Insecta: Coleoptera

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INTRODUCTION

The order Coleoptera, or beetles, is represented by some 350,000 known species (Lawrence *et al.* 1999), but recent estimates suggest there are hundreds of thousands or even millions of undescribed species (for a critical review see Ødegaard 2000). Beetles are not only rich in species, but also, or perhaps especially, extremely rich with respect to diversity in size, form, and ecological strategies. The largest beetles, Longhorn Beetles (Cerambycidae) from the Amazon, may be as long as 18 cm, while the smallest ones, Featherwing Beetles (Ptiliidae), measure less than half a millimetre (about 0.3 mm, acc. to Sörensson 1997). The oldest beetle fossils are known from the Lower Permian (about 280 million years) (Lawrence *et al.* 1999).

Beetles are holometabolous insects, i.e. their life stages are egg – larvae – pupa – adult. Adult beetles are usually easily recognized by their strongly sclerotized fore-wings, the so-called elytra, which form a strong protection shield.

Although the vast majority of beetles are terrestrial, at least 10,000 species are regarded to be aquatic in one or more of their developmental stages. The number of species with aquatic adults is very high as compared with other insect orders; the protective elytra and the generally very compact ectoskeleton obviously constituted an effective pre-adaptation to the invasion of the water by adults.

This chapter deals only with the "True Water Beetles" (TWB) sensu Jäch (1998), who provides a useful check-list of aquatic and riparian Coleoptera of the world, and defines them as submerged, or partly submerged, for most of the time of their adult stage. Larvae and pupae may be aquatic or terrestrial. Adults of other beetles usually associated with water (Phytophilous Water Beetles, Facultative Water Beetles, Parasitic Water Beetles, False Water Beetles, and Shore Beetles, sensu Jäch 1998, see also Dudgeon 1999) are not given detailed treatment herein. Adults of False Water Beetles are (except during oviposition and – if their pupa is aquatic – for a short period after hatching) more or less strictly terrestrial or riparian. Parasitic Water

Beetles are not yet recorded from Malaysia, and our knowledge of the Facultative Water Beetles and Phytophilous Water Beetles of Malaysia is still very scanty (Table 1). True Water Beetles may be found in the families given in Table 2 (Jäch 1998).

During their evolution, beetles have invaded the aquatic environment many times (Crowson 1981; Beutel 1995, 1997). True water beetles are diverse and inhabit a great variety of ecological niches. They can be encountered in virtually any kind of fresh and even brackish water habitat from the sea shore up to alpine lakes. Many new species are described every year, but there are only few large scale regional efforts to explore aquatic beetle diversity with China being one of the few exceptions (Jäch and Ji 1995, 1998, 2003; http:// www.nhm-wien.ac.at/nhm/2Zoo/coleoptera/publications/chinaindex.html).

Table 1. Phytophilous and False Water Beetles of Malaysia

	Stage / Aquatic or not		
	Larva	Pupa	Adult
Phytophilous Water Beetles			
Chrysomelidae		on or in water plants	
Curculionidae		on or in water plants	
False Water Beetles			
Psephenidae	+	+/-	-
Scirtidae[1]	+	+/-	+ /-
Eulichadidae	+	-	-

[1] Adults of the genus *Hydrocyphon* are generally terrestrial but are often found under water.

Table 2. World families of True Water Beetles, and their ocurrence in Malaysia

	Stage / Aquatic or not				Stage / Aquatic or not		
	Larva	Pupa	Adult		Larva	Pupa	Adult
MYXOPHAGA				POLYPHAGA			
? Lepiceridae***	?	?	?/+/-	Staphyliniformia			
Torridincolidae*	+	+	+	Epimetopidae	+	?	+
Hydroscaphidae**	+	?/+	+	Helophoridae***	+	-	+
ADEPHAGA				Hydraenidae	-(+)	-	+
Gyrinidae	+	-	+	Hydrochidae	+	-	+
Haliplidae**	+	-	+	Hydrophilidae	+	-	+
Noteridae	+	+	+	Spercheidae	+	-	+
Aspidytidae	+	-	+	Elateriformia			
Amphizoidae***	+	-	+	Elmidae	+	-	+
Hygrobiidae***	+	-	+	Dryopidae	-(+)	-	+
Dytiscidae	+	-	+	Lutrochidae***	+	-	+

* unconfirmed record (Bishop 1973) ** potentially occurring in Malaysia

*** not occurring in Malaysia or neighbouring countries

(+) very few larvae seem to be amphibious (facultatively aquatic)

Almost nothing is known about the preimaginal stages, species bionomics, habits, and the like of Oriental water beetles (Dudgeon 1999). On the other hand, our knowledge for example on the Central European fauna is comparatively good.

Respiration

Water Beetles display a wide array of respiratory adaptations (see Lawrence 1991; Wichard *et al.* 1995). Many larvae are able to breathe via the integument; and many of them are equipped with various kinds of gills (tracheal gills, spiracular gills), which may be even retractable, as in many Dryopoidea. Very rarely (e.g. in some Torridincolidae), larvae are provided with a plastron. Aquatic beetle larvae are frequently characterized by the loss or extreme reduction of spiracles: thoracic spiracles plus spiracle of eighth abdominal segment still functional (amphipneustic, e.g. many Psephenidae, Curculionidae), only spiracle of eighth abdominal segment functional (metapneustic, e.g. Dytiscidae, Amphizoidae, Noteridae, many Hydrophilidae, Scirtidae); all spiracles reduced to functionless vestiges (apneustic, e.g. Haliplidae, Hygrobiidae, Gyrinidae, many first instar larvae of Dytiscidae). Aquatic pupae of some species of Hydroscaphidae, Torridincolidae and Psephenidae are provided with spiracular gills bearing a plastron.

In contrast to the larvae, adults have no gills. Most species carry a smaller or larger air bubble with them, which is in contact with the tracheal system. This air supply may be stored in the subelytral space (e.g. Dytiscidae, Gyrinidae), underneath the coxal plates (Haliplidae), on the ventral surface (Hydrophilidae, Hydraenidae) or on any part of the body, where it is usually held by (often very specialized) hydrofuge pubescence or scales; some Dryopidae are even completely surrounded by the air bubble. In Elmidae, for instance, the air bubble can replace oxygen through diffusion of dissolved oxygen from the surrounding water while the beetle is fully submerged. In such a case the air bubble is called gas gill (or plastron) because it functions as a physical gill. Two kinds of plastron can be distinguished: microplastron (incompressible gas gill) and macroplastron (compressible gas gill).

Water beetles and mankind

Water beetles, especially Elmidae are gaining increasing recognition as indicators of water quality, water types (Moog and Jäch 1995; Verdonschot *et al.* 1992) and endangered habitats (Jäch, Dietrich and Raunig 2004). We have repeatedly urged that TWB are useful indicators and attractive tools for badly needed conservation assessments (Balke, Hendrich and Foster 1997, 1999; Balke and Hendrich 1999a; Jäch, Dietrich and Raunig 2004).

Water beetles can be used to control water plants that have become pests. *Agasicles hygrophila* Selman and Vogt, an alticine chrysomelid was, for instance, introduced into the USA from South America to control Alligatorweed (*Alternanthera*). Locally beetles may be of use in the control of the introduced water hyacinth (*Eichornia crassipes*). Species of Dytiscidae are predators and may play an important role in

controlling mosquitoes. Their actual importance is not yet understood, but at least some attention is nowadays paid to that problem (Mogi *et al.* 1999). Dytiscids were often blamed for causing considerable harm to fish fry (Wesenberg-Lund 1943), but there were few actual studies on that subject, and more research is needed to assess potential harm, as well as benefits, of water beetles to aquaculture (Vazirani 1972).

Adults of larger TWB, e.g. *Cybister*, *Eretes* (Dytiscidae) and *Hydrophilus* (Hydrophilidae), are still part of the diet of humans in China, Thailand, and New Guinea (Gressitt and Hornabrook 1977; Hill *et al.* 1982; Chen *et al.* 1998; Jäch and Easton 1998; Jäch 2003). Mjöberg (1916) reported on a gyrinid, *Aulonogyrus strigosus* F., roasted and eaten by Australian aborigines. Ochs (1924) believed these gyrinids to be an aphrodisiac. More than a century ago, a Riffle Beetle, *Austrelmis condimentarius* (Philippi) (Elmidae), was used as seasoning for food in South America. This species was reported to have considerable commercial value (Philippi 1864).

In Hong Kong, *Cybister* are sold as pets for use in the aquarium (Jäch and Easton 1998), a formerly common practice in Europe as well (Wesenberg-Lund 1943), which has unfortunately been forgotten. In Korea, a large *Cybister* species was (or still is) used for a kind of lottery, the so-called "Korean water beetle game" (Pemberton 1990) in which an oval container is filled with water. At the margin of the container, there are compartments, and above these, at the margin, either lie small prizes like sweets and cigarettes, or nothing. A participant pays a small amount of money, then lifts the beetle with a spoon and drops it in the middle of the container. The beetle will then swim around for a while and usually move to the edge to rest in one of the compartments. The participant wins the prize which is placed above that particular compartment – or loses if there is no prize.

KEY TO ADULTS OF MALAYSIAN FAMILIES OF TRUE WATER BEETLES AND PHYTOPHILOUS WATER BEETLES (modified after Jäch and Balke 2003)

Not every beetle that is collected in an aquatic habitat is a water beetle! Very many limnological samples taken from streams or swamps include Shore Beetles or even strictly terrestrial species. Specimens may be swept unintentionally from riparian vegetation when approaching the sample site and wind or rain may cause beetles to fall to the ground or into water, which is another reason why strictly terrestrial beetles are often encountered dead or still alive in aquatic samples. A general distinction between aquatic and terrestrial Coleoptera is not possible from preserved specimens because the morphological adaptations for aquatic life may be very cryptic and not readily detectable.

This key covers only adults of True Water Beetles and Phytophilous Water Beetles (sensu Jäch 1998). It is not a world key. All characters refer to aquatic species (potentially) occurring in Malaysia. The size ranges given for each family (or genus) are global maximum-minimum ranges, except where stated otherwise.

1. Head prolonged in front of eyes to form a distinct snout of variable length (always distinctly longer than wide). Antenna inserted on snout, geniculate between scape and pedicel (Fig. 1A). Size: 3.5–5.5 mm (Malaysian *Bagous* and *Neochtina*, length with rostrum) ..... CURCULIONIDAE
- Head anteriorly not prolonged into a distinct snout. Antenna not geniculate between scape and pedicel 2

2. Third tarsal segment bilobed (Fig. 1B,C). Size: 6.5–8.0 mm (Malaysian *Donacia*) ..... CHRYSOMELIDAE
- Third tarsal segment never bilobed. 3

3. Middle and hind-legs strongly modified (short and flat, oar-like), much shorter than fore-legs. Head with two pairs of well developed eyes, one on dorsal side and one on ventral side (Fig. 1D). Antenna with setose, enlarged pedicel (Fig. 1M). Size: ca 3.5–20.0 mm (Malaysian fauna). (Fig. 5A) ..... GYRINIDAE
- All legs approximately equally long (Fig. 2A–D). Head usually with only one pair of eyes (very rarely, e.g. in the hydrophilid genus *Amphiops* with two pairs of eyes) 4

4. Hind-coxa, hind-femur and basal abdominal ventrites concealed under conspicuous "hind-coxal plates" (Fig. 2B). Size: 2.5–3.5 mm. (Figs. 2B, 5D) ..... HALIPLIDAE
- Hind-coxa, hind-femur and basal abdominal ventrites never concealed (Fig. 2A,C,D) 5

5. Underside with conspicuously elevated metacoxal process (Fig. 2C). Size: 1.4–8.0 mm. (Fig. 5C), usually drop-shaped, apically acuminate ..... NOTERIDAE
- Metacoxal process – if present – never conspicuously elevated (Fig. 2A) 6

6. Metasternum with characteristic lateral "wings" (Fig. 2A). Metacoxae large, posteriorly with a paired posterior metacoxal process. Size: 1–50 mm. (Figs. 6–7) often streamlined ... DYTISCIDAE
- Metasternum never with characteristic lateral "wings" (Fig. 2D). Metacoxae smaller 7

7. Pronotum with a pronounced anteromedian projection that forms a shelf above the head. First ventrite very short and inconspicuous, so abdomen almost appearing as having only four visible sternites (ventrites). Size: 2.5–3.5 (Malaysian species). (Fig. 9A) ..... EPIMETOPIDAE
- Pronotum without a pronounced anteromedian projection. Abdomen with 4–7 visible sternites (ventrites) 8

8. Anterior margin of head (*i.e.* anterior margin of clypeus) distinctly emarginate with anterior corners upturned; labrum strongly deflected (not seen from above). Size: 1.9–4.2 mm (Malaysian species). (Fig. 10A) ..... SPERCHEIDAE
- Anterior margin of clypeus rarely emarginate, with anterior corners never upturned; labrum usually visible from above, rarely strongly deflected 9

9. Body form as in Fig. 9B. Middle of pronotum with three shallow impressions. Upper surface usually with metallic reflections. Size: 1.5–5.5 mm. (Fig. 9B) ..... HYDROCHIDAE
- Bodyform and pronotal structure not as in Fig. 9B: Hydrochidae. Upper surface very rarely with metallic reflections 10

10. Elytra truncate, thus posterior abdominal segments exposed (seen from above). Terminal abdominal segment triangular 11

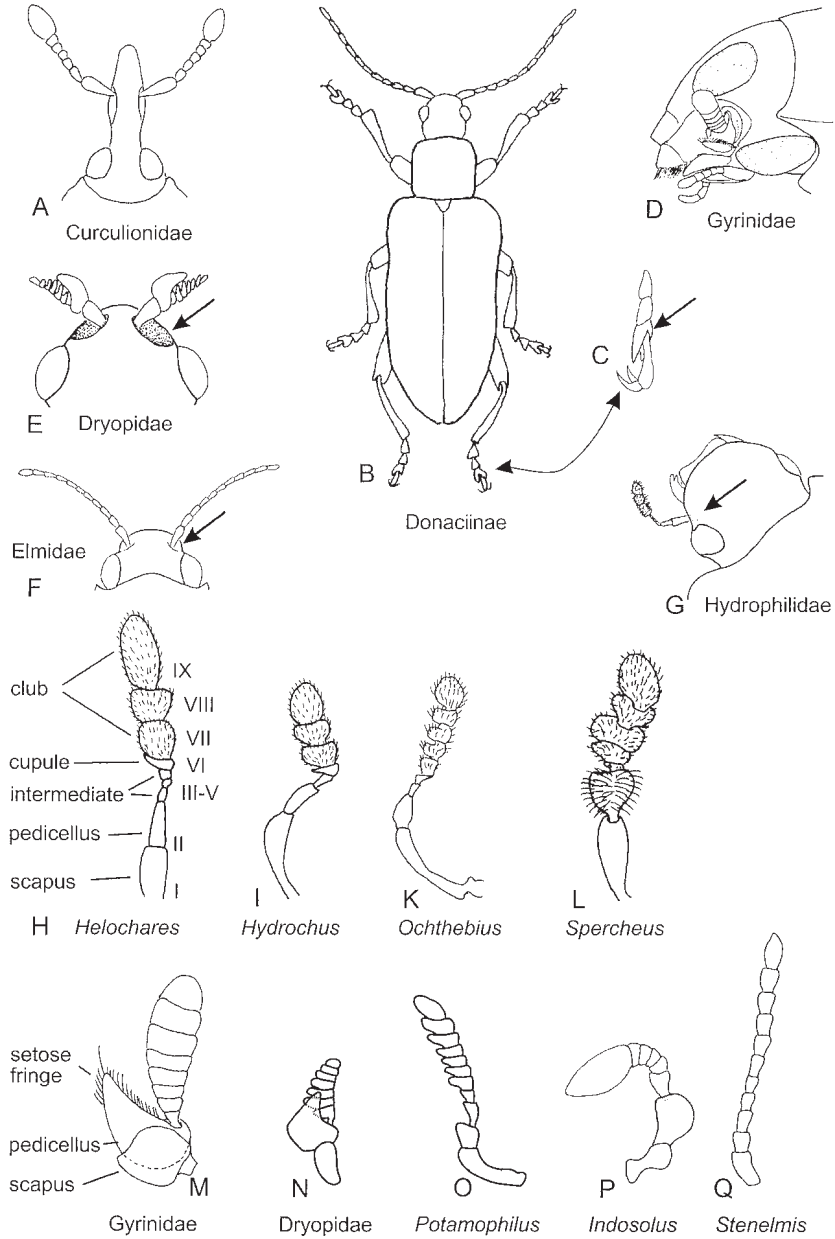

Figure 1. A – head of weevil, dorsal view; B – adult leaf beetle; C – hind-tarsus of leaf beetle, arrow points at bilobed tarsomere; D – head of Gyrinidae, lateral view; E – head of Dryopidae, dorsal view, arrow points at depression at antennal base; F – head of Elmidae, arrow points at antennal base; G – head of Hydrophilidae, dorsolateral view, arrow points at hidden antennal base; H–Q: antennae of various water beetle families.

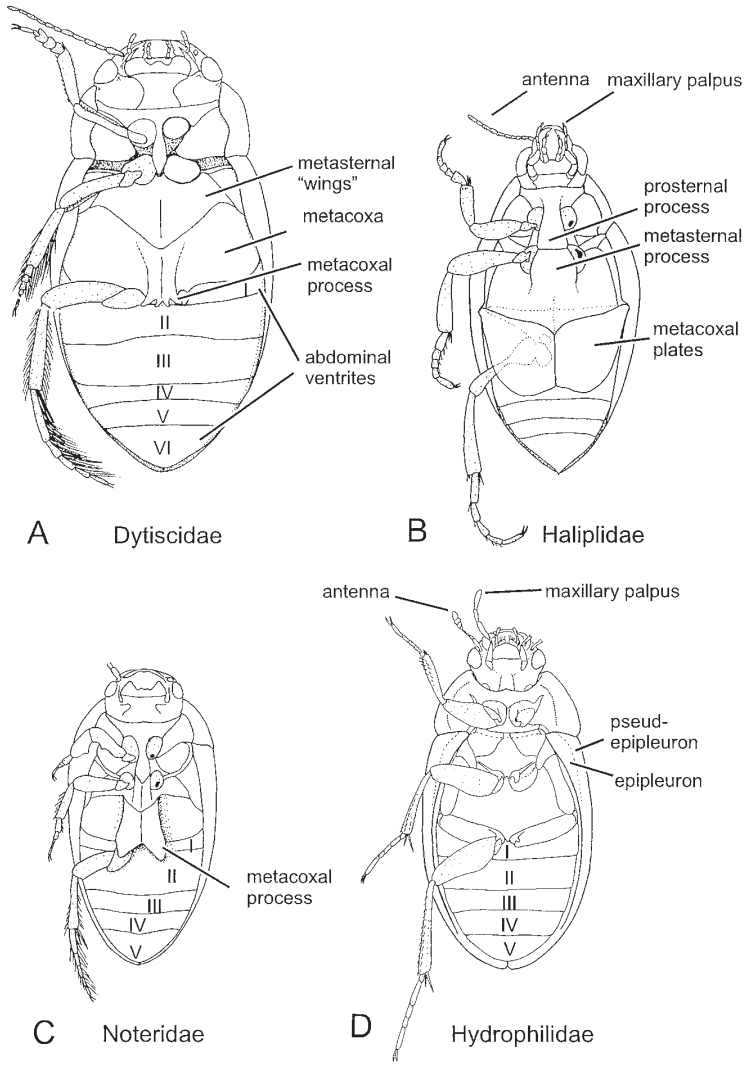

Figure 2. Ventral sides of water beetle families. A – Dytiscidae; B – Haliplidae; C – Noteridae; D – Hydrophilidae.

- Elytra not truncate. Terminal abdominal segment usually not seen from above and rarely long and triangular 12

11. Maxillary palpi very short, about half of the width of distance between eyes. Antenna straight, club not densely pubescent; antennal base exposed, seen from above. Size: < 2 mm. (Fig. 5B) ..... HYDROSCAPHIDAE
- Maxillary palpi rather long, about as long as distance between eyes. Antenna of hydrophiloid type (scapus long and curved, club pubescent, as in (Fig. 1K); antennal base not seen from

above (dorsally covered by lateral extension of frons and clypeus). Size: < 2 mm (Malaysian species). (Fig. 8A) ..... HYDRAENIDAE (genus *Limnebius*, partly)

12. Antenna typically hydrophiloid (see Fig. 1H,I,K); antennal base dorsally covered by lateral extension of head, therefore not seen from above (Fig. 1G). Claws often shorter than penultimate tarsal segment 13

- Antennae of varying appearance (see Fig. 1N–Q), if resembling hydrophiloid type (Elmidae: Larainae) then entirely pubescent; antennal base exposed, seen from above (Fig. 1E,F). Claws always longer than penultimate tarsal segment 14

13. Pubescent antennal club with 5 segments. Abdomen usually with 6 (very rarely, males of *Aulacochthebius* with 5) distinctly visible sternites (ventrites). In most cases shorter than 2 mm. Size: ca. 0.9–2.2 mm (Malaysian species). (Fig. 8B–D) ..... HYDRAENIDAE

- Pubescent antennal club with 3 segments (Fig. 1H). Abdomen usually with 4–5 (very rarely with 6, e.g. *Berosus*) clearly visible sternites (ventrites) (Fig. 2D). In most cases longer than 2 mm. Size: ca. 1.5–35 mm (Malaysian species). (Figs. 10B–D, 11) ..... HYDROPHILIDAE

14. Antenna very short, with 5–13 segments, pedicel greatly enlarged (Fig. 1N). Fronto-clypeal suture absent. Size: 1.3–9.5 mm. (Fig. 12D) ..... DRYOPIDAE

- Antenna long or short, 7–11 segments (Fig. 1O–Q), second segment never greatly enlarged. Frontoclypeal suture usually present. Size: 0.8–11 mm. (Fig. 12A–C) ..... ELMIDAE

KEY TO AQUATIC LARVAE OF MALAYSIAN WATER BEETLE FAMILIES

(modified after Dudgeon 1999)

It was stressed above (see key to adults) that not every beetle that is collected in an aquatic habitat is indeed a water beetle! The same is true for larvae. Terrestrial larvae are often encountered in benthic samples since there are numerous humicolous species, that are easily washed into the water by spates etc. Knowledge of the preimaginal stages of Oriental water beetles is extremely limited. The larvae of some families (e.g. Psephenidae, the so-called water pennies – Fig. 3I, or Scirtidae – Fig. 3K) are very conspicuous, however, for the non-specialist it is often very difficult to reliably identify aquatic larvae.

