

A new view on the generic classification of the *Agabus*-group of genera of the Agabini, aimed at solving the problem with a paraphyletic *Agabus* (Coleoptera: Dytiscidae)

A.N. NILSSON

Abstract

The generic classification of the *Agabus*-group of genera of the tribe Agabini (Coleoptera: Dytiscidae) is revised and presented as a checklist of the world species. In the new classification, the following six genera are recognized: *Agabus* LEACH, *Hydronebrius* JAKOVLEV, *Hydrotrupes* SHARP, *Ilybius* ERICHSON, *Ilybiosoma* CROTCH, and *Platambus* THOMSON. The concepts of *Ilybius* and *Platambus* have been expanded, and both genera now include additional species previously placed in *Agabus*. The genus *Agabus* is divided into the three subgenera: *Agabus* s.str., *Acatodes* THOMSON, and *Gaurodytes* THOMSON. The following new generic synonymies are given: *Agabinus* CROTCH, 1873, and *Colymbinectes* FALKENSTRÖM, 1936 = *Platambus* THOMSON, 1859; *Carrhydus* FALL, 1922 = *Agabus* LEACH, 1817. *Ilybius lenensis* nom.n. is proposed as replacement name for *I. aenescens* POPPIUS, 1905.

Key words: Coleoptera, Dytiscidae, Agabini, *Agabus*-group of genera, generic classification, checklist, key.

Introduction

Within the Colymbetinae, the Agabini are characterized by the derived presence of a linear group of short, stout setae near the posterior ventroexternal angle of the metafemur (BRINCK 1948). A few other potential autapomorphies of this tribe have been described from larvae (DE MARZO & NILSSON 1988, ALARIE & LARSON 1998). However, these characters have so far only been verified in relatively few species of the Agabini.

With respect to the delimitation of the tribe Agabini, I largely agree with BRINCK (1948), except that I find his arguments for treating *Hydronebriini* as a separate tribe weak. Besides the genus *Hydronebrius* JAKOVLEV, 1897 he included also the Nearctic *Agabus cordatus* group in this tribe. The species in the latter group have in fact the metafemoral row of setae, and the absence of these setae in *Hydronebrius* could be viewed as a reduction connected with the strong punctuation of the metafemur in this genus. This setal row is also absent in a few species of *Platambus* THOMSON, 1859 (BRANCUCCI 1988).

The Nearctic monobasic genus *Hydrotrupes* was excluded from the Agabini by BEUTEL (1994) based on larval characters. Later, ALARIE et al. (1998) analysed a larger set of larval characters which supported that *Hydrotrupes* belongs to the Agabini. I have included this genus in Agabini, admitting that its taxonomic position is uncertain.

The generic classification of Agabini needs to be revised. The chief problem being the large genus *Agabus* that so far not has been diagnosed by a single autapomorphy. Hopefully, my hypo-

thesis of relationships and the resulting classification given below will be tested by future studies, in which the use of molecular and morphological characters, including also larvae, will be combined. Based on my own experience, the application of parsimony analysis on characters from adult morphology only, will not lead to firmly based hypothesis of relationships within the Agabini.

Generic classification of Agabini

The tribe Agabini can be separated into two major groups of genera (NILSSON 1997): (1) those having a pair of elliptical, sublateral clypeal fovea, and female metatibia and -tarsus with a ventral fringe of natatorial setae present, viz. *Andonectes* GUÉORGUIEV, 1971, *Agametrus* SHARP, 1882, *Leuronectes* SHARP, 1882, and *Platynectes* RÉGIMBART, 1878; and (2) those having linear clypeal fovea near anterolateral angles or along entire anterior margin, and having female metatibia and -tarsus without the ventral setal fringe, i.e. the rest.

The only contradiction to this pattern known to me is *Ilybius discedens* SHARP, 1882, in which the female has the ventral setal fringe (LARSON 1987). As this species has all the advanced characters of the genus *Ilybius*, the presence of the setal fringe in the female is seemingly due to a reappearance of this character.

In this paper, I will only discuss the second group of genera to which *Agabus* belongs. My baseline is to neglect the generic classification currently in use (e.g. GUÉORGUIEV 1971, FRANCISCOLO 1979: 242, 243) and start to present characters that can be used for the basal splittings of the group. The new classification proposed for the *Agabus*-group of genera is presented in full below.

Review of some relevant characters

1. Clypeal bead continuous. LARSON (1975: Figs. 278, 279) introduced as a character within *Agabus* the development of a fine anterior marginal bead on the clypeus. As a continuous bead is unknown among other Colymbetinae, its presence is viewed as apomorphic. The apomorphic state occurs in all species here placed in the genus *Agabus*, except *A. striolatus*. The additional presence of the apomorphic state in the *Platambus glabrellus*- and *optatus*-groups is viewed as due to convergence.

2. Pronotum with anterior line continuous. NILSSON & LARSON (1990) introduced another important character in *Agabus*, i.e. the development of the fine line that follows close to the anterior margin of the pronotum. A continuous line is viewed as apomorphic as it is unknown in the Colymbetinae outside Agabini. The apomorphic state of this character is present in all species placed in the genus *Ilybius*. Moreover, it is present in the *Platambus semivittatus*-group, in *Ilybiosoma ilybiiformis*, and in the following species-groups of *Agabus* s.str.: *antennatus*, *bifarius*, *labiatus*, *punctulatus*, and *uliginosus*.

3. A third important character was first mentioned in SEMENOV'S (1899) description of *Aptator*. He noted the tiny hairs, pointing straight downward, which arise from punctures along the face of the epipleuron, except in the basal third and near the elytral apices. Later, LEECH (1942) observed these hairs also in other *Agabus* species than *A. bifarius*. These hairs are somewhat difficult to see, even on clean specimens. The absence of such hairs in other agabine genera suggests that their presence is apomorphic within *Agabus*. As the distribution of this character among *Agabus* species is congruent with other characters defining larger groups of species, these setae may have

evolved only once, i.e. they provide a synapomorphy for the species which have them, i.e. most *Agabus* s.str.

4. Most species of Agabini have a simple penis with a tapering apex. A ventral subapical spine is, however, present in many *Agabus* species, and I have used this character as a synapomorphy of the subgenus *Acatodes*. Its absence in *A. audeni* WALLIS, *A. anthracinus* (MANNERHEIM), *A. coxalis* SHARP, and possibly also *A. inexpectatus* NILSSON, is viewed as secondary loss (cf. LARSON 1989, 1991).

5. Saw-like female gonocoxae (ovipositor) provide an autapomorphy of *Ilybius* s.str. Moreover, FERY & NILSSON (1993) suggested a transformation series in the evolution of the ovipositor in which the row of denticles have evolved along the external ridge found in some species traditionally placed with *Agabus*. Externally ridged gonocoxae is here used as a unique synapomorphy of the species included in a more broadly delimited genus *Ilybius*.

6. In his key to Nearctic species-groups, LARSON (1989) characterized some groups of *Agabus* on the prosternal process having its lateral beads broadly inflated posterior of procoxae (cf. LARSON & WOLFE 1998: Figs. 21-26). Later, NILSSON (1997) used the same feature to characterize a redelimited *A. optatus*-group. I have found this character present also in the two species formerly assigned to the genus *Agabinus*, as well as in most species of *Platambus* as revised by BRANCUCCI (1988). The character is here used as a synapomorphy of the species included in a more broadly delimited genus *Platambus*.

7. In the same key, LARSON (1989) noted the broad separation of the mesocoxae present in his *Agabus obtusatus*-group. This character was given as a ratio of 1.5 or more between the narrowest distance between the mesocoxae and the narrowest distance between the procoxae. The character is here used as a synapomorphy of a more broadly delimited genus *Platambus*. It is most weakly developed in the *P. americanus*- and *P. confusus*-groups.

New limits for *Agabus*, *Ilybius* and *Platambus*

From my unpublished studies of the available morphological characters of the adults, it seems that no solution without much conflict is possible to find. A central problem is the conflict between the two characters represented by a continuous clypeal bead and a prosternal process with lateral bead inflated posteriorad of procoxae (NILSSON 1997). I now prefer to give priority to the last character, supported also by the wide mesocoxal separation of the species which have it. This character-complex is used to diagnose an expanded genus *Platambus*, adding to the species included by BRANCUCCI (1988) the dibasic Nearctic genus *Agabinus* CROTCH, 1873, plus the following species-groups traditionally placed with *Agabus*: *americanus*, *confusus*, *optatus*, *semivittatus* and *spinipes*. Besides the chiefly East Palearctic and Oriental *Platambus* s.str., and the *optatus*-group in eastern Asia and eastern North America, the resulting expanded genus *Platambus* includes also elements from western North America.

I suggest that the genus *Agabus* is restricted to the species not included in *Platambus* s.l. that have the clypeal bead continuous. Consequently, *Carrhydus* FALL, 1922, and *Metronectes* SHARP, 1882, will join *Agabus* (cf. BALKE et al. 1997), whereas many species currently placed in *Agabus* will have to be transferred to other genera.

