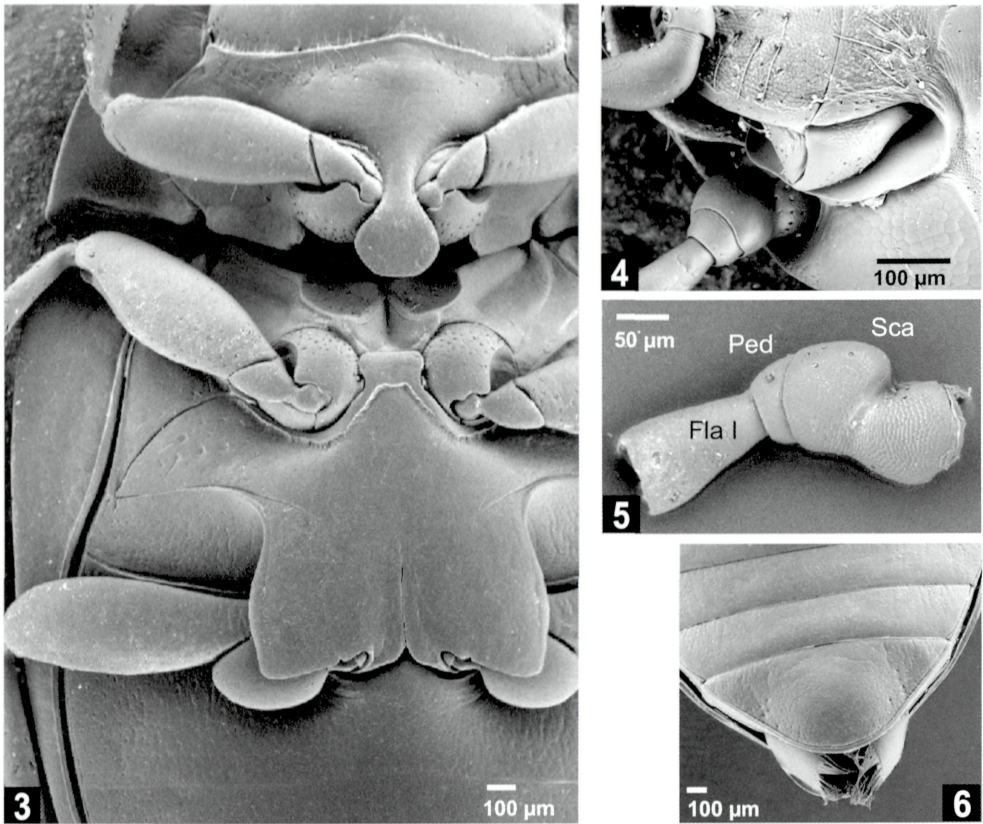
Another family which shows certain affinities with Aspidytidae is Amphizoidae. The shape of the apical part of the prosternal process, and the 'complex type' mesocoxal cavities are features shared by both groups. However, the former (carabid-like) condition cannot be considered a well defined apomorphy and is not unique to these groups, while the latter condition also is found in most dytiscids (except Laccophilinae and Vatellini) and † Eodromeinae (Trachypachidae) (PONOMARENKO 1977). The carabiform legs of Aspidytidae superficially are similar to those of *Amphizoa*, but swimming hairs are completely absent, whereas fringes of very fine hairs are present in amphizoid beetles. The head shape of *Amphizoa* is carabid-like (as in *Hygrobia*), with moderately protruding eyes, whereas the head of *Aspidytes* is short, broad, stream-lined and strongly retracted (as in Noteridae and Dytiscidae). Fusion of the mentum and submentum is an amphizoid autapomorphy (BEUTEL 1997) not shared by *Aspidytes*. The compound eyes of *Aspidytes* are emarginate anteriorly and the insertion of the scapus is covered by a lateral extension of the frons (as in Dytiscidae). The eyes are lacking an emargination in *Amphizoa* and the antennal insertion is exposed (as in *Hygrobia* or, e.g. *Carabus*).

The presence of a transverse internal ridge of the metaventre is a plesiomorphic feature shared with Amphizoidae, Hygrobiidae, Trachypachidae, Haliplidae, *Spanglerogyrus* and Carabidae. Complete reduction probably has occurred independently in Gyrininae, Noteridae, Dytiscidae and Rhyssodidae.