This key covers larvae of the families of True Water Beetles (Dryopidae and Hydraenidae included, although their larvae are hardly ever found under water), False Water Beetles, Facultative Water Beetles (Lampyridae only) and Phytophilous Water Beetles.

1. Legs absent or minute. Thorax and abdomen short, obese and without distinct sclerites (Fig. 3A–B) 2

- Legs present, with 3–6 well-defined segments. Body not as above (Figs. 3C–K, 4A–H) 3

2. Legs absent (Fig. 3B) ..... CURCULIONIDAE: Molytinae

- Legs very small. Last abdominal segment ventrally with a pair of large sclerotized hooks which are visible from below (Fig. 3A) ..... CHRYSOMELIDAE: Donaciinae

3. Legs with two claws 4

- Legs with a single claw 6

4. Abdomen with two pairs of stout hooks ventrally at the tip (on segment 10) and one pair of lateral tracheal gills on segments 1–9, two pairs of such gills on segment 9. Segment 10 rather short, lacking gills (Fig. 3G) ..... GYRINIDAE
- Abdomen lacks terminal hooks, with only eight segments. Lateral gills absent. Last abdominal segment not especially short 5

5. Last abdominal segment (no. 8) with paired terminal appendages (urogomphi) which are as long or longer than abdominal segment 1. Legs long and slender. Mandibles long narrow and sickle-shaped (Fig. 3E) ..... DYTISCIDAE
- Urogomphi very short and hardly visible. Legs short and stout. Mandibles stout and triangular, never sickle-shaped (Fig. 3F) ..... NOTERIDAE

6. Legs with five segments and a claw. Shape variable (Fig. 3C,D) ..... HALIPLIDAE
- Legs with three or four segments and a claw 7

7. Labrum and clypeus fused 8
- Labrum free, not fused to clypeus 9

8. Body flattened, with large, rather wide thoracic and abdominal tergites and a membraneous ventral surface. Pronotum expanded anteriorly. Head retractable, usually not visible when viewed from above (Fig. 4E) ..... LAMPYRIDAE
- Without the above combination of characteristics 16

9. First thoracic segment as well as abdominal segments 5 and 8 each with a pair of fleshy, articulated finger-like lobes laterally on the dorsal surface (Fig. 3H). Antenna very short with only two segments. Last instar larva smaller than 2 mm ..... HYDROSCAPHIDAE
- Abdominal segments without pairs of articulated finger-like lobes on the dorsal surface ... 10

10. Abdomen with 10 segments. Articulated cerci present ..... HYDRAENIDAE
- Abdomen with 9 segments. Articulated cerci lacking 11

11. Antenna long and conspicuous with many segments (Fig. 3K) ..... SCIRTIDAE
- Antenna short and inconspicuous, consisting of two or three segments only 12

12. Body greatly flattened with thoracic and abdominal tergites expanded laterally giving the larva a torpedo-shaped, ovoid or even circular outline and concealing legs and head when viewed from above (water pennies) (Fig. 3I) ..... PSEPHENIDAE
- Body more or less cylindrical or fusiform. Head and legs visible (at least in part) when viewed from above 13

13. Abdominal segment 9 with a ventral lid-like operculum concealing a chamber beneath. Abdominal segments 1–8 never with ventral gill tufts 14
- Abdominal segment 9 lacks a ventral operculum (= ovoid lid), but ventral gill tufts may be present on segments 1–8 15

14. Stemmata placed close together in one group. Segment 9 with tufts of retractile tracheal gills.. ..... ELMIDAE
- Six stemmata separated into three groups: dorsal (2), lateral (3), ventral (1). Segment 9 without tufts of retractile tracheal gills ..... DRYOPIDAE

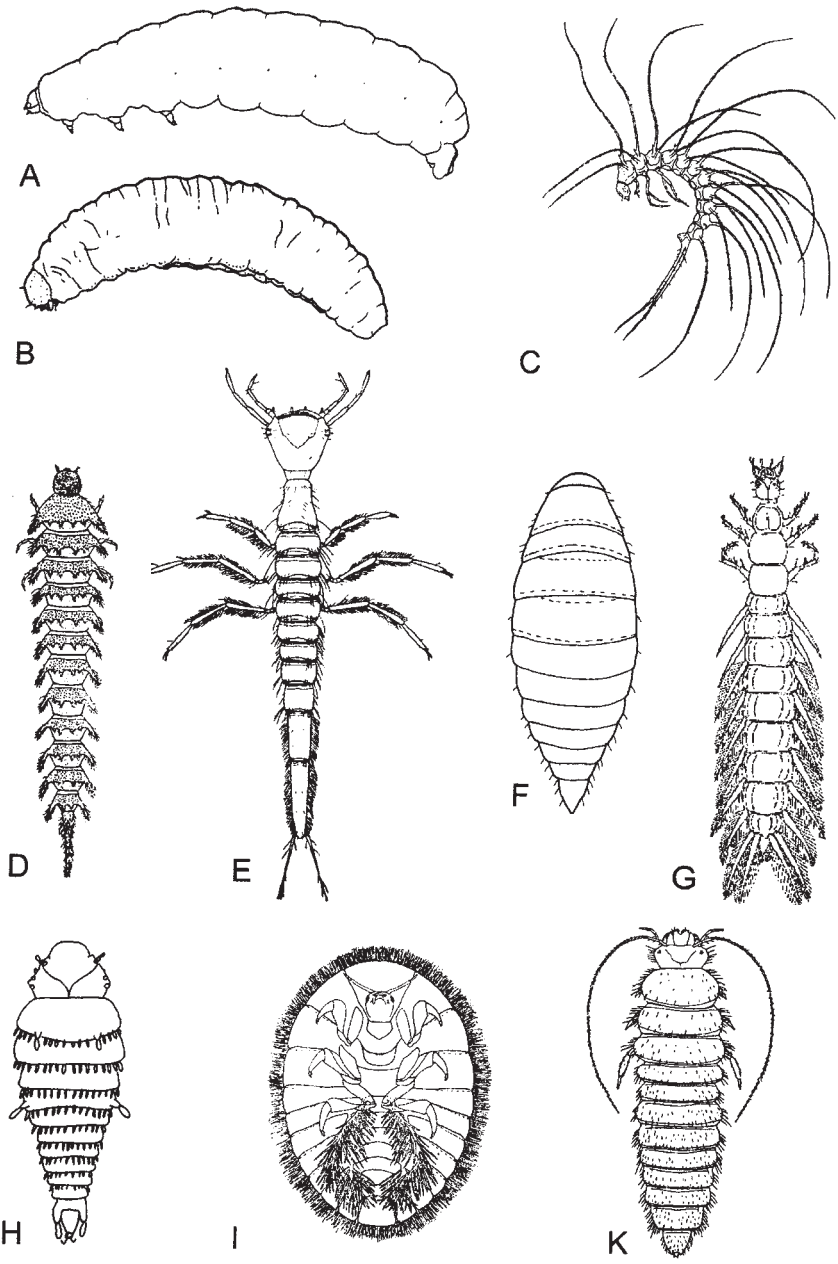

Figure 3. Larvae of A – *Donacia* Chrysomelidae; B – *Bagous* Curculionidae; C – *Peltodytes* Haliplidae; D – *Haliplus* Haliplidae; E – Dytiscidae; F – *Hydrocanthus* Noteridae; G – Gyrinidae; H – Hydroscaphidae; I – Psephenidae (ventral view); K – Scirtidae. (Source: C,D,E,G,I,K from Bertrand 1972)

15. Abdominal segments 1–8 with tufts of finger-like gills ventro-laterally (Fig. 4A) .... EULICHADIDAE
- Abdominal segments 1–8 without ventro-lateral gills, but a tuft of gills may be present on segment 9 (Fig. 4B) ..... PTILODACTYLIDAE

16. Habitus resembling an ant lion. Abdomen may be noticeably sclerotized, with nine complete segments, the tenth reduced (Fig. 4F) ..... SPERCHEIDAE
- Not like this. Abdomen membraneous or fleshy, with eight segments 17

17. Antenna inserted closer to the front of the head than mandibles. Labium and maxillae peculiarly positioned in a furrow beneath head (Fig. 4E) ..... HYDROCHIDAE
- Antenna arising behind insertion point of the mandibles. Labium and maxillae situated in usual location (i.e. the ventral anterior margin of the head) (Fig. 4D,H) ..... HYDROPHILIDAE

FAMILY HYDROSCAPHIDAE – Skiff Beetles

Diversity and Range This family of about 20 species contains three genera, two of which occur in the Americas only, while *Hydroscapha* is known from the Holarctic and Oriental Regions. Twelve species of *Hydroscapha* are known from the Old World (Löbl 1994).

Morphology (Figs. 3H, 5B). Egg very large relative to the beetle, occupying up to one quarter of the female abdomen. Larvae are, as far as is known, up to 1.8 mm long, elongate, fusiform and narrowing posteriorly; there are pairs of finger-like spiracular gills on prothorax and on abdominal segments 1 and 8 which are believed to support gas exchange (see Richoux and Doledec 1987; Lawrence and Reichardt 1991; White and Brigham 1996). The pupa has long spiracular processes and plastron-bearing spiracular gills (Lawrence and Reichardt 1991).

Adults are also rather small, the Oriental species being 0.6–1.9 mm long (Löbl 1994). They are, however, rather conspicuous beetles. The body outline is rather continuous, with the tip of elytra strongly truncate; the telescope-like abdomen usually well exceeds the elytra, and several segments are thus visible from above, or the abdomen can be rather retracted and thus more or less covered by the elytra.

Biology Larva, pupa and adult are aquatic, which is probably also true for the egg. Adults of *Hydroscapha* are able to move very quickly on water films; it seems, however, that they cannot swim freely. Because of its relatively large size, only one egg matures at a time. Larvae and adults feed on algae (Lawrence and Reichardt 1991; White and Brigham 1996).

Habitat Notes Members of this family are found on hygropetric rocks and in the interstitial of gravelly river margins and residual pools. They are also reported from hot springs up to a temperature of 46°C (Richoux and Doledec 1987; Lawrence and Reichardt 1991; Jäch 1995a; White and Brigham 1996).

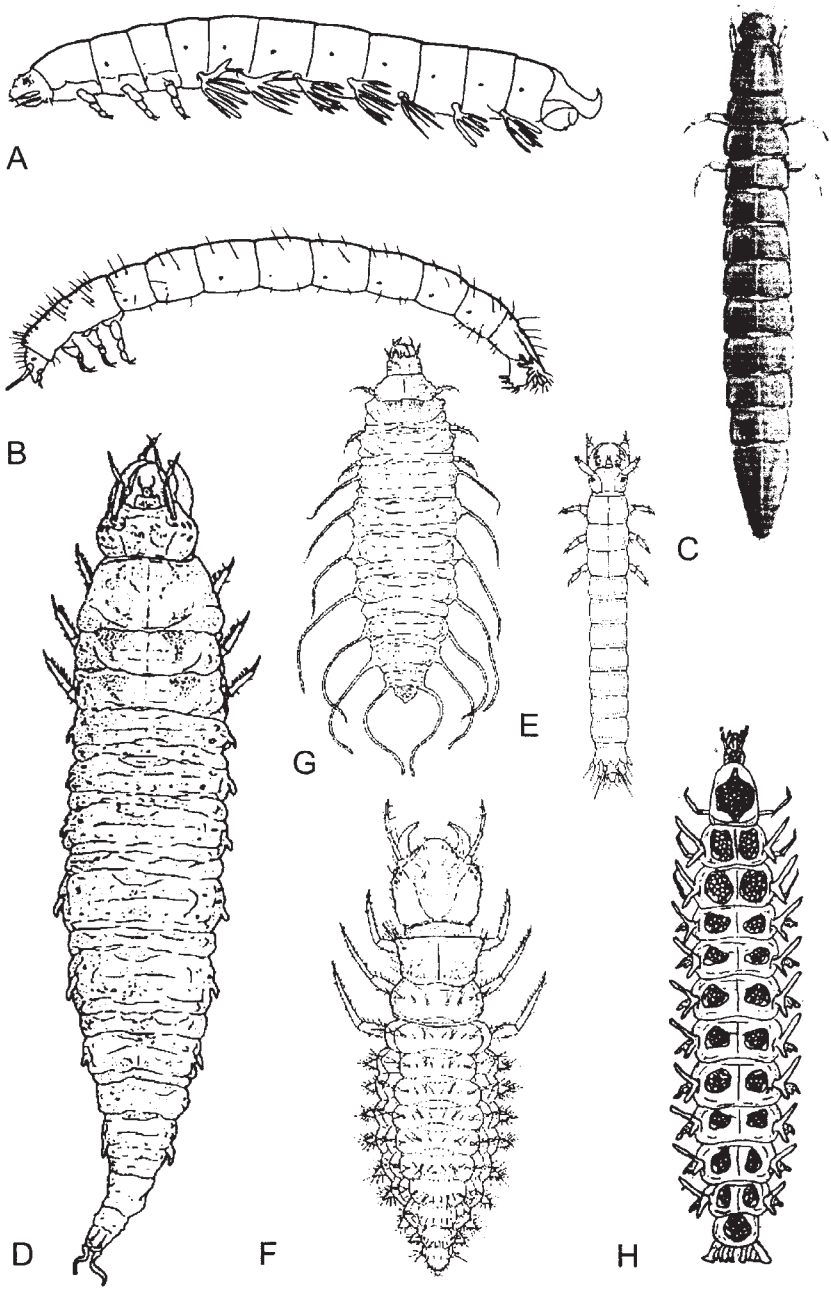

Figure 4. Larvae of A – Eulichadidae; B – Ptilodactylidae; C – Elmidae; D – *Hydrophilus* Hydrophilidae; E – Hydrochidae; F – Spercheidae; G – *Berosus* Hydrophilidae; H – Lampyridae. (Source: D from Hebauer and Klausnitzer 1998; E-H from Bertrand 1972)

Regional Taxa This group has not yet been reported from Malaysia, but its occurrence in India, China, the Philippines and Indonesia (Sulawesi) suggests presence in Malaysia as well. Oriental *Hydroscapha* were revised by Löbl (1994), see also Jäch (1995a).

FAMILY GYRINIDAE – Whirligig Beetles

Diversity and Range There are some 900 species in 13 genera worldwide with the greatest diversity in the tropics and subtropics. The family is traditionally divided into three subfamilies: Gyrininae, Orectochilinae, Enhydrinae. Although this arrangement has been recently disputed (see Lawrence and Newton 1995), it is useful for practical purposes.

Morphology (Figs. 1D, 3G, 5A). The eggs are elongate, whitish and with a reticulate surface on which an adhesive band is visible. Larvae are elongate, narrow and depressed, and bear conspicuous lateral tracheal gills on the abdominal segments 1–9, and a second pair of gills derived from the urogomphi is found on segment 9. Segment 10 is small, ventrally directed, and bears four sclerotised hooks. Pupa of exarate type, the eyes are divided.

The adults show striking adaptations to a life on the water surface. The middle and hind-legs are modified to form powerful oar-like swimming devices which allow them to move with considerable speed. Middle and hind-tibia and hind-tarsus are shortened and strongly expanded laterally to enlarge the surface effective for stroking. The compound eyes are usually broadly divided in a dorsal and ventral one to observe activity in both media to which the beetle is exposed. The antenna of adult gyrinids is very short; pedicel with large Johnston organ, acting as receptor for vibrations in the surface film.

Biology All stages except for the pupa are aquatic, with the adults spending the major part of their life on the water surface, being half submerged; the larvae, in contrast, are always fully submerged.

Larvae creep about on the vegetation or bottom substrate. They can also swim by up- and downward undulation of the body. Adults are fast swimmers who spend most of their time gyrating on the water surface, but when disturbed they quickly dive to the bottom of the habitat where they will hide for a while. For swimming, the hind-and middle legs are moved simultaneously, for medium speed only the middle legs are moved (cf. Holmen 1987). They often form huge aggregations of individuals. Interspecific swarms of up to eight species may occur (Spangler 1991a).

Larvae are apneustic, they breathe via the thin body cuticule and their tracheal gills so that they do not need to travel to the water surface for respiration. When diving, adults carry an air supply beneath the elytra; an air bubble is usually carried at the tip of the abdomen which serves as a physical gill. Eggs are laid in rows or bundles in the water, attached to plants, stones, wood etc. For European species, incubation takes 1–2 weeks, larval development has a duration of 15–35 days in *Gyrinus*,

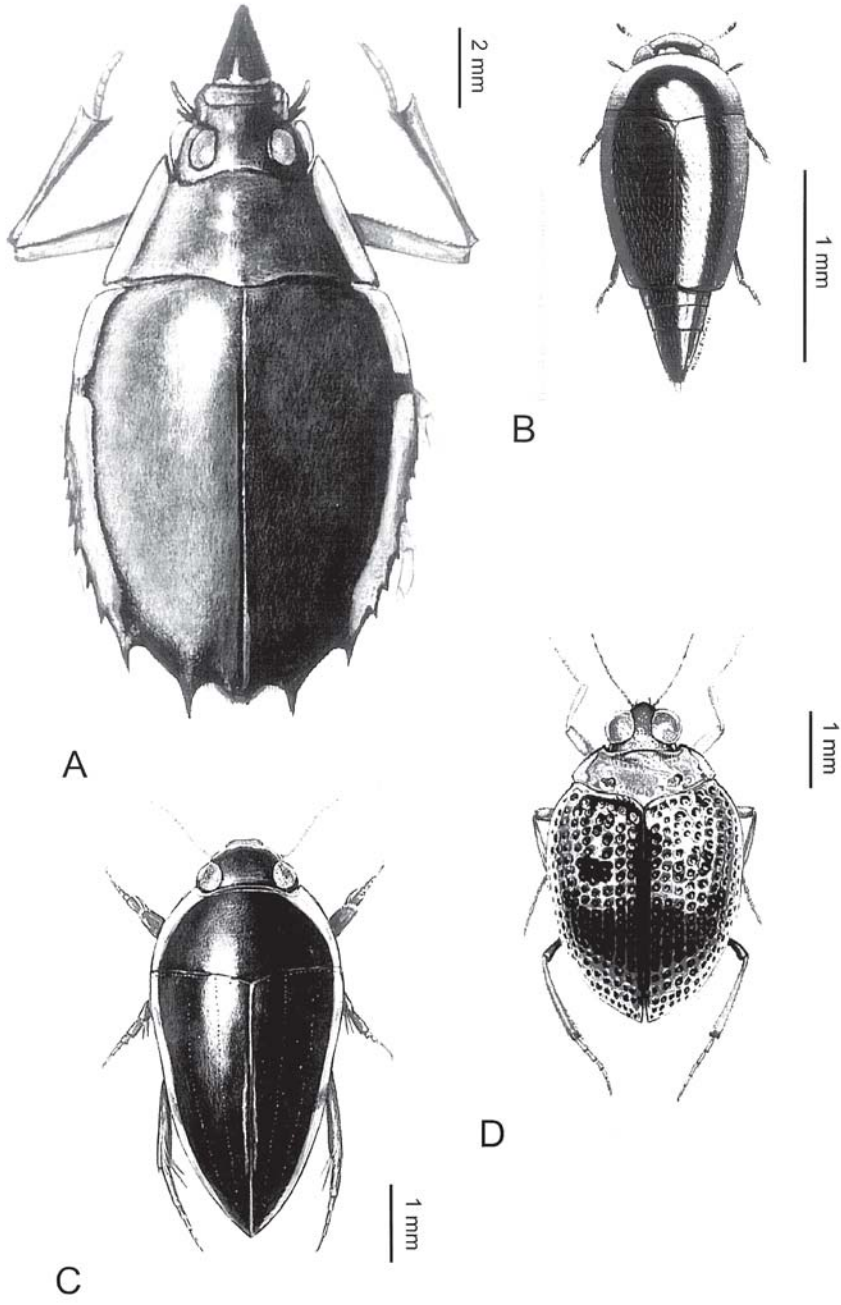

Figure 5. Adults of A – *Porrorhynchus* Gyrinidae ; B – Hydroscaphidae; C – *Hydrocanthus* Noteridae; D – *Peltodytes* Haliplidae.

while it is longer in *Orectochilus villosus* (Müller) in which larvae overwinter. Pupation takes place on land, in cocoons made of mud and debris. These cocoons are attached to stems of plants or other surfaces and the time span from cocoon formation to adult emergence is 8–14 days (Nilsson 1996).

Larvae are carnivorous and prey on oligochaetes and other smaller invertebrates. Adults prey on animals which live or have fallen on the water surface. In addition, gyrinids are also believed to be scavengers; Steiner and Anderson (1981) observed captured *Spanglerogyrus* feeding on bread crumbs. For more details on gyrinid bionomics, see Wesenberg-Lund (1943), Spangler (1991a) and Nilsson (1996).

Habitat Notes In ponds and lakes, gyrinids are often found between stands of emergent plants such as reeds, and also between *Pandanus* stems. Many species, especially in the tropics, are rheobiontic and will be found in different kinds of streams, often hiding in undercut river banks (*Orectochilus*) or in crevices of submerged wood during daytime. Several species are attracted to light traps.

Regional Taxa In Malaysia the family is represented by four genera: *Dineutus* (subg. *Spinosodineutes*), *Gyrinus*, *Orectochilus*, and *Porrorhynchus*. Except for *Dineutus* (*Spinosodineutes*) (see Brinck 1981) no modern keys to Malaysian species exist. However, a revision of the Southeast Asian species of the genus *Orectochilus* is in preparation by P. Mazzoldi. Original descriptions of Southeast Asian Gyrinidae were, among others, published by Régimbart (e.g. 1880, 1882a,b, 1883a,b, 1884, 1886, 1888, 1892, 1907), Ochs (e.g. 1927a,b, 1928, 1929, 1931, 1954) and Peschet (1923a,b). *Dineutus* and *Orectochilus* are quite frequently collected in Malaysia.