Moreover, I think that *Ilybius* should be expanded to include all species of Agabini with a continuous anterior line on pronotum and the clypeal bead broken (FERY & NILSSON 1993). The widened concept of this genus is also supported by a female ovipositor with a lateral ridge, and metacoxal lines reduced anteriorly. Consequently, the *Agabus chalconatus*-, *A. erichsoni*- (sensu

FRY & NILSSON 1993), and *A. opacus*-groups (sensu LARSON 1996) will have to be transferred to *Ilybius*.

Some species currently placed in *Agabus*, i.e. the *bifarius*-, *labiatus*-, *punctulatus*-, and *uliginosus*-groups, have both the clypeal and anterior pronotal beads continuous. Other characters will have to answer the question whether they belong to *Agabus* or *Ilybius*. For the moment they should better stay in *Agabus* s.str.

The remaining species

The species that fall outside these new concepts of *Platambus*, *Agabus* and *Ilybius* are those in *Hydronebrius*, and the *Agabus* (in traditional sense) groups *cordatus* (sensu NILSSON 1992), *seriatus* (sensu LARSON 1997), *striolatus* (monobasic), and *kermanensis* (monobasic). No unique synapomorphy has been found that could unite all the remaining species. Consequently, they have to be separated into two or more groups.

Besides the enigmatic SE Palearctic genus *Hydronebrius*, the remaining groups include 15 species, 12 of which are Nearctic. The three other species are the Ethiopian *A. discicollis* ANCEY, 1882, plus the Palearctic *A. striolatus* (GYLLENHAL, 1808) and *A. kermanensis* J.BALFOUR-BROWNE, 1939.

BALFOUR-BROWNE (1939) described *Ranagabus* as a subgenus of *Agabus*, with the single species *A. kermanensis*. The combination of characters found in this species was such that they "separate the species so sharply from all the groups of SHARP that I consider the only course to follow is the creation of a separate subgenus" (BALFOUR-BROWNE 1939: 106). The only subsequent reference to this species is GUÉORGUIEV (1965) who added to the original description and illustrated the penis.

My interest for *A. kermanensis* was triggered by the study of Afrotropical *Agabus* (NILSSON 1992), especially the search for close relatives of *A. discicollis*, and the other, Nearctic, species of the *A. cordatus*-group. I now believe that *A. kermanensis* belongs to the *A. cordatus*-group and that it is the sister-species of *A. discicollis*.

I have earlier (NILSSON 1992) placed *A. discicollis* together with the four Nearctic species in the *A. cordatus*-group (LARSON 1989). After the examination of *A. kermanensis* I am inclined to believe that it is the sister species of *A. discicollis*. The following characters separate *A. kermanensis* from *A. discicollis* and the other species of the *A. cordatus*-group: (1) head orientated anteriorly, (2) pronotum broad, (3) prosternal process long and received into well-defined impression on metasternum, and (4) legs short with punctuation weak.

The corresponding character states displayed by *A. discicollis* and the *A. cordatus*-group most probably represent adaptations to high altitudes that have evolved independently in *A. discicollis* and the Nearctic stock (NILSSON 1992). Character no. 3 is especially interesting as the reduction of the prosternal process and the metasternal groove is probably connected with the more ventrally orientated head of the high-altitude specialists. A similar reduction has probably occurred in the species of the Ethiopian *A. ambulator*-group (cf. NILSSON 1992), that I now think should be included in the *A. confinis*-group. The Afrotropical species of the group are seemingly closely related to *A. turcmenus* GUIGNOT, 1957.

The parameres of *A. discicollis* and *A. kermanensis* are very similar, and more strongly setose than in the Nearctic species. The median lobes are also quite similar, although the basal apodeme is much larger in *A. kermanensis*. The broad metafemur with its laminar posteroexternal angle and the medially truncate or slightly excavate last abdominal segment are unique to *A. kermanensis*.

The morphological differences between *A. kermanensis* and *A. discicollis* are in the Nearctic paralleled by those between the *A. cordatus*- and *A. seriatus*-groups (sensu LARSON 1989), with the high-altitude specialists found in the *A. cordatus*-group. Phylogenetically, it would probably make sense to assign the Old and New World species to one species-group each, viz. the *Ilybiosoma discicollis*- and *seriatum*-groups, respectively. This solution has been used in my classification (see below).

The only apomorphic character (within the *Agabus*-group of genera) found in all species of the redelimited *seriatus*-, *discicollis*-, and *striolatus*-groups is the presence of anteroventral spiniferous punctures along the entire length of the metatibia. Consequently, this character is used to diagnose a genus with the available name *Ilybiosoma* CROTCH, 1873, with the type species *Ilybius regularis* CROTCH, 1852. These punctures are fewer and more sparsely set in *A. striolatus* than in the other species, in which they form a more or less continuous row. As these punctures also occur in several other *Agabus* species, like those in the *tristis*-group, the possibility to place *A. striolatus* in *Agabus* (*Gaurodytes*) should also be considered further. Until more evidence will become available, I prefer a conservative view, and have consequently kept *A. striolatus* in this position in my classification (see below).

Revised key to *Agabus*-group of genera and subgenera

1. Female metatibia and -tarsus with ventral setal fringe present. Clypeus with pair of sublateral, elliptical fovea..... *Platynectes*-group of genera
- Female metatibia and -tarsus with ventral setal fringe reduced (except in *Ilybius discedens*). Clypeus with medially broken or continuous linear fovea along anterior margin (*Agabus*-group of genera).....2
2. Prosternal process in most species with lateral bead broadly inflated posterior of procoxae. Mesocoxae widely separated. Epipleuron broad in many species, also in posterior half... *Platambus*
- Prosternal process with lateral bead not broadly inflated posterior of procoxae. Mesocoxae more narrowly separated. Epipleuron narrow in posterior half.....3
3. Metafemur with linear group of setae at posteroexternal angle reduced..... *Hydronebrius*
- Metafemur with linear group of setae at posteroexternal angle present.....4
4. Clypeus with linear fovea more or less continuous (*Agabus*).....5
- Clypeus with linear fovea broadly interrupted medially.....7
5. Penis with subapical ventral spine..... subgenus *Acatodes*
- Penis without subapical ventral spine.....6
6. Paramere stylate. Pronotum with anterior bead broadly interrupted medially.. subgenus *Gaurodytes*
- Paramere strap-like. Many species with pronotum having anterior bead continuous, and/or metasternal wing narrow..... subgenus *Agabus* s.str.
7. Pronotum with continuous fine line along anterior margin.....*Ilybius*
- Pronotum with anterior bead broadly interrupted medially.....*Ilybiosoma*

Classification of *Agabus*-group of genera

Distributions coded as: (E) Ethiopian, (EP) East Palearctic (Asian part), (H) Holarctic, (NA) Nearctic (including Mexico), (O) Oriental, (P) Palearctic, and (WP) West Palearctic (European plus North African parts). As in the forthcoming new Palearctic Coleoptera catalogue (Eds. Löbl & Smetana), all of China and the Himalayan provinces of India are included in the Palearctic

Region. The type region is given for each species. Synonyms are given in alphabetical order. Names are categorized as: [HN] preoccupied homonym, [IN] indication to, i.e. new name for misidentification, [NO] nomen oblitum, [RN] replacement name. Only available names based on extant species are listed. When possible, names of species groups are based on species with Holarctic distributions.

Genus *Agabus* LEACH, 1817 (E, H, O)

Autapomorphy: clypeus with fine marginal bead more or less continuous.

Subgenus *Acatodes* THOMSON, 1859 (E, H, O)

Autapomorphy: penis with subapical spine.