The presence of metacoxal plates, which cover the coxo-trochanteral articulation, probably is a derived groundplan feature of Adephaga excl. Gyrinidae (BEUTEL 1995). They are fairly extensive in Aspidytidae and similar to those of extant and some fossil Trachypachidae (e.g. *Eodromeus*), Amphizoidae and *Liadytes avus* (PONOMARENKO 1985), whereas they are largely reduced in Charonoscapinae, *Coptoclava* (PONOMARENKO 1977), Hygrobiidae (BEUTEL 1986) and Dytiscidae. Greatly enlarged plates with rounded posterior margin, which function as an additional storage room for breathing air, are present in Haliplidae, and a similar condition is present in representatives of the fossil taxa Triaplidae, Necronectinae (in part), *Karadromeus*, and *Psacodromeus* (Trachypachidae) (PONOMARENKO 1977).

It is obvious that Aspidytidae are immensely important for the understanding of the evolution of Dytiscoidea (RIBERA et al. 2002). They have originated many millions of years ago, presumably in the Jurassic period, when the first radiation of Dytiscoidea took place (e.g. Liadytidae, Noteridae: Toarcian; LABANDEIRA 1994). Considering this recent finding of a comparatively large and even more characteristic family of beetles, it appears likely that more phylogenetically, highly interesting extant taxa remain undiscovered. Therefore, we argue strongly for a comprehensive survey of habitats which may have largely escaped the attention of collectors in the past. Hygropetric surfaces may be such a type of largely under-recorded habitat, and we are confident that intensive investigations will yield more spectacular discoveries in the future.

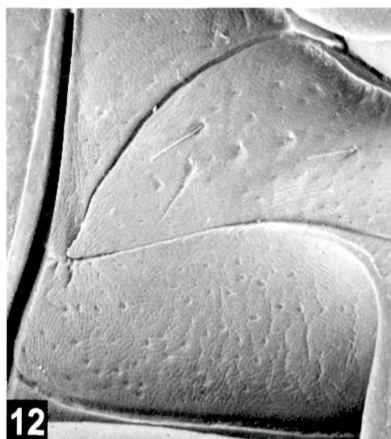
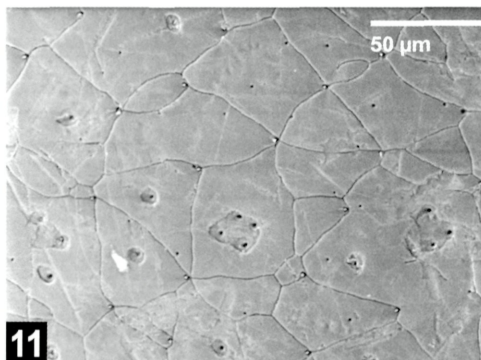
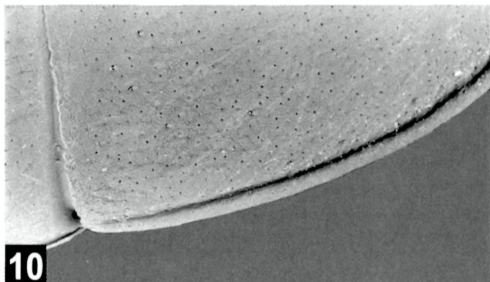
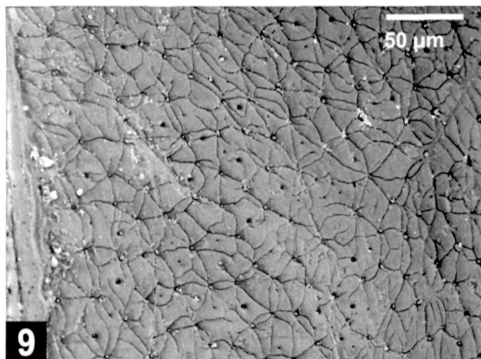
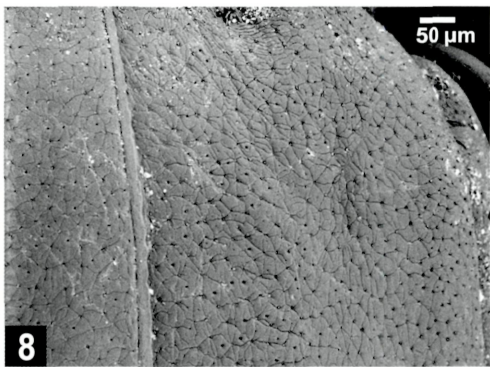
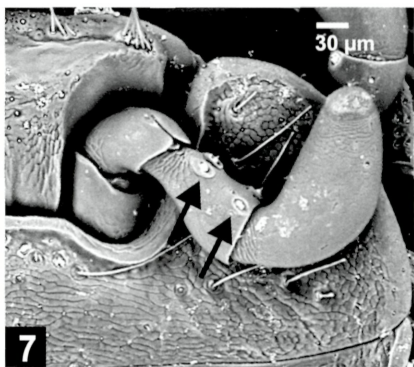