Key to genera of Malaysian Gyrinidae (adults)

1. Last abdominal segment elongated, triangular, with a distinct longitudinal row of hairs on its ventral side. Surface of pronotum and elytra partially hairy ..... *Orectochilus*
- Last abdominal segment semicircular, without a longitudinal row of hairs on its ventral side. Surface of pronotum and elytra completely glabrous 2

2. Scutellum visible. Posterior corner of pronotum without bristle-carrying pit (caution: the tuft of bristles is often inconspicuous and the bristles may be worn out, so the character may be difficult to appreciate). Maxilla with galea. Relatively small, globular species (length 3.7–5.2 mm).. *Gyrinus*
- Scutellum invisible. Posterior corner of pronotum with bristle-carrying pit. Maxilla without galea. Species less globular, more elongated or more flattened. Larger species, size medium to big (length 6–20 mm) 3

3. Labrum triangular, longer than wide (Fig. 5A). Length 13–20 mm ..... *Porrorhynchus*
- Labrum short and wide, distinctly wider than long. Length 6–8 mm ..... *Dineutus*

Genus *Gyrinus*

The genus includes only three species in Southeast Asia: *Gyrinus smaragdinus* Régimbart, *G. sericeolimbatus* Régimbart and *G. convexiusculus* MacLeay. The first of these species is restricted to the mountains of northern Indochina and Assam

and is surely not present in Malaysia. *Gyrinus sericeolimbatus* is known from Malaysia (specimens from Pahang and Sabah deposited in the Natural History Museum of Vienna). *Gyrinus convexiusculus* could be present, since it has a wide distribution from North India and southern China to Java, Sumatra, Australia and New Zealand; however, it has not been recorded from Malaysia so far. *Gyrinus convexiusculus* is easily distinguished from *G. sericeolimbatus* by the dorsal side, which is uniformly black and shiny in the former, but distinctly microreticulated and provided with metallic lustre in the latter.

Genus *Dineutus*

In Malaysia this genus is represented by two species, *Dineutus unidentatus* Aubé and *D. spinosus* (F.), both in the subgenus *Spinosodineutes*, which is characterized by the epipleural (postero-lateral) angle of the elytra being produced into a distinct spine. The two species are easily distinguished by the yellow margin of the elytra of *D. unidentatus*, while *D. spinosus* is evenly dark and bronzed (see also Brinck 1981).

Genus *Porrorhynchus* (Fig. 5A)

The genus includes very few species, with a distribution covering Southeast Asia and New Guinea. One species, *P. marginatus* Castelnau, is represented in Malaysia. This species is recorded from Indochina, Peninsular Malaysia and most of Indonesia. It is highly variable and seems to give rise to local races (in particular in the southernmost part of Peninsular Malaysia the subspecies known as *Porrorhynchus marginatus tenuirostris* Régimbart seems to predominate). Whether these taxa really deserve subspecific (or even specific) status must be solved by a detailed taxonomic revision.

Genus *Orectochilus*

This genus contains at present about 200 species, distributed mainly in Southeast Asia (only 3–4 species reach the Palearctic Region and one is found in the Congo Basin in Africa). The genus is actually divided into two subgenera: *Orectochilus* s.str. (which is not recorded from Malaysia, although one species is known from Sumatra), characterized by pronotum and elytra totally covered by hairs, and *Patrus*, characterized by pronotum and elytra only partially covered by hairs. However, this systematic arrangement might be subject to change as a consequence of the revision now in progress. Peninsular Malaysia is relatively poor in species (12 species recorded at present), while by comparison Sabah and Sarawak are home to about 40 species.

FAMILY HALIPLIDAE – Crawling Water Beetles

Diversity and Range This is a moderately large family of True Water Beetles, with some 220 known species in five genera. Haliplidae occur in all biogeographical regions, with the highest species diversity in the temperate zones of the northern hemisphere (Vondel 1995, 1997).

Morphology (Figs. 2B, 3C,D, 5D). Eggs are white and oval or roundish, their surface structure seems to be more or less identical in different species (Nilsson 1996; Vondel 1997). Larvae are elongate. In *Peltodytes*, the body bears numerous long appendages (tracheal gills, Fig. 3C); in *Haliplus* (Fig. 3D), there are minute, pea-shaped structures on the dorsal and ventral side of the body (micro-tracheal gills) (Wichard *et al.* 1995). The third instar is up to 14 mm long. For a detailed account of the different types of haliplid larvae, see Bertrand (1972), White and Brigham (1996) and Vondel (1997).

Adults are usually elongate or drop-shaped, the body being oval in cross section. The head of haliplids appears small with large eyes, which sometimes protrude strongly. The antenna is long and filiform. The scutellum is concealed. The hind-coxal plates are a very good character to identify the family: these plates are largely covering the coxa, hind-femur and at least sternites 2–4. The prosternal process has a broad, straight posterior margin, which tightly fits on the broad, straight foremargin of the metasternal process between the mesocoxae.

Biology All stages except for the pupa are aquatic. Larvae cannot swim, rather they can be observed creeping over the substrate or on water plants. Adults move rather quickly in the water by alternately moving their hind-legs. This produces the impression of water walking.

Larvae do not need to access atmospheric air, they breathe via the integument and their gills (Nilsson 1996). Adults carry an air supply beneath the elytra and under the coxal plates; this supply has to be renewed at the surface from time to time. Eggs are placed into plants, usually into existing holes, or the female bites a hole into the plant prior to oviposition. For European species, incubation takes 1–2 weeks, the first and second instars last 1–2 weeks, while the third instar may last for more than a year. Pupation takes place on land in a pupal cavity in soil or moss, where the third instar may rest for a month or so. Actual pupation takes 5–10 days (Nilsson 1996).

Larvae are phytophagous and eat filamentous algae, characeans and perhaps even seed-plants; some species are rather specialised with respect to their preferred diet. Adults of some species are phytophagous, while others are carnivorous (Seeger 1971a; Vondel 1997). Ecology of European haliplids was reviewed in detail by Seeger (1971a,b,c), see also Vondel (1997).

Habitat Notes Freshwater habitats such as pools and puddles, and margins of slowly flowing streams (cf. Vondel 1997). One will encounter most species at the edge of pools and ditches, where they live among water plants. Sometimes, it is possible to observe plenty of specimens “water walking” between stalks of *Phragmites*, usually in water depths up to half a metre. *Haliplus confinis* (Europe) was recorded from down to 5 m depth (Nilsson 1996).

Regional Taxa Surprisingly, this family has not yet been recorded from Malaysia, although two genera and several species very likely occur there. Oriental Haliplidae were revised by Vondel (1992, 1993, 1995).

Key to genera and subgenera of Haliplidae (adults) potentially occuring in Malaysia
(modified after Vondel 1993, 1997)

1. Elytra with sutural line on apical half. Metacoxal plates covering at least part of the sixth abdominal sternite, only the seventh remains completely visible ..... *Peltodytes*
- Elytra without sutural line, or with faint line apically. Metacoxal plates shorter, leaving at least three abdominal sternites visible ..... *Haliplus*

Genus *Peltodytes*
Four Oriental species are currently known (Vondel 1992). *Peltodytes sumatrensis* Régimbart (Fig. 5D) is known from Sumatra and Thailand, and perhaps from Sulawesi (Vondel 1992).

Genus *Haliplus*, subgenus *Liaphlus*
Twenty Oriental species of *Liaphlus* (Vondel 1993) are currently known. At least three species are known from adjacent areas (see Vondel 1993, 1995; Mazzoldi and Vondel 1997): *H. philippinus* Chapin, 1930 (Burma, Thailand, Laos, Vietnam, Philippines, Indonesia), *H. pulchellus* Clark (Oriental, including Thailand, Indonesia), and *H. samosirensis* Vondel (Sumatra, Kalimantan).

FAMILY NOTERIDAE – Burrowing Water Beetles

Diversity and Range A cosmopolitan family of about 300 species in about 13 genera, most of which occur in the tropics. There are two subfamilies, i.e. the stygobiontic Phreatodytinae (Japan), and the Noterinae (cosmopolitan).

Morphology (Figs. 2C, 3F, 5C). Eggs are oval and whitish, but nothing is known beyond this (Dettner 1997). The larvae are fusiform, with short legs and no obvious urogomphi (Bertrand 1972; Spangler 1991b; Dettner 1997). Pupa of exarate type. Adults are 1.4–8.0 mm long, the body is rather convex dorsally and with a flattened ventral side. Shape in dorsal view oval, elongate with tapered apex, or drop-shaped. The antenna is long and filiform in the Oriental species, the scutellum is concealed. The strongly elevated metacoxal process is an apomorphy for the family and makes adult noterids easy to recognize. A detailed description of noterid morphology was provided by Nilsson (1996) and Dettner (1997).

Biology All stages are aquatic, however, the pupa is protected by a mud cocoon, which can be filled with air. The larvae cannot swim, but crawl rapidly on the substrate or among water plants, and larvae of some species (*Noterus*) are active burrowers (Spangler 1982, 1991b; Dettner 1997), which led to the popular name of the family. Larvae of other genera are apparently also burrowers. Adult noterids are usually good swimmers, simultaneously moving their hind-legs.

For European species, larvae receive air from roots and plant stems which they penetrate with the tip of their abdomen (Nilsson 1996). The third instar constructs a cocoon of plant material and debris, which is adhered to submerged roots or stems of aquatic plants. These are pierced by the larva so that escaping air fills the cocoon,

later supporting gas exchange of the pupa. Adults carry an air supply under the elytra, they have to travel to the water surface for renewal of this supply from time to time. Dettner (1997) notes that females may oviposit by piercing stalks of *Carex*, otherwise it is believed that eggs are laid on roots and other plant material. Larval life is believed to take 4–6 weeks, but little is known of noterid ecology.

Larvae are carnivorous and were fed with Oligochaeta and Diptera larvae in the lab (Dettner 1997), while some authors suggest the larvae are mixed feeders (Spangler 1991b). Adults are carnivorous, but there are reports that they also eat plant material.

Habitat Notes Most species inhabit stagnant or slowly flowing water rich in emergent and floating vegetation. The dense network of roots latter are often inhabited by numerous noterids. It seems that semi-exposed or fully sunny habitats are preferred. However, there are also stygobiontic species, which are so far known from Japan and Indonesia (Sulawesi) (Spangler and Decu 1998). One will usually encounter many specimens when sweeping aquatic vegetation with a heavy dip net. Larvae can usually be collected by washing roots of aquatic plants. Spangler (1991b) notes that larvae of some American genera perhaps prefer burrowing between the roots of floating aquatic plants. Noterids are often attracted by light traps.

Regional Taxa The last comprehensive works on Indo-Malayan Noteridae were published by Sharp (1882) and Régimbart (1899), Indian species were reviewed by Vazirani (1969a). A modern revision is badly needed. Several species are very common, especially in exposed lowland habitats, such as mud pools or abandoned paddy fields.

Key to genera of Malaysia Noteridae (adults)

1 Body elongate and tapering at apex, or oval, egg-shaped. Foretibia at foremargin with strong spines, but these not strongly curved or hooked. Prosternal process apically pointed. Metacoxal process without hairs 2

\- Body drop shaped; foretibia at foremargin with a strong spine which is strongly curved and thus hook-like. Prosternal process apically truncate. Metacoxal process densely setose 3

2 Very small elongate species, TL < 2 mm. Beetle elongate, body tapering apically.....*Notomicrus*

\- Beetle larger than 2 mm. Shape in dorsal view distinctly oval, egg-shaped.....*Neohydrocoptus*

3 Large beetle, TL > 4.0 mm. Prosternal process without hairs ..... *Hydrocanthus*

\- Smaller, prosternal process with hairs ..... *Canthydrus*

Genus *Hydrocanthus*

A speciose and pantropical genus of about 50 species. The only Malaysian species is *H. indicus* Wehncke (Fig. 5C). It is widely distributed in the Oriental Region (Vazirani 1977).

Genus *Notomicrus*

Currently, nine species are recognized, eight of them in the New World, and one widespread species in the Oriental and Australian Realms. The latter, *N. tenellus* (Clark) also occurs in Malaysia (Vazirani 1977; Hebauer *et al.* 1999).

Genus *Canthydrus*

Cosmopolitan, with most of the about 100 species in the tropics. In Malaysia, there are two species, i.e. *C. angularis* Sharp and *C. ritsemai* Régimbart (Vazirani 1977). Some Southeast Asian species of *Canthydrus* (*C. flavus*-group) were revised by Wewalka (1992).

Genus *Neohydrocoptus*

A genus of the Old World tropics, there are about 30 species, some of which occur in Malaysia: *N. bivittis* (Motschulsky); *N. boschae* (Régimbart); *N. frontalis* (Régimbart); *N. sharpi* (Wehncke); *N. scapularis* (Régimbart), and perhaps *N. bivittulus* (Motschulsky).

FAMILY DYTISCIDAE – Diving Beetles

Diversity and Range More than 3700 species in about 150 genera are known (Pederzani 1995; Nilsson 2001), so that this is the most diverse family of True Water Beetles. The range is cosmopolitan.

Morphology (Figs. 2A, 3E, 6A–E, 7A–E). Eggs oval to elongate and whitish to brown. Larvae up to 8 cm long. Body usually elongate and broadest in the middle, then tapering towards head and posterior end. Head with long, sickle-shaped mandibles, these either with a groove, or a closed channel that opens anteriorly and posteriorly. Legs are long and slender, forelegs usually the shortest pair and hind-legs the longest one. The eight-segmented abdomen bears a pair of usually long, two-segmented appendages called urogomphi (Nilsson 1996). Pupa of exarate type.

Adults 1–48 mm long, the largest Malaysian specimens (*Cybister* sp.) reach about 3 cm. The shape is oval or elongately oval and continuous, sometimes interrupted by an angle between pronotum and elytra. Many species are rather depressed dorso-ventrally, but other morphotypes appear globular (e.g. *Hyphydrus*, *Microdytes*). The antenna is long and filiform in the Oriental species; the scutellum is either concealed (subfamily Hydroporinae), or visible. Males possess stalked suction palettes ventrally on fore- and middle tarsomeres 1–3; in the Hydroporinae, these devices may also be present in the female; the largest palettes are found in Colymbetinae and Dytiscinae. The hind-legs are often flattened to form paddles. Usually, there are fringes of long golden swimming hairs dorsally on the hindtarsomeres, often, especially in the males, also ventrally. Middle and hindlegs are the principal swimming devices in Dytiscidae, and these are modified according to the bionomics of the species. Species that hunt in open water have very strongly flattened hindlegs while those living on wet rocks or in damp soil may have lost their swimming hairs completely (Nachtigall 1974; Balke and Hendrich 1996; Balke, Dettner and Hendrich 1997; Ribera *et al.* 1997). *Agabus bifarius* (Kirby), a Palearctic species, is known to be wing dimorphic, i.e. species in which there are fully winged individuals and beetles with reduced, shorter wings.

Moreover, numerous cases of brachyptery (= short winged) are known, and also species with atrophy of flight muscles (Jackson 1952, 1956).

Biology Eggs, larvae and adults are aquatic. However, adults of a few species from India, Australia and New Caledonia were described as terrestrial. Larvae of the smaller species creep about on the bottom of their habitat, usually close to the edge of the water, while larvae of the larger species, such as *Hydaticus* and *Cybister*, can swim rather quickly by alternately moving their legs, and/or stroking with the abdomen, the latter case being escape behaviour. Adults are usually good swimmers. This is especially true for adult *Cybister* species. Adults swim by simultaneously moving their middle (stirring) and hind-legs; or only the hind-legs.

Dytiscids utilize atmospheric air which they obtain at the water surface with the tip of the abdomen. Larvae store air in the main ducts of the tracheae, while adults can carry air in the space between the elytra and the abdomen. Adults hold an air bubble at the end of the abdomen which functions as a physical gill. However, the bubble must be renewed at the surface from time to time as with increasing depths there will be an increase of the pressure and O_2 and N_2 diffuse into the water. As the beetle consumes oxygen, the partial pressure of N_2 increases even more, and more N_2 diffuses into the water, thus leading to a decrease of the bubble volume (Dettner and Peters 1999). Cuticular respiration occurs in smaller larvae. The air supply (adults) together with a rectal ampulla are a means of hydrostatic control (Hicks and Larson 1991).

Dytiscidae deposit their eggs singly or in small groups, either on the substrate, or into water plants which were previously pierced by the female ovipositor (Wesenberg-Lund 1943; Nilsson 1996). There are no egg cases or silk-like covers for the eggs. Eggs usually hatch within 10 days up to 6 weeks after oviposition, with the duration strongly depending on the temperature of the environment (study of European *Dytiscus*, Korschelt 1924). The latter is true for all immature stages. The first instar was found to last about 5 days (at 20°C) up to 39 days (at 11°C), the second instar lasts 4–5 days (20°C) up to 13 days (13°C, but may be 44 days if cooled down to 5°C); while the third instar lasts 13–14 days (18°C) up to 35 days (14°C). Duration of larval life also strongly depends on the amount of food available. Pupation takes place on land, but close to the water, in cells that are formed by the larva in damp soil, under wood and plants. Actual pupation takes 10 days up to half a year, again depending on the temperature (Korschelt 1924). Little is known about life cycle of other species, especially the smaller ones, and we did not find any information on the Oriental species.

Larvae are carnivorous, the kind of prey is more or less related to the body size of the larva and its capability of catching a particular animal. Thus, small larvae feed on small crustaceans, Diptera larvae, etc., while large ones (*Cybister* sp.) may well attack tadpoles and small fish. Digestion is extraintestinal, and the derived fluids are ingested by means of the suctorial mandibles (Wesenberg-Lund 1943; Nilsson 1996). Adults are usually carnivorous, but sometimes also scavengers.

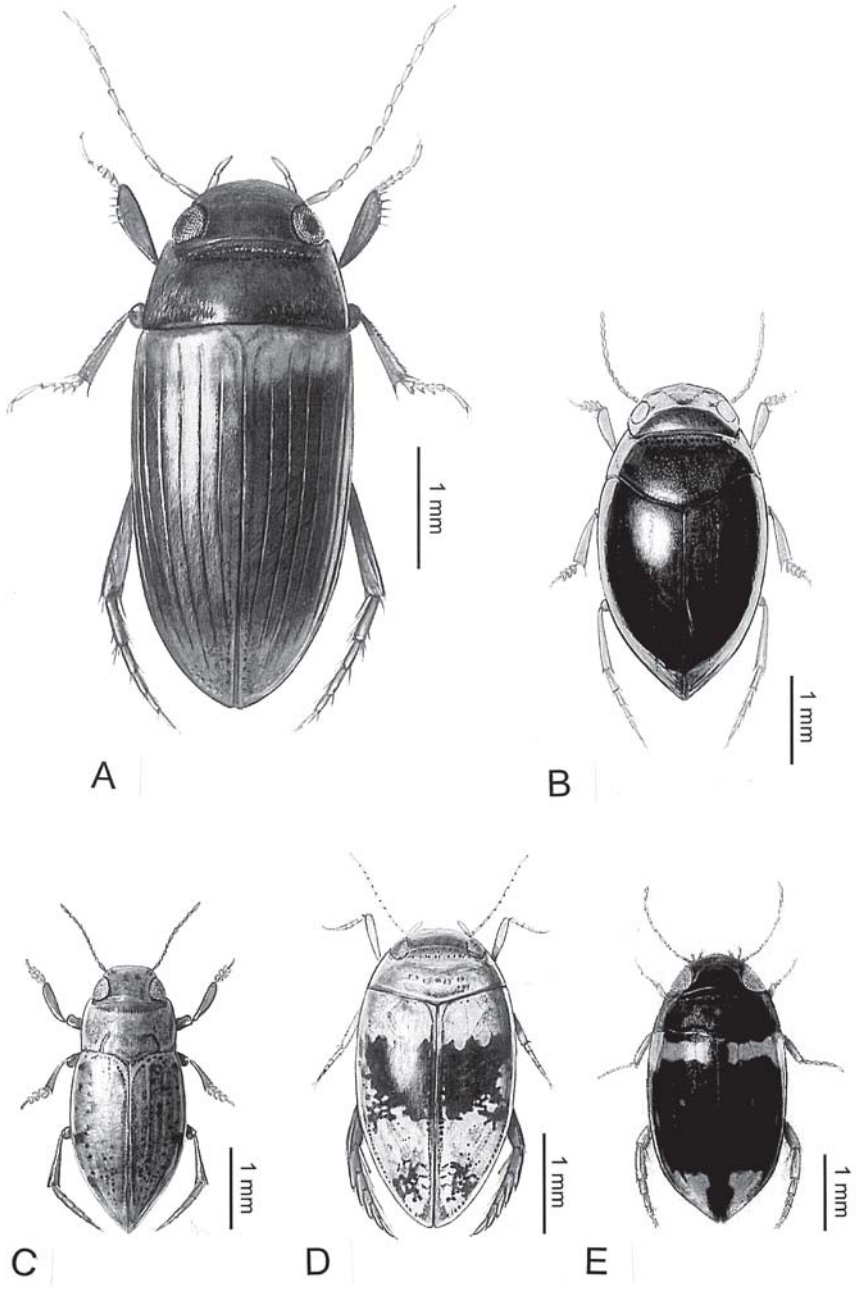

Figure 6. Adults of Dytiscidae. A – *Copelatus*; B – *Hydrovatus*; C – Bidessini; D – *Laccophilus*; E –*Neptosternus*.

Many species of Dytiscidae are supposed to be capable of sound production. There are, however, few bioacoustical studies that have explored this assumption (Larson and Pritchard 1974; Aiken 1985; Biström 1996a). In stressful situations, some species of *Rhantus* were found to be buzzing (Smith 1973).

Adult Dytiscidae produce antimicrobial secretions with their pygidial glands. These secretions are applied to the body on land, where the beetle cleans and brushes his body with the legs (Kovac and Maschwitz 1990). The actual composition of the secretions varies among different taxa (Dettner 1985). Also, adult Dytiscidae possess prothoracal glands which produce milk-like defensive secretions that irritate predators, in large dytiscid species even irritate amphibians and fish (Klausnitzer 1984).

Detailed accounts of dytiscid ecology can be found in Korschelt (1923, 1924); Wesenberg-Lund (1943); Galewski (1971); Schmidl (1992); Dudgeon (1999) and Larson *et al.* (2000).