[Syn.: *Arctodytes* THOMSON, 1874; *Heteronychus* SEIDLITZ, 1887; *Scytodytes* SEIDLITZ, 1887; *Allonychus* ZAITZEV, 1905; *Mesogabus* GUÉORGUIEV, 1969]

arcticus-group (H)

anthracinus MANNERHEIM, 1852:304, Alaska (NA)

= *scapularis* MANNERHEIM, 1852:303

arcticus arcticus (PAYKULL, 1798:201) (*Dytiscus*), Sweden (H)

= *reticulatus* (KIRBY, 1837:71) (*Colymbetes*)

arcticus alpinus (MOTSCHULSKY, 1860:102) (*Colymbetes*), Mongolia (EP)

= *insignis* GUÉORGUIEV, 1969:62

= *punctipennis* (J.SAHLBERG, 1880:56) (*Gaurodytes*)

= *sibiricus* (J.SAHLBERG, 1880:56) (*Gaurodytes*)

arcticus ochoticus POPPIUS 1908:54, Siberia (EP)

browni KAMIYA, 1934:181, Manchuria (EP)

= *brunneus* KAMIYA, 1935:8 [HN]

= *orientalis* KAMIYA, 1938:36 [RN]

conspicuus SHARP, 1873:48, Japan (EP)

= *deplanatus* GUIGNOT, 1952:18

= *procerus* (RÉGIMBART, 1883:229) (*Platynectes*)

granulatus (FALKENSTRÖM, 1936:95) (*Gaurodytes*), China (EP)

sturmii (GYLLENHAL in SCHÖNHERR, 1808:18) (*Dytiscus*), Sweden (P)

= *fallax* MUNSTER, 1932:85

= *goedellii* (VILLA & VILLA, 1833:33) (*Colymbetes*)

confinis-group (E, H, O)

ambulator RÉGIMBART, 1895:152, Ethiopia (E)

angusi NILSSON, 1994:172, Siberia (EP)

approximatus FALL, 1922:26, Colorado (NA)

audeni WALLIS, 1933:270, British Columbia (NA)

bergi ZAITZEV, 1913:195, Transcaucasus (P)

bicolor (KIRBY, 1837:70) (*Colymbetes*), North America (NA)

= *mutus* SHARP, 1882:513

canadensis FALL, 1922:27, Manitoba (NA)

clypealis (THOMSON, 1867:107) (*Gaurodytes*), Sweden (H)

= *scholzi* KOLBE, 1916:253

confinis (GYLLENHAL, 1808:511) (*Dytiscus*), Sweden (H)

= *longulus* (LECONTE, 1878:596) (*Gaurodytes*)

= *ovoideus* (CROTCH, 1873:418) (*Gaurodytes*)

congener (THUNBERG, 1794:75) (*Dytiscus*), Sweden (P)

= *congener* (PAYKULL, 1798:214) (*Dytiscus*) [HN]

= *daisetsuzanus* KAMIYA, 1938:34

= *foveolatus* MULSANT & Godart, 1860:177

- = *funkii* SEIDLITZ, 1887:92
 = *fuscotestaceus* DALLA TORRE, 1877:63
 = *venturii* BERTOLINI, 1870:242
costulatus (MOTSCHULSKY, 1859:541) (*Colymbetes*), Siberia (EP)
 = *tunkunensis* (ZIMMERMANN, 1928:178) (*Gaurodytes*)
discolor (HARRIS, 1828:164) (*Colymbetes*), North America (H)
 = *levanderi* HELLÉN, 1929:40
elongatus (GYLLENHAL in C.R.SAHLBERG, 1826:169) (*Dytiscus*), Scandinavia (H)
 = *bryanti* CARR, 1930:278
immaturus LARSON, 1991:1263, New Brunswick (NA)
inexpectatus NILSSON, 1990:157, Siberia (H)
inscriptus (CROTCH, 1873:422) (*Gaurodytes*), Labrador (NA)
kootenai LARSON, 1991:1279, British Columbia (NA)
lapponicus (THOMSON, 1867:108) (*Gaurodytes*), Norway (P)
 = *obovatus* (J.SAHLBERG, 1875:176) (*Gaurodytes*)
 = *obscuripennis* (J.SAHLBERG, 1875:177) (*Gaurodytes*)
loeffleri WEWALKA & NILSSON, 1990:152, Ethiopia (E)
mackenziensis LARSON, 1991:1267, Northwest Territories (NA)
matsumotoi SATÔ & NILSSON, 1990:193, Japan (EP)
moestus (CURTIS, 1835:LX) (*Colymbetes*), Northwest Territories (H)
 = *borealis* SHARP, 1882:513
 = *nigripalpis* J.SAHLBERG, 1880:56
phaeopterus (KIRBY, 1837:70) (*Colymbetes*), North America (NA)
pseudoclypealis SCHOLZ, 1933:74, Russia (P)
 = *haraldi* HÅK.LINDBERG, 1933:121
sasquatch LARSON, 1991:1285, California (NA)
setulosus (J.SAHLBERG, 1895:39) (*Gaurodytes*), Finland (WP)
slovzovi (J.SAHLBERG, 1880:59) (*Gaurodytes*), Siberia (EP)
smithi BROWN, 1930:88, British Columbia (NA)
subfuscatus SHARP, 1882:514, Massachusetts (NA)
thomsoni (J.SAHLBERG, 1871:407) (*Gaurodytes*), Finland (H)
 = *coriaceus* (J.SAHLBERG, 1875:174) (*Gaurodytes*)
tibetanus ZAITZEV, 1908:425, Tibet (EP)
turcmenus GUIGNOT, 1957:93, Turkestan (EP)
zetterstedti THOMSON, 1856:216, Scandinavia (H)
 = *browni* LEECH, 1938:126 [HN]

***fuscipennis*-group (H)**

- ajax* FALL, 1922:30, Alberta (NA)
coxalis coxalis SHARP, 1882:535, Siberia (H)
 = *splichali* REITTER, 1899:196
coxalis ermaki (ZAITZEV, 1953:259) (*Gaurodytes*), Siberia (EP)
coxalis schmidti ZAITZEV, 1913:197, Georgia (P)
fuscipennis fuscipennis (PAYKULL, 1798:209) (*Dytiscus*), Sweden (P)
 = *eversmanni* BALLION, 1855:237
 = *fossarum* (GERMAR, 1824:29) (*Dytiscus*)
 = *obscurior* (J.SAHLBERG, 1875:199) (*Acatodes*)
fuscipennis ontarionis FALL, 1922:30, Ontario (NA)
infuscatus AUBÉ, 1838:330, North America (H)
 = *dubiosus* POPPIUS, 1905:20
 = *gelidus* U.SAHLBERG, 1906:15
kaszabi GUÉORGUIEV, 1972:37, Mongolia (EP)

japonicus-group (EP, O)

- aequabilis* (GSCHWENDTNER, 1923:105) (*Gaurodytes*), Tien Shan (EP)
aequalis SHARP, 1882:501, Siberia (EP)
amoenus amoenus SOLSKY, 1874:142, Turkestan (EP)
amoenus sinuaticollis RÉGIMBART, 1899:278, India (EP)
bakeri (ZIMMERMANN, 1924:743) (*Gaurodytes*), Philippines (O)
fulvipennis RÉGIMBART, 1899:277, China (EP)
 = *chinensis* (ZIMMERMANN, 1919:211) (*Gaurodytes*)
hummeli (FALKENSTRÖM, 1936:2) (*Gaurodytes*), China (EP)
japonicus japonicus SHARP, 1873:50, Japan (EP)
japonicus ezo NAKANE, 1989:23, Japan (EP)
japonicus continentalis GUÉORGUIEV, 1970:259 [RN], Primorye (EP)
 = *falkenstromi* (ZAITZEV, 1953:254) (*Gaurodytes*) [HN]
japonicus shiroumanus (NAKANE, 1959:98) (*Gaurodytes*), Japan (EP)
kokoosson FENG, 1936:8, China (EP)
mucronatus (FALKENSTRÖM, 1936:89) (*Gaurodytes*), China (EP)
philippensis (ZIMMERMANN, 1924:743) (*Gaurodytes*), Philippines (O)
regimbarti ZAITZEV, 1906:174, China (EP)
rufipennis (GSCHWENDTNER, 1933:163) (*Gaurodytes*), China (EP)

lutosus-group (NA)

- griseipennis* LECONTE, 1859:5, Wyoming (NA)
lutosus LECONTE, 1853:31 [RN], California (NA)
 = *discolor* LECONTE, 1852:204 [HN]
 = *lecontei* (CROTCH, 1873:417) (*Gaurodytes*) [RN]
 = *mimus* LEECH, 1942:132
rumppi LEECH, 1964:79, California (NA)

obsoletus-group (NA)

- ancillus* FALL, 1922:24, Oregon (NA)
hoppingi LEECH, 1942:135, California (NA)
morosus LECONTE, 1852:204, California (NA)
 = *fossiger* (MOTSCHULSKY, 1859:170) (*Colymbetes*)
obliteratus obliteratus LECONTE, 1859:5, Wyoming (NA)
obliteratus nectris LEECH, 1942:133, British Columbia (NA)
obsoletus LECONTE, 1858:15, California (NA)

raffrayi-group (E)

- dytiscoides* RÉGIMBART, 1908:6, Tanzania (E)
pallidus OMER-COOPER, 1931:786, Ethiopia (E)
raffrayi SHARP, 1882:501, Ethiopia (E)
 = *limbicollis* RÉGIMBART, 1905:224
ruwenzoricus GUIGNOT, 1936:49, Uganda (E)
sjostedti RÉGIMBART, 1908:5, Tanzania (E)

Subgenus *Agabus* s. str. (H)

No autapomorphy found. The following characters occur within the group: male antenna clavate; pronotum with anterior bead continuous; metasternal wing narrow; epipleuron with row of fine setae; larval legs provided with secondary swimming hairs.

