

Cladistics 20 (2004) 123-138

Cladistics

www.blackwell-synergy.com

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

Kee-Jeong Ahn<sup>a,b,\*</sup> and James S. Ashe<sup>b</sup>

<sup>a</sup>Department of Biology, Chungnam National University, Daejeon 305-764, South Korea

<sup>b</sup>Natural History Museum and Biodiversity Research Center, Snow Hall, 1460 Jayhawk Boulevard, University of Kansas,

Lawrence, KS 66045-7573, USA

Accepted 5 March 2004

#### 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 Willi Hennig Society 2004.

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 myllaeninelike 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-

<sup>\*</sup>Corresponding author: Department of Biology, Chungnam National University, Daejeon 305-764, South Korea. *E-mail address:* kjahn@cnu.ac.kr

Table 1						
Generic classification	of th	e Myll	aenini	and	related	taxa

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

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 *Brachy*pronomaea 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*, *Camaco*palpus, *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 navicul*- are (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 manausensi	sriparian	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 (?	P)Nepal
Masuria chinensis	riparian (?	P)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	riparian	Costa Rica (Alajuela)
multiserrata		
Pseudomniophilia	riparian (?	P)Costa Rica (Puntarenas,
sulcata		Monteverde)
Pseudomniophilia unidentata	riparian (?	P)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 < 0.35times 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. 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

		1		2	4
	0		2	3	4
		0	U	U	U
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	000000300	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
Tricken series fronti	0001200110	0000001210	0001200030	0112000000	000022-000
Amazonopora loschoni	2101200000	1000100000	0001200002	0112010001	3131101000
Amazonopora tescheni	0000100000	1000100000	0001121420	0221013000	0051002100
Rrachypronomaga asakii	0000000000	1000100000	0001121420	1221013000	0031002100
Bruchypronomaea esaka Bryothinusa catalinae	00000000000	1000000100	0001121421	1221001000	0040003100
Bryothinusa minuta	0000100000	1000100100	0001121421	1221011000	004102 100
Dimonomera indica	10000000000	1000100100	0001121421	0221011000	0041002100
Dysacrita problematica	10000000000	0000200120	00001120421	0122001000	004012-100
Lautaea murphyi	0000200000	0000000100	0001121422	2221021000	0041203100
Masuria chinensis	0000000000	0000000100	0000020420	0121001000	0041202100
Masuria loebli	0000000000	0000000100	0000021420	0121011000	0041203100
Mvllaena brevicornis	1000000000	1000110100	0001120421	1221011000	0041001100
Mvllaena gracilicornis	1000000000	1000110100	0001120421	1221011000	0041001100
Nopromaea africana	00000000?	1000100100	0100010440	0220011000	014002-100
Nopromaea aleocharoides	00000000?	0000100100	0000010440	0220011000	014002-100
Philomina torrentum	1000000000	000000100	0000021421	0121011000	0040?02100
Polypea coralli	0000000000	0000??0100	0001120421	1121001000	0040001100
Pronomaea cariniventris	0000000000	100000100	0000010440	0230011000	011002-100
Pronomaea congoensis	0000000000	100000100	0000010440	0230011000	011002-100
Pronomaea rostrata	0000000000	100000100	0000010440	0230011000	011002-100
Pseudomniophilia multiserrata	1000200001	100000100	0000010440	0221011000	0140003100
Pseudomniophilia sulcata	1000200001	100000100	0000010440	0221011000	0140003100
Pseudomniophilia unidentata	1000200001	100000100	0000010440	0221011000	0140003100
Rothium ashlocki	0000000000	100000100	0001121421	1121011000	0040001010
Rothium evansi	0000000000	1000000100	0001121421	1121001000	004002-010
Rothium giulianii	0000000000	000000100	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	100000001	0000110000	0010000050	0032002000	013222-022
Aleochara sulcicollis	000000001	0000110000	0010000050	0032002000	0132200022
Ambiopusa alaskana	0000100000	0000000100	0000000541	1140001000	024012-100
Halorhadinus aequalis	0000000000	0000110320	0001000141	1240001000	0240102101
Digiotta mersa Phutogua animifan	0000200000	0000000100	0002100141	1140001000	024001-100
Athota arassiaornis	0000000000	0000110100	0000000050	0132000000	0120101112
Ameria crassicornis	0000100000	0000110100	0000000050	0032000000	0120101112
Arypada langinas	100010001	0000110100	0000000050	0032000000	0110100022
Calodera riparia	0010200000	0000110100	0000000050	0030000000	0110201022
Homalota plana	0010200000	0000110000	0100000050	0030000000	0100100021
I entusa lombarda	0000000000	0000110100	0100000050	0131001000	00/0103101
Drusilla canaliculata	0010100000	0000110100	0002200050	2231000000	0110100021
Zvras laticollis	0000000000	0000110000	0002200050	2131000000	0100100020
Brvohiota hicolor	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