Habitat Notes Dytiscidae occur in a great variety of habitats from groundwaters, damp jungle soil, steppe lakes, ponds, forest puddles, large lakes, rivers, small streams, springs, hygropetric sites, to alpine lakes up to 4700 m altitude. Many species can be found hiding among emergent vegetation or submerged plants, in thick layers of leaves at the margin of water bodies, while others dwell in the interstitial of gravelly river margins, stream ponds, and the like. In general, most species prefer habitats with abundant aquatic vegetation, so meso- and eutrophic sites will usually feature a rich diving beetle community. The occurence of some species is related to acidity or salinity of water; water temperature and habitat microstructures are other factors of interest. Many species are attracted to light traps.

Regional Taxa Oriental Dytiscidae as a whole were revised by Sharp (1882) and Régimbart (1899). Later, Vazirani (1969a, b, 1970, 1971, 1977) revised several groups and also presented a catalogue of Oriental Dytiscidae. Several authors published revisions and other taxonomic works on various genera. These works are cited under the respective genera. Dytiscidae are the most common of all Malaysian water beetles, especially in stagnant water.

Key to subfamilies of Malaysian Dytiscidae (adults)

1. Scutellum visible 2
- Scutellum not visible 4
2. Eyes in anterior view laterally not emarginate ..... Dytiscinae
- Eyes in anterior view laterally emarginate 3
3. Space between the metacoxal lines very narrow, or metacoxal lines faint, or reduced. Beetle often with longitudinal lines and/or strioles on elytra ..... Copelatinae
- Space between the metacoxal lines broader, at narrowest point broader than postcoxal process. Elytra without longitudinal lines and/or strioles ..... Colymbetinae
4. Fore- and middle-tarsus appearing four-segmented as the 4th joint is small and concealed by 3rd joint ..... Hydroporinae
- Fore- and middle-tarsus both distinctly with five joints. Hind-tarsomeres 1–4 with distinct apical lobes ..... Laccophilinae: *Laccophilus*

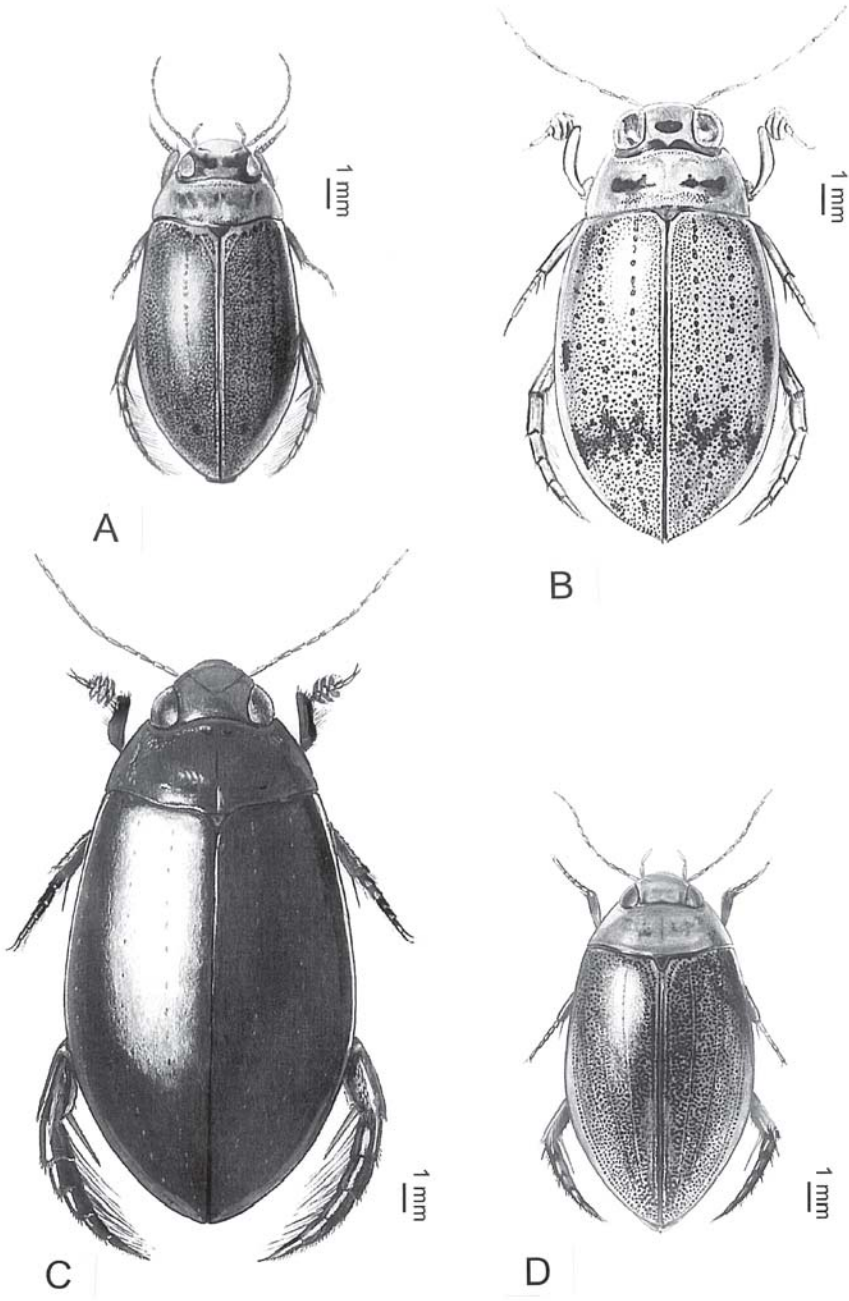

Figure 7. Adults of Dytiscidae. A – *Rhantus*; B – *Eretes*; C – *Cybister*; D – *Hydaticus*.

Subfamily Copelatinae

Genus *Copelatus*

This is a diverse, cosmopolitan genus with the highest species diversity in the tropics. About 400 species have so far been described (Nilsson 1995). Most of these species inhabit primary forest sites and riverine forests. They are usually encountered in puddles of which the bottom is covered with leaves and debris. Most species have conspicuous longitudinal lines on the elytra (Fig. 6A). Metacoxal lines are present. Five named species are known to occur in Peninsular Malaysia, Sabah and Sarawak: *C. minutissimus* Balfour-Browne, *C. oblitus* Sharp, *C. tenebrosus* Régimbart, *C. doriae* Sharp, *C. irinus* Régimbart (Régimbart 1899; Balfour-Browne 1939; Balke *et al.* 1999). A synoptic review of *Copelatus* species was published by Guéorguiev (1968).

Genus *Lacconectus*

This genus is confined to the Oriental Region and includes 41 species (Hendrich 1998). All seven species (*L. basalis* Sharp, *L. corayi* Brancucci, *L. krikkeni* Brancucci, *L. muluensis* Brancucci, *L. ponti* Brancucci, *L. pulcher* Brancucci and *L. sabahensis* Brancucci) currently known from Peninsular Malaysia, Sabah and Sarawak can be identified with the key provided by Brancucci (1986); in this genus, the metacoxal lines are faint or absent. The beetles inhabit smaller forest streams and springs, where they can often be found in leaf packs, or in stream pools. Species of *Lacconectus* are keen flyers that are often found in very small water bodies in the forest (Hendrich and Yang 1999, Hendrich *et al*. 2004).

Subfamily Hydroporinae

This subfamily comprises most of the smaller Dytiscidae, usually shorter than 4 mm. More than 500 species are known in this cosmopolitan group.

Tribe Vatellini

Genus *Derovatellus* Sharp

This genus is widely distributed in Africa and America, containing some 30 species. One species, *Derovatellus orientalis* Wehncke, occurs in the Oriental Region where it is known from Peninsular Malaysia (Hebauer *et al.* 1999), Kalimantan and Sumatra (Biström 1979). It inhabits more or less shaded (? temporary) puddles in primary swamps. The distribution of this rare species is extremely patchy.

Tribe Hyphydrini

Genus *Hyphydrus*

This large genus is widely distributed in the Old World with most of the about 110 species in the Afrotropical Region. The revision of Biström (1982) and updates deal with the 29 Oriental species (Biström *et al.* 1997). So far three species have been reported from Malaysia (*H. holomelas* Biström, *H. lyratus lyratus* Swartz, *H. sumatrae* Régimbart). *Hyphydrus* species inhabit pools and puddles, usually with some aquatic vegetation.

Genus *Hyphovatus*

A small genus of three Oriental species, *H. dismorphus* (Biström) and *H. manfredi* Wewalka and Biström from Thailand, and *H. prapatensis* Wewalka and Biström from Indonesia (Sumatra) (Wewalka and Biström 1994). It probably occurs in Malaysia.

Genus *Allopachria*

An Oriental genus with most of the 32 described species in the Indomalayan Region. The revision of Wewalka (2001) deals with all known Malaysian species. Four species have been recorded from Peninsular Malaysia, Sabah and Sarawak (*A. abnormipenis* Wewalka, *A. balkei* Wewalka, *A. kodadai* Wewalka, *A. zetteli* Wewalka). All the species inhabit small springs and streams in forests and their ranges are usually small.

Genus *Anginopachria*

The single species of the genus is only known from the type locality in Pahang, Peninsular Malaysia (Balke and Hendrich 1999; Wewalka *et al*. 2001).

Genus *Microdytes*

An Oriental genus with most of the 34 described species in the Indomalayan Region. The revision of Wewalka (1997) and the last update (Wewalka and Wang 1998) treat all Malaysian species. So far, four species have been recorded from West Malaysia, Sabah and Sarawak (*M. elgae* Hendrich, Balke and Wewalka, *M. hendrichi* Wewalka, *M. pasiricus* Csiki and *M. sarawakensis* Wewalka). All the species inhabit small springs and streams in forests and their ranges are usually small.

Tribe Hydrovatini

Genus *Hydrovatus*

This large genus has an almost world wide distribution, with most of the 200 or so species inhabiting the Old World tropics. The revision of Biström (1996b) deals with all of the Oriental species (Fig. 6B). So far, 13 species have been recorded from Malaysia. *Hydrovatus* species can be found usually in stagnant water, such as pools, irrigation ditches which would only have very slowly flowing water, puddles and paddy fields. They are often encountered in slightly swampy situations with dense vegetation, such as emergent grasses and weeds (Hendrich *et al*. 2004). Most species are rather widely distributed.

Tribe Bidessini

Genus *Borneodessus*

A monobasic genus with only one species (separated into two subspecies) endemic to the central mountains of northern Borneo. The subspecies *B. zetteli zetteli* occurs in Sabah, while *B. zetteli kalimantanensis* is recorded from Kalimantan (Balke *et al*. 2002). The species inhabits forest rivers.

Genus *Clypeodytes*

This genus includes about 36 species from Africa, Asia and Australia (Biström 1988; Nilsson 1995). The Oriental and Australasian species are in great need of total

revision. So far, only one species, *C. javanus* Régimbart, has been reported from Malaysia but at least four species are known from Vietnam, Myanmar, Thailand and the Sunda Islands of Indonesia (Vazirani 1977; Biström 1988). *Clypeodytes bufo* Sharp is widespread in the lowland and coastal areas of Vietnam and Thailand so it should be expected in Malaysia as well. The species appear to be inhabitants of all kind of stagnant waters.

Genus *Hydroglyphus*

This large genus is distributed in the Palearctic, Ethiopian, Oriental and Australasian Realms with most of the ca. 80 species inhabiting the Old World tropics (Régimbart 1899; Biström 1988). No key has been published for the Oriental species yet. Only one species has been reported from Malaysia: *H. inconstans* (Régimbart). However, at least eight species are known from Vietnam, Myanmar, Thailand and the Sunda Islands (Vazirani 1977; Biström 1988; Hendrich and Balke 1995). Some of these species such as *H. orientalis* (Clark) and *H. flammulatus* (Régimbart) are widespread in lowland and coastal areas of the afore-mentioned countries and can be expected to occur in Malaysia. The species appear to be inhabitants of all kinds of stagnant waters, especially swamps. They are frequently caught at light.

Genus *Leiodytes*

A small genus with 19 species which occur in the Ethiopian and Oriental Regions (Biström 1988; Nilsson 1995). The Oriental species need to be revised. Only one species, *Leiodytes nicobaricus* (Redtenbacher), is known from Malaysia (Balke *et al*. 1999), collected from pools and puddles.

Genus *Limbodessus*

The only species of the genus, *L. compactus* (Clark), is distributed over the Indomalayan Region, New Guinea, the Pacific Islands and northern Australia (Balke and Satô 1995). It occurs among grasses and weeds at the margin of pools and puddles.

Genus *Liodessus*

A widespread genus, including about 44 species (Biström 1988). There are two new species (Fig. 6C) known from Malaysia, which were collected from lowland habitats (Balke and Hendrich, in prep.).

Genus *Pseuduvarus*

This genus contains only one species, and *Pseuduvarus* is perhaps even a synonym of *Hydroglyphus*. *Pseuduvarus vitticollis* (Boheman) is distributed from Africa, Madagascar, Réunion, Mauritius, Pakistan, India, Sri Lanka, Malaysia and China (Nilsson 1995). The species inhabits pools and puddles rich in emergent vegetation (Hendrich *et al*. 2004).

Genus *Uvarus*

At the moment 55 species are recognized in this widely distributed genus. The distribution is almost world wide with centers of diversity in Africa, North and Central

America (Biström 1988). Two species (*U. gentilis*, *U. livens*) have been recorded from Malaysia (Vazirani 1977). However, the occurrence of *Uvarus* in Malaysia is rather doubtful: *Uvarus gentilis* (Sharp) is a synonym of *Pseuduvarus vitticollis* (see Nilsson 1995), while *U. livens* (Régimbart) probably belongs to another genus.

Subfamily Laccophilinae

Genus *Neptosternus*

This Afrotropical–Oriental genus currently comprises >80 species (Fig. 6E). Southeast Asian representatives were most recently revised by Hendrich and Balke (1997). The fauna of that region had to be updated soon afterwards, indicating the remarkable species richness of *Nepstosternus*. Sixty one species are now known from Southeast Asia (Hendrich and Balke 2003). Two species are known from Peninsular Malaysia and 14 from Sabah and Sarawak. All of them inhabit smaller to medium sized forest streams, where they hide under stones, logs and among mats of floating roots and grasses. The ranges of the species are rather small, except for the widespread *N. hydaticoides* Régimbart.

Genus *Laccophilus*

This genus has a worldwide distribution and includes more than 250 species (Fig. 6D). The Oriental species were revised by Brancucci (1983). Twelve species have been recorded from Malaysia. They inhabit stagnant and running water.

Subfamily Colymbetinae

Tribe Agabini

Genus *Platynectes*

Platynectes species are known from South America, as well as the Oriental and Australasian Realms and were revised by Guéorguiev (1972). Nilsson (1998) and Šťastný (2003) revised the Oriental taxa of the *Platynectes dissimilis*-group. Some 17 species are known to occur in the Oriental Region (Hendrich and Balke 2000b). The genus is currently in need of a comprehensive revision and many species or subspecies especially in Melanesia are still unnamed. Two species, *P. javanus* Nilsson and an unidentified species of the *P. decempunctatus*-group, are recorded from higher altitudes (above 1000 m) in Malaysia. The beetles inhabit streams and riverine swamps, as well as irrigation ditches.

Tribe Colymbetini

Genus *Rhantus*

This is a large genus with almost 100 species (Fig. 7A), known from all major zoogeographic regions of the world (Nilsson 1995). In the Oriental Region the genus is confined to higher altitudes. In Malaysia there is just a single record of the widespread *Rhantus suturalis* MacLeay from Mt. Kinabalu, Sabah (Balke 1998). Oriental *Rhantus* species inhabit pools at higher altitudes.

Subfamily Dytiscinae
Tribe Eretini
Genus *Eretes*
This is a small genus with one species in Australia, one species in North America and two widespread species in the Palearctic and Oriental Realms (Miller 2002). *Eretes griseus* (F.) (Fig. 7B) is recorded from Peninsular Malaysia and Singapore (Hendrich *et al*. 2004) and may occur in Borneo. It is an inhabitant of stagnant waters, usually insolated pools.

Tribe Hydaticini
Genus *Pleurodytes*
This small genus has two rare Oriental species (Vazirani 1969b). *Pleurodytes dineutoides* (Sharp) has been reported from Indonesia: Kalimantan, Java and Nias; *Pleurodytes epipleuricus* (Régimbart) is only known from the type locality Myanmar (Régimbart 1899; Vazirani 1969b). It may occur in Malaysia. Both species occur in forest pools.

Genus *Hydaticus*
This large genus has an almost worldwide distribution, with most of the about 150 species inhabiting the Old World tropics. No recent revision is available that deals with all the Oriental species (Nilsson 1995). So far, eight species and two subspecies have been recorded from Malaysia (Régimbart 1899; Vazirani 1977). The revisions of the *H. vittatus*- and *H. fabricii*-groups (Fig. 7D) published by Wewalka (1975, 1979) are very useful for identification of the respective species, while the remaining ones can be identified to some degree with Régimbart (1899). *Hydaticus* species inhabit pools, puddles, margins of lakes, riverine forest pools and intermittent stream pools. They can also be caught in paddy fields. Ecology varies greatly from species to species, with the rare ones being confined to forest habitats (Hendrich *et al*. 2004).

Tribe Thermonectini
Genus *Rhantaticus*
This monobasic genus is widespread in the Old World tropics (Nilsson 1995); *Rhantaticus congestus* (Klug), inhabiting stagnant, mainly insolated water, is recorded from Vietnam, Thailand and Myanmar (Vazirani 1977) and may occur in Malaysia.

Genus *Sandracottus*
This small Oriental and Australian genus has 12 species. Three species, *S. mixtus* Balfour-Browne, *S. maculatus* Wehncke, *S. bizonatus* Régimbart, are recorded from Peninsular Malaysia, Sabah and Sarawak (Régimbart 1899; Vazirani 1977). *Sandracottus* species inhabit pools and puddles in forests.

Tribe Cybistrini
Genus *Cybister*
This is a large genus with about 100 species, chiefly confined to the Old World tropics (Fig. 7C). Four species have been recorded from Malaysia. No key has been

published for the Oriental species. However, the majority of the species can reliably be identified with the works of Régimbart (1899), Vazirani (1969b) or Mori and Kitayama (1993). Species of *Cybister* are inhabitants of stagnant waters, such as forest pools, margins of lakes, and ditches.

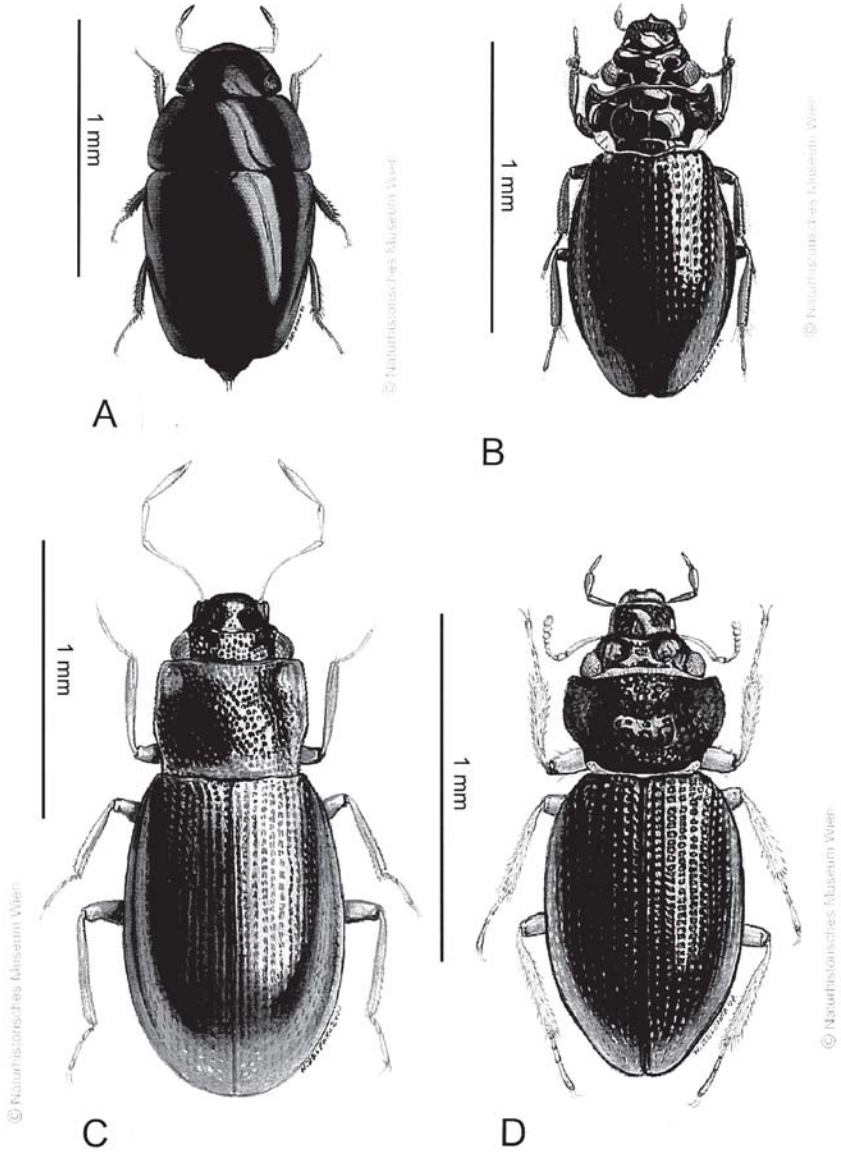

Figure 8. Adults of Hydraenidae. A – *Limnebius*; B – *Aulacochthebius*; C – *Hydraena*; D – *Ochthebius*.

FAMILY HYDRAENIDAE – Minute Moss Beetles

A detailed synopsis of the morphology and biology of the Hydraenidae can be found in Jäch, Beutel, Delgado and Díaz (2004).

Diversity and range This cosmopolitan family, with some 1200 known species in about 40 genera, is arranged in four subfamilies: Hydraeninae, Ochthebiinae, Orchymontiinae, Prosthetopinae; the last two are not represented in the Oriental Region. It can be estimated that there are still more than 1000 undescribed species globally. A world catalogue has been published by Hansen (1998). A revised generic check-list was compiled by Jäch, Beutel, Delgado and Díaz (2004).

