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Phylogeny of the Myllaenini and related taxa (Coleoptera: Staphylinidae: Aleocharinae)

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Abstract

A cladistic analysis of the tribe Myllaenini Ganglbauer and related genera is presented. Monophyly of the Myllaenini is tested, and the tribe is hypothesized to be a monophyletic group consisting of nine genera (*Myllaena* Erichson, *Amazonopora* Pace, *Dimonomera* Cameron, *Bryothinusa* Casey, *Philomina* Blackwelder, *Polypea* Fauvel, *Brachypronomaea* Sawada, *Rothium* Moore and Legner, and *Lautaea* Sawada), based on the synapomorphy of antero-lateral angles of mentum prolonged into spinose processes. A history of the classification of the Myllaenini is discussed. The data set for phylogenetic analysis comprised 99 characters representing 297 character states derived from adult morphology. The analysis agrees on the monophyly of the Myllaenini and the monophyly of the Pronomaeini Ganglbauer (*Pronomaea* Erichson, *Pseudomniophila* Pace, *Nopromaea* Cameron and *Tomoxelia* Bernhauer). The tribe Dimonomerini (*Dimonomera* Cameron) is confirmed to be a member of the Myllaenini. Masuriini is a possible sister group of the Myllaenini. *Stylopalpus* Cameron shows a sister group relationship to the Pronomaeini. Several other clades are also consistently recovered. However, the phylogenetic relationships of the genus *Dysacrita* are ambiguous. The rogue genus *Diglotta* Champion is not recovered as a member of the Myllaenini or Pronomaeini. On the contrary, it forms a monophyletic clade with the liparocephaline genera *Halorhadinus* Sawada and *Amblopusa* Casey. Evolution of the defensive gland on abdominal tergite VII among aleocharine lineages is reconsidered, and the origin of an intertidal habitat in the Myllaenini is discussed.

The beetle family Staphylinidae represents one of the truly remarkable radiations in the history of life; it currently includes over 46 200 described species, placed in 3200 genera (Newton et al., 2000), organized into about 32 subfamilies. All recent works indicate that this is only a small fraction of the true contemporary diversity. Among staphylinids, the subfamily Aleocharinae is the largest, most poorly known, and taxonomically the most difficult lineage. It comprises 52 tribes, over 1000 described and probably valid genera, and over 12 000 described species (Ashe, 1998). Within the Aleocharinae, members of the tribe Myllaenini Ganglbauer and related genera are characterized by unusual styliform mouthparts; the maxillary lobes and labial palpi are particularly elongated and stylet-like (Fenyes, 1918; Seevers, 1978; Pace, 1999). This set of myllaenine-like genera has a confusing taxonomic history. They have been variously classified as comprising several separate tribes, placed with the tribe Pronomaeini Ganglbauer or its equivalent, or they have been taxonomically dispersed among several lineages of riparian or intertidal aleocharines (Table 1). Consequently, they comprise one of the most complex and confusing staphylinid groups.

Ganglbauer (1895) first mentioned the Myllaenini; he included only one genus *Myllaena* Erichson 1837 in this distinct aleocharine tribe. Later, Fenyes (1918–20) placed the genera *Camacopselaphus* Gemminger and Harold 1868 and *Myllaena* in the tribe Myllaenini, based on the number of tarsomeres (4-4-5), the number of antennomeres (11), the number of maxillary palpo-

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Table 1
Generic classification of the Myllaenini and related taxa

	Myllaenini	Pronomaeini	Diglottini
Ganglbauer (1895)	*Myllaena*	*Pronomaea*, *Mataris*	*Diglotta* (= *Diglossa*)
Fenyes (1918)	*Myllaena*, *Camacopselaphus*	*Pronomaea*, *Mataris*	*Diglotta*
Scheerpeltz (1933)	*Myllaena*, *Polypea*, *Camacopalus*	*Pronomaea*, *Mataris*	*Diglotta*
Moore and Legner (1976)	*Myllaena*, *Brachypronomaea*, *Actocharis*, *Bryothinusa*, *Halorhadinus*		*Diglotta*
Seevers (1978)	*Myllaena*, *Camacopalpus*, *Mniophila*, *Polypea*	*Pronomaea*, *Mataris*	*Diglotta*
Klimaszewski (1982)	*Myllaena*, *Pseudomniophila*,		*Diglotta*,
Klimaszewski and Ashe (1992)	*Philomina* (= *Mniophila*)		*Polypea*
Pace (1986, 1999)	**Pronomaeini (= Myllaenini)** *Pronomaea*, *Mataris*, *Nopromaea*, *Masuria*, *Amazonopora*, *Stylopalpus*, *Pseudomniophila*, *Philomina*, *Tomoxelia*, *Dysacrita*, *Myllaena*		**Diglottini** *Diglotta*, *Bryothinusa*, *Polypea*, *Corallis*, *Halorhadinus*, *Brachypronomaea*
This study	*Myllaena*, *Amazonopora*, *Bryothinusa*, *Dimonomera*, *Lautaea*, *Philomina*, *Polypea*, *Rothium*, *Brachypronomaea*	*Pronomaea*, *Nopromaea*, *Pseudomniophila*, *Tomoxelia*	*Diglotta*

meres (4), the number of labial palpomeres (2 or indistinctly 3), and front head forming a beak.

Scheerpeltz (1933) classified *Myllaena*, *Polypea* Fauvel 1878 and *Camacopalpus* Motschulsky 1858 in the tribe Myllaenini. Klimaszewski (1982) transferred *Camacopalpus* to the Zyrasini (= Lomechusini) and separated the genus *Polypea* from the Myllaenini and placed it in the tribe Diglottini. Later, Klimaszewski and Ashe (1992) added the genera *Philomina* Blackwelder 1952 (= *Mniophila* Cameron 1939) and *Pseudomniophila* Pace 1985 to the tribe Myllaenini.

Moore and Legner (1976) placed the genera *Brachypronomaea* Sawada 1956, *Myllaena*, *Actocharis* Fauvel 1869, *Bryothinusa* Casey 1904 and *Halorhadinus* Sawada 1971 in the Myllaenini based on the corneous galea and lacinia. The genus *Halorhadinus* was transferred to the tribe Liparocephalini by Ahn (2001).

Seevers (1978) placed the genera *Myllaena*, *Camacopalpus*, *Philomina* (= *Mniophila*) and *Polypea* in the tribe Myllaenini in his revision of North American Aleocharinae. In addition, he mentioned that *Dimonomera* Cameron 1933 (Dimonomerini), *Masuria* Cameron 1928 (Masuriini), *Pronomaea* Erichson 1837 and *Mataris* Fauvel 1886 (Pronomaeini Mulsant & Rey 1873) should probably be included in the Myllaenini.

Pace (1986) and Haghebaert (1991) placed the genera *Diglotta* Champion 1887, *Brachypronomaea*, *Halorhadinus*, *Bryothinusa*, *Polypea*, *Corallis* Fauvel 1878 in the tribe Diglottini. However, they did not provide sufficient evidence by which the Diglottini could be differentiated from the Myllaenini.

Recently, Pace (1999) synonymized the tribe Myllaenini under the tribe Pronomaeini and placed within it the genera *Pronomaea*, *Mataris*, *Nopromaea* Cameron 1930, *Tomoxelia* Bernhauer 1901 (= *Afropronomaea* Klimaszewski and Jansen 1994), *Amazonopora* Pace 1996, *Stylopalpus* Cameron 1932, *Pseudomniophila*, *Philomina*, *Myllaena* and *Masuria* (Masuriini). He defined the group based on: ligula entire, labial palpi elongate with 1, 2 or 3 palpomeres, maxilla very long and tarsal formula 4-4-5 or 4-5-5. Curiously, Pace did not mention the genus *Dysacrita* Pace which he himself described in 1992 and placed in the tribe Myllaenini.

On the other hand, Sawada (1989) described the genus *Lautaea* and mentioned its relationship with *Pronomaea* and *Bryothinusa*. Ahn and Ashe (1996a) transferred the genus *Rothium* Moore and Legner 1977 to the tribe Myllaenini from the Homalotini. Ashe (1999) transferred the genus *Dimonomera* to the tribe Myllaenini from the monotypic tribe Dimonomerini.

To date, as a result, the tribe Myllaenini and related taxa contains 19 genera (*Pronomaea*, *Mataris*, *Nopromaea*, *Diglotta*, *Masuria*, *Amazonopora*, *Stylopalpus*, *Bryothinusa*, *Pseudomniophila*, *Philomina*, *Myllaena*, *Polypea*, *Corallis*, *Tomoxelia*, *Dysacrita*, *Rothium, Dimonomera, Lautaea*, *Brachypronomaea*), whose phylogenetic relationships have not been tested by modern cladistic methodology.

The objectives of this paper are to test the monophyly of the tribe Myllaenini, to reconstruct the phylogenetic relationships of genera included in the Myllaenini and among related genera, to hypothesize the sister taxa of the Myllaenini, and to present a hypothesis of the origin of intertidal habitat among the myllaenines and related taxa. These results, taken together, provide a background for future studies of aleocharine phylogeny and the evolution of intertidal habitat among the Aleocharinae.