Community D	(continued)	5	6	7	0	0
Gymmaa variegata 0	(commuea)	0	0	0	0	9
Gymman variegata 011011223 201230320 1100 202-00000 000002000   Deinogis erosa 0110001223 2012001200 0004220110 102-10000 002002200   Amarynus testaeus 010001223 2012001200 0004220110 102-11000 001001100   Parasonsoma muteilar 1020101220 0021204012 101000-011 002-010000 00110100   Cypha discutter 1000101220 0032202112 000300-010 0000001100 012002201   Cypha discutter 1000101220 0031214212 000310100 100001000 01002201   Chechangine 100010120 0031214212 000301000 100000100 012002201   Amacompora manazaextis 103102000 100000002 002210001 0010001100 012002201   Amacompora manazaextis 103103000 100000002 01-2011000 0010001100 12202201   Paynhima cardinae 1030103000 100000002 01-2011000 001001100 12202201   Resigna passi 1031013000 1000000002 01-2011000 0010011		~	~	~		
Stylegyminiad dualminerian 0.1001/22.3 0.112/001/200 112-001-00 102-11000 0.012002200   Amacypna testareus 1000101223 2012/201412 0.00001010 0.02-010000 0.01101100   Paraconssom markidare 1000101223 2012/201412 10000100 0.02-010000 0.01101100   Cyba lascidies 1000101220 0.032/201212 0.00300-010 0.00001010 0.12/002201   Cyba lascidies 100010120 0.032/2012412 0.00300-010 0.000070100 0.72??????   Holbas fusicientis 1000101210 0.032/2012412 0.00301010 0.100001700 0.11002201   Trickopsenia frosti 100010220 0.013-3-121 0.003010010 0.10001100 0.12/002201   Amaconyora manasemis 103102/200 0.10000002 0.1-2/011000 0.011001100 12/002201   Brachtypromonace cashi 1031012/200 0.02/000002 0.1-2/011000 0.011001100 12/002201   Brachtypromonace cashi 1031012/200 0.02/010000 0.02/01100 0.02/012/0220 0.02/012/0100 0.02/012/010 0.02/012/010 </th <th>Gymnusa variegata</th> <th>0110012223</th> <th>2012303200</th> <th>0000021110</th> <th>202-00000</th> <th>000002000</th>	Gymnusa variegata	0110012223	2012303200	0000021110	202-00000	000002000
Demonsk erola O11001123 2012001200 0004221110 102-11100 001010100   Paragonas traitesia 100010123 2012204212 0002001001 002-00000 001010100   Cyplan discular 1000101220 0031214212 000300-010 0000007100 072777777   Cyplan discular 1000101220 0031214212 000300-010 000007100 072777777   Olgena infina 100010120 0031214212 0003010010 0100001200 011002201   Origena infina 1000101210 0031214212 0003010010 0100001200 011002201   Amacamopra manaseavis 1031012000 100000002 002010001 0010001100 012002201   Bryothimas arcalibae 1031013000 100000002 01-2011000 0010001100 012002201   Bryothimas arcalibae 1030103000 100000002 01-2011000 001001100 01202201   Bryothimas arcalibae 1030103001 00210213111 01-1011001 00210100 012002201   Bryothimas arcalibae 1000103010 0212131110 01-101000 <th>Stylogymmusa subantarctica</th> <th>0100012223</th> <th>1012003202</th> <th>11-000-100</th> <th>102-10000</th> <th>002002200</th>	Stylogymmusa subantarctica	0100012223	1012003202	11-000-100	102-10000	002002200