Morphology (Fig. 1K, 8A–D) The eggs are oval; in many species they are covered with an egg-case or protective coat. Larvae are up to 4 mm long (Delgado and Soler 1997a); their body is elongate, almost cylindrical in cross-section and narrowed posteriorly. Head with five stemmata. Urogomphi (cerci) are two-segmented. Last abdominal segment usually with anal hooks. Spiracles are present on mesothorax, metathorax (not functional) and abdominal segments 1–8. Good accounts of larval morphology (incl. chaetotaxy) were recently presented by Delgado and Soler (1997a–c).

The pupae of two European species of *Ochthebius* were described by Bøving and Henriksen (1938) and Beier and Pomeisl (1959). A detailed study of the morphology and chaetotaxy of hydraenid pupae is currently being carried out by J.A. Delgado (in prep.)

Adult hydraenids are generally small, 0.8–3.3 mm long. Body outline with a distinct discontinuity between elytra and pronotum (most genera) or continuously curved and oval (*Limnebius*). Dorsal surface usually more or less glabrous and rather sparsely setose; ventral side usually with short and dense pubescence. Head usually abruptly constricted and retracted into prothorax behind level of eyes (not in Orchymontiinae), forming a “neck region”. Ventral side of head with antennal grooves near eyes. Compound eyes usually well developed, often distinctly protruding. In several genera, there is a pair of glabrous ocelli on the frons. The antennae are short, with 7–11 antennomeres and modified in most species for breathing purposes (hydrophiloid type). Antennal base not seen from above (covered by lateral extension of clypeus and frons). Maxillary palpi always well developed, sometimes very long (e.g. *Hydraena*). Pronotum laterally more or less equally rounded or strongly narrowing anteriorly (*Limnebius*), or distinctly constricted or excised posteriorly (*Aulacochthebius*, some *Ochthebius* spp.). Pronotal margins are often fringed with a narrow, fragile hyaline membranous cuticle in *Aulacochthebius* and *Ochthebius*. One of the most conspicuous morphological features of hydraenid adults is the presence of a pair of hypomeral antennal pockets (these are absent in several genera not represented in Malaysia). Anterior margin of prosternum with acute median projection in many species of *Hydraena*. Procoxal cavities posteriorly open in most hydraenids, but in *Hydraena* closed. Elytra well sclerotized, leaving one or two tergites exposed, or covering abdomen completely.

Abdomen usually with six (rarely with five, e.g. males of *Aulacochthebius*) well developed ventrites; however, an additional, usually small sclerite is observed behind the last ventrite in both sexes (in females this terminal sclerite represents the more or less strongly fused gonocoxites).

Biology Eggs and adults of most species are aquatic; there is however a number of strictly terrestrial and riparian genera (not in Malaysia). The larvae of the aquatic adults usually inhabit damp sites close to the water. Many of the riparian larvae are however able to stay submerged for some time if necessary and several taxa were reported to be aquatic in at least the first two larval stages (Spangler 1982; Hansen 1997a, b; Jäch 1998).

Adults of most species of Hydraenidae can be regarded as True Water Beetles (sensu Jäch 1998). They cannot swim. If one washes them loose, they float to the surface, where they usually cling upside down to the underside of the water surface trying to reach the next stone, leaf and the like, to search for a foothold and shelter.Certain adults, especially those living in well oxygenated streams use an incompressible gas gill (or microplastron), which enables them to stay permanently submerged (see below, under Elmidae). Other aquatic Hydraenidae use their antennae to replenish their air reservoir at the water surface (see below, under Hydrophilidae).

The life cycles of three Neotropical species of *Hydraena* were studied by Delgado *et al.* (1997); the average developmental period (egg to adult) of the Neotropical *H. particeps* Perkins lasted about three weeks; the three larval stages were completed in about 17 days. Cocoons are constructed on land, close to the water (Beier and Pomeisl 1959; Spangler 1991c; Hansen 1996). Larvae and adults mainly feed on algae, but some are saprophagous (Hansen 1997a). However, it is still not absolutely clear whether carnivory occurs (Spangler 1991c; Hansen 1997b).

Habitat Notes The aquatic species are found in a variety of habitats: e.g. saline coastal rock pools, swamps, streams, seepage water. Often, numerous beetles can be encountered in leaf packs, between roots or any kind of wood in lentic and lotic situations. It seems that many Hydraenidae are adapted to a particular particle size of the substrate so that they can dwell in the interstitial to some degree. They may disappear when streams are polluted with sediment (Brigham 1982).

Regional Taxa At least one genus, *Hydraena*, is very common in Malaysia; however, due to the small size and cryptic behaviour, this family is very rarely collected by inexperienced ecologists.

Key to genera of Malaysian Hydraenidae (adults)

1. Frons with a pair of ocelli. Last segment of maxillary palpi peg-like, thinner than penultimate one. Pronotum narrowly margined by transparent membrane 2
- Frons without ocelli. Last segment of maxillary palpi not peg-like, not thinner than penultimate one. Pronotum without a distinct lateral membrane 3

2. Pronotum with two sharply defined transverse impressions. (Fig. 8B) ..... *Aulacochthebius*
- Pronotum without sharply defined transverse impressions. (Fig. 8D) ..... *Ochthebius*

3. Body outline continuous, without evident angle between pronotum and elytron (shape drop-shaped or ovate); maxillary palpi not exceedingly long, last segment not distinctly longer than penultimate one; pronotum broadest at base; elytra without distinct punctation. (Fig. 8A) .. .. *Limnebius*
- Body outline not continuous, with distinct angle between pronotum and elytron; maxillary palpi exceedingly long, last segment almost twice as long as penultimate one; pronotum broadest near middle; elytra always distinctly punctate. (Fig. 8C) ..... *Hydraena*

Genus *Aulacochthebius* (Fig. 8B)
Eleven species of this Palearctic-Afrotropical-Oriental genus are currently known, but none have been recorded from Malaysia. However, we have seen numerous specimens (probably belonging to *A. asiaticus* d'Orchymont) from southern Thailand and Java in various museum collections.

Genus *Limnebius* (Fig. 8A)
This genus contains some 130 known species but has not yet been recorded from Malaysia. A few unidentified specimens from Sabah are deposited in the Natural History Museum Vienna. Six species were described from adjacent areas, most of them from Java. Species of *Limnebius* occur in stagnant water, and at the edges of streams, for example in gravel banks.

Genus *Ochthebius* (Fig. 8D)
About 360 species of *Ochthebius* are currently known. There are no reports from Malaysia, but several species occur in adjacent areas, i.e. *O. masatakasatoi* Jäch (Thailand), *O. subinteger* Mulsant and Rey (Andaman Islands) and *O. sumatrensis* Jäch (Sumatra). These beetles inhabit streams, swamps, marine coastal rock pools and hygropetric sites.

Genus *Hydraena* (Fig. 8C)
With about 550 described species, this is the most speciose water beetle genus worldwide. A phylogenetic analysis of the subgeneric classification and a world check-list of species was published by Jäch *et al.* (2000). So far, species of this genus have not been reported from Malaysia. However, numerous unidentified specimens from various areas of Malaysia are deposited in museum collections. Several species are known from adjacent areas, and a revision as well as more sampling will surely reveal more than 100 new species in Malaysia. Three unidentified species were reported from Singapore (Balke *et al.* 1999). Oriental *Hydraena* species are found at the margin of streams, in springs, in forest puddles, abandoned paddy fields and flooded meadows (see Balke *et al.* 1999; Balke and Hendrich 1999a).

FAMILY EPIMETOPIDAE – Jewel Water Beetles

Diversity and Range This family is represented by 19 species in the Americas (genus *Epimetopus* Lacordaire), eight in the Oriental Region (genus *Eumetopus* Balfour-Browne) and two in Africa (genus *Eupotemus* Ji and Jäch) (Hansen 1991b; Jäch 2002; Ji and Jäch 1998a,b; Skale and Jäch 2003).

Morphology (Fig. 9A) Preimaginal stages of South American species were treated by Archangelsky (1997), those of the Oriental Epimetopidae are unknown. Adult *Eumetopus* are 2.5–3.5 mm long. The body outline is rather discontinuous, with a great angle between pronotum and elytra. The eyes are partly divided by a lateral canthus, or shelf-like projection. The pronotum is widest close to its anterior angles, and the anterior margin has a large median, shelf-like projection which covers parts of the head. Some species of *Eumetopus* are provided with colourful elytral tubercles (Hansen 1991b; Ji and Jäch 1998b).

Biology Eggs, larvae and adults are aquatic. Eggs are carried by the female in an egg case underneath the abdomen (brood care); these cases contain up to 17 eggs as far as is known (see Archangelsky 1997). Little else is known about their biology.

Habitat Notes *Eumetopus flavidulus* (Sharp) was collected "in a dried-up river bed hiding under stones that lay on fine moist sand with algae" (Hansen 1991b). In Laos, specimens of *Eumetopus* were collected by washing river banks (Jendek, pers. comm.). *Epimetopus* species were found "among the vegetation at the edge of streams, where

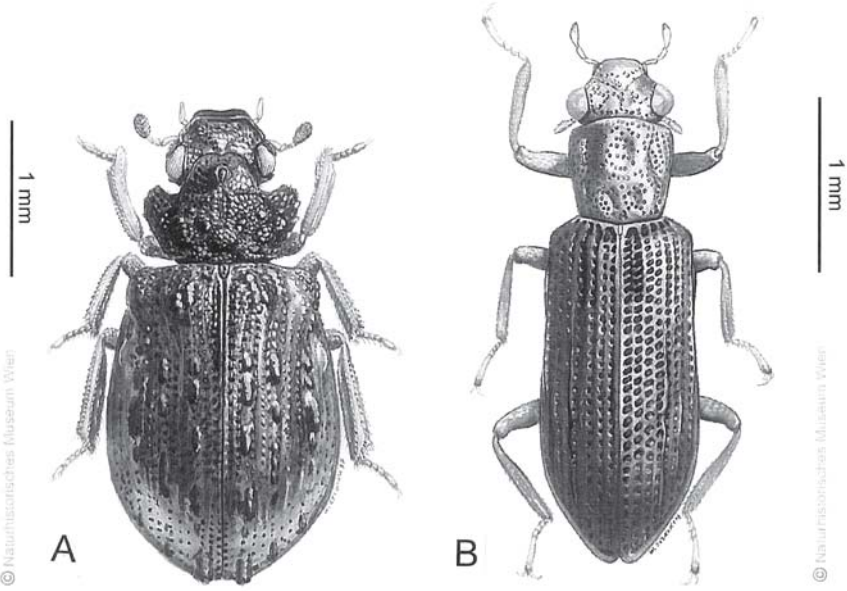

Figure 9. Adults of A – *Eumetopus Epimetopidae;* B – *Hydrochus Hydrochidae.*

they crawl about"; *E. thermarum* was collected at the margins of warm streams (up to 38°C) (Archangelsky 1997). Large numbers of Epimetopidae are sometimes attracted be light traps.

Regional Taxa No species has been reported from Malaysia. One species, *Eumetopus tibialis* Ji and Jäch, is known from northern Thailand, and *E. schuelkei* Jäch was described recently from Laos. The Oriental species were treated by Ji and Jäch (1998b), Jäch (2002) and Skale and Jäch (2003).

FAMILY HYDROCHIDAE – Elongated Water Scavenger Beetles

Diversity and Range There are some 200 species of Hydrochidae, all in the genus *Hydrochus*. They are known from all biogeographic regions (Hansen 1999a).

Morphology (Figs. 4F, 9B) The larvae have an elongate, parallel-sided body. The pupa is not described. Adult hydrochids are elongate, 1.5–5.5 mm long, sometimes rather narrow, and more or less roundish in cross section. The body outline is interrupted between pronotum and elytra; the pronotum has a characteristic shape, it is widest before the middle. The antenna is 7-segmented with three club segments.

Biology Eggs, larvae and adults are aquatic. Larvae and adults cannot swim, but are sluggish crawlers. Egg cases were found to contain one egg each; the cases are attached to plants, tree roots and the like at the water's edge (Archangelsky 1997). Adults feed on algae, the larval diet is not known (Archangelsky 1997).

Habitat Notes Both larvae and adults inhabit stagnant or slowly flowing waters including the margins of rivers. Some species prefer open situations, while others live in shaded habitats (Hebauer and Klausnitzer 1998). Specimens crawl about on water plants, leaves, and roots. Adults are sometimes attracted by light traps.

Regional Taxa One species, *H. rishi* Makhan (Hansen 1999a), is currently reported from Malaysia. This family is obviously very rare in Malaysia.

FAMILY SPERCHEIDAE – Filterfeeding Water Scavenger Beetles

Diversity and Range There are 17 species which occur in the Old World and one in the New World (Hansen, 1999a). All of them belong to the genus *Spercheus*.

Morphology (Figs. 4G, 10A) The larvae are very conspicuous, as they resemble ant lions (Neuroptera), with a narrow thorax and a sac-like abdomen which bears short, setose lateral appendages. Pupa of exarate type. Adults are broadly oval, with a rather convex body, 1.5–7.0 mm long. The head is strongly narrowed posteriorly just behind the eyes; anterior margin of clypeus distinctly emarginate with anterior corners upturned; labrum strongly deflected (not seen from above). The antenna is seven-segmented; antennomeres II and IV (cupula), as well as all three club segments pubescent. Elytra in some species with ridges or large tubercles (Hansen 1991b).

Biology Eggs, larvae and adults are aquatic. Larvae and adults cannot swim but rather crawl about upside-down under the water surface and on the underside of floating plant material such as *Lemna*. The female carries an egg cocoon (brood care) which contains up to 60 eggs until the larvae hatch (Hebauer and Klausnitzer 1998). Females can produce up to six cocoons within two months.

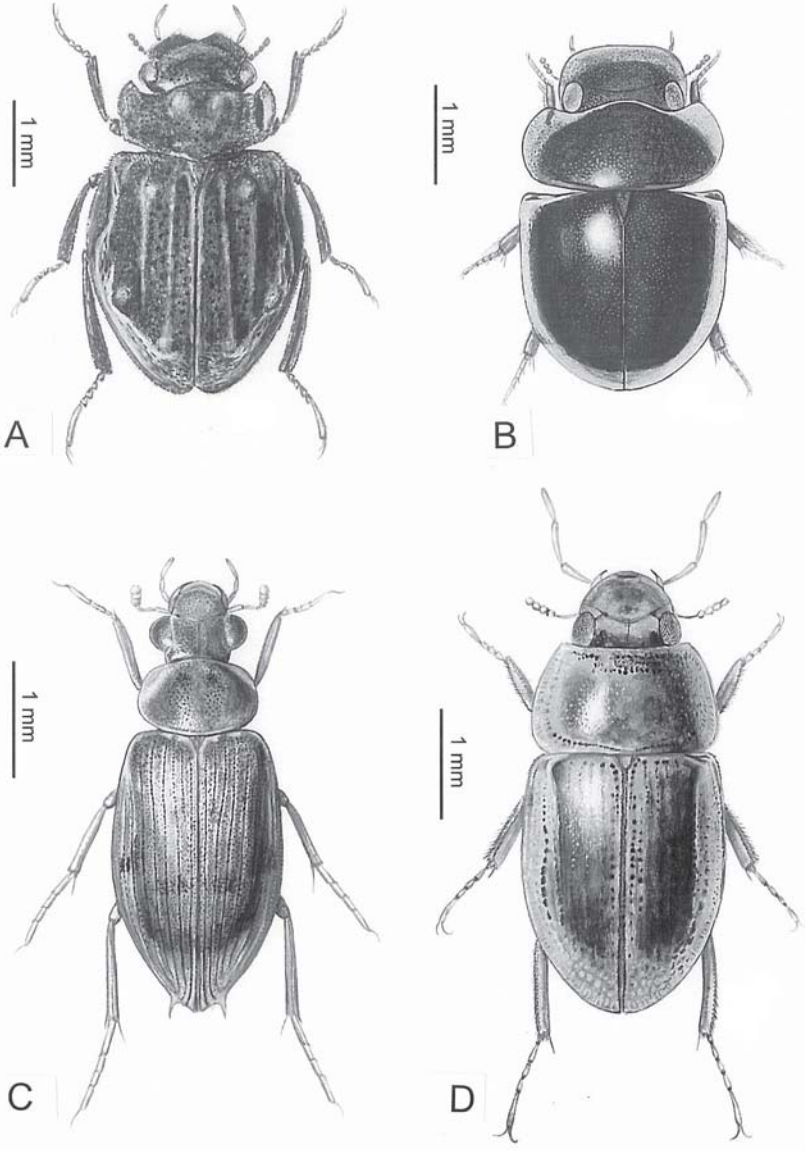

Figure 10. Adults of A – *Spercheus* Spercheidae; B – *Amphiops* Hydrophilidae; C – *Berosus* Hydrophilidae; D – *Helochares* Hydrophilidae.

Larvae and adults are filter-feeders. Living prey, such as small crustaceans, are also caught by the larvae (Rothmeier and Jäch 1986; Wesenberg-Lund 1943; Hansen 1996). Adults of both sexes are capable of producing a sound which can readily be heard when the beetles are disturbed.

Habitat Notes Usually to be found between water plants in insolated pools and puddles; sometimes they are abundant in paddy fields (Hendrich and Balke 1995).

Regional Taxa Two species were reported from "Malaysia" by Hebauer (1997) but his records were based on specimens from surrounding areas (Philippines, Indonesia). However, *S. stangli* Schwarz and Barber was reported from Brunei, and we have seen specimens from Singapore (Hendrich *et al.* 2004) and Sarawak. *Spercheus platycephalus* MacLeay occurs in Indonesia and the Australian Region; we found it in abundance in paddy fields in Bali (Hendrich and Balke 1995). There are two species in Thailand, which perhaps also occur in Malaysia: *S. spangleri* Hebauer, and *S. siamensis* Hebauer (Hebauer 1997; Hansen 1999a). A review of the genus *Spercheus* was published by Hebauer (1997).

FAMILY HYDROPHILIDAE – Water Scavenger Beetles

Diversity and Range This is another major family of aquatic Coleoptera. There are more than 2500 known species, and many new ones are being added every year (see Hansen 1999b). Currently 171 genera are known. The family is diverse not only in number of species, but also with respect to variety of form, size and ecological strategies (cf. Hansen 1991b, 1996). Hydrophilids occur in all biogeographic regions.

Four subfamilies are currently recognized (Horelophinae: 1 sp., New Zealand, Horelophopsinae: 1 sp., New Guinea, Hydrophilinae, Sphaeridiinae) (Hansen 1999a). The vast majority of Sphaeridiinae are terrestrial; they can frequently be encountered in all kinds of rotting organic matter (fruit, fungi, dung, carrion etc.) (Gentili *et al.* 1995). A check-list and key to the aquatic genera of the Hydrophilidae of the Palearctic and Oriental Realms has been published by Komarek (2003).

Morphology (Figs. 1G,H,L 2D, 4D,H, 10B–D, 11) Some of the largest and most conspicuous species (*Hydrophilus* spp.) of TWB belong to this family. Eggs are whitish and oval, often with a small process or a filiform appendage at one end (Hansen 1996). The body of the larva is usually widest somewhere in the middle, and slightly tapering at both ends, thus often giving the impression of a slightly subparallel shape in dorsal view. Larvae of many species have short legs which are not visible in dorsal view, and such larvae have a somewhat maggot-like appearance. This is also because only head and parts of the thorax are sclerotized, the rest of the body has a rather soft, elastic cuticle. Long lateral abdominal appendages may be present (e.g. *Berosus*, *Hydrophilus*) and are usually interpreted as gills.

Adults are 1–50 mm long. The body is usually oval to elongately oval, as well as slightly to very strongly (*Amphiops*) arched dorsally. The dorsal surface is mainly glabrous, ventrally typically with fine and dense pubescence (Hansen 1996).

Biology The hydrophilids treated here are aquatic, except for the pupal stage. Larvae crawl about on the substrate and among water plants. Adults of most genera are capable of swimming by alternately moving their legs, but with the exception of only a few genera (e.g. *Berosus*) they are rather sluggish.

Larvae of all hydrophilids except for *Berosus* have one pair of functional spiracles, situated on the eighth abdominal segment. It appears that many of these larvae are in fact connected to the water surface with the tip of the abdomen most of the time, while the rest of the body is submerged. Thus the larva can creep around on the vegetation, breathe, and still look for prey. *Berosus* larvae have long abdominal appendages (tracheal gills), and therefore do not need to travel to the surface for air supply. Some species of *Hydrophilus* and *Hydrochara* (Palearctic) also bear such appendages which were interpreted as tracheal gills (see Hebauer and Klausnitzer 1998), but there are no studies exploring this possibility to the best of our knowledge (cf. Wesenberg-Lund 1943). Cuticular respiration perhaps plays an important role in hydrophiloid larvae (Hebauer and Klausnitzer 1998). Adults renew their air supply which is stored in the tracheae and a ventral air bubble by attaching one or both antennae with the setose antennal club to the water surface, breaking the surface film, and then pumping air via the antennae to the air bubble on the underside of the beetle and into the tracheae (Crowson 1981; Hansen 1987).

Berosus species place their egg cases in small groups on the substrate, and cover these with a thin silk-like layer. Many of the remaining genera construct more elaborate egg cases, which are attached to the substrate or to water plants; in some of the larger genera, such as *Hydrophilus*, very special devices are constructed by the female, i.e. floating egg cases, or egg boats which feature an exhaust for air supply. Species of *Helochares* and related genera do not deposit their egg cases, which are carried by the female ventrally on the abdomen (brood care, see also Epimetopidae and Spercheidae). Females produce up to five egg cases during their life, and these may, depending on the species, contain 1–100 or more eggs. They usually hatch 1–2 weeks after deposition, and larval life is thought to take but a few weeks (Wesenberg-Lund 1943; Hansen 1996), however, little is known about the biology of the Oriental species.

Larvae are mainly carnivorous and digest their prey (small invertebrates) extraintestinally. Unlike in Dytiscidae, they do not possess mandibular channels which would enable them to feed under water. Rather, hydrophilid larvae emerge to eat, more precisely: the head is emerged, and the prey is then soaked with a brownish digestive secretion. The digested, fluid prey is then sucked in by the larva. Third instars of *Hydrophilus* prey more or less exclusively on shell-bearing freshwater snails, and these can be digested under water, as the larva enters the shell with its

head, sealing the latter against the water with its body (Wesenberg-Lund 1943). Adults are scavengers and feed on all kinds of plant material.