Figs. 3 – 6: SEM photographs of *Aspidytes wrasei*, 3) parts of venter; 4) lateral margin of head in ventrolateral view with eye in the lower right corner and labial palp in upper left; 5) removed antennal base, dorsal aspect: scapus, pedicellus, flagellomere I; 6) tip of abdomen, ventral view, gonocoxosterna with long setae partly extracted.

### Key to adults of extant and fossil families of Adepaga

- 1 Compound eyes completely divided, at least by a narrow cuticular bridge, with one portion on dorsal side and one portion on ventral side..... 2
- Compound eyes not divided..... 5
- 2 Antenna strongly modified: with ear-shaped pedicellus and flagellum transformed into compact club. Middle- and hind legs either with oar-shaped femoral extension and feather-like swimming hairs (Spanglerogyrinae) or transformed into short paddle-like structures. .... **Gyrinidae**
- Antenna filiform. Middle- and hind legs without femoral oar-shaped extension and not paddle-like, with unmodified swimming hairs..... 3
- 3 With large rounded metacoxal plates (= femoral cover sensu PONOMARENKO 1977), which almost reach the elytral epipleura laterally. Hind tibiae and tarsi long and thin..... † **Coptoclavidae (Necronectinae)**
- Metacoxae without femoral covers. Hind tibiae and tarsi at least partly modified..... 4