Materials and methods

The specimens for this study are deposited in the Chungnam National University Insect Collection, Daejeon (CNUIC) and Snow Entomological Collection, Division of Entomology, KU Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence (KSEM), or they were borrowed from the following institutions: Institut Royal des Sciences Naturelles de Belgique, Bruxelles (ISNB), Field Museum of Natural History, Chicago (FMNH), Muséum d'Historie Naturelle, Genève (MHNG), Natural History Museum, London (NHM), Naturhistorisches Museum Wien, Wien (NMW), Deutsches Entomologisches Institut (DEI) and Humboldt-Universität Museum für Naturkunde, Berlin (HUMN).

Due to the small size of most aleocharines, dissections of specimens are essential for observing microscopic structural features. Our techniques for mounting and studying dissected specimens on microscope slides followed the methods of Ahn and Ashe (1996b) and Hanley and Ashe (2003).

Choice of taxa

One to several exemplar species of each known genus hypothesized to be in the Myllaenini and related taxa were included, with the exception of the genera *Lautaea* Sawada, *Mataris* Fauvel and *Corallis* Fauvel, which were not available for study. Repeated attempts to obtain a loan of specimens of these taxa were not successful. In addition, the South African genus *Stenectinobregma* Scheerpeltz 1974, which was originally described in the Pronomaeini, is not known to the authors; specimens for dissection and complete study were not available. We used Sawada's description (1989) for the character coding of *Lautaea murphyi* Sawada. Exemplar taxa of polytypic genera were chosen from several areas within the overall generic distribution to include character variation within the genera in the analyses. The type species of each genus was included whenever possible, depending on the availability of specimens for dissection and full character study. The genera *Philomina*, *Brachypronomaea*, *Lautaea*, *Polypea* and *Dimonomera* are monotypic, and all species are included.

We included the genera *Pronomaea* and *Pseudomniophila* (variously placed in the Myllaenini or Pronomaeini), and *Masuria* (Masuriini) in order to test the monophyly of the Myllaenini. Phylogenetic relationships among the tribes of Aleocharinae are not generally known except for the basal groups (Ashe, 1998). Therefore, the exemplar taxa of 12 tribes (Mesoporini, Hypocyphtini, Trichopseniini, Aleocharini, Liparocephalini, Phytosini, Athetini, Oxypodini, Homalotini, Lomechusini, Falagriini, Hoplandriini) and 25 genera [*Anacyptus testaceus* (LeConte), *Paraconosoma naviculare* (Bernhauer), *Cypha discoides* (Erichson), *Cypha longicornis* (Paykull), *Holobus flavicornis* (Lacordaire), *Oligota inflata* Mannerheim, *Oligota pusillima* (Gravenhorst), *Trichopsenius frosti* Seevers, *Aleochara curtula* (Goeze), *Aleochara sulcicollis* Mannerheim, *Amblopusa alaskana* Ahn and Ashe, *Halorhadinus aequalis* Sawada, *Phytosus spinifer* Curtis, *Atheta crassicornis* (Fabricius), *Pontomalota opaca* Casey, *Oxypoda longipes* (Mulsant and Rey), *Calodera riparia* Erichson, *Homalota plana* (Gyllenhal), *Leptusa lombarda* Bernhauer, *Drusilla canaliculata* (Fabricius), *Zyras laticollis* Märkel, *Bryobiota bicolor* (Casey), *Myrmecocephalus arizonicus* (Casey), *Hoplandria laeviventris* Casey, *Platandria mormonica* Casey] were chosen to represent the major clades of the other "higher Aleocharinae" as well as basal representatives of the tribe Gymnusini (*Gymnusa variegata* Kiesenwetter, *Stylogymnusa subantarctica* Hammond) and the tribe Deinopsini [*Deinopsis erosa* (Stephens)] as outgroups (Ashe, 2000). The taxa studied, with their habitats and distributions, are listed in Appendix A.

Selection of characters

Adult morphological characters are exclusively used in these analyses; larvae are not known for most taxa, and sufficient specimens for molecular studies are not available for most myllaenine genera and related taxa. For example, no more than three specimens, including types, of each of the genera *Brachypronomaea*, *Polypea*, *Lautaea*, *Dimonomera*, and *Philomina* are available. The mouthparts have been shown to contain many phylogenetically informative characters by various aleocharine systematists (Sawada, 1972; Ashe, 1984, 1992; Ahn and Ashe, 1996b; Hanley, 2002) and have provided a substantial number of the characters used in this study (see Appendixes B and C).

Phylogenetic analysis

The phylogenetic analysis was performed using NONA 2.0 (Goloboff, 1998), run within WinClada (Beta) 0.99 (Nixon, 1999). Tree search options of HOLD 10000, HOLD/100, MULT*1000 were used.

Multistate characters were treated as unordered. To test the monophyly of the Myllaenini, we included all outgroup and ingroup taxa in the analysis during tree construction in a simultaneous analysis (Nixon and Carpenter, 1993). All cladograms were rooted on *Gymnusa variegata*.

In order to estimate clade support on a cladogram we calculated Bremer support (Bremer, 1988) value and relative Bremer support (Goloboff and Farris, 2001; Kitching, 2002). In Nona we calculated these values using the following command sequence to avoid an overestimation of the values. After finding the most

parsimonious cladograms, the commands "hold 32760; sub 3; find*" are used to find suboptimal trees. The number 3 of the "sub" command was found heuristically by gradual increase to avoid a saturation of computer memory with suboptimal trees. Twenty most parsimonious trees with 584 steps, 747 trees with 584–585 steps (sub 1) and 12419 trees with 584–586 (sub 2) steps were found, respectively. However, the number 32760 of the hold command were used, although more than 100000 trees with 584–587 steps (sub 3) could be retained, because NONA can not calculate the Bremer support and relative Bremer support values of more than 32760 trees. Therefore, several values are indicated as ">3" and ">100". Character distributions were studied using WinClada (Beta) 0.99 (Nixon, 1999). All illustrated cladograms were prepared using WinClada and edited using Microsoft Power Point and Word 2002.

Results

We propose new concepts of the tribes Myllaenini and Pronomaeini here, not only to make the discussion more efficient, but also to avoid confusion. Our results show that Myllaenini is a monophyletic group. Its members share synapomorphic characters which are not shared with the Pronomaeini and other related taxa. Therefore, we redefine the tribe Myllaenini to contain the genera *Myllaena*, *Amazonopora*, *Dimonomera*, *Bryothinusa*, *Philomina*, *Polypea*, *Brachypronomaea*, *Rothium* and *Lautaea*, and hypothesize them to be a monophyletic assemblage based on synapomorphy. In addition, we newly define the tribe Pronomaeini to comprise the genera *Pronomaea*, *Pseudomniophila*, *Nopromaea* and *Tomoxelia*, based on shared apomorphies.

In the following sections we only discuss the phylogenetic relationships of the Myllaenini and related genera; the data set is not designed to capture the full range of character variation among the representatives of basal lineages and other higher aleocharine tribes, so the phylogenetic patterns produced among these taxa may be spurious. Only unambiguously optimized characters are presented, and the apomorphies discussed are unique (Fig. 1), unless stated otherwise specifically.

The analysis resulted in 20 most parsimonious cladograms with a length of 584, a consistency index of 0.33 and a retention index of 0.69. For discussion, we produced one of these 20 trees in Fig. 1 with the unambiguously optimized characters mapped. A strict consensus tree of these 20 most parsimonious trees with Bremer support values and Relative Bremer support values is presented in Fig. 2.

The myllaenine lineage is well supported as a whole, based on a unique apomorphy (52-3, antero-lateral angles of mentum prolonged into spinose processes) and a single homoplastic character (29-1). However, the generic relationships are poorly resolved. *Philomina* is a sister group of the remaining myllaenine genera, and the species of *Rothium* do not form a monophyletic group. *Dysacrita* and the tribes Masuriini and Myllaenini (clade A, Fig. 3) form a monophyletic group based on two apomorphies (25-2, lacinia with distinct interdigitating setae; 82-1, gland opening on tergite VII small, 0.2–0.4 times width of tergite) and two homoplastic characters (27-4, 46-2); however, the relationships among these three lineages have not been unambiguously resolved.

Pronomaeini is also well supported as a monophyletic group, based on one apomorphy (25-1, lacinia with small and indistinct interdigitating setae) and six homoplastic characters (27-4, 28-4, 31-2, 33-0, 41-1 and 89-1). Within Pronomaeini, *Pronomaea*, *Nopromaea africana* and *Tomoxelia nairobiensis* form a monophyletic clade based on three homoplastic characters (58-0, 63-1 and 66-3). The genus *Nopromaea* is not recovered as monophyletic. *Stylopalpus* shows a sister group relationship to the Pronomaeini based on three homoplastic characters (35-1, 44-0, 45-2).

Dysacrita, Masuriini and Myllaenini (clade A) shows a sister group relationship to *Stylopalpus*, the Pronomaeini and other higher aleocharine lineages (clade B, Fig. 3) based on three apomorphies (28-2, 32-2 and 57-0) and 11 homoplastic characters (0-0, 1-0, 3-0, 4-0, 36-1, 47-1, 66-2, 68-0, 69-0, 75-1 and 78-0). The clade of Pronomaeini and *Stylopalpus* is recovered as a sister group of other higher aleocharine lineages (clade C, Fig. 3), based on two homoplastic characters (14-1, 72-1).

Diglotta is not recovered as a member of the Myllaenini or Pronomaeini. On the contrary, *Diglotta* forms a monophyletic group with the liparocephaline genera *Halorhadinus* and *Amblopusa*, although this study is not designed to fully test the phylogenetic relationships of this group.