[Syn.: *Eriglenus* THOMSON, 1859; *Apator* SEMENOV, 1899; *Carrhydrus* FALL, 1922; *Neonecticus* GUIGNOT, 1951]

aeruginosus-group (NA)

- aeruginosus* AUBÉ, 1838:298, North America (NA)

= *dispositus* GUIGNOT, 1936:189

punctatus MELSHEIMER, 1844:27, North America (NA)

antennatus-group (NA)

antennatus LEECH, 1939:217 [RN], Nebraska (NA)

= *clavatus* LECONTE, 1859:4 [HN]

bifarius-group (H)

bifarius (KIRBY, 1837:71) (*Colymbetes*), North America (H)

= *kessleri* HOCHHUTH, 1871:238

clavicornis-group (H)

clavicornis SHARP, 1882:536, Siberia (H)

= *verus* BROWN, 1931:115

crassipes (FALL, 1922:35) (*Carrhydrus*) Alberta (NA)

serricornis (PAYKULL, 1799:49) (*Dytiscus*), Finland (P)

= *clavatus* (LATREILLE, 1804:166) (*Dytiscus*)

= *minor* J.SAHLBERG, 1875:199

= *paykullii* LEACH, 1817:72 [RN]

disintegratus-group (NA)

disintegratus (CROTCH, 1873:416) (*Gaurodytes*), North America (NA)

taeniolatus (HARRIS, 1828:164) (*Colymbetes*), North America (NA)

= *taeniatus* AUBÉ, 1838:311

falli-group (NA)

falli (ZIMMERMANN, 1934:186) (*Gaurodytes*) [RN], Manitoba (NA)

= *sharpi* FALL, 1922:19 [HN]

labiatus-group (H)

fulvaster ZAITZEV, 1906:26, Russia (P)

labiatus (BRAHM, 1791:27) (*Dytiscus*), Germany (P)

= *assimilis* (STURM, 1834:112) (*Colymbetes*)

= *femorialis* (PAYKULL, 1798:215) (*Dytiscus*)

= *hochhuti* ZAITZEV, 1908:CLX [IN; *brunneus* F. sensu HOCHHUTH 1871]

= *impressus* (ZOUBKOFF, 1833:317) (*Colymbetes*)

= *transcaucasicus* ZAITZEV, 1927:28

mandsuricus (GUIGNOT, 1956:139) (*Ilybius*), Manchuria (EP)

= *charini* (LAFER, 1988:54) (*Erigenus*)

pallens POPPIUS, 1905:22, Siberia (H)

= *hudsonicus* LEECH, 1938:123

= *mongolicus* GUÉORGUIEV, 1968:27

= *zaitzewi* POPPIUS, 1909:12

undulatus (SCHRANK, 1776:70) (*Dytiscus*), Germany (WP)

= *abbreviatus* (FABRICIUS, 1787:191) (*Dytiscus*)

= *imperfectus* MEIER, 1899:98

= *interruptus* SCHILSKY, 1888:183

= *pictus* MEIER, 1899:98

= *ruficeps* (MÉNÉTRIES, 1832:141) (*Colymbetes*)

zimmermanni SCHOLZ, 1920:15, Asia Minor (P)

lineatus-group (EP)

desertorum F.MORAWITZ, 1863:169, Russia (EP)

lineatus GEBLER, 1848:75, Siberia (EP)

punctulatus-group (H)

colymbus LEECH, 1938:125, Manitoba (NA)

luteaster ZAITZEV, 1906:27, Siberia (EP)
oblongulus FALL, 1922:18, Oregon (NA)
pisobius LEECH, 1949:246, British Columbia (NA)
punctulatus AUBÉ, 1838:332, North America (NA)
 = *aeneolus* (CROTCH, 1873:417) (*Gaurodytes*)

uliginosus-group (H)

ammicola (J.SAHLBERG, 1880:58) (*Gaurodytes*), Siberia (H)
 = *triton* FALL 1922:17
jacobsoni ZAITZEV, 1905:225, Russia (P)
margaretae LARSON, 1975:344, Alberta (NA)
uliginosus (LINNAEUS, 1761:216) (*Dytiscus*), Sweden (P)
 = *aeratus* STEPHENS, 1828:79 (*Colymbetes*)
 = *dispar* BOLD, 1849:XXIV
 = *reichei* AUBÉ, 1837:138
vereschaginae ANGUS, 1984:193, Siberia (EP)

Subgenus *Gaurodytes* THOMSON, 1859 (E, H, O)

Autapomorphy: paramere stylate.

[Syn.: *Necticus* HOPE, 1839 (preocc.); *Metronectes* SHARP, 1882; *Dichodytes* THOMSON, 1886; *Xanthodytes* SEIDLITZ, 1887; *Gabinectes* GUIGNOT, 1931; *Agabinectes* GUIGNOT, 1932; *Dichonectes* GUIGNOT, 1945]

adpressus-group (H)

adpressus AUBÉ, 1837:169, Dauria (H)
 = *angusticollis* (J.SAHLBERG, 1871:408) (*Gaurodytes*)
 = *haeffneri* AUBÉ, 1837:170
 = *sahlbergi* SHARP, 1882:517
 = *solus* LEECH, 1949:248
 = *subquadratus* (MOTSCHULSKY, 1860:102) (*Colymbetes*)
udege NILSSON, 1994:170, Primorye (EP)

affinis-group (H)

affinis (PAYKULL, 1798:211) (*Dytiscus*), Sweden (P)
 = *branchiatus* (BABINGTON, 1832:329) (*Colymbetes*)
 = *guttulus* (SCHÖNHERR, 1808:19) (*Dytiscus*) [IN; *guttatus* PAYKULL sensu ILLIGER 1801]
biguttulus (THOMSON, 1867:110) (*Gaurodytes*), Scandinavia (P)
 = *boreellus* (J.SAHLBERG, 1871:409) (*Gaurodytes*)
 = *ovalis* (J.SAHLBERG, 1875:178) (*Gaurodytes*)
kholini NILSSON, 1994:45, Primorye (EP)
laferi NILSSON, 1994:47, Primorye (EP)
semipunctatus (KIRBY, 1837:69) (*Colymbetes*), North America (NA)
 = *stridulator* SHARP, 1882:509
sikhotealinensis (LAFER, 1988:56) (*Gaurodytes*), Primorye (EP)
unguicularis (THOMSON, 1867:101) (*Eriglenus*), Sweden (P)
velox LEECH, 1939:219, Manitoba (NA)
yakutiae NILSSON & LARSON, 1990:229, Siberia (EP)

ambiguus-group (NA)

ambiguus (SAY, 1823:96) (*Colymbetes*), North America (NA)
 = *fimbriatus* LECONTE, 1850:214 [RN]
 = *reticulatus* AUBÉ, 1838:355 [HN]
austinii SHARP, 1882:516, Utah (NA)
erythropterus (SAY, 1823:95) (*Colymbetes*), North America (NA)
klamathensis LARSON & LEECH, 1989:875, Oregon (NA)

strigulosus (CROTCH, 1873:422) (*Gaurodytes*), California (NA)
= *nanus* (LECONTE, 1878:452) (*Gaurodytes*)

aubei-group (WP)

aubei PERRIS, 1869:6, Corsica (WP)
= *parallelipennis* DESBROCHERS DES LOGES, 1871:337

brunneus-group (WP)

brunneus (FABRICIUS, 1798:64) (*Dytiscus*), Morocco (WP)
= *castaneus* (GYLLENHAL in SCHÖNHERR, 1808:21) (*Dytiscus*)
= *ferrugineus* (STEPHENS, 1828:79) (*Colymbetes*)
= *marginicollis* FAIRMAIRE, 1860:631
= *rotundatus* WEHNCKE, 1872:136
= *rufulus* FAIRMAIRE, 1859:272
didymus (OLIVIER, 1795:26) (*Dytiscus*), France (WP)
= *chalybaeus* J.SAHLBERG, 1903:12
= *vitreus* (PAYKULL, 1798:217) (*Dytiscus*)

guttatus-group (P)

africanus PEDERZANI & SCHIZZEROTTO, 1998:88, Tunisia (WP)
balcanicus HLISNIKOVSĀY, 1955:101, Bulgaria (WP)
basalis (GEBLER, 1830:65) (*Colymbetes*), Turkestan (EP)
= *abnormicollis* BALLION, 1871:329
= *pallidipennis* JAKOVLEV, 1897:40 [HN]
= *songoricus* GEBLER, 1859:450 (*Colymbetes*) [RN]
biguttatus (OLIVIER, 1795:26) (*Dytiscus*), France (P)
= *alligator* NORMAND, 1933:299
= *annulatus* (ZOUBKOFF, 1833:318) (*Colymbetes*)
= *concii* FRANCISCOLO, 1942:137
= *consanguineus* WOLLASTON, 1864:81
= *fontinalis* (STEPHENS, 1828:66) (*Colymbetes*)
= *indicus* RÉGIMBART, 1899:272
= *melas* AUBÉ, 1837:168
= *nigricollis* (ZOUBKOFF, 1833:317) (*Colymbetes*)
= *nitidus* (FABRICIUS, 1801:265) (*Dytiscus*)
= *nubiensis* RÉGIMBART, 1895:154
= *olivieri* ZAITZEV, 1908:121 [RN]
= *pauper* SCHILSKY, 1888:184
= *picicornis* (STEPHENS, 1828:66) (*Colymbetes*)
= *silesiacus* LETZNER, 1844:173
= *subaquilus* GOZIS, 1912:60
binotatus AUBÉ, 1837:161, Sardinia (WP)
blatta JAKOVLEV, 1897:39, Turkestan (EP)
= *picea* JAKOVLEV, 1897:40
brandti HAROLD, 1880:148, China (EP)
= *jeholensis* KAMIYA, 1935:8
caraboides SHARP, 1882:494, Syria or Mesopotamia (EP)
= *merkli* RÉGIMBART, 1885:XIX
cephalotes REICHE, 1861:202, Corsica (WP)
dilatatus (BRULLÉ, 1832:127) (*Colymbetes*), France (P)
= *castaneus* SHARP, 1882:500 [HN]
= *gory* AUBÉ, 1837:162
faldermanni ZAITZEV, 1927:22, Transcaucasia (P)
= *iranicus* GUÉORGUIEV, 1965:257
= *palaestinus* (ZIMMERMANN, 1934:164) (*Gaurodytes*)