Habitat Notes Like Dytiscidae, hydrophilids can be found in a great range of habitats. Many species are terrestrial, and some are hygropetric. However, there are no groundwater species reported so far. They are very often attracted to light traps.

Regional Taxa Hydrophilidae are very common in Malaysia, especially in all kinds of stagnant water, even in rain puddles. However, the majority of the Malaysian genera have not been revised taxonomically and faunistic surveys are largely lacking.

Key to tribes of Oriental Hydrophilidae (adults) (after Hansen 1991b)

1. Labrum well sclerotized, of same colour as clypeus, and usually not concealed by clypeus .. .. Hydrophilinae...2
- Labrum soft, paler than clypeus, hidden under clypeus ..... Sphaeridiinae: *Coelostoma* (*Coelostoma* is the only aquatic genus here)
2. Elytral margins finely serrate or denticulate, at least anteriorly, seldom only weakly so. Pronotum with double punctation consisting of evenly mixed, fine and coarse punctures, sometimes almost rugulose-punctate, but without systematic punctures. Tarsi without fringe of long swimming hairs on dorsal side. Elytra with 10 well defined punctate striae. Spines on ventral face of tarsi modified to rather fine and dense setae, not arranged in rows ..... Sperchopsini (not Oriental)
- Elytral margins not distinctly serrate. Pronotum usually with simple punctation consisting of equal punctures, sometimes impunctate; except sometimes for systematic punctures laterally, if punctation is double, then beetle with middle and hind-tarsi with row of long swimming hairs on dorsal side; or elytra are not punctato-striate. Spines on ventral face of tarsi arranged in a pair of rows, only exceptionally modified to form fine setae 3
3. Middle and hind-tibia each with a distinct row of long swimming hairs on dorsal side. Scutellum much longer than wide ..... Berosini
- Middle and hind-tibia without swimming hairs; or in *Amphiops* with two rows on middle tibia, but not on hind-tibia; if swimming hairs are present on hind-tibiae, then scutellum hardly longer than wide and with a well developed prosternum 4
4. 2nd and/or 1st ventrite with a large cavity on each side which is normally filled with a hyaline mass, and is covered by a fringe of long setae which rise from the basal margin of the 1st ventrite; if not, first ventrite very short and the eyes are completely divided into a dorsal and a ventral part by a lateral canthus ..... Chaetharthriini
- Basal ventrites simple, without cavities, hyaline mass, or long setae; 1st ventrite not especially short. Eyes not divided 5
5. Head, pronotum and elytra without systematic punctures. Pseudepipleuron narrow throughout, much narrower than true epipleuron anteriorly, not delimited from it by a ridge. The 5th ventrite without apical emargination ..... Anacaenini
- Head, pronotum and elytra with systematic punctures; but not neccessarily evident on all three of these parts, sometimes obscured by a dense ground punctation. If systematic punctures absent, the pseudepipleuron at least approximately as wide as the true epipleuron anteriorly, or sharply defined from it by a sharp ridge (Laccobiini); or the 5th ventrite has a small apical emargination (Hydrophilini) 6

6. Posterior margin of 5th ventrite simply rounded, there is no apical emargination. Meso- and metasternal elevations not forming a common sternal keel. Elytra without striae or well defined rows of serial punctures (except some *Laccobius* with 6 abdominal ventrites). Apical segment of maxillary palpus longer than the preceeding one. Pseudepipleuron at least approximately as wide as the true epipleuron (except *Pelthydrus*) ..... Laccobiini

- Posterior margin of 5th ventrite with a small apical emargination fringed with stiff yellowish setae; if not: meso- and metasternal elevations raised to form a common sternal keel; or: elytra with 10 well defined rows of serial punctures (or striae); or: apical segment of maxillary palpus not much longer than the preceeding one. Pseudepipleuron usually much narrower than the true epipleuron ..... Hydrophilini

Subfamily Hydrophilinae

Tribe Berosini

The genus *Berosus* (Fig. 10C) is represented by five species in Malaysia and Borneo. It was recently revised by Schödl (1992, 1993). A second genus, *Allocotocerus* Kraatz, has two species in the region (Hansen 1999a). Finally, there is one species of *Regimbartia*, i.e. *R. attenuata* (F.), which is widespread in the Oriental Region.

Tribe Chaetarthrini

There are four species of *Chaetarthria* which are known from Sarawak and Peninsular Malaysia (Hebauer 1995a). The genus *Amphiops* is only represented by one very common species, *A. mater* Sharp (Fig. 10B) (Hansen 1999a).

Tribe Anacaenini

Three species of *Paracymus* are known from Sabah and Peninsular Malaysia (Wooldridge 1977; Hansen 1999a). We have seen Malaysian specimens of *Anacaena* which remain to be revised taxonomically. There are a few species known from neighbouring countries (Hansen 1999a).

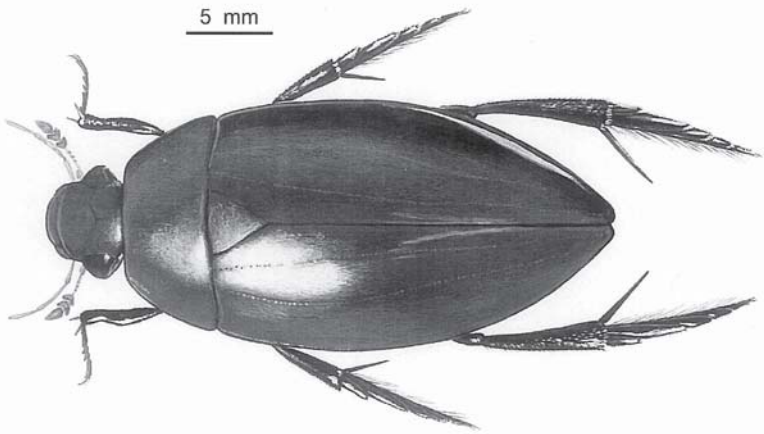

Figure 11. *Hydrophilus* Hydrophilidae.

Tribe Laccobiini
Eighteen species of *Pelthydrus* are known from Borneo and Peninsular Malaysia. This genus was revised by Schönmann (1994, 1995). The species of *Pelthydrus* are associated with small forest streams. Two species of *Laccobius* were reported from Peninsular Malaysia and Sabah (Gentili 1979; Hansen 1999a), as well as one species of *Oocyclus*, the widespread *O. sumatrensis* d'Orchymont (key, taxonomy: Hebauer and Wang 1998). *Laccobius* are in stagnant waters, but often associated with streams and larger, gravelly rivers where they can be found in abundance in floating vegetation, pools on gravel banks, etc.; species of *Oocyclus* are hygropetric (Hebauer and Wang 1998; Hendrich and Yang 1999).

Tribe Hydrophilini
There are eight genera of this tribe known from Malaysia (approximate number of Malaysian species in parentheses, after Hansen 1999a,b and Hebauer 1995b, 2000b; and unpublished data): *Agraphydrus* (1); *Megagraphydrus* (3); *Helochares* (8) (Fig. 10D); *Chasmogenus* (1); *Enochrus* (5); *Sternolophus* (2); *Hydrobiomorpha* (5 spp. in adjacent areas); *Hydrophilus* (3) (Fig. 11). A preliminary review of *Chasmogenus* was presented by Hebauer (1992).

Beetles of the genus *Hydrophilus* (Fig. 11) are among the largest Malaysian water beetles, and are used as food for humans (see introduction). They can at present not be reliably identified to species level due to lack of a modern revision. Hydrophilini inhabit stagnant and running waters, depending on the species.

Subfamily Sphaeridiinae
Tribe Coelostomatini
There are 10 species of *Coelostoma* in the region (Hansen 1999a), which usually inhabit richly vegetated ponds and puddles.

FAMILY ELMIDAE – Riffle Beetles
A comprehensive synopsis of the morphology and biology of Elmidae can be found in Kodada and Jäch (2004a).

Diversity and Range This rather large cosmopolitan family (with ca. 130 genera and more than 1200 described species) includes two subfamilies: Elminae and Larainae. A world check-list of genera has been published by Kodada and Jäch (2004a).

Morphology (Figs. 1F,O–Q, 4C, 12A–C) Eggs of the European *Elmis aenea* Müller were described by Beier (1948) as yellowish white, stout and regularly oval with abutted ends, 0.35–0.40 mm long and 0.22–0.25 mm wide. Mature larvae are 3–16 mm long; they can be elongate and slender (triangular or round in cross section), or flattened and onisciform or almost trilobite-like; head often partly retracted into pronotum, but always partly visible from above; mandible with well developed prostheca; spiracles present on mesothorax and abdominal segments 1–8; ninth abdominal segment with clawed operculum and with three bunches of retractile anal

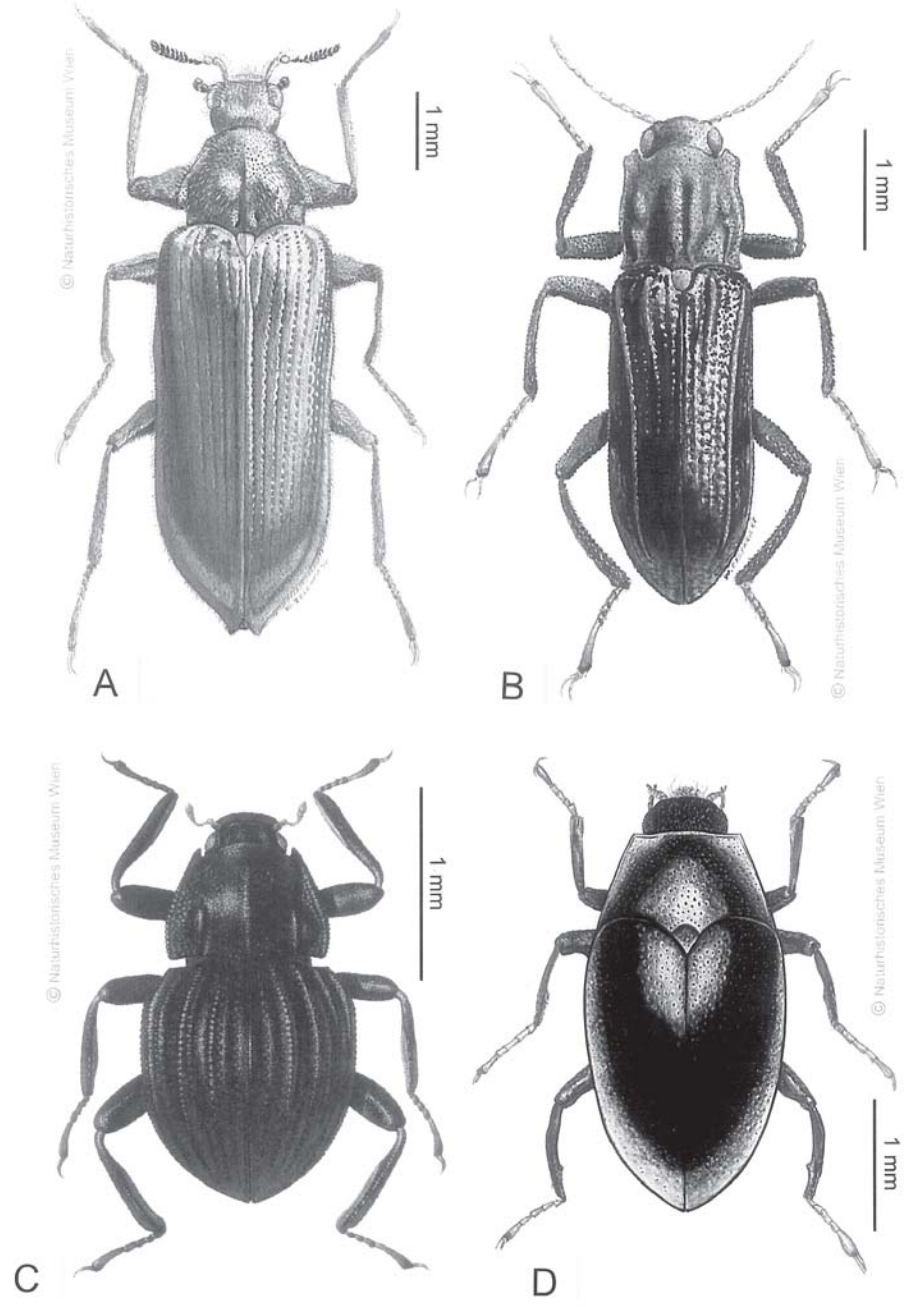

Figure 12. A – C adults of Elmidae. A – *Potamophilus*; B – *Stenelmis*; C – *cf. Grouvellinus*. D – *Elmomorphus* Dryopidae.

tracheal gills; tracheal system with conspicuous tracheal bulbs (oxygen reservoirs, according to Beier 1948) in last instar. One South American genus, *Stegoelmis*, is reported to have spiracular gills (Spangler 1990). For more information on the different types of elmid larvae, see Beier (1948), Bertrand (1972), Brown (1972, 1991), Olmi (1976), White and Brigham (1996), Kodada and Jäch (1999, 2004a). Pupae are of exarate type and, so far known, characterized by the pronotum bearing 2–4 filamentous projections and by the presence of a pair of caudal appendages. For more information on the types of elmid pupae, see Bertrand (1972) and Olmi (1976).

Adults are 0.8–11.0 mm long, short to elongately oval or sometimes even strongly elongate and parallel-sided. The colouration is usually dark, there are however numerous species with vividly yellowish colour patterns or even conspicuously metallic species. Head usually more or less strongly retracted into pronotum. The fronto-clypeal suture is usually distinct (absent in *Elmis*, *Stenelmis*). Antenna seven- to 11-segmented, variously shaped, e.g. filiform, incrassate, clavate, or of hydrophiloid-like appearance (scapus long and curved, apex loosely clubbed) or dryopid-like. Prosternum is usually slightly produced anteriad. Legs are usually very long, with long apical tarsal segment and claws. Larainae are usually entirely and densely pubescent, thus superficially resembling certain dryopids. Elminae are often largely subglabrous; their vestiture is usually confined to certain body parts (usually head, lateral body parts, and legs), being composed of (sometimes strongly modified) setae, which often can be seen only by means of SEM. Wing polymorphism occasionally occurs.

Biology Eggs and larvae of Elmidae are strictly aquatic. Pupation generally takes place above the water line – however, during spates they are frequently found fully submerged. Except for the period of a short dispersal flight (see Jäch 1997) adults of Elminae are strictly aquatic, whereas adults of Larainae are often encountered a little above the water line (preferably on partly submerged wood) or in spray zones of water falls and cascades. Strictly terrestrial representatives, which are not uncommon in other TWB families (e.g. Dytiscidae, Hydrophilidae, Hydraenidae, Dryopidae) are unknown among elmids. Elmidae are not capable of swimming during any developmental stage. Their large claws, however, enable them to cling to the substrate (stones, submerged wood) even in the fastest current.

Larvae breathe by means of anal retractile tracheal gills, and (very rarely) by spiracular gills; tracheal bulbs serve as oxygen reservoirs in the last instar (Beier 1948). Adults of Elmidae generally use a gas gill (plastron) for breathing. A gas gill is an air bubble or a very thin film of air, which (1) is in contact with the tracheal system, (2) is held by very small hydrofuge hairs or other cuticular structures, and (3) functions as physical gill (by replacing oxygen through diffusion of dissolved oxygen from the surrounding water while the beetle is submerged). In Elminae this gas gill is formed by a very thin film of air (incompressible gas gill, microplastron), which cannot shrink and therefore does not have to be replenished by atmospheric air from the surface, a fact which enables the beetles to stay permanently submerged.

Adults of Larainae are less well adapted for a life under water; they use a comparatively large respiratory bubble (compressible gas gill, macroplastron), which needs to be replenished when conditions become unfavourable.

Few observations of elmid ovipositions have been reported, but it is probable that most Elminae glue their eggs singly or in small clusters to the undersides of submerged rocks, wood or plant stems, depending upon habitat preference of the species; females of *Lara avara* (Larainae) were reported to lay 100–150 eggs on submerged wood (Brown 1987). Incubation time is rather short (5–15 days), varying with the temperature. Duration of larval stage (6–36 months) and number of instars (5–8) vary with temperature, as well as with body size and available food. Pupation requires 1–2 weeks in Elminae and at least two weeks in *Lara* (Larainae). Adult life span is remarkably diverse: *Lara avara* (Larainae) lives approximately three weeks, whereas representatives of two genera of Elminae (*Macronychus*, *Microcylloepus*) survived for more than 10 years under laboratory conditions (Brown 1973).

Larvae and adults feed mainly on detritus and algae, which they scrape from the substrate. Some species of Elminae and most (or all) species of Larainae are strictly xylophagous, probably gaining most nutrition from fungi and bacteria responsible for the decay of wood. Few species of Elminae were reported to eat submerged moss.

Habitat notes Members of this family live almost exclusively in lotic habitats. Within running waters they prefer the fast flowing reaches (especially shallow riffles or rapids), where they can be found on rocks, wood, leaf packs, vegetation (e.g. moss) and on rootlets trailing in water beneath undercut stream banks. Few species are encountered in wave-washed lake shores or ponds, a few species are recorded from subterranean waters and very few are found in hygropetric environments. They have been found in a depth of more than 10 m below the water surface. Many species are capable of flight. They are often attracted by light traps.

Regional Taxa Elmidae (especially Elminae) are very common in Malaysia and they are most abundantly found in samples taken from running waters. The taxonomy of the Elmidae of Malaysia is not well known. Although several genera were described or revised recently (e.g. Jäch 1993, 1994, Jäch and Boukal 1996, 1997a, b, Jäch and Kodada 1996a, b, 1997, Kodada and Ciampor 2000) the majority of species belongs to unrevised genera. Many new species and a few new genera still await description. Twenty two genera are now known to occur in Malaysia: Elminae: *Ancyronyx*, *Aulacosolus*, *Graphelmis*, *Graphosolus*, *Grouvellinus*, *Haraldaria*, *Hedyselmis*, *Homalosolus*, *Indosolus*, *Leptelmis*, *Loxostirus*, *Macronevia*, *Nesonychus*, *Podelmis*, *Prionosolus*, *Rhopalonychus*, *Stenelmis* (Fig. 12B), *Vietelmis*, *Zaitzeviaria*; Larainae: *Dryopomorphus*, *Potamophilinus*, *Potamophilus* (Fig. 12A).

Three genera, *Haraldaria*, *Hedyselmis*, *Macronevia*, are so far known only from Peninsular Malaysia. Three genera seem to be endemic to Borneo: *Homalosolus*, *Loxostirus*, *Rhopalonychus*. Some genera which are known from neighbouring areas may occur in Malaysia (e.g. *Jaechomorphus*, *Macronychus*).

Revisions of *Graphelmis* and *Potamophilus* (Fig. 12A) are in preparation. The speciose genera *Grouvellinus*, *Indosolus*, *Potamophilinus*, *Stenelmis*, *Zaitzeviaria* are in need of taxonomic revisions.

FAMILY DRYOPIDAE – Longtoed Water Beetles

A comprehensive synopsis of the morphology and biology of Dryopidae can be found in Kodada and Jäch (2004b).

Diversity and Range This is a moderately large cosmopolitan family (with about 30 genera and about 250 described species). A world check-list of genera has been published Kodada and Jäch (2004b). Since then one Oriental genus, *Stenomystax* Kodada *et al*., has been added (Kodada *et al.* 2003).

Morphology (Figs. 1E,N, 12D) Photographs of eggs of the European *Pomatinus substriatus* (Müller) were published by Olmi (1976), who described them as 0.73 mm long. Mature larvae are up to about 12 mm long; they are elongate and slender, cylindrical, anteriorly and posteriorly rounded; head slightly rectracted into pronotum, visible from above; mandibles without prostheca; spiracles present on mesothorax and abdominal segments 1–8; first seven abdominal spiracles lateral; abdomen without pleura; ninth abdominal segment with operculum, without retractile gills. For more information on the different types of dryopid larvae, see Bertrand (1972), Brown (1972, 1991), Olmi (1976), White and Brigham (1996).

Pupae are of exarate type and characterized by so-called gin traps: pigmented, tergal, abdominal sclerotizations, which can bite together by the contraction of longitudinal muscles. The gin traps were regarded as a protective device by Hinton (1946), however, according to Ulrich (1986) the gin traps are used to anchor the pupa in the larval exuvia, which obviously plays a crucial role in the development.

Adults are approximately 1.3–9.5 mm long, short to elongately oval or sometimes even strongly elongate and parallel-sided. The colouration is usually dark; vivid colour patterns or metallic species are unknown among the aquatic species. Most dryopids are entirely and densely pubescent, however, some of the aquatic genera are subglabrous, the vestiture being confined to certain body parts and composed of (sometimes strongly modified) microtrichia. Head usually partly retracted into pronotum. Fronto-clypeal suture absent. Antenna very short, five- to 13-segmented, and morphologically quite characteristic: pedicel greatly enlarged, remaining segments forming a densely set pectinate club. Prosternum usually slightly produced anteriad. Legs sometimes very long, with long apical tarsal segment and claws. Females of many species with blade-shaped ovipositor.

Biology Larvae and pupae of Dryopidae are usually terrestrial or riparian, occuring in wet sand, soil, wood or leaf litter; larvae of *Dryops* are apparently more or less amphibious (facultatively aquatic) (Nilsson 1996). According to Lawrence *et al.* (1999) “all stages of *Stygoparnus* (a cave-dwelling genus from Texas, USA) are

known to be truly aquatic", however, according to Spangler and Decu (1998), the larvae of this species are "presumed to be terrestrial", and the pupa is still unknown! Many adult dryopids are aquatic, but many species are riparian or strictly terrestrial (e.g. *Geoparnus*, *Monstrosostea*, *Sostea*). Dryopidae are not capable of swimming during any developmental stage.

Adults of the aquatic species breathe by means of a gas gill. As in Elmidae two types of gas gills, compressible and incompressible (micro- and macroplastron), can be observed. The distinction between these two types may not always be very obvious. The use of the antennae in replenishing the beetles macroplastron was reported for *Elmoparnus* from Central and South America.