Discussion

Monophyly of Myllaenini

The classification of Myllaenini and related taxa has been one of the most complex and confused in aleocharine systematics (Table 1). For example, the intertidal genus *Bryothinusa* Casey has been classified in several tribes by various entomologists: tribe Myllaenini by Moore and Legner (1976); the Phytosini by Moore (1956) and Seevers (1978); and the Diglottini by Pace (1986) and Haghebaert (1991). As Ahn and Ashe (1999) mentioned, the presence of elongated and stylate mouthparts among aleocharines probably resulted from parallel development, and these have had a confusing effect on the complex classification system of these tribes.

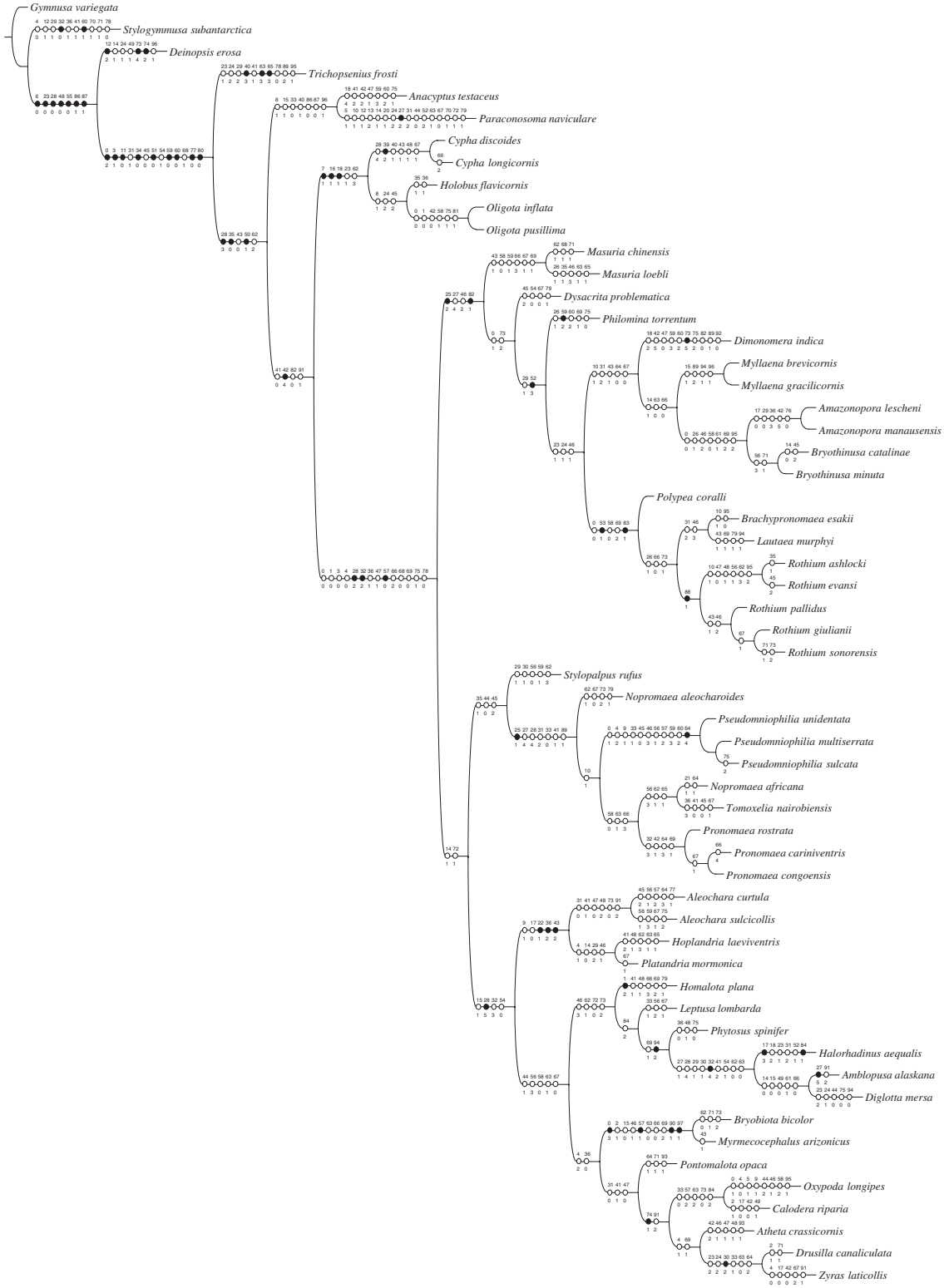

Fig. 1. One of 20 most parsimonious cladograms. Only unambiguously optimized characters are shown. Unique characters are indicated by closed circles, homoplasies by open circles.

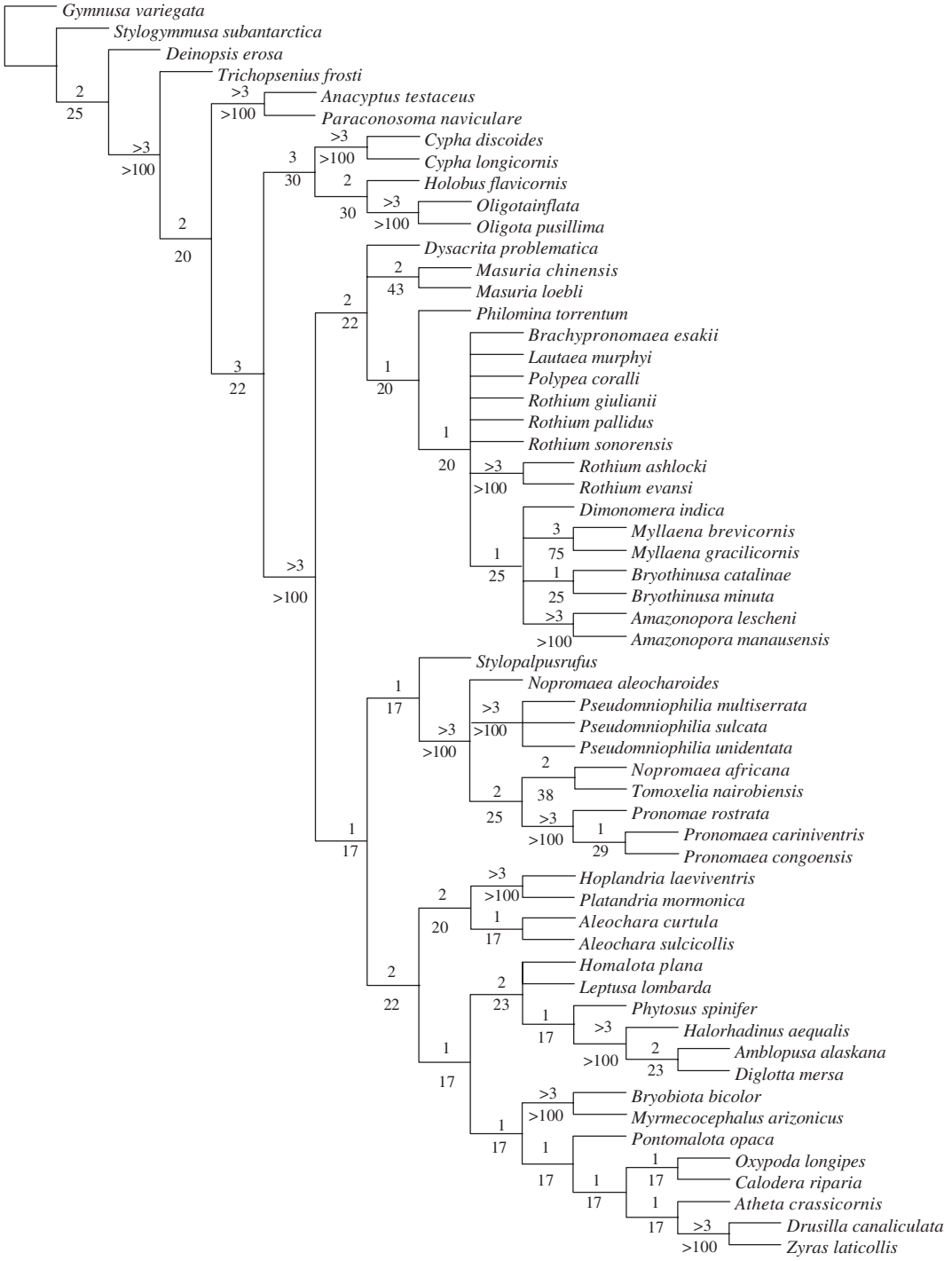

Fig. 2. The strict consensus tree of 20 most parsimonious cladograms with Bremer support (above branches) and relative Bremer support values (below branches).

The monophyly of Myllaenini has not been rigorously demonstrated. However, we obtained consistent results from this study that a group of genera including *Myllaena*, *Amazonopora*, *Dimonomera*, *Bryothinusa*, *Philomina*, *Polypea*, *Brachypronomaea*, *Rothium* and *Lautaea* forms a monophyletic group. Our new concept of the Myllaenini is based on the synapomorphy of antero-lateral angles of mentum prolonged into spinose processes, a character that is, to our knowledge, unique throughout the aleocharines.