- freudei* GUÉORGUIEV, 1975:97, Nepal (EP)
glacialis HOCHHUTH, 1846:218, Caucasus (P)
 = *armeniacus* SHARP, 1882:497
 = *inguttatus* REITTER, 1908:223
glazunovi (ZAITZEV, 1953:228) (*Gaurodytes*), Uzbekistan (EP)
guttatus guttatus (PAYKULL, 1798:211) (*Dytiscus*), Sweden (P)
 = *didymoides* ROUBAL, 1919:15
 = *nigripes* (COSTA, 1847:97) (*Colymbetes*)
 = *picinus* (MARSHAM, 1802:428) (*Dytiscus*)
 = *septemseriatus* (J.SAHLBERG, 1875:180) (*Gaurodytes*)
 = *signatus* (GRIMMER, 1841:32) (*Colymbetes*)
 = *styriacus* SHARP, 1882:496
 = *unicolor* DALLA TORRE, 1877:64
guttatus baudii SEIDLITZ, 1887:85, Italy (WP)
heydeni WEHNCKE, 1872:135, Spain (WP)
 = *parvulus* FRESNEDA & HERNANDO, 1989:14
lobonyx GUIGNOT, 1952:17, Sikkim (EP)
longissimus RÉGIMBART, 1899:275, Tibet (EP)
maderensis WOLLASTON, 1854:85, Madeira (WP)
ommani ZAITZEV, 1908:424, Tibet (EP)
picotae FOSTER & BILTON, 1997:113, Portugal (WP)
svenhedini (FALKENSTRÖM, 1932:192) (*Gaurodytes*), China (EP)
winkleri (GSCHWENDTNER 1923:104) (*Gaurodytes*), Turkestan (EP)
 = *pamiricus* GUIGNOT, 1955:274

nebulosus-group (P)

- conspersus* (MARSHAM, 1802:427) (*Dytiscus*), England (P)
 = *bulgaricus* (CSIKI, 1943:214) (*Gaurodytes*)
 = *corsicus* GUIGNOT, 1932:571
 = *gougeletii* REICHE, 1863:474
 = *luniger* KOLENATI, 1845:82
 = *perlautus* GOZIS, 1912:53
 = *subnebulosus* (STEPHENS, 1828:72) (*Colymbetes*)
dichrous SHARP, 1878:169, Pamir (EP)
 = *lederii* SEIDLITZ, 1887:94
 = *luteolus* RÉGIMBART, 1899:275
friedrichi (FALKENSTRÖM, 1936:91) (*Gaurodytes*), China (EP)
godmanni CROTCH, 1867:385, Azores (WP)
nebulosus (FORSTER, 1771:56) (*Dytiscus*), Germany (P)
 = *abdominalis* RAGUSA, 1888:7 [HN]
 = *bipunctatus* (FABRICIUS, 1787:190) (*Dytiscus*) [HN]
 = *immaculatus* (GSCHWENDTNER, 1927:92) (*Gaurodytes*) [HN]
 = *mixtus* GUIGNOT, 1949:6
 = *naevius* (GMELIN, 1790:1957) (*Dytiscus*)
 = *nigromaculatus* (GOEZE, 1777:625) (*Dytiscus*)
 = *notatus* (BERGSTRÄSSER, 1778:31) (*Dytiscus*)
 = *pratensis* SCHAUFUSS, 1881:620
 = *ragusai* ZAITZEV, 1908:123 [RN]
 = *tesselatus* (GEOFFROY in FOURCROY, 1785:68) (*Dytiscus*)
safei ABDUL-KARIM & ALI, 1986:277, Iraq (EP)

paludosus-group (P)

- alinae* (LAFER, 1988:58) (*Gaurodytes*), Primorye (EP)
paludosus (FABRICIUS, 1801:266) (*Dytiscus*), Germany (WP)

- = *marginalis* SHARP, 1882:502
- = *pallidipennis* (LAPORTE, 1834:103) (*Colymbetes*)
- = *politus* (MARSHAM, 1802:419) (*Dytiscus*)

ragazzii-group (E)

- abessinicus* (ZIMMERMANN, 1928:177) (*Gaurodytes*), Ethiopia (E)
- crypticoides* RÉGIMBART, 1895:152, Ethiopia (E)
- galamensis* NILSSON, 1992:174, Ethiopia (E)
- perssoni* NILSSON, 1992:172, Ethiopia (E)
- ragazzii* RÉGIMBART, 1887:638, Ethiopia (E)
- = *ferrugatus* RÉGIMBART, 1905:225

striolatus-group (WP)

- striolatus* (GYLLENHAL, 1808:508) (*Dytiscus*), Sweden (WP)
- = *costatus* GERHARDT, 1910:42
- = *rectus* (BABINGTON, 1841:53) (*Colymbetes*)

taiwanensis-group (EP)

- taiwanensis* NILSSON & WEWALKA, 1994:993, Taiwan (EP)

tristis-group (H)

- adustus* GUIGNOT, 1954:223, Kashmir (EP)
- bipustulatus* (LINNAEUS, 1767:667) (*Dytiscus*), Sweden (E, P)
- = *abdominalis* (COSTA, 1847:134) (*Colymbetes*)
- = *acuductus* (MARSHAM, 1802:416) (*Dytiscus*)
- = *alpestris* HEER, 1837:53
- = *alpicola* ZAITZEV, 1927:24
- = *alticola* BRUNEAU DE MIRÉ & LEGROS, 1963:875
- = *callosus* (THOMSON, 1884:1031) (*Gaurodytes*)
- = *carbonarius* (FABRICIUS, 1801:263) (*Dytiscus*)
- = *dolomitanus* SCHOLZ, 1935:37
- = *falcozi* GUIGNOT, 1931:7
- = *immaculatus* (SCHRANK, 1781:201) (*Dytiscus*)
- = *kiesenwetterii* SEIDLITZ, 1887:88
- = *latus* (GEBLER, 1841:371) (*Colymbetes*)
- = *luctuosus* (GEOFFROY IN FOURCROY, 1785:67) (*Dytiscus*)
- = *maurus* (ZIMMERMANN, 1919:209) (*Gaurodytes*)
- = *peyerimhoffi* BRUNEAU DE MIRÉ & LEGROS, 1963:875
- = *picipennis* J.SAHLBERG, 1903:5
- = *pyrenaeus* FRESNEDA & HERNANDO, 1988:35
- = *regalis* PETRI, 1903:49
- = *remotus* J.SAHLBERG, 1913:45
- = *sexualis* REICHE, 1857:IX
- = *snowdonius* (NEWMAN, 1833:55) (*Colymbetes*)
- = *solieri* AUBÉ, 1837:183
- debilipes* RÉGIMBART, 1899:273, Simla (EP)
- = *skarduensis* GUIGNOT, 1958:30
- = *subsericatus* RÉGIMBART, 1899:274
- leptapsis* (LECONTE, 1878:596) (*Gaurodytes*), Michigan (NA)
- melanarius* AUBÉ, 1837:180, Russia (WP)
- = *frigidus* SCHIÖDTE, 1841:477
- = *kotschyi* LETZNER, 1849:95
- = *tarsatus* (ZETTERSTEDT, 1837:132) (*Dytiscus*)
- = *tatricus* ROUBAL, 1938:19
- nevadensis* HÅK.LINDBERG, 1939:32, Spain (WP)

solskii JAKOVLEV, 1897:40, Turkestan (EP)
tristis AUBÉ, 1838:356, North America (H)
 = *atratus* MANNERHEIM, 1853:157
 = *crotchi* ZAITZEV, 1905:212
 = *dubius* MANNERHEIM, 1843:221
 = *kurilensis* KAMIYA, 1938:35
 = *picea* ZAITZEV, 1905:212 [HN]
 = *piceolus* ZAITZEV, 1908:123 [RN]
wollastoni SHARP, 1882:531, Madeira (WP)
 = *dissimilis* (FALKENSTRÖM, 1938:13) (*Gaurodytes*)
 = *falkenstromi* J.BALFOUR-BROWNE, 1944:352 [RN]

Genus *Hydronebrius* JAKOVLEV, 1897 (EP)

Autapomorphy: body punctuation very strong; setal row at posterolateral angle of metafemur reduced.

ampliocollis TOLEDO, 1994:207, China (EP)
cordaticollis (REITTER, 1896:233) (*Agabus*), Uzbekistan (EP)
kashmirensis (VAZIRANI, 1964:145) (*Amphizoia*), Kashmir (EP)
 = *guignoti* VAZIRANI, 1970:346
mattheyi mattheyi BRANCUCCI, 1980:171, Pakistan (EP)
mattheyi nepalensis BRANCUCCI, 1980:174, Nepal (EP)

Genus *Hydrotrupes* SHARP, 1882 (NA)

palpalis SHARP, 1882:492, California (NA)

Genus *Ilybiosoma* CROTCH, 1873 (E, H)

Autapomorphy: metatibia with anteroventral spiniferous punctures along entire length.