Very little is known about oviposition and larval development of Dryopidae. Eggs of the aquatic species can be found above or below the water surface. Duration of the larval development for two North American *Helichus* spp. was recorded as 2–3 years and 4–5 years (Ulrich 1986). The number of instars is not exactly known. *Dryops* species were reported to feed on more or less decayed plant tissue. Adults of the Oriental genus *Elmomorphus* are almost exclusively found on wood, in leaf packs and on trailing rootlets.

Habitat Notes The aquatic adults of this family are found in flowing water (e.g. *Elmomorphus*, *Helichus*) or stagnant water, such as abandoned paddy fields, swamps, etc. (e.g. *Pachyparnus*). *Elmomorphus* is often collected in packs of leaves and twigs that have accumulated in riffle areas in forest streams. One American genus (*Stygoparnus*) is stygobiontic. Many dryopid species are capable of flight. They are often attracted by light traps.

Regional Taxa Our knowledge of the Malaysian Dryopidae is still very poor. Only three aquatic genera, *Elmomorphus*, *Pachyparnus* and *Stenomystax* have been recorded. A revision of *Elmomorphus* is in preparation; this revision will include descriptions of many new species. *Pachyparnus* and *Stenomystax* are represented by very few species. A few aquatic genera from Malaysia are still undescribed. At least *Elmomorphus* (Fig. 12D) is common in Malaysia.

REFERENCES

Aiken R.B. (1985) Sound production by aquatic insects. *Biological Reviews* **60**: 163–211.

Aiken R.B. and Wilkinson C.W. (1984) Bionomics of *Dytiscus alaskanus* J. Balfour-Browne (Coleoptera: Dytiscidae) in a central Alberta lake. *Canadian Journal of Zoology* **63**: 1316–1323.

Archangelsky M. (1997) Studies on the biology, ecology, and systematics of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). *Bulletin of the Ohio biological survey* N.S. **12**(1): 1–207.

Balfour-Browne J. (1939) On *Copelatus* Erichson and *Leiopterus* Stephens (Col. Dytiscidae) with description of new species. *Transactions of the Royal Entomological Society London* **88**: 57–88.

Balke M. (1998) Updating the Pacific, Indomalayan and Neotropical *Rhantus*-fauna (Dytiscidae). *Koleopterologische Rundschau* **68**: 71–80.

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

Balke M. and Hendrich L. (1996) A new *Geodessus* from Southern India. *Aquatic Insects* **18**: 91–99.

Balke M. and Hendrich L. (1999a) Singapore Water Beetles Tell A Story. *Nature Watch* **7**: 14–17.

Balke M. and Hendrich L. (1999b) An enigmatic new species of the genus *Allopachria* Zimmermann, 1923 from West Malaysia (Col. Dytiscidae). *The Raffles Bulletin of Zoology* **47**: 283–286.

Balke M., Hendrich L. and Foster G.N. (1997) Water Beetles and EIAs: Southeast Asian Projects. *Species* **29**: 54.

Balke M., Hendrich L., Mazzoldi P. and Biström O. (2002) Biogeography and taxonomy of *Borneodessus* gen.n., from Borneo (Insecta: Coleoptera: Dytiscidae). *Journal of Natural History* **36:** 963–978.

Balke M., Hendrich L. and Yang C.M. (1999) Water beetles (Insecta: Coleoptera) in the Nature Reserves of Singapore. Proceedings of the Nature Reserves Survey Seminar. *Gardens' Bulletin Singapore* **49**(2)(1997): 321–331.

Balke M. and Satô M. (1995) *Limbodessus compactus* (Clark): a Widespread Austro-Oriental Species, as Revealed by its Synonymy with two other Species of Bidessini (Coleoptera: Dytiscidae). *Aquatic Insects* **17**: 187–192.

Beier M. (1948) Zur Kenntnis von Körperbau und Lebensweise der Helminen (Col. Dryopidae). *"EOS", Revista española de Entomologia* **XXIV**(2): 123–211.

Beier M. and Pomeisl E. (1959) Einiges über Körperbau und Lebensweise von *Ochthebius exsculptus* Germ. und seiner Larve (Col. Hydroph. Hydraen.). *Zeitschrift für Morphologie und Ökologie der Tiere* **48**: 72–88.

Bertrand H. (1972) *Larves et nymphes des Coléoptères aquatiques du globe*. Paillart, Paris. Pp 804.

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

Beutel R.G. (1995) The Adephaga (Coleoptera): phylogeny and evolutionary history. *In* Pakaluk J. and Slipinski S.A. (Eds) *Biology, Phylogeny, and Classification of Coleoptera: Papers celebrating the 80th birthday of R.A. Crowson*. Muzeum i Instytut Zoologii PAN, Warszawa. Pp 173–217.

Beutel R.G. (1997) Über Phylogenese und Evolution der Coleoptera (Insecta). *Abhandlungen des naturwissenschaftlichen Vereins in Hamburg* (NF) **31**: 1–164.

Beutel R.G. and Haas A. (1996) Phylogenetic analysis of larval and adult characters of Adephaga (Coleoptera) using cladistic computer programs. *Entomologica scandinavica* **27**: 197–205.

Beutel R.G. and Ruhnau S. (1990) Phylogenetic analysis of the genera of Haliplidae (Coleoptera) based on characters of adults. *Aquatic Insects* **12**: 1–17.

Bishop J.E. (1973) *Limnology of a small Malayan river Sungai Gombak*. W. Junk, The Hague. Pp 485.

Biström O. (1979) A revision of the genus *Derovatellus* Sharp (Coleoptera, Dytiscidae) in Africa. Contribution to the study of Dytiscidae 1. *Acta Entomologica Fennica* **35**: 1–28.

Biström O. (1982) Revision of the genus *Hyphydrus* Illiger (Coleoptera, Dytiscidae). *Acta Zoologica Fennica* **165**: 1–121.

Biström O. (1988) Generic review of the Bidessini (Coleoptera, Dytiscidae). *Acta Zoologica Fennica* **184**: 1–41.

Biström O. (1996a) Morphology and function of a possible stridulation apparatus in genus *Hydrovatus* (Coleoptera: Dytiscidae). *Entomologica Basiliensia* **19**: 43–50.

Biström O. (1996b) Taxonomic revision of the genus *Hydrovatus* Motschulsky (Coleoptera, Dytiscidae). *Entomologica Basiliensia* **19**: 57–584.

Biström O., Hendrich L. and Kirk-Spriggs A.H. (1997) A new *Hyphydrus* species from Indonesia, with a list of and a key to the Oriental and Australasian species (Coleoptera, Dytiscidae). *The Raffles Bulletin of Zoology* **45**: 305–313.

Bøving A.G. and Henriksen K.L. (1938) The developmental stages of the Danish Hydrophilidae (Ins., Coleoptera). *Videnskabelige Meddelelser Naturhistorisk Forening* **102**: 27–162.

Brancucci M. (1983) Revision des éspèces est-paléarctiques, orientales et australiennes du genre *Laccophilus* (Col. Dytiscidae). *Entomologische Arbeiten des Museums Georg Frey* **31/32**: 241–426.

Brancucci M. (1986) Revision of the genus *Lacconectus* Motschulsky (Coleoptera, Dytiscidae). *Entomologica Basiliensia* **11**: 81–202.

Brigham W.U. (1982) Aquatic Coleoptera. Pp 10.1–10.136. *In* Brigham A.R., Brigham W.U., and Gnilka A. (Eds) *Aquatic insects and oligochaetes of North and South Carolina*. Midwest Aquatic Enterprises, Mahomet, Illinois.

Brinck P. (1981) *Spinosodineutes* (Coleoptera: Gyrinidae) in New Guinea and adjacent islands. *Entomologica scandinavica, Supplement* **15**: 353–364.

Brown H.P. (1972) Aquatic Dryopoid beetles of the United States. *Biota of Freshwater Ecosystems, Identification Manual* **6**: 1–82.

Brown H.P. (1973) Survival records for elmid beetles with notes on laboratory rearing of various dryopoids (Coleoptera). *Entomological News* **84**: 278–284.

Brown H.P. (1987) Biology of riffle beetles. *Annual Review of Entomology* **32**: 253–273.

Brown H.P. (1991) Elmidae (Dryopoidea) (= Elminthidae, Helminthidae). Pp 404–407. *In* Stehr F.R. (Ed.) *Immature Insects*. Kendall/Hunt, Dubuque.

Chen P.P., Wongsiri S., Jamyanya T., Rinderer T.E., Vongsamanode S., Matsuka M., Sylvester H.A. and Oldroyd B.P. (1998) Honey bees and other edible insects used as human food in Thailand. *American Entomologist* **44**(1): 24–29.

Crowson R.A. (1955) *The natural classification of the families of Coleoptera*. Nathaniel Lloyd, London.

Crowson R.A. (1981) *The biology of the Coleoptera*. Academic Press, London. Pp 802.

Delgado J.A., Collantes F. and Soler A.G. (1997) Distribución y ciclo vital de tres especies del género *Hydraena* en Nicaragua (Coleoptera: Hydraenidae). *Revista de Biologica Tropica* **44**(3) / **45**(1) (1996/1997): 645–649.

Delgado J.A. and Soler A.G. (1997a) Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) I: Genus *Limnebius* Leach, 1815 based on a description of *Limnebius cordobanus* d'Orchymont. *Aquatic Insects* **19**: 37–49.

Delgado J.A. and Soler A.G. (1997b) Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) III: The Genus *Calobius* Wollaston, 1854. *Aquatic Insects* **19**: 165–175.

Dettner K. (1985) Ecological and phylogenetic significance of defensive compounds from pygidial glands of Hydradephaga. *Proceedings of the Academy of Natural Sciences, Philadelphia* **137**: 156–171.

Dettner K. (1997) Insecta: Coleoptera: Noteridae. *In* Schwoerbel J. and Zwick P. (Eds) *Süßwasserfauna von Mitteleuropa*, Vol. 20/ 2, 3, 4: Pp 98–126.

Dettner K. and Peters W. (Eds) (1999) *Lehrbuch der Entomologie*. Fischer, Stuttgart. Pp 921.

Dudgeon D. (1999) *Tropical Asian streams: Zoobenthos, ecology and conservation*. Hong Kong University Press, Hong Kong. Pp 844.

Folkerts G.W. and Donovan L.A. (1973) Resting sites of stream dwelling gyrinids (Coleoptera). *Entomological news* **84**(5): 198–201.

Galewski K. (1971) A study of the morphobiotic adaptations of European species of the Dytiscidae (Coleoptera). *Polskie pismo entomologiczne* **41**: 487–702.

Gentili E. (1979) I *Laccobius* della regione orientale (Coleoptera, Hydrophilidae). *Annuario Osservatorio di Fisisca terrestre e Museo Antonio Stoppani del Seminario Arcivescoville di Milano* (N.S.) **3**(1978): 27–50.

Gentili E., Hebauer F., Jäch M.A., Ji L. and Schödl S. (1995) Hydrophilidae: 1. Checklist of the Hydrophilidae recorded from China. *In* Jäch M.A. and Ji L. (Eds) *Water beetles of China*. Vol. 1. Pp 207–219. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp 410.

Gressitt J.L. and Hornabrook R.W. (1977) *Handbook of Common New Guinea Beetles*. Wau Ecology Institute, Handbook No. 2. Wau. Pp 87.

Guéorguiev V.B. (1968) Essai de classification des Coléoptères Dytiscidae, Tribus Copelatini (Colymbetinae). *Izvestija na Zoologitjeskija Institut s Musei Sofia* **28**: 5–45.

Guéorguiev V.B. (1972) Notes sur les Agabini (Coleoptera, Dytiscidae). II. Révision des genres *Platynectes* Régimbart et *Colymbinectes* Falk. *Izvestija na Zoologitjeskija Institut s Musei Sofia* **34**: 33–62.
Hansen M. (1987) The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* **18**: 1–254.
Hansen M. (1991a) A review of the genera of the beetle family Hydraenidae (Coleoptera). *Steenstrupia* **17**: 1–52.
Hansen M. (1991b) The hydrophilid beetles, Phylogeny, Classification and a revision of the genera (Coleoptera: Hydrophiloidea). *Biologiske Skrifter* **40**: 1–367.
Hansen M. (1996) Coleoptera Hydrophiloidea and Hydraenidae, Water Scavenger Beetles. *In* Nilsson A.N. (Ed.) *Aquatic Insects of North Europe*. Apollo, Stenstrup. Pp 173–194.
Hansen M. (1997a) Evolutionary trends in "staphyliniform" beetles (Coleoptera). *Steenstrupia* **23**: 1–52.
Hansen M. (1997b) Phylogeny and classification of the staphyliniform beetle families (Coleoptera). *Biologiske Skrifter* **48**: 1–339.
Hansen M. (1998) Hydraenidae. In *World catalogue of insects* 1. Apollo, Stenstrup. Pp 169.
Hansen M. (1999a) Hydrophiloidea (s.str.) (Coleoptera). In *World Catalogue of Insects* 2, Apollo, Stenstrup. Pp 416.
Hansen M. (1999b) Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. *Entomologica scandinavica* **30**: 121–172.
Hebauer F. (1992) The species of the genus *Chasmogenus* Sharp, 1882 (Coleoptera, Hydrophilidae). *Acta Coleopterologica* **8**: 61–92.
Hebauer F. (1995a) Oriental *Chaetarthria*. *Latissimus* **5**: 7–9.
Hebauer F. (1995b) Neues zu den Acidocerina Hansen (Helocharae d'Orchymont) der indomalaiischen Region (Coleoptera, Hydrophilidae). *Acta Coleopterologica* **11** (3): 3–14.
Hebauer F. (1997) Revision der Arten der Familie Spercheidae Erichson, 1837 (Coleoptera: Hydrophiloidea). *Entomologische Blätter für Biologie und Systematik der Käfer* **93**: 9–42.
Hebauer F. (2000) The genus *Megagraphydrus* Hansen, 1999, with description of new species (Coleoptera: Hydrophiloidea). *Acta Coleopterologica* **16**(2): 14–22.
Hebauer F., Hendrich L. and Balke M. (1999) A contribution to the knowledge of the water beetle fauna of a tropical freshwater lake: Tasek Cini, Pahang, West Malaysia (Coleoptera: Hydradephaga, Hydrophiloidea and Staphylinoidea). *The Raffles Bulletin of Zoology* **47**: 333–348.
Hebauer F. and Klausnitzer B. (1998) Insecta: Coleoptera: Hydrophiloidea (exkl. *Helophorus*). *In* Schwoerbel J. and Zwick P. (Eds) *Süßwasserfauna von Mitteleuropa*, Vol. 20/ 7, 8, 9, 10–1. Pp 134.
Hebauer F. and Wang L.-J. (1998) New species of the genus *Oocyclus* Sharp, 1882 from India, Sri Lanka and Taiwan with a key to all known species (Coleoptera: Hydrophilidae). *Acta Coleopterologica* **14**(1): 37–46.
Heinrich B. and Vogt F.D. (1980) Aggregation and foraging behaviour of whirligig beetles. *Behavioural Ecology and Sociobiology* **7**: 179–186.
Hendrich L. (1995) Malaysia's predaceous water beetles. *Nature Malaysiana* **20**(2): 46–50.
Hendrich L. (1998) Dytiscidae: IV. Notes on Chinese *Lacconectus* Motschulsky, 1855 with description of a new species from Hainan (Coleoptera: Dytiscidae: Copelatinae). Pp 101–105. *In* Jäch M.A. and Ji L. (Eds) *Water Beetles of China*. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein. Wien.
Hendrich L. and Balke M. (1995) Die Schwimmkäfer der Sundainsel Bali: Faunistik, Taxonomie, Ökologie, Besiedlungsgeschichte und Beschreibung von vier neuen Arten (Coleoptera: Dytiscidae). *Faunistische Abhandlungen* **20**(5): 29–56.
Hendrich L. and Balke M. (1997) Taxonomische Revision der südostasiatischen Arten der Gattung *Neptosternus* Sharp, 1882 (Coleoptera: Dytiscidae: Laccophilinae). *Koleopterologische Rundschau* **67**: 53–97.
Hendrich L. and Balke M. (2000) The genus *Platynectes* Régimbart in the Moluccas (Indonesia): taxonomy, faunistics and zoogeography (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* **70**: 37–52.

Hendrich L. and Balke M. (2003) *Neptosternus arnecornelii* sp.n. from Borneo and notes on other species of the genus (Coleoptera: Dytiscidae). *Linzer biologische Beiträge* **35**(1): 181-187.

Hendrich L., Balke M. and Yang C.M. (2004) Aquatic Coleoptera of Singapore: species richness, ecology and conservation. *The Raffles Bulletin of Zoology* in press.

Hendrich L. and Yang C.M. (1999) A contribution to the knowledge of the water beetle fauna of Pulau Tioman, Peninsular Malaysia (Coleoptera: Noteridae, Dytiscidae, Hydrophilidae, Hydraenidae, Scirtidae, Limnichidae). *The Raffles Bulletin of Zoology, Supplement* **6**: 253–262.

Hicks B.J. and Larson D.L. (1991) The rectum as a hydrostatic organ in the predaceous diving beetle genus *Ilybius* Erichson (Coleoptera: Dytiscidae). *The Coleopterists Bulletin* **45**(3): 274–278.

Hill D.S., Hore P. and Thornton I.W.B. (1982) *Insects of Hong Kong*. Hong Kong University Press, Hong Kong, China. Pp 503.

Hinton H.E. (1946) The "gin-traps" of some beetle pupae; a protective device which appears to be unknown. *Transactions of the Royal Entomological Society London* **97**: 473–496.

Holmen M. (1987) The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* **20**: 1–168.

Jackson D.J. (1952) Observations on the capacity for flight of water beetles. *Proceedings of the Royal Entomological Society London* A **27**: 57–70.

Jackson D.J. (1956) Observations on flying and flightless water beetles. *Journal of the Linnean Society, Zoology* **43**: 18–42.

Jäch M.A. (1993) *Ancyronyx* (Coleoptera: Elmidae) – The spider riffle beetle of the Malaysian forest rivers. *Nature Malaysiana* **18**(3): 86–89.

Jäch M.A. (1994) A taxonomic review of the Oriental species of the genus *Ancyronyx* Erichson, 1847 (Coleoptera, Elmidae). *Revue Suisse de Zoologie* **101**(3): 601–622.

Jäch M.A. (1995) Hydroscaphidae. *In* Jäch M.A. and Ji L. (Eds) *Water beetles of China, Vol. 1*. Pp 33–34. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien.

Jäch M.A. (1997) Daytime swarming of rheophilic water beetles in Austria (Coleoptera: Elmidae, Hydraenidae, Haliplidae). *Latissimus* **9**: 10–11.

Jäch M.A. (1998) Annotated check list of aquatic and riparian/littoral beetle families of the world. In Jäch M.A. and Ji L. (Eds) *Water beetles of China.* Vol. 2. Pp 25–42. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. http://www.nhm-wien.ac.at/nhm/2Zoo/coleoptera/publications/chinaindex.html

Jäch M.A. (2002) First record of Epimetopidae in Laos. *Koleopterologische Rundschau* **72**: 161–164.

Jäch M.A. (2003) Fried water beetles Cantonese style. *American Entomologist* **49**(1): 34-37. http://www.nhm-wien.ac.at/nhm/2Zoo/coleoptera/publications/183.pdf

Jäch M.A. and Balke M. (2003) Key to adults of Chinese water beetle families (Coleoptera). *In* Jäch M.A. and Ji L. (Eds) *Water Beetles of China*, Vol. 3. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp VI + 572.

Jäch M.A., Beutel R.G., Delgado J.A. and Díaz J.A. (2004) Hydraenidae. *In* Beutel R.G. and Leschen R.A.B. (Eds) *Handbook of Zoology.* Vol. 3 (Coleoptera). De Gruyter, Berlin, in prep.

Jäch M.A., Beutel R.G., Díaz J.A. and Kodada J. (2000) Subgeneric classification, description of head structures, and world check list of *Hydraena* Kugelann (Insecta: Coleoptera: Hydraenidae). *Annalen des Naturhistorischen Museums Wien* **102**(B): 177–258.

Jäch M.A. and Boukal D.S. (1996) Description of two new riffle beetle genera from Peninsular Malaysia (Coleoptera: Elmidae). *Koleopterologische Rundschau* **66**: 179–189.

Jäch M.A. and Boukal D.S. (1997a) Description of two new genera of Macronychini: *Aulacosolus* and *Nesonychus* (Coleoptera: Elmidae). *Koleopterologische Rundschau* **67**: 207–224.

Jäch M.A. and Boukal D.S. (1997b) The genus *Hedyselmis* Hinton (Coleoptera: Elmidae). *Entomological Problems* **28**(2): 111–116.

Jäch M.A., Dietrich F. and Raunig B. (2004): *Rote Liste der Zwergwasserkäfer* (*Hydraenidae*) *und Krallenkäfer* (*Elmidae*) *Österreichs* (*Insecta: Coleoptera*). Umweltbundesamt, Wien, in press.

Jäch M.A. and Easton E.R. (1998) Water beetles of Macao (Coleoptera). *In* Jäch M.A. and Ji L. (Eds) *Water beetles of China, Vol. 2*. Zoologisch–Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp 43–50.

Jäch M.A. and Ji L. (Eds) (1995) *Water beetles of China*, Vol. 1. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp 410.

Jäch M.A. and Ji L. (Eds) (1998) *Water beetles of China*, Vol. 2. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp 371.

Jäch M.A. and Ji L. (Eds) (2003) *Water beetles of China*, Vol. 3. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp VI + 572.

Jäch M.A. and Kodada J. (1996a) Three new riffle beetle genera from Borneo: *Homalosolus*, *Loxostirus* and *Rhopalonychus* (Insecta: Coleoptera: Elmidae). *Annalen des Naturhistorischen Museums Wien* **98** B: 399–419.

Jäch M.A. and Kodada, J. (1996b) *Graphosolus* gen. nov. from Southeast Asia (Coleoptera: Elmidae). *Entomological Problems* **27**(2): 93–98.

Jäch M.A. and Kodada J. (1997) *Prionosolus* and *Podonychus*, two new genera of Macronychini (Coleoptera: Elmidae). *Entomological Problems* **28**(1): 9–23.