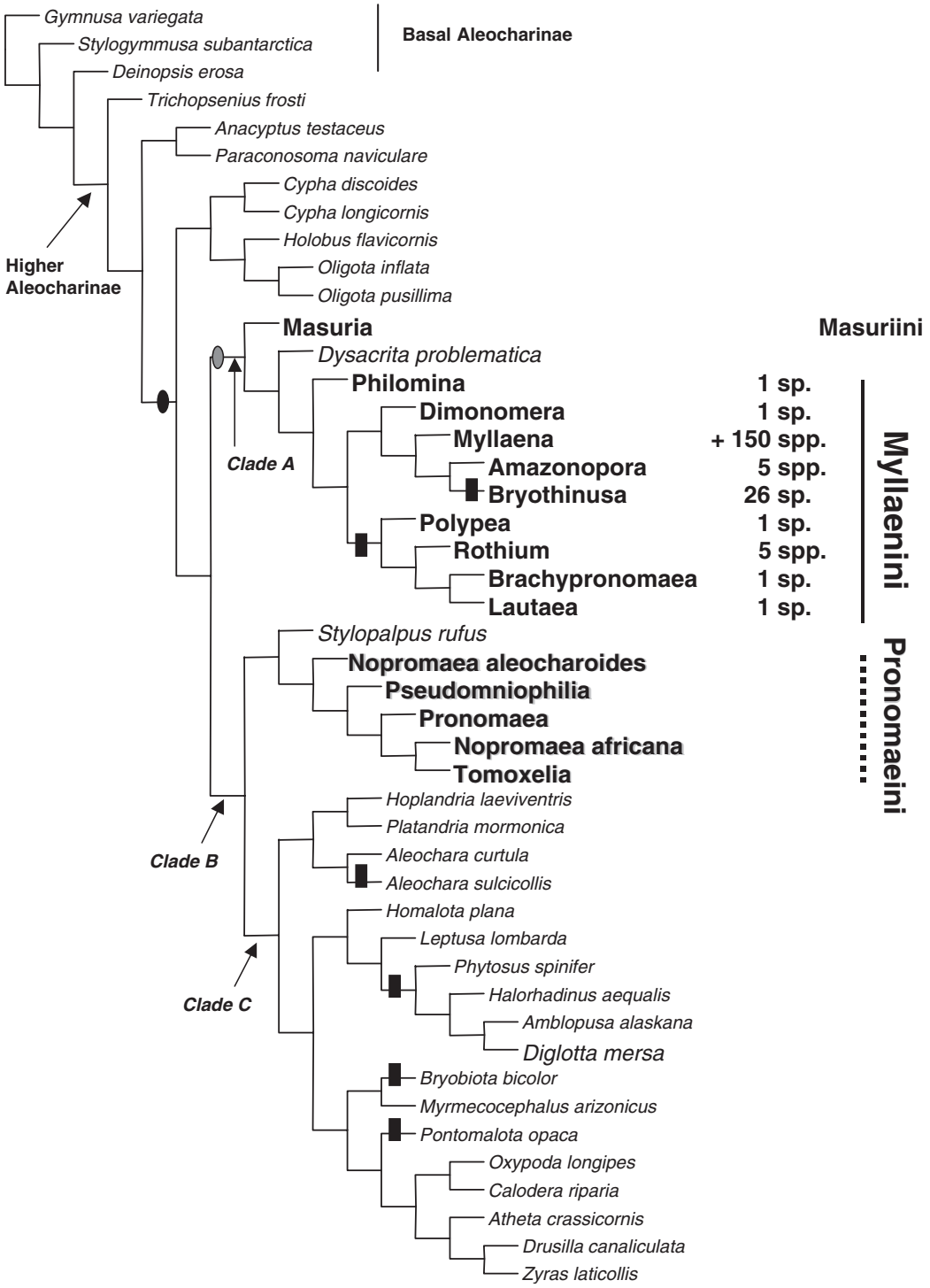

Fig. 3. The evolution of the defensive gland on abdominal tergite VII and intertidal habitat association in the aleocharine lineages. The origin of intertidal habitat in the Myllaenini is represented by a single optimization of two origins. Black circle indicates the origin of the large defensive gland on abdominal tergite VII, while the gray circle indicates small size. Black rectangular marks indicate the origin of the intertidal habitat. One of 20 most parsimonious cladograms.

However, intergeneric relationships among the Myllaenini were not well resolved, though the genera *Dimonomera*, *Myllaena*, *Bryothinusa* and *Amazonopora* formed a monophyletic group.

Phylogenetic position and sister taxa of Myllaenini

The position of the tribe Myllaenini among Aleocharinae has been problematic. Seevers (1978) and Klimaszewski (1982) mentioned that the Myllaenini is a member of the "basal" Aleocharinae and is related to the Gymnusini and Deinopsini. They based this hypothesis primarily on a similarity in body form (all are teardrop-shaped, with a strongly deflexed head), stylate mouthparts, and the fact that all are found in riparian habitats. However, Hammond (1975) and Ashe and Newton (1993) presented evidence that they are actually members of the "higher" Aleocharinae. Presence of a tergal gland in both larvae and adults of Myllaenini supports the latter conclusion. Steidle and Dettner (1993) suggested that the Myllaenini are the most basal group of the higher aleocharines that they examined, based on the very small opening of the tergal gland of *Myllaena* (the only taxon of the Myllaenini sampled).

On the other hand, Seevers (1978) proposed that the Pronomaeini, Masuriini and Dimonomerini are related to the Myllaenini, based on a similarity in mouthpart structure. The single dimonomerine genus *Dimonomera* was hypothesized to belong to the Myllaenini by Ashe (1999), and this hypothesis was supported by our study. The results of cladistic analysis suggests that the sister group of the Myllaenini is not certain. Masuriini and *Dysacrita* are possible sister groups, which form a monophyletic group with the Myllaenini (Figs. 2 and 3). However, we consider the tribe Masuriini more convincing, since only one female paratype of *Dysacrita* was available to study, and this resulted in many missing characters in the data matrix for phylogenetic analyses. At present, the systematic position of *Dysacrita* is uncertain.

Monophyly of Pronomaeini, and systematic position of Stylopalpus and Diglotta

The tribe Pronomaeini, comprising *Pronomaea, Pseudomniophila, Nopromaea* and *Tomoxelia* has been well recovered as a monophyletic group. Pronomaeini is supported by the synapomorphy of lacinia with small and indistinct interdigitating setae.

Inter-generic relationships among Pronomaeini are not well resolved and reveal the following patterns: (((*Nopromaea africana*, *Tomoxelia nairobiensis*) *Pronomaea*), *Pseudomniophila*, *Nopromaea aleocharoides*). The included species of the genus *Nopromaea* are not recovered as a monophyletic group. *Stylopalpus* is recovered as the sister group to Pronomaeini. However, we hypothesize that the genus is not a member of Pronomaeini, since it does not share the synapomorphy with the other members of the tribe and the Bremer support value is low (Fig. 2). The systematic position of *Stylopalpus* should be studied in greater detail.

Diglotta is not recovered as a member of Myllaenini nor Pronomaeini. On the contrary, *Diglotta* forms a monophyletic group with the liparocephaline genera *Halorhadinus* and *Amblopusa*, although this study was not designed to hypothesize the phylogenetic relationships of the Liparocephalini.

Evolution of the defensive gland on abdominal tergite VII

Steidle and Dettner (1993) studied the evolutionary trend of development of the opening for the defensive gland on abdominal tergite VII, based on the chemistry and morphology of adult aleocharines. They hypothesized that the size of reservoir and its openings represented gradual development, with incremental increases in size, in conjunction with the evolution of an efficient chemical defense system. Their arguments on this trend were based on a hypothesized evolutionary scenario of the size of gland opening, from the absence of the defensive gland in Gymnusini and Deinopsini, the most primitive aleocharine tribes, to a large one in the "higher" Aleocharinae. They placed the Myllaenini at the base of the "higher Aleocharinae", because of the small size of the opening to the tergal gland reservoir. However, they admitted that their cladistic analysis had some limits because they sampled only a few aleocharine members of several tribes from central Europe.

Our phylogenetic analysis includes more comprehensive characters and a broader range of taxa and their distributions, and provides an opportunity to study the evolutionary trend of gland opening size on abdominal tergite VII among aleocharines. The cladograms produced (Figs 1–3) confirm that the defensive gland evolved from the absence of a defensive gland in the most primitive aleocharines (Gymnusini and Deinopsini). In addition, the members of the relatively primitive tribes, Trichopseniini and Mesoporini, do not have the glands. However, Steidle and Dettner's (1993) hypothesis of gradual increases in the size of gland opening during the diversification of aleocharines is not directly supported by the cladistic analyses. Instead, the cladograms are consistent with the hypothesis that a reduced size of the tergal gland openings in the aleocharine tribes Myllaenini, Masuriini and *Dysacrita* (clade A, Fig. 3) are derived conditions. The taxa in these groups have very small defensive glands and small gland openings on tergite VII that comprise less than the half width of tergite VII.

The Origin of the intertidal habitat in the Myllaenini

Aleocharine staphylinids are distributed throughout the world, and represent one of the great monophyletic radiations in the history of life. This radiation is characterized by dramatic habitat, microecological and behavioral specialization in various lineages.

While many aleocharines are dominant generalist predators in leaf litter and soil communities, others have very specialized habits and habitats. For example, aleocharines are one of very few lineages of insects to invade and diversify in seashore habitats (Moore and Legner, 1976; Ahn and Ashe, 1992, 1995, 1996a,b; Ahn, 1996, 1997; Hammond, 2000).