[Syn.: *Nebriogabus* GUIGNOT, 1936; *Ranagabus* J.BALFOUR-BROWNE, 1939]

discicollis-group (E, EP)

discicollis (ANCEY, 1883:70) (*Agabus*), Ethiopia (E)
kermanensis (J.BALFOUR-BROWNE, 1939:107) (*Agabus*), Iran (EP)

seriatum-group (NA)

amaroides (SHARP, 1882:33) (*Agabus*), Mexico (NA)
bjorkmanae (HATCH, 1939:104) (*Agabus*), British Columbia (NA)
 = *recta* (LECONTE, 1869:374) (*Anisomera*) [HN]
brevicollis (LECONTE, 1857:34) (*Agabus*), California (NA)
 = *sobrinus* (MOTSCHULSKY, 1859:170) (*Colymbetes*)
cordatum (LECONTE, 1853:226) (*Anisomera*), New Mexico (NA)
flohrianum (SHARP, 1887:756) (*Agabus*), Mexico (NA)
 = *flohri* (ZIMMERMANN, 1919:207) (*Gaurodytes*)
ilybiiformis (ZIMMERMANN, 1928:176) (*Gaurodytes*), California (NA)
lugens (LECONTE, 1852:203) (*Agabus*), New Mexico (NA)
 = *suturalis* (CROTCH, 1873:423) (*Gaurodytes*)
minnesotensis (WALLIS, 1933:268) (*Agabus*), ?Minnesota (NA)
pandurum (LEECH, 1942:128) (*Agabus*), California (NA)
perplexus (SHARP, 1882:498) (*Agabus*), California (NA)
regularis (LECONTE, 1852:203) (*Ilybius*), California (NA)
 = *oblongus* (MOTSCHULSKY, 1859:169) (*Ilybius*)
rogus (LARSON, 1997:123) (*Agabus*), Oregon (NA)
seriatum (SAY, 1823:97) (*Colymbetes*), New York (NA)

- = *arctus* (MELSHEIMER, 1844:27) (*Agabus*)
- = *intersectus* (CROTCH, 1873:419) (*Gaurodytes*)
- = *parallelus* (LECONTE, 1850:213) (*Agabus*)

Genus *Ilybius* ERICHSON, 1832 (H)

Autapomorphies: female ovipositor with lateral ridge; pronotum with fine anterior bead continuous; metacoxal lines reduced anteriorad.

[Syn.: *Ilyobius* GEMMINGER & HAROLD, 1868; *Idiolybius* GOZIS, 1886; *Agabidius* SEIDLITZ, 1887; *Asternus* GUIGNOT, 1931; *Parasternus* GUIGNOT, 1936; *Ilybidius* GUIGNOT, 1948]

chalconatus-group (H)

- albarracinensis* (FERY, 1986:345) (*Agabus*), Spain (WP)
- = *maestroae* (FRESNEDA & HERNANDO, 1987:67) (*Agabus*)
- bedeli* (ZAITZEV, 1908:121) (*Agabus*) [RN], Algeria (WP)
- = *politus* (REICHE, 1861:369) (*Agabus*) [HN]
- chalconatus* (PANZER, 1797:38/17) (*Dytiscus*), Germany (P)
- = *aterrimus* (STEPHENS, 1828:79) (*Colymbetes*)
- = *fuscoaenescens* (RÉGIMBART, 1877:CXLVII) (*Agabus*)
- = *nigroaeneus* (MARSHAM, 1802:428) (*Dytiscus*)
- dettneri* (FERY, 1986:342) (*Agabus*), Portugal (WP)
- gagates* (AUBÉ, 1838:306) (*Agabus*), North America (NA)
- hozgargantae* (BURMEISTER, 1983:133) (*Agabus*), Spain (WP)
- hulae* (WEWALKA, 1984:137) (*Agabus*), Israel (EP)
- jaechi* (FERY & NILSSON, 1993:94) (*Agabus*), Turkey (EP)
- lagabrunensis* (SCHIZZEROTTO & FERY, 1990:148) (*Agabus*), Italy (WP)
- larsoni* (FERY & NILSSON, 1993:98) (*Agabus*), Québec (NA)
- lenensis* nom.n. [RN] Siberia (EP)
- = *aenescens* (POPPIUS, 1905:18) (*Agabus*) [HN]
- lenkoranensis* (FERY & NILSSON, 1993:95) (*Agabus*), Azerbaijan (WP)
- montanus* (STEPHENS, 1828:76) (*Colymbetes*), England (WP)
- = *melanocornis* (ZIMMERMANN, 1915:223) (*Agabus*)
- neglectus* (ERICHSON, 1837:158) (*Agabus*), Germany (WP)
- pederzani* (FERY & NILSSON, 1993:95) (*Agabus*), Italy (WP)
- pseudoneglectus* (FRANCISCOLO, 1972:84) (*Agabus*), Italy (WP)
- = *skiathos* (HINTERSEHER, 1981:87) (*Agabus*)
- samokovi* (FERY & NILSSON, 1993:91) (*Agabus*), Bulgaria (WP)
- satunini* (ZAITZEV, 1913:196) (*Agabus*), Transcaucasia (WP)
- wewalkai* (FERY & NILSSON, 1993:85) (*Agabus*), Turkey (EP)

erichsoni-group (H)

- balkei* (FERY & NILSSON, 1993:103) (*Agabus*), Siberia (EP)
- erichsoni* (GEMMINGER & HAROLD, 1868:454) (*Agabus*), [IN; *nigroaeneus* MARSHAM sensu ERICHSON 1837], Germany (H)
- = *cincticollis* (MÄKLIN, 1881:22) (*Agabus*)
- = *lutosus* (CROTCH, 1873:419) (*Gaurodytes*) [HN]
- subtilis* (ERICHSON, 1837:157) (*Agabus*), Germany (P)
- = *altaicus* (GEBLER, 1848:73) (*Agabus*)

opacus-group (H)

- austrodiscors* (LARSON, 1996:635) (*Agabus*), California (NA)
- confertus* (LECONTE, 1861:340) (*Agabus*), California (NA)
- discors* (LECONTE, 1861:341) (*Agabus*), Washington (NA)
- euryomus* (LARSON, 1996:639) (*Agabus*), California (NA)
- hypomelas* (MANNERHEIM, 1843:221) (*Agabus*), Alaska (NA)

= *irregularis* (MANNERHEIM, 1853:159) (*Agabus*)
jimzim (LARSON, 1996:643) (*Agabus*), Arizona (NA)
lineellus (LECONTE 1861:340) (*Agabus*), California (NA)
opacus (AUBÉ, 1837:173) (*Agabus*), Finland (H)
= *gelidus* (FALL, 1926:142) (*Agabus*) [HN]
= *mimmi* (J.SAHLBERG, 1875:182) (*Gaurodytes*)
= *pseudoconfertus* (WALLIS, 1926:90) (*Agabus*)
= *sachalinensis* (KAMIYA, 1938:37) (*Agabus*)
= *sharpi* (JAKOBSON, 1908:430) (*Agabus*) [RN]
= *sibericus* (SHARP, 1882:519) (*Agabus*) [HN]
vancouverensis (LEECH, 1937:146) (*Agabus*), British Columbia (NA)
vandykei (LEECH, 1942:129) (*Agabus*), California (NA)
verisimilis (BROWN, 1932:4) (*Agabus*), British Columbia (NA)
walsinghami (CROTCH, 1873:419) (*Gaurodytes*), Oregon (NA)
wasastjernae (C.R.SAHLBERG, 1824:167) (*Dytiscus*), Finland (H)
= *kenaiensis* (FALL, 1926:141) (*Agabus*)
= *palustris* (WALLIS, 1926:92) (*Agabus*)

subaeneus-group (H)