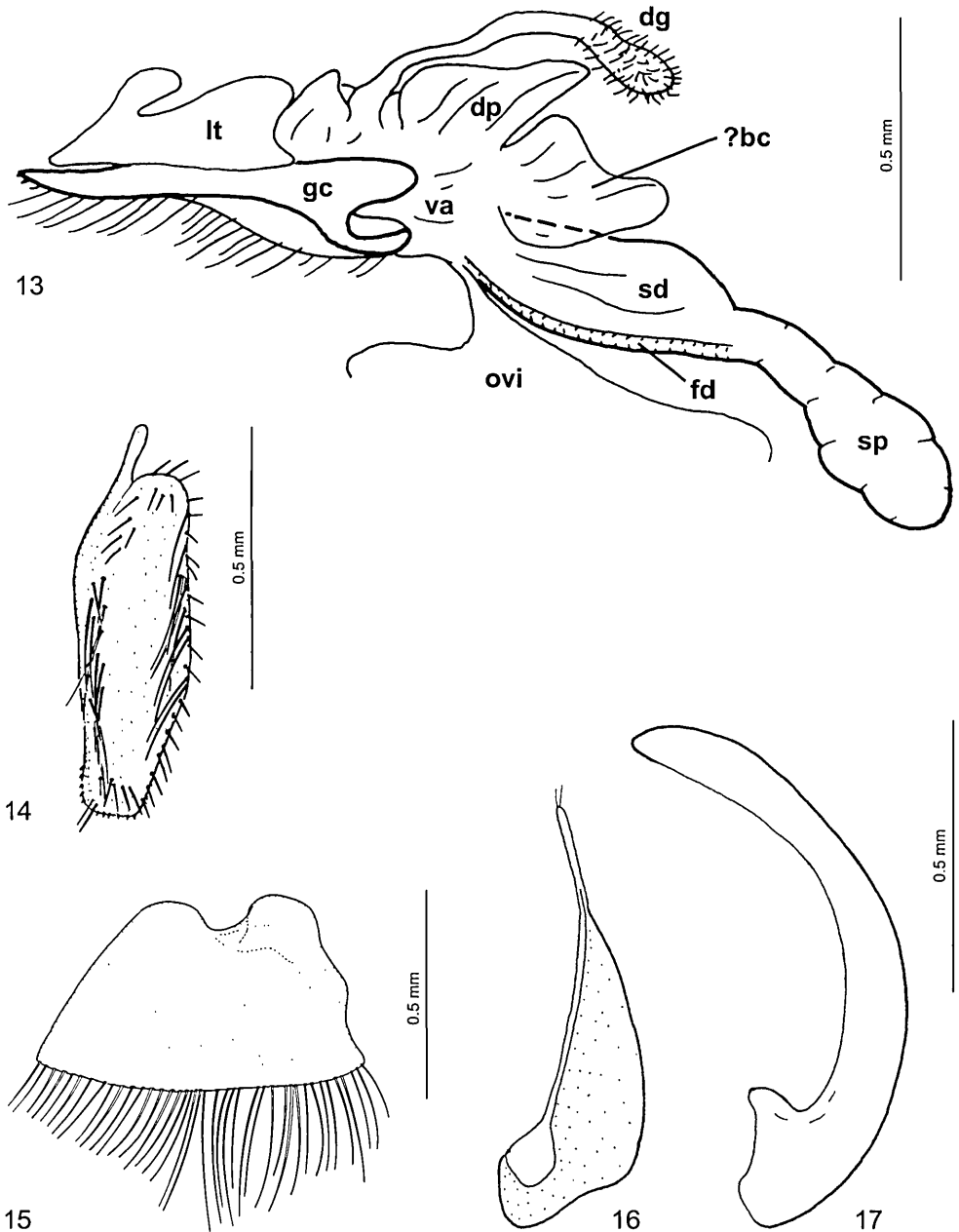
Figs. 7 – 12: SEM photographs of *Aspidytes wrasei*, 7) left lateral half of head in part, ventral view, arrows point on sensilla on labial palp; 8) anteromedian part of pronotum and frons, dorsal view; 9) frons showing the surface sculpture; 10) lateral part of pronotum, dorsal view, showing broad lateral bead and surface sculpture; 11) elytron, posterosublateral position, showing elytral surface sculpture; 12) ventral view, showing metacoxa, lateral part of praepisternum and anepisternum.

- 4 Hind tibiae widened and flattened, with long swimming hairs. Hind tarsi flattened but not widened, much narrower than tibia..... † **Coptoclavidae (Charonoscapinae)**
- Hind tibiae and tarsi flattened and strongly widened, without swimming hairs..... † **Coptoclavidae (Coptoclavinae)**