Approximately 47 genera and 192 species (Hammond, 2000; Ahn, unpublished data) are known to be confined to seashore habitats. Regular inhabitants of the seashore can be divided into submarine and littoral species (Moore and Legner, 1976). Submarine species are those that tolerate submergence in seawater and may continue their activities at a reduced rate when submerged (Meyerdick, 1969; Topp and Ring, 1988). This contrasts with those of the littoral zone which are killed by submergence in seawater (Topp and Ring, 1988). All of those aleocharine species which inhabit the rocky reef area are submarine, in that they live in the intertidal region and are subsequently submerged by seawater for at least part of each day.

Tribe Myllaenini contains several seashore inhabiting genera: *Bryothinusa*, *Brachypronomaea*, *Rothium*, *Lautaea* and *Polypea*. They are found exclusively in the intertidal region. The other four genera, *Myllaena*, *Amazonopora*, *Philomina* and *Dimonomera*, are terrestrial, and primarily associated with freshwater riparian habitats.

The ecological association of intertidal habitat was mapped onto a cladogram to hypothesize the number of origins in the myllaenine lineage (Fig. 3). The evolution of intertidal habitat in the Myllaenini is represented by a single optimization of two origins. The first origin applies to a clade of *Lautaea*, *Polypea*, *Brachypronomaea*, and *Rothium*. Each of the first three genera contain only a single species from Singapore, Aru Islands (New Guinea), and Ryukyu Island (Japan), respectively, and five *Rothium* species are known from the Pacific coasts of Mexico and Central America. The second origin applies to the genus *Bryothinusa* within a clade of *Dimonomera*, *Myllaena*, *Amazonopora* and *Bryothinusa*. Members of the genus *Bryothinusa* are found in intertidal regions throughout the Pacific Basin and in the Red Sea; *Bryothinusa* is the most specious genus among the intertidal aleocharines. Most of the *Bryothinusa* are found in the intertidal zone, but some are found in estuarine habitats (Ahn, personal observation).

The ancient myllaenine genera *Amazonopora*, *Myllaena*, *Dimonomera* and *Philomina* have been recorded from the riparian habitats. Therefore, we hypothesize that ancestors of the Myllaenini appear to have arisen in riparian habitats and colonized intertidal habitats later. However, the low species diversity of most of myllaenine intertidal genera suggests that most have not successfully diversified in the harsh intertidal environment. The genus *Bryothinusa*, which has about 26 known species, is the most successful one in terms of the species number and broad distribution.

In addition, our cladistic analyses show that multiple origins of seashore habitats (Fig. 3) have occurred throughout the Aleocharinae: *Phytosus* (Phytosini), *Aleochara* (Aleocharini), *Bryobiota* (Falagriini), *Pontomalota* (Athetini), *Diglotta* (Diglottini), *Amblopusa* and *Halorhadinus* (Liparocephalini), as many entomologists have noted previously (Moore and Legner, 1976; Ahn and Ashe, 1992, 1995, 1996a,b; Ahn, 1996, 1997; Hammond, 2000).

Appendix A. Myllaenini and related taxa studied with their habitats and distribution

Taxa	Habitats	Distribution
Amazonopora lescheni	riparian	Peru
Amazonopora manausensis	riparian	Brazil
Brachypronomaea esakii	intertidal	Japan (Ryukyu Islands)
Bryothinusa catalinae	intertidal	USA (California)
Bryothinusa minuta	intertidal	Korea, Japan
Diglotta mersa	intertidal	Europe
Dimonomera indica	riparian (?)	India (North-western)
Dysacrita problematica	terrestrial	Thailand (Chiang Mai)
Lautaea murphyi	intertidal	Singapore
Masuria loebli	riparian (?)	Nepal
Masuria chinensis	riparian (?)	China
Myllaena brevicornis	riparian	Europe
Myllaena gracilicornis	riparian	Europe
Nopromaea africana	terrestrial	West Africa
Nopromaea aleocharoides	terrestrial	
Philomina torrentum	riparian	India
Polypea coralli	intertidal	New Guinea (Aru Islands)
Pronomaea cariniventris	terrestrial	Congo
Pronomaea congoensis	terrestrial	Africa
Pronomaea rostrata	terrestrial	Europe, Northern Africa
Pseudomniophilia multiserrata	riparian	Costa Rica (Alajuela)
Pseudomniophilia sulcata	riparian (?)	Costa Rica (Puntarenas, Monteverde)
Pseudomniophilia unidentata	riparian (?)	Venezuela
Rothium ashlocki	intertidal	Ecuador (Galapagos)
Rothium evansi	intertidal	Ecuador (Punta Galera, Salinas), Peru (Paita)
Rothium giulianii	intertidal	Mexico (Sinaloa, Guerrero)
Rothium pallidus	intertidal	Mexico (Acapulco)
Rothium sonorensis	intertidal	Mexico (Sonora)
Stylopalpus rufus	terrestrial	Namibia
Tomoxelia nairobiensis	terrestrial	Kenya

Appendix B. Character analysis

Terms for adult microstructures follow Sawada (1972) and Ashe (1984). Ninety nine characters were used. Inapplicable characters and missing characters were coded (–) and (?), respectively.

(0) *Body form*: 0. more or less parallel-sided; 1. fusiform; 2. limuloid; 3. falagroid.

(1) *Head deflexed or not*: 0. slightly deflexed; 1. strongly deflexed into vertical plane; 2. prognathous.

(2) *Neck*: 0. absent; 1. present.

(3) *Head covered by apex of pronotum or not*: 0. not covered; 1. partially covered.

(4) *Infraorbital carina*: 0. complete; 1. not complete; 2. absent.

(5) *Frontal suture*: 0. absent; 1. present.

(6) *Setigerous pores on head*: 0. absent; 1. six setigerous pores present (pair in middle of frons, at inner margin of each eye, at inner margin of each antennal fossa).

(7) *Number of antennomeres*: 0. 11; 1. 10.

(8) *Antenna forming club*: 0. not forming club; 1. antennomeres 8–10 forming club.

(9) *Coeloconic sensory structures on antennae*: 0. absent; 1. present.

(10) *Labrum shape*: 0. transverse; 1. more or less circular; 2. elongate.

(11) *Apico-lateral margin of epipharynx*: 0. not modified to setose or spinose process; 1. modified to setose or spinose process.

(12) *Meso-lateral region of epipharynx*: 0. without elongate setose processes; 1. with a few scattered long setose processes on each side of midline; 2. with dense patch of setose processes on each side of midline.

(13) *Middle basal region of epipharynx*: 0. without setose processes or spinules; 1. with orally directed short spinules; 2. with dense patch of orally directed setose processes.

(14) *Basal region of epipharynx*: 0. without medial transverse single row of sensory pores; 1. with medial transverse single row of 4–6 sensory pores; 2. with medial transverse single row of 8–10 sensory pores; 3. with medial transverse single row of numerous small sensory pores.

(15) *Medial region of epipharynx*: 0. with a few irregularly scattered pores, or pores absent; 1. with numerous pores in a linear or rectangular array.

(16) *Mandible shape*: 0. apical half not narrower than basal half; 1. apical half narrower than basal half.

(17) *Number of subapical teeth on right mandible*: 0. absent; 1. 1 small; 2. 1 large; 3. 1 large, 1 small; 4. 2 large; 5. 3 large

(18)*Number of subapical teeth on left mandible*: 0. absent; 1. indistinctly present; 2. 1 small; 3. 1 large; 4. 2 large; 5. 3 large

(19) *Prostheca*: 0. with fringe of filiform setulae; 1. with fringe of small teeth; 2. with a few large teeth.

(20) *Molar lobe*: 0. absent; 1. small; 2. large.

(21) *Molar denticles*: 0. absent; 1. present.

(22) *Number of maxillary palpomeres*: 0. 4; 1. 4 and pseudo-palpomere.

(23) *Maxillary palpomere 3 shape*: 0. dilated; 1. ovoid; 2. elongate.

(24) *Maxillary palpomere 4*: 0. longer than half of maximum with of 3 but shorter than maximum width of 3; 1. shorter than half of maximum width of 3; 2. longer than width of 3.

(25) *Spine distribution and shape of lacinia*: 0. not interdigitating; 1. interdigitating setae small and indistinct; 2. interdigitating setae distinct.

(26) *A pair of hook-like setae on lacinia*: 0. absent; 1. present.

(27) *Distribution of teeth or spines on apical third of lacinia*: 0. row of large setae, contiguous with the apical spine and with each other; 1. widely dispersed small to moderate teeth; 2. numerous moderate to small teeth in linear row; 3. large apical spine, subapical patch of small spines, and 3 large teeth more basally; 4. widely dispersed small spines with a spinose scale on each side of each spine; 5. large apical spine, 4 short spines more apically, and 1 larger spine behind these 4.

(28) *Distribution of teeth on middle third of lacinia*: 0. spines and setae absent; 1. row of very small widely separated setae or spinose setae; 2. row of 4–5 large widely separated setae or spinose setae; 3. single row of large recurved spinose setae; 4. one row of large and one row of small setae; 5. numerous intermixed curved spines and large setae.

(29) *Galea width to lacinia*: 0. more or less same; 1. narrower than lacinia; 2. wider than lacinia.

(30) *Galea length to lacinia*: 0. more or less same; 1. galea shorter than lacinia; 2. galea longer than lacinia.

(31) *Galea length*: 0. very short and broad, length 3 times width at base or less; 1. moderate in length, length 4–6 times width at base or less; 2. long, slender and stylate, length 8–10 times width at base; 3. very long, slender, and stylate, length 14 or more times width at base.

(32) *Apical setae on galea*: 0. greatly reduced to vestigial setae and single large sensillum; 1. single row of moderate to large spines; 2. single row of moderate setae; 3. numerous setae and spinose sensillae in moderate to large membranous patch; 4. dense row of moderate to large setae or spines.