aenescens THOMSON, 1870:125, Scandinavia (P)
= *kiesenwetteri* KRAATZ, 1871:166
angustior (GYLLENHAL, 1808:500) (*Dytiscus*), Sweden (H)
anjae NILSSON, 1999:36, Sakhalin (EP)
apicalis SHARP, 1873:51, Japan (EP)
= *intermediatus* FENG, 1936:10
ater (DE GEER, 1774:401) (*Dytiscus*), Sweden (P)
= *ater* (PANZER, 1797:38/15) (*Dytiscus*) [HN]
= *ungularis* (LECONTE, 1862:521) (*Colymbetes*)
biguttulus (GERMAR, 1824:29) (*Dytiscus*), North America (NA)
= *laramaeus* LECONTE, 1859:4
cinctus SHARP, 1878:169, Central Asia (EP)
= *angustulus* RÉGIMBART 1899:289
= *chinensis* CSIKI 1901:102
= *deplanatus* (STEVEN, 1829:26) (*Colymbetes*) [NO]
chishimanus KÔNO, 1944:80, Kuril Islands (EP)
= *weymarni* J.BALFOUR-BROWNE, 1947:446
churchillensis WALLIS, 1939:195, Manitoba (NA)
confusus AUBÉ, 1838:280, North America (NA)
= *denikei* WALLIS, 1933:271
crassus THOMSON, 1856:224, Sweden (WP)
discedens SHARP, 1882:557, Hudson Bay (NA)
fenestratus (FABRICIUS, 1781:294) (*Dytiscus*), Germany (P)
= *aeneus* (PANZER, 1797:38/16) (*Dytiscus*) [HN]
= *ciliatus* (OLIVIER, 1791:311) (*Dytiscus*)
= *evanescens* DALLA TORRE, 1877:63
= *prescottii* (MANNERHEIM, 1829:21) (*Colymbetes*)
fraterculus LECONTE, 1862:521, North Red River (NA)
fuliginosus fuliginosus (FABRICIUS, 1792:191) (*Dytiscus*), Germany (P)
= *foetidus* (O.F.MÜLLER, 1776:71) (*Dytiscus*) [NO]
= *lacustris* (PANZER, 1797:38/14) (*Dytiscus*) [HN]
= *pirinicus* GUÉORGUIEV, 1957:25
fuliginosus turcestanicus GSCHWENDTNER, 1934:74, Kyrgyzstan (EP)
guttiger (GYLLENHAL, 1808:499) (*Dytiscus*), Sweden (P)
= *immunis* (STEPHENS, 1828:81) (*Colymbetes*)

- = *kiesenwetteri* WEHNCKE, 1872:136 [HN]
 = *quadrinotatus* (STEPHENS, 1828:83) (*Colymbetes*)
ignarus (LECONTE, 1862:521) (*Colymbetes*), Lake Superior (NA)
incarinatus ZIMMERMANN, 1928:181, Illinois (NA)
lateralis (GEBLER, 1832:40) (*Colymbetes*), Dauria (EP)
 = *limbatus* SHARP, 1882:557
meridionalis AUBÉ, 1837:126, France (WP)
 = *hispanicus* SHARP, 1872:260
nakanei NILSSON, 1994:58, Sakhalin (EP)
oblitus SHARP, 1882:560, North America (NA)
obtusus SHARP, 1882:558, Siberia (EP)
ovalis GSCHWENDTNER, 1934:74, Siberia (EP)
picipes (KIRBY, 1837:71) (*Colymbetes*), North America (H)
pleuriticus LECONTE, 1850:213, Lake Superior (NA)
 = *inversus* SHARP, 1882:552
poppiusi ZAITZEV, 1907:208, Siberia (EP)
quadriguttatus (LACORDAIRE, 1835:316) (*Colymbetes*), France (P)
 = *obscurus* (MARSHAM, 1802:414) (*Dytiscus*) [HN]
 = *sexdentatus* SCHIÖDTE, 1841:487
quadrinotatus AUBÉ, 1838:274, North America (NA)
similis THOMSON, 1856:225, Sweden (P)
 = *ovatus* HOCHHUTH, 1871:237
subaeneus ERICHSON, 1837:156, Germany (H)
 = *badenii* WEHNCKE, 1871:164
 = *chalybeatus* THOMSON, 1860:48
 = *lapponicus* SCHOLZ, 1917:251
 = *suffusus* CROTCH, 1873:411
 = *viridiaeneus* CROTCH, 1873:411
vittiger (GYLLENHAL, 1827:379) (*Dytiscus*), Sweden (H)

Genus *Platambus* THOMSON, 1859 (H, O)

Autapomorphy: Prosternal process with lateral bead broadly inflated posterior of procoxae and/or mesocoxae widely separated.

[Syn.: *Agabinus* CROTCH, 1873; *Anagabus* JAKOVLEV, 1897; *Colymbinectes* FALKENSTRÖM, 1936; *Stictogabus* GUIGNOT, 1948; *Allogabus* GUIGNOT, 1951; *Agraphis* GUIGNOT, 1954; *Neoplatynectes* VAZIRANI, 1970; *Paraplatynectes* VAZIRANI, 1970]

americanus-group (NA)

- americanus* (AUBÉ, 1838:334) (*Agabus*), Mexico (NA)
 = *obscurior* (ZIMMERMANN, 1919:212) (*Gaurodytes*) [HN]

confusus-group (NA)

- confusus* (BLATCHLEY, 1910:229) (*Rhantus*), Indiana (NA)
 = *amplus* (FALL, 1922:12) (*Agabus*)

glabrellus-group (NA)

- glabrellus* (MOTSCHULSKY, 1859:171) (*Colymbetes*), California (NA)
 = *morulus* (LECONTE, 1861:340) (*Agabus*)
sculpturellus (ZIMMERMANN, 1919:205) (*Agabinus*), California (NA)

maculatus-group (O, P)

- angulicollis* (RÉGIMBART, 1899:273) (*Agabus*), Tibet (EP)
balfourbrowni VAZIRANI 1965:28, Assam (EP)
biswasi VAZIRANI, 1965:32, Nepal (EP)

- excoffieri* RÉGIMBART, 1899:281, China (EP)
fimbriatus SHARP, 1884:445, Japan (EP)
 = *kansouis* FENG, 1936:9
fletcheri ZIMMERMANN, 1928:176, India (O)
guttulus (RÉGIMBART, 1899:283) (*Platynectes*), China (EP)
incrassatus GSCHWENDTNER, 1935:62, Burma (O)
lindbergi GUÉORGUIEV, 1963:218, Afghanistan (EP)
 = *guignoti* VAZIRANI, 1965:27
lunulatus (STEVEN, 1829:26) (*Agabus*), Caucasus (P)
 = *simulatus* (AUBÉ, 1837:148) (*Agabus*)
maculatus (LINNAEUS, 1758:412) (*Dytiscus*), Europe (P)
 = *biocellatus* (O.F.MÜLLER, 1776:72) (*Dytiscus*)
 = *cantalicus* PIC, 1912:57
 = *caucasicus* ZAITZEV, 1927:18
 = *escalerai* RÉGIMBART, 1900:121
 = *glacialis* (GRAËLLS, 1858:42) (*Agabus*) [HN]
 = *graellsii* (GEMMINGER & HAROLD, 1868:455) (*Agabus*) [RN]
 = *hebraicus* (GEOFFROY in FOURCROY, 1785:70) (*Dytiscus*)
 = *inornatus* SCHILSKY, 1888:183
 = *ornatus* (HERBST, 1784:125) (*Dytiscus*)
 = *praetextus* (DALLA TORRE, 1877:63) (*Agabus*)
 = *pulchellus* (HEER, 1839:149) (*Colymbetes*) [HN]
nepalensis (GUÉORGUIEV, 1968:42) (*Stictogabus*), Nepal (EP)
 = *bhutanensis* WEWALKA, 1975:157
pictipennis (SHARP, 1873:49) (*Agabus*), Japan (EP)
satoi BRANCUCCI, 1982:226, Nepal (EP)
schaefleini BRANCUCCI, 1988:188, China (EP, O)
strbai HENDRICH & BALKE, 1998:107, Laos (O)
wittmeri WEWALKA, 1975:158, Bhutan (EP)

optatus-group (H, O)

- ater* (FALKENSTRÖM, 1936:97) (*Colymbinetes*), China (EP)
coriaceus (RÉGIMBART, 1899:282) (*Platynectes*), Assam (O)
ikedai (NILSSON, 1997:635) (*Agabus*), Japan (EP)
insolitus (SHARP, 1884:444) (*Agabus*), Japan (EP)
jilanzhui WEWALKA & BRANCUCCI, 1995:98, China (EP)
koreanus (NILSSON, 1997:636) (*Agabus*), Primorye (EP)
nakanei (NILSSON, 1997:631) (*Agabus*), Japan (EP)
obtusatus (SAY, 1823:99) (*Colymbetes*), North America (NA)
 = *nitidus* (SAY, 1823:98) (*Colymbetes*)
optatus (SHARP, 1884:445) (*Agabus*), Japan (EP)
 = *miyamotoi* (NAKANE, 1959:95) (*Gaurodytes*)
planatus (SHARP, 1882:503) (*Agabus*), North America (NA)
princeps (RÉGIMBART, 1888:615) (*Platynectes*), Burma (EP, O)
schillhammeri WEWALKA & BRANCUCCI, 1995:99, China (EP)
stygius (RÉGIMBART, 1899:279) (*Agabus*), China (EP)
ussuriensis (NILSSON, 1997:632) (*Agabus*), Primorye (EP)

sawadai-group (EP, O)