- 5 Metacoxal plates very large, posteriorly rounded, reaching the lateral margin of the metaventrite and at least partly cover the metafemora..... 6
- Metacoxal plates absent, if present moderately sized, not reaching lateral margin of metaventrite..... 7
- 6 Head strongly inclined. Prosternal process absent, procoxae thus contiguous. Length of beetle 7-14 mm. .... † **Triaplidae**
- Head prognathous. Prosternal process broad, apically truncate, separating procoxae. Length of beetle < 7 mm..... **Haliplidae**
- 7 Protibia with antennal cleaner in distal 2/3 of tibia or between two apical tibial spurs (isochaet condition). Antenna pubescent, at least terminal segment. Metacoxae fused or not, if fused not extensively with only a narrow midcoxal septum..... (Geadephaga) 8
- Protibia without antennal cleaner. Antenna without pubescence. Metacoxae extensively fused, with large midcoxal septum. .... (Dytiscoidea) 11
- 8 Metacoxae mesally fused. Transverse suture of metaventrite laterally reduced. .... 9
- Metacoxae not fused, but usually in contact. Transverse suture of metaventrite generally complete or if completely absent, metacoxae widely separated. .... (Carabidae) 10
- 9 Metathoracic anepisternum reaching mesocoxal cavity..... † **Trachpyachidae (Eodromeinae)**
- Metathoracic anepisternum not reaching mesocoxal cavity. .... **Trachpyachidae (Trachypachinae)**
- 10 Transverse suture complete. Metacoxae almost always in contact. Body shape various..... **Carabidae excl. Rhysodini**
- Transverse suture absent. Metacoxae widely separated. Body cylindrical. .... **Rhysodini**
- 11 Metaventrite strongly narrowed by cranial extension of metacoxae, lateral part wing-like<sup>2</sup>, transverse suture absent. Metacoxae strongly extended anteriorly, with evenly rounded anterior margin. Metacoxal plates obsolete<sup>3</sup>. .... **Dytiscidae**
- Metaventrite not narrowed by cranial extension of metacoxae, lateral part not wing-like. If metacoxae strongly extended anteriorly, not with rounded anterior margin, and with distinct metacoxal plates and separate inner lamina of metacoxae..... 12
- 12 Body length < 2 mm long. Eyes absent. Lateral parts of metaventrite absent, displaced by metacoxal extension. Suture separating sternite II from III and IV absent..... **Noteridae (Phreatodytinae)**
- Body length > 2 mm long. If small and eyeless (*Speonoterus* SPANGLER from Sulawesi), then lateral parts of metaventrite present and fused with metacoxa. Suture separating sternite II from III and IV distinct. .... 13
- 13 Transverse suture of metaventrite absent. Metacoxae with anterior paramedian angle and very clearly defined inner lamina, which is converging anteriorly. Suture separating abdominal sternites III and IV faint or absent ..... **Noteridae (Noterinae)**
- Transverse suture of metaventrite present, but sometimes very indistinct. Metacoxae without anterior paramedian angle, inner lamina diverging before meeting anterior coxal margin or parallel-sided. Suture separating abdominal sternites III and IV distinct (i.e. with six ventrites). .... 14
- 14 Eyes strongly protruding. Body dorsally and ventrally strongly convex. Front tibia with a pair of flattened burrowing spurs. Hind tarsi flattened. Elytron ventrally with row of short transverse ridges in posterolateral position used for sound production (BEUTEL 1986, WICHARD et al. 1995). All legs with dense fringes of long swimming hairs. .... **Hygrobiidae**

<sup>2</sup> Lateral part of praepisternum = "metasternal wings" in the taxonomic literature.

<sup>3</sup> Metacoxal plates – The structure homologous to the extensive metacoxal plates e.g. in Haliplidae. Erroneously, the dytiscid-type metacoxae are often referred to as "metacoxal plates" in the taxonomic literature.



Figs. 13 – 15: Female genitalia of *Aspidytes wrasei*, 13) genital tract in lateral view, simplified (bc, bursa copulatrix; dg, dorsal gland; dp, dorsal pocket; fd, fertilization duct; gc, gonocoxa; lt, laterotergite; ovi, common oviduct; sd, spermathecal duct; sp, spermatheca; va, vagina); 14) gonocoxa, ventral view, some setae omitted; 15) gonocoxosternite, ventral view.

Figs. 16 – 17: Male Genitalia of *Aspidytes wrasei*, 17) paramere, internal view; 18) median lobe of aedeagus in lateral view.

- Eyes slightly or not protruding. Body dorsally slightly convex, ventrally rather flat. Front tibia without burrowing spurs. Hind tarsi long and slender, not flattened. Elytron without sound production devices. Legs with only short swimming hairs or swimming hairs absent..... 15
- 15 With distinct pronoto-clytral angle. Beetle with rugulose surface structure. Length of beetle 11.0 - 15.5 mm. .... **Amphizoidae**
- Without pronoto-clytral angle. Surface comparably smooth, not rugulose. Length of beetle less than 10 mm. .... 16
- 16 Legs with swimming hairs. Metaventricle with or without flattened median platform... † **Liadytidae**
- Legs without swimming hairs. Metaventricle without flattened median platform. .... **Aspidytidae**

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Fig. 18: Andreas Pütz at type locality of *Aspidytes wrasei*: bottom of hypogetric cliff [photograph by M. Schülke].

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