(33) *Mesal setae on galea*: 0. row of filiform setae on most of galea; 1. row of filiform setae on apical 1/4; 2. absent; 3. widely scattered short setae and minute spines.

(34) *Adoral base of galea*: 0. without notch or indentation; 1. with hook-like notch.

(35) *Cardo shape*: 0. more or less triangular; 1. more or less rectangular.

(36) *Number of labial palpomeres*: 0. 3; 1. 2 (1 and 2 fused); 2. 3 and pseudopalpomere; 3. 1 (1, 2, and 3 fused).

(37) *Longitudinal row of setae laterally on adoral side of labial palpomere 1*: 0. absent; 1. present.

(38) *Labial palpomere 1 length*: 0. subequal to, or shorter than 2 and 3 together; 1. much longer than 2 and 3 together.

(39) *Labial palpomere 1 shape*: 0. elongate, more or less parallel-sided; 1. expanded apically, base narrower than apex; 2. more or less quadrate.

(40) *Labial palpomere 2*: 0. elongate, more or less parallel-sided; 1. subglobose or globose; 2. minute (less than 0.2 times length of 1); 3. half moon shape.

(41) *Ligula length*: 0. shorter than palpomere 1; 1. almost same as palpomere 1; 2. longer than palpomere 1; 3. extremely long, reaching the tip of palpus.

(42) *Ligula apex*: 0. acutely emarginate into 2 lobes in apical third or less; 1. acutely emarginate in apical half to third; 2. divided in apical three-fourths to half; 3. divided to base, or near base; 4. elongate and rounded; 5. more or less triangular.

(43) *Number of setae on ligula*: 0. absent; 1. two; 2. four to eight.

(44) *Posterior margin of labium*: 0. rounded; 1. pointed, but not thin; 2. pointed and very thin.

(45) *Number of medial setae on prementum*: 0. two medial setae present; 1. one medial seta present; 2. medial setae absent.

(46) *Distance between medial setae on prementum*: 0. large, greater than 2 times width of setal pore; 1. small, 1–2 times width of setal pore; 2. contiguous; 3. one behind the other.

(47) *Medial pseudopore field on prementum*: 0. broad (greater than 2 times width of medial setal pore); 1. narrow (less broad than 2 times width of medial setal pore).

(48) *Number of pseudopores on median region of prementum*: 0. absent; 1. less than 8 scattered pseudopores present; 2. numerous pseudopores present

(49) *Lateral pseudopore field on prementum*: 0. absent; 1. less than 8 scattered pseudopores present; 2. numerous pseudopores present.

(50) *Setae on hypopharynx*: 0. with irregularly scattered setae on each side of midline; 1. with well-differentiated row of setae on each side of midline.

(51) *Mentum width to gula*: 0. greatest width about equal to apex of gula; 1. greatest width much greater than apex of gula.

(52) *Antero-lateral angles of mentum*: 0. truncate (not deeply emarginate), broadly rounded, or broadly and shallowly emarginated; 1. broadly U-shaped emarginated; 2. prolonged into broad lobes; 3. prolonged into spinose processes.

(53) *Numerous pores on mentum*: 0. absent; 1. present.

(54) *Two long medial setae on mentum*: 0. absent; 1. present.

(55) *Antero-lateral margins on mentum*: 0. on same plane as discal areas; 1. on different plane from discal areas.

(56) *Pronotum width to length ratio*: 0. width to length ratio about 2.0; 1. width to length ratio more than 1.5; 2. width to length ratio between 1.5 and 1.2; 3. width to length ratio between 1.2 and 1.0; 4. width to length ratio less than 1.0.

(57) *Pronotum shape*: 0. not narrowed behind middle, broadest near center; 1. distinctly narrowed behind middle, broadest in anterior 0.5–0.3; 2. narrowed anteriorly, broadest in posterior 0.5–0.3.

(58) *Hypomera*: 0. visible in lateral view; 1. slightly visible in lateral view; 2. not visible in lateral view.

(59) *Medial carina on mesosternum*: 0. absent; 1. strong, but present only on basal 0.5–0.3 of mesosternum; 2. strong, but present only on apical 0.5–0.3 of mesosternum; 3. strong, complete to apex of mesosternal process.

(60) *Numerous microsetae associated with medial carina on mesosternum*: 0. absent; 1. present, especially in basal half; 2. present, especially in apical half.

(61) *Mesocoxal acetabula*: 0. completely margined posteriorly by fine ridge; 1. not margined posteriorly, open.

(62) *Degree of separation of middle coxae*: 0. contiguous; 1. narrowly separated (separation less than 0.15 total length meso- and metasternal processes); 2. middle coxae moderately separated (separation $> 0.15 < 0.35$ times combined length of processes); 3. middle coxae widely separated (separation greater than 0.35 times combined length of processes).

(63) *Mesosternal process*: 0. extended to less than 0.3 times total length of mesocoxae; 1. extended to 0.4–0.6 times total length of mesocoxae; 2. extended to more than 0.7 times total length of mesocoxae; 3. connected to metasternal process.

(64) *Mesosternal process shape*: 0. apex pointed; 1. apex rounded; 2. apex truncated; 3. apex emarginate with obtuse lateral margin; 4. apex emarginate with spinose lateral margin.

(65) *Metasternal process*: 0. extended to less than 0.3 times total length of mesocoxae; 1. extended to 0.4–0.6 times of total length of mesocoxae; 2. extended to more than 0.8 times total length of mesocoxae; 3. connected to mesosternal process.

(66) *Metasternal process shape*: 0. absent; 1. apex pointed; 2. apex broadly rounded; 3. apex narrowly rounded; 4. apex truncated; 5. apex emarginate with blunt lateral margin; 6. apex emarginate with spinose lateral margin.

(67) *Isthmus*: 0. distinctly present, isthmus length greater than 0.1 times combined length of processes; 1. slightly present, isthmus length 0.1–0.05 times combined length of processes; 2. virtually to completely absent, processes in contact or separation not greater than 0.02 times combined length of processes.

(68) *Elytra shape*: 0. longer than wide; 1. more or less quadrate.

(69) *Postero-lateral margin of elytra*: 0. markedly or deeply sinuate; 1. slightly or moderately sinuate; 2. rectilinear, not at all sinuate.

(70) *Epipleural ridge on elytra*: 0. absent; 1. present.

(71) *Hind wings*: 0. present; 1. absent; 2. rudimentary.

(72) *Flabellum on hind wings*: 0. absent; 1. present.

(73) *Tarsal formula*: 0. 5-5-5; 1. 4-5-5; 2. 4-4-5; 3. 4-4-4; 4. 3-3-3; 5. 1-1-5.

(74) *Tarsal claws*: 0. simple; 1. with small basal tooth; 2. with medial and subbasal tooth.

(75) *Number of empodial setae*: 0. absent; 1. 1 seta; 2. 2 setae.

(76) *Shape of empodial setae*: 0. not spatulate; 1. spatulate.

(77) *Pre-apical longitudinal ctenidium of setulae on protibia*: 0. absent; 1. present.

(78) *Ventral lamella (ventral plate) on hind coax*: 0. small or absent; 1. large, covering part of trochanter.

(79) *Macrosetae on abdomen*: 0. small, difficult to distinguished from microsetae; 1. larger, easily distinguished from microsetae.

(80) *Pectinate or not (comb of cuticular projections) on abdomen*: 0. not pectinate; 1. pectinate, one type; 2. pectinate, two types.

(81) *Tergal gland on abdominal tergites III–VI*: 0. absent; 1. present.

(82) *Gland opening on abdominal tergite VII*: 0. large, greater than 0.5 times width of tergite; 1. small, 0.2–0.4 times width of tergite; 2. absent.

(83) *Gland opening shape on abdominal tergite VII*: 0. more or less trapezoidal; 1. oblong.

(84) *Male abdominal sternite VIII*: 0. round, not modified; 1. slightly prolonged; 2. prolonged.

(85) *Number of paratergites on abdominal segments III-VII*: 0. two; 1. one.

(86) *Male abdominal tergite IX*: 0. entire; 1. divided by tergite X.

(87) *Female abdomen tergite IX*: 0. entire; 1. divided by tergite X.

(88) *Setal pattern of abdominal tergite IX*: 0. not circular; 1. circular.

(89) *Abdominal tergite X shape*: 0. not divided; 1. divided into two lobes but not pointed; 2. divided into two long pointed lobes.

(90) *External gland on basal region of abdominal sternite IV*: 0. absent; 1. present.

(91) *Ventral area of median lobe*: 0. completely membranous (compressor plate not apparent); 1. with short, well-defined compressor plate; 2. with long compressor plate (extended entire length of median lobe).

(92) *Median lobe attachment for paramere*: 0. with pair of very large processes distal to basal bulb; 1. with single large medial process; 2. process single, small or insignificant.

(93) *Athetine bridge on median lobe*: 0. absent; 1. present.

(94) *Apical process of paramere*: 0. round; 1. pointed; 2. more or less diamond shape.

(95) *Apical process length of paramere*: 0. long and slender (longer, or as long as paramerite); 1. medium length (less than length of paramerite, but more than 0.5 times as long); 2. short, less than 0.5 times as long as paramerite.

(96) *Apical process articulation of paramere*: 0. not articulated; 1. articulated proximal to anterior edge of velum; 2. clearly articulated distal to anterior edge of velum.