- kempi* (VAZIRANI, 1970:330) (*Agraphis*), India (O)
khukri BRANCUCCI, 1990:240, Nepal (EP)
punctatipennis BRANCUCCI, 1984:153, China (EP)
regulae BRANCUCCI, 1991:345, Vietnam (O)
sawadai (KAMIYA, 1932:6) (*Agabus*), Japan (EP)

= *confossus* (GUIGNOT 1954:200) (*Agraphis*)

semenowi-group (EP)

lineatus GSCHWENDTNER, 1935:62, India (EP)

= *striatus* (ZENG & PU, 1992:482) (*Hydronebrius*)

semenowi (JAKOVLEV, 1897:38) (*Anagabus*), Turkestan (EP)

sogdianus (JAKOVLEV, 1897:39) (*Anagabus*), Turkestan (EP)

= *holzschuhi* WEWALKA, 1975:155

= *jucundus* (GUIGNOT, 1954:222) (*Agabus*)

= *ledouxii* (LEGROS, 1977:14) (*Anagabus*)

= *limbibasis* (REITTER, 1900:226) (*Anagabus*)

= *vatelloides* (RÉGIMBART, 1899:270) (*Agabus*)

wewalkai BRANCUCCI, 1982:120, India (EP)

semivittatus-group (NA)

strictovittatus (LARSON & WOLFE, 1998:40) (*Agabus*), Florida (NA)

flavovittatus (LARSON & WOLFE, 1998:44) (*Agabus*), Tennessee (NA)

johannis (FALL, 1922:10) (*Agabus*), Florida (NA)

semivittatus (LECONTE, 1852:204) (*Agabus*), Florida (NA)

= *spilotus* (LECONTE, 1859:5) (*Agabus*)

= *texanus* (SHARP, 1882:505) (*Agabus*)

stagninus (SAY, 1823:100) (*Colymbetes*), North America (NA)

= *striola* (AUBÉ, 1838:308) (*Agabus*)

texovittatus (LARSON & WOLFE, 1998:46) (*Agabus*), Texas (NA)

spinipes-group (NA)

apache (YOUNG, 1981:349) (*Agabus*), Arizona (NA)

spinipes (SHARP, 1882:32) (*Agabus*), Mexico (NA)

Acknowledgements

I am grateful to R. Brett, San Francisco, and P.J. Spangler, Washington D.C., who supported this study by loan of material. Thanks are also due to D.J. Larson, St. John's, for helpful discussions.

References

- ALARIE, Y. & LARSON, D.J. 1998: Larvae of *Agabinus* Crotch: Generic characteristics, description of *A. glabrellus* (Motschulsky), and comparison with other genera of the subfamily Colymbetinae (Coleoptera: Adepaga: Dytiscidae). - The Coleopterists Bulletin 52: 339-350.
- ALARIE, Y., SPANGLER, P.J. & PERKINS, P.D. 1998: Study of the larvae of *Hydrotrupes palpalis* Sharp (Coleoptera: Adepaga, Dytiscidae) with implications for the phylogeny of the Colymbetinae. - The Coleopterists Bulletin 52: 313-332.
- BALFOUR-BROWNE, J. 1939: A contribution to the study of the Dytiscidae. I. (Coleoptera, Adepaga). - Annals and Magazine of Natural History (11) 3: 97-114.
- BALKE, M., DETTNER, K. & HENDRICH, L. 1997: *Agabus* ("*Metronectes*") *aubei* Perris: Habitat, morphological adaptations, systematics, evolution, and notes on the phanerofluicolous fauna (Coleoptera: Dytiscidae). - Aquatic Insects 19: 75-90.
- BEUTEL, R.G. 1994: On the systematic position of *Hydrotrupes palpalis* Sharp (Coleoptera: Dytiscidae). - Aquatic Insects 16: 157-164.
- BRANCUCCI, M. 1988: A revision of the genus *Platambus* Thomson (Coleoptera, Dytiscidae). - Entomologica Basiliensia 12: 165-239.

- BRINCK, P. 1948: Coleoptera of Tristan Da Cunha. - Results of the Norwegian Scientific Expedition to Tristan Da Cunha 1937-1938 17: 1-121 + 1 pl.
- DE MARZO, L. & NILSSON, A.N. 1988: Structure of the "preoral comb" in larvae of European Agabini (Coleoptera, Dytiscidae). - Entomologica, Bari 23: 191-205.
- FERY, H. & NILSSON, A.N. 1993: A revision of the *Agabus chalconatus*- and *erichsoni*-groups (Coleoptera: Dytiscidae), with a proposed phylogeny. - Entomologica Scandinavica 24: 79-108.
- FRANCISCOLO, M.F. 1979: Coleoptera. Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae. - Fauna d'Italia 14: 1-804.
- GUÉORGUIEV, V.B. 1965: Zoologische Ergebnisse der Österreichischen Iran-Expedition 1949/50 Karakorum-Expedition 1958 und Irak-Expedition 1963 (Coleoptera: Dytiscidae et Gyrinidae). - Reichenbachia 5: 114-118.
- GUÉORGUIEV, V.B. 1971: Notes sur les Agabini (Coleoptera, Dytiscidae). I. Les genres *Agametrus* Sharp, *Leuronectes* Sharp et *Andonectes* gen. n. - Izvestija na Zoologitjeskija Institut s Musei Sofia 33: 165-176.
- LARSON, D.J. 1975: The predaceous water beetles (Coleoptera: Dytiscidae) of Alberta: systematics, natural history and distribution. - Quaestiones Entomologicae 11: 245-498.
- LARSON, D.J. 1987: Revision of North American species of *Ilybius* Erichson (Coleoptera: Dytiscidae), with systematic notes on Palearctic species. - Journal of the New York Entomological Society 95: 341-413.
- LARSON, D.J. 1989: Revision of North American *Agabus* Leach (Coleoptera: Dytiscidae): introduction, key to species groups, and classification of the *ambiguus*-, *tristis*-, and *arcticus*-groups. - The Canadian Entomologist 121: 861-919.
- LARSON, D.J. 1991: Revision of North American *Agabus* Leach (Coleoptera: Dytiscidae): *elongatus*-, *zetterstedti*-, and *confinis*-groups. - The Canadian Entomologist 123: 1239-1317.
- LARSON, D.J. 1996: Revision of North American *Agabus* Leach (Coleoptera: Dytiscidae): the *opacus*-group. - The Canadian Entomologist 128: 613-665.
- LARSON, D.J. 1997: Revision of North American *Agabus* Leach (Coleoptera: Dytiscidae): the *seriatus*-group. - The Canadian Entomologist 129: 105-149.
- LARSON, D.J. & WOLFE, G.W. 1998: Revision of North American *Agabus* (Coleoptera: Dytiscidae): the *semivittatus*-group. - The Canadian Entomologist 130: 27-54.
- LEECH, H.B. 1942: Key to the Nearctic genera of water beetles of the tribe Agabini, with some generic synonymy (Coleoptera: Dytiscidae). - Annals of the Entomological Society of America 35: 355-362.
- NILSSON, A.N. 1992: A revision of Afrotropical *Agabus* Leach (Coleoptera, Dytiscidae), and the evolution of tropicoalpine super specialists. - Systematic Entomology 17: 155-179.
- NILSSON, A.N. 1997 (1996): A redefinition and revision of the *Agabus optatus*-group (Coleoptera, Dytiscidae); an example of Pacific intercontinental disjunction. - Entomologica Basiliensia 19: 621-651.
- NILSSON, A.N. & LARSON, D.J. 1990: A review of the *Agabus affinis* group (Coleoptera: Dytiscidae), with the description of a new species from Siberia and a proposed phylogeny. - Systematic Entomology 15: 227-239.
- SEMENTOV, A. 1899: Notes on morphological peculiarities of *Agabus kessleri* Hochh. (Coleoptera, Dytiscidae). - Horae Societatis Entomologicae Rossicae 32: 510-514. (In Russian.)

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Koleopterologische Rundschau](#)

Jahr/Year: 2000

Band/Volume: [70_2000](#)

Autor(en)/Author(s): Nilsson Anders N.

Artikel/Article: [A new view on the generic classification of the Agabus-group of genera of the Agabini, aimed at solving the problem with a paraphyletic Agabus \(Dytiscidae\). 17-36](#)