Ji L. and Jäch M.A. (1998a) Description of *Eupotemus* gen. nov. (Coleoptera: Epimetopidae) and world checklist of the species of Epimetopidae. *Entomological Problems* **29**(2): 95–97.

Ji L. and Jäch M.A. (1998b): Epimetopidae: Synopsis of the genus *Eumetopus* Balfour-Browne (Coleoptera). *In* Jäch M.A. and Ji L. (Eds) *Water Beetles of China*, Vol. 1. Pp 195–205. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein. Wien.

Kodada J. (1993) *Jaechomorphus*, a new riffle beetle genus from Sumatra (Coleoptera: Elmidae: Larainae). *Entomological Problems* **24**(2): 1–17.

Kodada J. and Ciampor F. (2000) Review of the genus *Vietelmis* (Coleoptera: Elmidae). *Entomological Problems* **31**(1): 65–90.

Kodada J. and Jäch M.A. (1999) *Roraima carinata* gen. et sp.nov. and *Neblinagena doylei* sp.nov., two Larainae from Mount Roraima, Venezuela (Coleoptera: Elmidae). *Entomological Problems* **30**(1): 13-29.

Kodada J. and Jäch M.A. (2004a): Elmidae. *In* Beutel R.G. and Leschen R.A.B. (Eds) *Handbook of Zoology*. Vol. 3 (Coleoptera). De Gruyter, Berlin, in prep.

Kodada J. and Jäch M.A. (2004b): Dryopidae. *In* Beutel R.G. and Leschen R.A.B. (Eds) *Handbook of Zoology*. Vol. 3 (Coleoptera). De Gruyter, Berlin, in prep.

Kodada J., Jäch M.A. and Ciampor F. (2003) Dryopidae: I. *Stenomystax*, a new aquatic genus (Coleoptera). Pp. 431-472. *In* Jäch M.A. and Ji L. (Eds) *Water Beetles of China*, Vol. 3. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp VI + 572.

Komarek, A. (2003) Hydrophilidae: I. Check list and key to Palearctic and Oriental genera of aquatic Hydrophilidae (Coleoptera), pp. 383-395. *In* Jäch M.A. and Ji L. (Eds) *Water Beetles of China*, Vol. 3. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp VI + 572.

Klausnitzer B. (1984) *Käfer im und am Wasser*. Neue Brehm Bücherei 567. Ziemsen, Wittenberg Lutherstadt. Pp 148.

Korschelt E. (Ed.) (1923–24) *Bearbeitung einheimischer Tiere. Erste Monographie. Der Gelbrand Dytiscus marginalis L.* Engelmann, Leipzig. Pp 836 (Band 1). Pp 964 (Band 2).

Kovac D. and Maschwitz U. (1990) Secretion-grooming in aquatic beetles (Hydradephaga): a chemical protection against contamination of the hydrofuge respiratory region. *Chemoecology* **1**: 131–138.

Larsen O. (1966) On the morphology and function of the locomotor organs of the Gyrinidae and other Coleoptera. *Opuscula entomologica* **30**: 1–242.

Larson D.J., Alarie Y. and Roughley R.E. (2000) *Predaceous diving beetles* (*Coleoptera: Dytiscidae*) *of the Nearctic region, with emphasis on the fauna of Canada and Alaska.* NRC Research Press, Ottawa. Pp 982.

Larson D.J. and Pritchard G. (1974) Organs of possible stridulatory function in water beetles (Coleoptera: Dytiscidae). *The Coleopterists Bulletin* **28**: 53–63.

Lawrence J.F. (1991) Order Coleoptera. Introduction. *In* Stehr F.W. (Ed.) *Immature Insects*. Vol. 2. Kendall / Hunt, Dubuque. Pp 144–184.
Lawrence J.F. and Britton E.B. (1991) Coleoptera (Beetles). *In* CSIRO *The Insects of Australia* Vol. 2. 2nd Ed. Melbourne University Press. Pp 542–1137.
Lawrence J.F. and Britton E.B. (1994) *Australian Beetles*. Melbourne University Press. Pp 192.
Lawrence J.F., Hastings A.M., Dallwitz M.J., Paine T.A. and Zurcher E.J. (1999) *Beetles of the World*: *A Key and Information System for Families and Subfamilies*. CD-ROM, Version 1.0 for MS-Windows. CSIRO Publishing, Melbourne.
Lawrence J.F. and Newton A.F. Jr. (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). *In* Pakaluk J. and Slipinski S.A. (Eds) *Biology, Phylogeny, and Classification of Coleoptera: Papers celebrating the 80th birthday of R.A. Crowson*. Muzeum i Instytut Zoologii PAN, Warszawa. Pp 779–1006.
Lawrence J.F. and Reichardt H. (1991) Hydroscaphidae (Myxophaga). *In* Stehr F.W. (Ed.) *Immature Insects*. Vol. 2. Kendall / Hunt, Dubuque. Pp 303–304.
Löbl I. (1994) Les espèces asiatiques du genre *Hydroscapha* Leconte (Coleoptera, Hydroscaphidae). *Archives de Sciences, Genève* **47**(1): 15–34.
Matthes D. (1978) *Tiersymbiosen und ähnliche Formen der Vergesellschaftung*. Fischer, Stuttgart and New York. Pp 241.
Matthes D. and Guhl W. (1972) *Orbopercularia robusta* nov.sp. (Ciliata, Peritrichia), ein neuer obligater symphoriont. *Protistologica* **8**(4): 471–476.
Mazzoldi P. and Vondel B. van (1997) *Haliplus samosirensis* Vondel recorded from Kalimantan. *Koleopterologische Rundschau* **67**: 119–120.
Miller K.B. (2002) Revision of the Genus *Eretes* Laporte, 1833 (Coleoptera: Dytiscidae). *Aquatic Insects* **24**: 247-272.
Mjöberg E. (1916) Results of Dr. E. Mjöberg's Swedish Scientific Expedition to Australia 1910 – 1913. 9. Cicindelidae, Gyrinidae, Lucanidae, Paussidae. *Arkiv för Zoologi* **10**(10): 1–16.
Mogi M., Sunahara T. and Selomo M. (1999) Mosquito and aquatic predator communities in ground pools on lands deforested for rice field development in Central Sulawesi, Indonesia. *Journal of the American Mosquito Control Association* **15**(2): 92–97.
Moog O. and Jäch M.A. (1995) Elmidae. *In* Moog O. (Ed.) *Fauna Aquatica Austriaca*. May 1995. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Wien.
Mori M. and Kitayama A. (1993) *Dytiscoidea of Japan*. Osaka, Kankyo-Kagaku Ltd. Pp 217.
Nachtigall W. (1974) Locomotion: Mechanics and hydrodynamics of swimming in aquatic insects. *In* Rockstein M. (Ed.) *The physiology of Insecta*. 2nd Ed. Academic Press, New York. Pp 381–432.
Nilsson A.N. (1995) Noteridae and Dytiscidae: An Annotated check list of the Noteridae and Dytiscidae of China. Pp 35–96. *In* Jäch M.A. and Ji L. (Eds) *Water Beetles of China*. Vol. 1. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein. Wien. Pp 371.
Nilsson A.N. (Ed.) (1996) *Aquatic Insects of North Europe – A Taxonomic Handbook*. Stenstrup: Apollo Books.
Nilsson A.N. (1998) Dytiscidae: V. The genus *Platynectes* Régimbart in China, with a revision of the dissimilis-complex (Coleoptera). Pp 107–121. *In* Jäch M.A. and Ji L.(Eds) *Water Beetles of China*, Vol. 2. Wien: Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein. Pp 410.
Nilsson A. N. (2001) Dytiscidae (Coleoptera). In *World Catalogue of Insects* 3, Apollo, Stenstrup. Pp 395.
Nilsson A.N. and Persson S. (1990) Dimorphism of the metasternal wing in *Agabus raffrayi* and *A. labiatus* (Coleoptera: Dytiscidae) questioned. *Aquatic Insects* **12**: 135–144.
Ochs G. (1924) Über neue und interessante Gyriniden aus dem British Museum in London. *Entomologische Blätter für Biologie und Systematik der Käfer* **20**: 228–244.
Ochs G. (1927a) Papers on Malayan Aquatic Biology. IV. On the Gyrinidae of the Malay Peninsula. *Journal of the Federated Malay States Museums*, Kuala Lumpur **13**: 242–245.
Ochs G. (1927b) Fauna sumatrensis, Gyrinidae (Coleoptera). *Supplementa Entomologica* **15**: 114–122.

Ochs G. (1928) Über die Gyriniden Borneo's. *Entomologische Blätter für Biologie und Systematik der Käfer* **24**(3): 98–103.
Ochs G. (1929) Papers on Malayan Aquatic Biology. X. Additional notes on the Gyrinidae. *Journal of the Federated Malay States Museums* **14**: 401–403.
Ochs G. (1931) Über die Gyriniden-Ausbeute der Deutschen Limnologischen Sunda-Expedition mit einer Übersicht über die Gyriniden-Fauna Javas und Larvenbeschreibungen. *In* Thienemann, A. (Ed.) Tropische Binnengewässer. *Archiv für Hydrobiologie, Supplement-Band* **1**: 461–485.
Ochs G. (1954) Die Sunda-Gyriniden des Museum Zoologicum Bogoriense (Coleoptera, Gyrinidae). *Treubia* **22**: 217–223.
Ødegaard F. (2000) How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society* **71**: 583–597.
Oygur S. and Wolfe G.W. (1991) Classification, distribution, and phylogeny of North American (North of Mexico) species of *Gyrinus* Müller (Coleoptera: Gyrinidae). *Bulletin of the American Museum of Natural History* **207**: 1–97.
Pederzani F. (1995) Keys to the identification of the genera and subgenera of adult Dytiscidae (sensu latu) of the world. *Atti dell'Accademia Roveretana degli Agiati*, ser. VII, vol. **IV**, B: 5–83.
Pemberton R.W. (1990) The Korean Water Beetle Game. *Pan-Pacific Entomologist* **66**: 172–174.
Peschet R. (1923a) Fauna Entomologique de l'Indochine, Gyrinidae. *Opuscules de l'Institut Scientifique de l'Indochine, Saigon* **1**: 1–18.
Peschet R. (1923b) Description d'un *Orectochilus* nouveau de Sumatra (Col. Gyrinidae). *Bulletin de la Société Entomologique de France* **1922**: 293–294.
Philippi R.A. (1864) Ein Käferchen, daß als Gewürz dient. *Stettiner Entomologische Zeitung* **25**: 93–96.
Régimbart M. (1880) The new Dytiscidae and Gyrinidae collected during the recent scientific Sumatra expedition. *Notes from the Leyden Museum* **2**: 209–216.
Régimbart M. (1882a) Gyrinides nouveaux de la collection du Musée Civique de Gênes. *Annali del Museo Civico di Storia Naturale di Genova* **18**: 70–74.
Régimbart M. (1882b) New species of Gyrinidae in the Leyden Museum. *Notes from the Leyden Museum* **4**: 59–71.
Régimbart M. (1883a) Essai monographique de la Famille des Gyrinidae, 1ere partie. *Annales de la Société Entomologique de France* (6) **2**(1882): 379–458.
Régimbart M. (1883b) Essai monographique de la Famille des Gyrinidae, 2eme partie. *Annales de la Société Entomologique de France* (6) **3**: 121–190.
Régimbart M. (1884) Essai monographique de la famille des Gyrinidae. 3eme partie. *Annales de la Société Entomologique de France* (6) **3**: 381–482.
Régimbart M. (1886) Essai monographique de la Famille des Gyrinidae, 1er Supplement. *Annales de la Société Entomologique de France* (6) **6**: 247–272.
Régimbart M. (1888) Viaggio di Leonardo Fea in Birmania e regioni vicine. X. Dytiscidae et Gyrinidae. *Annali del Museo Civico di Storia Naturale di Genova*, Serie 2, **6**: 609–623.
Régimbart M. (1892) Essai monographique de la Famille des Gyrinidae, 2eme Supplement. *Annales de la Société Entomologique de France*, **60**: 663–752.
Régimbart M. (1899) Révision des Dytiscidae de la région indo-sino-malaise. *Annales de la Société Entomologique de France* **68**: 186–367.
Régimbart M. (1901) Révision des grands Hydrophiles. *Annales de la Société Entomologique de France* **70**: 188–232.
Régimbart M. (1907) Essai monographique de la Famille des Gyrinidae, 3e Supplement. *Annales de la Société Entomologique de France* **76**:137–245.
Ribera I., Foster G.N. and 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. and Nilsson A.N. (1995) Morphometric patterns among diving beetles (Coleoptera: Noteridae, Hygrobiidae, and Dytiscidae). *Canadian Journal of Zoology* **73**: 2343–2360.

Ribera I. and Vogler A.P. (2000) Habitat type as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. *Biological Journal of the Linnean Society* **71**: 32–53.

Richoux P. and Doledec S. (1987) *Hydroscapha granulum* (Motschulsky, 1855). Description of the larva and ecological notes. *Aquatic insects* **9**: 137–144.

Rothmeier G. and Jäch M.A. (1986) Spercheidae, the only filter-feeders among Coleoptera. *Proceedings of the IV. European Congress of Entomology, Amsterdam*. Pp 133–137.

Schmidl J. (1992) *Vergesellschaftung und Habitatwahl adephager Wasserkäfer in Abhängigkeit von physikalischen und chemischen Wasserparametern. Eine canonische Korrespondenzanalyse*. MSc Thesis, Erlangen University. Pp 185.

Schödl S. (1993) Revision der Gattung *Berosus* Leach. 3. Teil: Die paläarktischen und orientalischen Arten der Untergattung *Berosus* s.str. (Coleoptera: Hydrophilidae). *Koleopterologische Rundschau* **63**: 189–233.

Schönmann H. (1994) Revision der Gattung *Pelthydrus* Orchymont 1. Teil: *Globipelthydrus* subgen. n. (Coleoptera: Hydrophilidae). *Koleopterologische Rundschau* **64**: 189–222.

Schönmann H. (1995) Revision der Gattung *Pelthydrus* Orchymont 2. Teil: *Pelthydrus* s.str. (Coleoptera: Hydrophilidae). *Koleopterologische Rundschau* **65**: 105–144.

Seeger W. (1971a) Morphologie, Bionomie und Ethologie von Halipliden, unter besonderer Berücksichtigung funktionsmorphologischer Gesichtspunkte (Haliplidae; Coleoptera). *Archiv für Hydrobiologie* **68**: 400–435.

Seeger W. (1971b) Autökologische Untersuchungen an Halipliden mit zoogeographischen Anmerkungen (Haliplidae; Coleoptera). *Archiv für Hydrobiologie* **68**: 528–547.

Seeger W. (1971c) Die Biotopwahl bei Halipliden, zugleich ein Beitrag zum Problem der syntopischen (sympatrischen s.str.) Arten (Haliplidae; Coleoptera). *Archiv für Hydrobiologie* **69**: 175–199.

Sharp D. (1882) On aquatic carnivorous Coleoptera or Dytiscidae. *Transactions of the Royal Dublin Society* (2)**2**: 179–1003.

Skale A. and Jäch M.A. (2003) A new species of *Eumetopus* Balfour-Browne, 1949 from Nepal (Insecta: Coleoptera: Epimetopidae). *In* Hartmann M. and Baumbach H. (Eds) *Biodiversität und Naturausstattung im Himalaya*.Verein der Freunde and Förderer des Naturkundemuseums Erfurt e.V. 391 Pp., XVI plts.

Smith R.L. (1973) Aspects of the biology of three species of the genus *Rhantus* (Coleoptera: Dytiscidae) with special reference to the acoustical behaviour of two. *Canadian Entomologist* **105**: 909–919.

Sörensson M. (1997) Morphological and taxonomical novelties in the world's smallest beetles, and the first Old World record of Nanosellini (Coleoptera: Ptiliidae). *Systematic Entomology* **22**: 257–283.

Spangler P.J. (1982) Coleoptera. *In* Hurlbert S.H., Rodriguez G. and Dos Santos N.D. (Eds) *Aquatic biota of tropical South America. Part 1. Arthropoda*. San Diego State University, San Diego. Pp. 129–220.

Spangler P. (1990) A revision of the Neotropical aquatic beetle genus *Stegoelmis* (Coleoptera: Elmidae). *Smithsonian Contributions to Zoology* **502**: 1–52.

Spangler P.J. (1991a) Gyrinidae. *In* Stehr F.W. (Ed.) *Immature Insects*. Vol. 2. Kendall / Hunt, Dubuque. Pp 319–320.

Spangler P.J. (1991b) Noteridae. *In* Stehr F.W. (Ed.) *Immature Insects*. Vol. 2. Kendall / Hunt: Dubuque. Pp 314–315.

Spangler P.J. (1991c) Hydraenidae. *In* Stehr F.W. (Ed.) *Immature Insects*. Vol. 2. Kendall / Hunt: Dubuque. Pp 320–322.

Spangler P.J. and Decu V. (1998) Coleoptera aquatica. *In* Juberthie C. and Decu V. (Eds) *Encyclopaedia Biospeologica. Tom II*. Moulis, Bucarest: Société de Biospéologie. Pp 1031–1046.

Šťastný J. (2003) Dytiscidae: X. Review of *Platynectes* subgen. *Gueorguievtes* Vazirani from South-east Asia (Coleoptera). Pp 217-259. *In* M.A. Jäch and L. Ji (Eds) *Water Beetles of China*. Vol. 3. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Pp VI + 572.

Steiner W.E. and Anderson J.J. (1981) Notes on the natural history of *Spanglerogyrus albiventris* Folkerts, with a new distribution record (Coleoptera: Gyrinidae). *Pan-Pacific Entomologist* **57**(1): 124–132.

Ulrich G. (1986) The larvae and pupae of *Helichus suturalis* Leconte and *Helichus productus* Leconte (Coleoptera: Dryopidae). *The Coleopterists Bulletin* **40**(4): 325–334.
Vazirani T.G. (1969a) Contribution to the study of aquatic beetles (Coleoptera). 2. A review of the subfamilies Noterinae, Laccophilinae, Dytiscinae and Hydroporinae (in part) from India. *Oriental Insects* **2**: 221–341.
Vazirani T.G. (1969b) Contribution to the study of aquatic beetles IV. A Review of *Pleurodytes* Régimbart (Col. Dytiscidae). *Annales de la Société Entomologique de France* (N.S.) **5**(1): 137–141.
Vazirani T.G. (1970) Contribution to the study of aquatic beetles (Coleoptera) V. A review of Hydroporinae: Dytiscidae in part, from India. *Oriental Insects* **4**(1): 93–129.
Vazirani T.G. (1971) Contributions to the study of aquatic beetles (Coleoptera). VII. A revision of Indian Colymbetinae (Dytiscidae). *Oriental Insects* **4**(3): 303–362.
Vazirani T.G. (1972 [?]) Aquatic insects in relation to fisheries in India. *Cheetal, Journal of the Wildlife and Fisheries Service of India* **17**(2): 14–24.
Vazirani T.G. (1977) Catalogue of Oriental Dytiscidae. *Records of the zoological Survey of India, Miscellaneous Publications, Occasional Papers*, **6.** Pp 111.
Verdonschot P.F.M., Higler L.W.G., Van der Hook W.F. and Cuppen J.G.M. (1992) A list of macroinvertebrates in Dutch water types: a first step towards an ecological classification of surface waters based on key factors. *Hydrobiological Bulletin* **25**(3): 241–259.
Vondel B. van (1992) Revision of the Palaearctic and Oriental species of *Peltodytes* Régimbart (Coleoptera: Haliplidae). *Tijdschrift voor Entomologie* **135**: 275–297.
Vondel B. van (1993) Revision of the *Liaphlus* species of the Oriental region excluding China (Coleoptera: Haliplidae). *Tijdschrift voor Entomologie* **136**: 289–316.
Vondel B. van (1995) Haliplidae: Review of the Haliplidae of China. *In* Jäch M.A. and Ji L. (Eds) *Water beetles of China.* Vol. 1. Pp 111–154. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien.
Vondel B. van (1997) Insecta: Coleoptera: Haliplidae. *In* Schwoerbel J. and Zwick P. (Eds) *Süßwasserfauna von Mitteleuropa*, Volume 20/ 2, 3, 4. Fischer, Stuttgart. Pp 1–95.
Wewalka G. (1975) Revision der Artengruppe des *Hydaticus vittatus* (Fabricius) (Dytiscidae, Coleoptera). *Koleopterologische Rundschau* **52**: 87–100.
Wewalka G. (1979) Revision der Artengruppe des *Hydaticus* (*Guignotites*) *fabricii* (MacLeay), (Coleoptera, Dytiscidae). *Koleopterologische Rundschau* **54**: 119–139.
Wewalka G. (1992) Die *Canthydrus flavus* (Motschulsky) – Gruppe aus Südostasien (Coleoptera: Noteridae). *Linzer biologische Beiträge* **24**(2): 803–811.
Wewalka G. (1997) Taxonomic revision of *Microdytes* Balfour-Browne (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* **67**: 13–51.
Wewalka G. (2001) Taxonomic revision of *Allopachria* (Coleoptera: Dytiscidae). *Entomological Problems* **31**(2): 97–128.
Wewalka G., Balke M. and Hendrich L. (2001) *Anginopachria*, a new genus for an enigmatic species previously assigned to *Allopachria* (Coleoptera: Dytiscidae). *Entomological Problems* **32**(1): 91–92.
Wewalka G. and Biström O. (1994) *Hyphovatus* gen.n. from Southeast Asia, with description of two new species (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* **64**: 37–43.
Wewalka G. and Wang L.-J. (1998) Three new species of *Microdytes* Balfour-Browne from Laos and Borneo (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* **68**: 59–63.
Wesenberg-Lund C. (1943) *Biologie der Süßwasserinsekten*. Springer, Berlin. Pp 682.
White D. and Brigham W.U. (1996) Aquatic Coleoptera. *In* Merritt R.W. and Cummins K.W. (Eds) *An introduction to the aquatic insects of North America.* Kendall/Hunt. Dubuque. Pp 399–473.
Wichard W., Arens W. and Eisenbeis G. (1995) *Atlas zur Biologie der Wasserinsekten*. Fischer, Stuttgart. Pp 338.
Wooldridge D.P. (1977) *Paracymus* of the Oriental Faunal Region. *Journal of the Kansas Entomological Society* **50**(1): 119–128.