(97) *Velum of paramerite and condylite of paramere*: 0. not separated; 1. separated.

(98) *Condylite articulation with paramerite of paramere*: 0. not apparently articulated; 1. clearly articulated.

Appendix C. Character data matrix

	0	1 0	2 0	3 0	4 0
Gymnusa variegata	1100201000	1102200231	2002000110	0213110110	2330?2-010
Stylogymmusa subantarctica	1100001000	2112000441	2002000111	0202111000	0131?2-010
Deinopsis erosa	1100200000	0121100552	1000100300	0212110110	0331?2-001
Anacyptus testaceus	1012000100	0000105400	0000000300	1100000011	2202001001
Paraconosoma naviculare	2101210010	1012110000	1000200230	0210000001	1330000000
Cypha discoides	2101200100	0000001410	0001000040	0112000002	1041200010
Cypha longicornis	2101200100	0000001410	0001000040	0112000002	1041200010
Holobus flavicornis	2101200110	0000001410	0001200030	0112011000	004022-000
Oligota inflata	0001200110	0000001110	0001200030	0112000000	000022-000
Oligota pusillima	0001200110	0000001210	0001200030	0112000000	000022-000
Trichopsenius frosti	2101200000	0000000000	0001200002	0112010001	3131101000
Amazonopora lescheni	0000100000	1000100000	0001121420	0221013000	0051002100
Amazonopora manausensis	0000000000	1000100000	0001121420	0221013000	0051002100
Brachypronomaea esakii	0000000000	1000000100	0001121421	1221001000	0040003100
Bryothinusa catalinae	0000100000	1000000100	0001121421	1221011000	004102-100
Bryothinusa minuta	0000100000	1000100100	0001121421	1221011000	0041002100
Dimonomera indica	1000000000	1000000120	0001120421	0221011000	0051?01000
Dysacrita problematica	1000000000	0000?00100	0000020420	0122001000	004012-100
Lautaea murphyi	0000?00000	0000000100	000112142?	?2210?1000	0041?03100
Masuria chinensis	0000000000	0000000100	0000020420	0121001000	0041202100
Masuria loebli	0000000000	0000000100	0000021420	0121011000	0041203100
Myllaena brevicornis	1000000000	1000110100	0001120421	1221011000	0041001100
Myllaena gracilicornis	1000000000	1000110100	0001120421	1221011000	0041001100
Nopromaea africana	000000000?	1000100100	0100010440	0220011000	014002-100
Nopromaea aleocharoides	000000000?	0000100100	0000010440	0220011000	014002-100
Philomina torrentum	1000000000	0000000100	0000021421	0121011000	0040?02100
Polypea coralli	0000000000	0000??0100	0001120421	1121001000	0040001100
Pronomaea cariniventris	0000000000	1000000100	0000010440	0230011000	011002-100
Pronomaea congoensis	0000000000	1000000100	0000010440	0230011000	011002-100
Pronomaea rostrata	0000000000	1000000100	0000010440	0230011000	011002-100
Pseudomniophilia multiserrata	1000200001	1000000100	0000010440	0221011000	0140003100
Pseudomniophilia sulcata	1000200001	1000000100	0000010440	0221011000	0140003100
Pseudomniophilia unidentata	1000200001	1000000100	0000010440	0221011000	0140003100
Rothium ashlocki	0000000000	1000000100	0001121421	1121011000	0040001010
Rothium evansi	0000000000	1000000100	0001121421	1121001000	004002-010
Rothium giulianii	0000000000	0000000100	0001121421	11210?1000	0041002100
Rothium pallidus	0000000000	0000000100	0001121421	11210?1000	0041002100
Rothium sonorensis	0000000000	0000000100	0001121421	1121001000	0041002100
Stylopalpus rufus	0000000000	0000100100	0000000021	1122011000	004002-100
Tomoxelia nairobiensis	000000000?	1000?00100	0000010440	0220013000	0040000100
Aleochara curtula	1000000001	0000110000	0010000050	0032002000	013222-022
Aleochara sulcicollis	0000000001	0000110000	0010000050	0032002000	0132200022
Amblopusa alaskana	0000100000	0000000100	0000000541	1140001000	024012-100
Halorhadinus aequalis	0000000000	0000110320	0001000141	1240001000	0240102101
Diglotta mersa	0000200000	0000000100	0002100141	1140001000	024001-100
Phytosus spinifer	0000000000	0000110100	0000000050	0132000000	0040103111
Atheta crassicornis	0000100000	0000110100	0000000050	0032000000	0120101112
Pontomalota opaca	0000200000	0000110100	0000000050	0032000000	0110100022
Oxypoda longipes	1000010001	0000110100	0000000050	0030000000	0110201022
Calodera riparia	0010200000	0000110000	0000000050	0030000000	0100100021
Homalota plana	0200000000	0000110100	0100000050	0130001000	0100103111
Leptusa lombarda	0000000000	0000110100	0100000050	0131001000	0040103101
Drusilla canaliculata	0010100000	0000110100	0002200050	2231000000	0110100021
Zyras laticollis	0000000000	0000110000	0002200050	2131000000	0100100020
Bryobiota bicolor	3010200000	0000100100	0000000050	0132000000	0010101120
Myrmecocephalus arizonicus	3010200000	0000100100	0000000050	0132000000	0011101102
Hoplandria laeviventris	1000100001	0000010000	0010000052	0132002000	0202201110
Platandria mormonica	1000100001	0000010000	0010000052	0132002000	0012201100

(*continued*)	5 0	6 0	7 0	8 0	9 0
Gymnusa variegata	0110012223	2012303200	0000021110	202-00000	000002000
Stylogymmusa subantarctica	0100012223	1012003202	11-000-100	102-10000	002002200
Deinopsis erosa	0110001223	2012001200	0004220110	102-11100	001000100
Anacyptus testaceus	1000101223	2022204212	0000010010	002-000000	001010100
Paraconosoma naviculare	1020101220	0021204012	101000-011	002-010000	001010100
Cypha discoides	1000100220	0032204112	000300-010	0000001100	012002201
Cypha longicornis	1000100220	0032202112	000300-010	0000?0?100	0????????
Holobus flavicornis	1000101220	0031214212	000300-010	0000?0?100	0????????
Oligota inflata	1000101210	0032204212	0003010010	0100001?00	011002201
Oligota pusillima	1000101210	0031214212	0003010010	0100001?00	011002201
Trichopsenius frosti	0000102220	0013-3-212	000000-000	002-011102	0??011201
Amazonopora lescheni	1030102000	0100000002	0002010001	0010001100	012002201
Amazonopora manausensis	1030102000	0100000002	0002010001	0010001100	012002201
Brachypronomaea esakii	1031102000	0122300002	01-1021000	0011001100	012000201
Bryothinusa catalinae	1030103000	0100000002	01-2011000	0010001100	012002201
Bryothinusa minuta	1030103000	0100000002	01-2011000	0010001100	012002201
Dimonomera indica	1030102223	2012002000	00?5021000	0000?01101	010001201
Dysacrita problematica	1000002020	0022102000	00?20??001	0010?0?100	0????????
Lautaea murphyi	103?1020??	????????01	01-1011001	00??001100	012011201
Masuria chinensis	1000103001	0012103111	01-1010000	0010001100	012002201
Masuria loebli	1000101001	0021113101	0001010000	0010001100	012002201
Myllaena brevicornis	1030102220	0000000000	0002011001	0010001102	012011101
Myllaena gracilicornis	1030102220	0000000000	0002011001	0010001102	012011101
Nopromaea africana	1020103000	0011113200	00?10??000	0?00?01101	012002201
Nopromaea aleocharoides	1020102020	0012202000	00?200-001	0000001101	012002201
Philomina torrentum	1030102222	2022102201	00?200-000	0010?0?100	0????????
Polypea coralli	1031102000	0022102202	01-2011000	0011?0?100	0????????
Pronomaea cariniventris	1020102000	0021304101	001100-000	0100001101	012002201
Pronomaea congoensis	1020102000	0?21303101	001100-000	0100001?01	012002201
Pronomaea rostrata	1020102000	0021303201	001100-000	0100001?01	012002201
Pseudomniophilia multiserrata	1020101223	2022402200	0011010000	0100001101	012002201
Pseudomniophilia sulcata	1020101223	2022402200	0011020000	0100001101	012002201
Pseudomniophilia unidentata	1020101223	2022402200	0011010000	0100001101	012002201
Rothium ashlocki	1031101000	0032200202	0001021000	0011001110	012002201
Rothium evansi	1031101000	0032200202	0001021000	0011001110	012002201
Rothium giulianii	1031102000	0022100102	0001021001	0011001110	012001201
Rothium pallidus	1031102000	0022100202	00?10??00?	0011001110	012001201
Rothium sonorensis	1031102000	0022100102	01-2021001	0011001110	012001201
Stylopalpus rufus	1010100021	0032202200	00?1010000	0100001100	012002201
Tomoxelia nairobiensis	1020103000	0011213100	00?10??000	0?00001101	0????????
Aleochara curtula	1000001220	0022302202	0010010100	0000001100	022002201
Aleochara sulcicollis	1000002013	0022103101	0010020000	0000001100	022002201
Amblopusa alaskana	1000103000	0100000001	01-2010000	0000201100	022022201
Halorhadinus aequalis	1010103000	0000002001	0202010000	0000101100	012022201
Diglotta mersa	1000103000	0100000001	01-200-000	0000201100	012002201
Phytosus spinifer	1000003000	0011002001	000200-000	0000201100	012022201
Atheta crassicornis	1000002000	0011002001	0011110001	0000001100	022102201
Pontomalota opaca	1000003000	0121102000	01-1010000	0000001100	012102201
Oxypoda longipes	1000001220	0012002000	0010110001	0000201100	022001201
Calodera_riparia	1000004200	0012002000	0010110000	0000201100	022002201
Homalota plana	1000003000	0011003002	0002010001	0000001100	012002201
Leptusa lombarda	1000002000	0011002100	01-2010000	0000201100	012002201
Drusilla canaliculata	1000004000	0020213001	01-1110001	0000001100	022002201
Zyras laticollis	1000002000	0030224201	0011110001	0000001100	012002201
Bryobiota bicolor	1000003100	0100000002	01-2010000	0000001100	112002211
Myrmecocephalus arizonicus	1000003100	0120000002	0011010000	0000001100	112002211
Hoplandria laeviventris	1000002020	0031114200	0011010000	0000001100	012002201
Platandria mormonica	1000002020	0022103100	0011010000	0000001100	012002201

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References

Ahn, K.-J., 1996. A review of *Diaulota* Casey (Coleoptera: Staphylinidae: Aleocharinae), with description of new species and known larvae. Coleopt. Bull. 50, 270–290.

Ahn, K.-J., 1997. A review of *Liparocephalus* Mäklin (Coleoptera: Staphylinidae: Aleocharinae) with descriptions of larvae. Pan-Pac. Entomol. 73, 79–97.

Ahn, K.-J., 2001. Phylogenetic relationships of the intertidal genus *Halorhadinus* Sawada and key to the genera of the Liparocephalini (Coleoptera: Staphylinidae: Aleocharinae). Insect Syst. Evol. 32, 123–132.

Ahn, K.-J., Ashe, J.S., 1992. Revision of the intertidal aleocharine genus *Pontomalota* Casey (Coleoptera: Staphylinidae) with a discussion of its phylogenetic relationships. Ent. Scand. 23, 347–359.

Ahn, K.-J., Ashe, J.S., 1995. Revision of the genus *Bryobiota* and a revised phylogeny of the falagriine genera of America north of Mexico. Ann. Entomol. Soc. Am. 88, 143–154.

Ahn, K.-J., Ashe, J.S., 1996a. A revision of *Rothium* Moore and Legner (Coleoptera: Staphylinidae: Aleocharinae) with a discussion of its phylogenetic relationships. J. Kans. Entomol. Soc. 69, 234–256.

Ahn, K.-J., Ashe, J.S., 1996b. Phylogeny of the intertidal aleocharine tribe Liparocephalini (Coleoptera: Staphylinidae). Syst. Entomol. 21, 99–114.

Ahn, K.-J., Ashe, J.S., 1999. Two new species of *Amazonopora* Pace 1996 (Coleoptera Staphylinidae Aleocharinae) from Peru and French Guiana with a discussion of its phylogenetic relationships. Trop. Zool. 12, 125–136.

Ashe, J.S., 1984. Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with review of the described subgenera and major features of evolution. Quaest. Entomol. 20, 129–349.

Ashe, J.S., 1992. Phylogeny and revision of genera of the subtribe Bolitocharina (Coleoptera: Staphylinidae: Aleocharinae). Univ. Kans. Sci. Bull. 54, 335–406.

Ashe, J.S., 1998. Aleocharinae. Tree of Life: http://tolweb.org/tree/phylogeny.html.

Ashe, J.S., 1999. Redescription and phylogenetic position of the unusual aleocharine staphylinid *Dimonomera indica* Cameron, 1933 (Coleoptera: Staphylinidae: Aleocharinae: Dimonomerini). J. N.Y. Entomol. Soc. 107, 55–63.

Ashe, J.S., 2000. Mouthpart structure of *Stylogymnusa subantarctica* Hammond, 1975 (Coleoptera: Staphylinidae: Aleocharinae) with a reanalysis of the phylogenetic position of the genus. Zool. J. Linn. Soc. 130, 471–498.

Ashe, J.S., Newton, A.F., 1993. Larvae of *Trichophya* and phylogeny of the tachyporine group of subfamilies (Coleoptera: Staphylinidae) with a review, new species and characterization of the Trichophyinae. Syst. Entomol. 18, 267–286.

Bremer, K., 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution, 42, 795–803.

Fenyes, A., 1918–20. Genera Insectorum, Coleoptera, Fam. Staphylinidae, Subfam. Aleocharinae. Fasc. 173a,b,c, pp. 1–453. Brussels.

Ganglbauer, L., 1895. Die Käfer Von Mitteleuropa, 2, pp. 1–88. Wien: Carl Gerold's Sohn.

Goloboff, P.A., 1998. NONA 2.0: a tree searching program. Program and documentation vailable at ftp.unt.edu.ar/pub/parsimony.

Goloboff, P.A., Farris, J.S., 2001. Methods for quick consensus estimation. Cladistics, 17, S26–S34.

Haghebaert, G., 1991. A review of the *Diglotta* of the world (Coleoptera, Staphylinidae, Aleocharinae). Bull. Ann. Soc. R. Belge. Ent. 127, 223–234.

Hammond, P.M., 1975. The phylogeny of a remarkable new genus and species of gymnusine staphylinid (Coleoptera) from the Auckland Islands. J. Ent. 44, 153–173.

Hammond, P.M., 2000. Coastal Staphylinidae (rove beetles) in the British Isles, with special reference to saltmarshes. In: Sherwood, B.R., *et al*., (Eds.), British Saltmarshes. Forrest Text, London, pp. 247–302.

Hanley, R.S., 2002. Phylogeny and higher classification of Hoplandriini (Coleoptera: Staphylinidae: Aleocharinae). Syst. Entomol. 27, 301–321.

Hanley, R.S., Ashe, J.S., 2003. Techniques for dissecting adult aleocharine beetles (Coleoptera: Staphylinidae). Bull. Ent. Res. 93, 11–18.

Kitching, I.J., 2002. The phylogenetic relationships of Morgan's Sphinx, *Xanthopan morganii* (Walker), the tribe Acherontiini, and allied long-tongued hawkmoths (Lepidoptera: Sphingidae, Sphinginae). Zool. J. Linn. Soc. 135, 471–527.

Klimaszewski, J., 1982. A redefinition of Myllaenini Ganglbauer and redescriptions of *Camacopalpus* Motschulsky and *Polypea* Fauvel (Coleoptera: Staphylinidae). Can. Entomol. 114, 411–429.

Klimaszewski, J., Ashe, J.S., 1992. Two new species of the myllaenine genus *Pseudomniophila* Pace from the montane forests of Costa Rica (Coleoptera: Staphylinidae: Aleocharinae). Elytron 6, 77–85.

Meyerdick, D.E., 1969. Adaptations of a rove beetle *Diaulota fulviventris* Moore (Coleoptera: Staphylinidae), to the marine environment. MSc Thesis. San Diego State Coll, CA.

Moore, I., 1956. A revision of the Pacific coast Phytosi with review of the foreign genera (Coleoptera: Staphylinidae). Trans. San Diego Soc. Nat. Hist. 12, 103–152.

Moore, I., Legner, E.F., 1976. Intertidal rove beetles (Coleoptera: Staphylinidae). In: Cheng, L., (Ed.), Marine Insects. North Holland Publishers, Amsterdam, pp. 521–551.

Newton, A.F., Thayer, M.K., Ashe, J.S., Chandler, D.S., 2000. 22. Staphylinidae Latreille, 1802. In: Arnett, R.H., Thomas, M.C., (Eds.), American Beetles, Vol. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, FL, pp. 272–418.

Nixon, K.C., Carpenter, J.M., 1993. On outgroups. Cladistics, 9, 413–426.

Nixon, K., 1999. WinClada. Cornell University Herbarium, Ithaca.
Pace, R., 1986. Revisione di quattro specie della Tribu′ Diglottini (Coleoptera: Staphylinidae) descritte da Fauvel. Estratto Ann. Mus. Civ. St. Nat. Verona, 86, 273–280.
Pace, R., 1999. Aleocharinae della Namibia raccolte dalla spedizione entomologica 'Namibia 1992' del Museo di Storia Naturale di Berlino (Coleoptera Staphylinidae). Mem. Soc. Entomol. Ital. 77, 161–212.
Sawada, K., 1972. Methodological research in the taxonomy of Aleocharinae. Contr. Biol. Laboratory Kyoto University, 24, 31–59.
Sawada, K., 1989. On a new genus and new species of Aleocharinae (Coleoptera: Staphylinidae) from mangrove forests in Singapore. Raffles Bull. Zool. 37, 83–86.
Scheerpeltz, O., 1933. Staphylinidae VII: Supplementum I. In: Coleopterorum Catalogus, Pars 129, 990–1500. Dr W. Junk, Berlin.
Seevers, C.H., 1978. A generic and tribal revision of the North American Aleocharinae (Coleoptera: Staphylinidae). Fieldiana: Zool. 71, 1–289.
Steidle, J.L., Dettner, K., 1993. Chemistry and morphology of the tergal gland of freeliving adult Aleocharinae (Coleoptera: Staphylinidae) and its phylogenetic significance. Syst. Entomol. 18, 149–168.
Topp, W., Ring, R.A., 1988. Adaptations of Coleoptera to the marine environment. II. Observations on rove beetles (Staphylinidae) from rocky shores. Can. J. Zool. 66, 2469–2474.