Anacympin texteens 100010122 2022/20412 00000010 002-010000 001010100   Cypha longicomis 100010220 003204112 003300-010 000000100 012002201   Copha longicomis 100010220 003204112 003300-010 0000072100 07272777   Holosa fancemis 10001020 003204112 003300-010 0000072100 07272777   Holosa fancemis 100010120 003204112 003310010 0100001700 011002201   Olipota inflan 100010120 003204112 003310010 0100001700 011002201   Maceympora Issee 00010120 003214212 003310010 010000170 011002201   Maceympora lesslemi 101010200 010000002 01-311000 001001100 12202201   Brachymporase sokal 131102000 010000002 01-321000 001001100 12200201   Brachymporase sokal 133102027 777227701 01-311000 001001100 12202201   Dynacrite probenatics 1030102220 000000000 002311001 <	Deinopsis erosa	0110001223	2012001200	0004220110	102-11100	001000100
Particinionina functimize 1020101220 000320-011 000300-010 000000100 012002201   Cypha discodes 1000100220 000330-010 0000001100 012002201 000300-010 0000001100 012002201   Cypha discodes 1000110220 0033200112 000300-010 0000001100 011002201   Oligota pusitima 1000110210 003124212 000310010 0100001700 011002201   Trichopsenia frosti 0000102200 010320002 000201001 0010001100 012002201   Amaconopora manaaceskii 030102000 0100000002 010201001 001001100 012002201   Broyhimsa catalinae 103102000 012200002 01-2011000 001001100 12002201   Disacrita probientae assekii 103102020 010000002 01-2011000 001001100 12002201   Disacrita probientai 1031012020 000220000 00727701 001-101001 027027001   Disacrita probientai 1031012020 00002000 007277701 001-101001 027027001   Disacrita probientai	Anacyptus testaceus	1000101223	2022204212	101000 011	002-000000	001010100
Cyphal longiconis 100010220 0032202112 000300-010 0000707100 0777777   Holoss flavicornis 100010220 003202112 000300-010 0000707100 07777777   Holoss flavicornis 100010120 0031214212 000310010 0100001700 011002201   Digota inflata 100010120 00122024212 000310010 0100001700 011002201   Amaconopora kscheni 103010200 0100000002 0002010001 001001100 012002201   Amaconopora anamasensis 1031102000 0100000002 01-2011000 001001100 012002201   Bryohimsar anamasensis 1031102000 0100000002 01-2011000 010001100 012002201   Bryohimsar anamasensis 1030103000 0100000002 01-2011000 001001100 012002201   Bryohimsar anamasensis 100010220 00272772777 010107100 07727777 01000100 012002201   Masaria chinensis 100010100 012102101 00120100 012201201 0727010 012072100 7777777 07070110 12202201 </th <th>Paraconosoma naviculare</th> <th>1020101220</th> <th>0021204012</th> <th>101000-011</th> <th>002-010000</th> <th>001010100</th>	Paraconosoma naviculare	1020101220	0021204012	101000-011	002-010000	001010100
Cybrin inglemins 100010220 0022422112 000300-010 0000707100 0777777   Oligota ingllana 1000101220 0031242112 000300-010 00000707100 01777777   Oligota ingllana 1000101220 003124212 000300-010 000001700 011002201   Trickopsenia frosti 000010220 0013124212 000000-000 00000010 0100001700 011002201   Amaztonopora manasensis 1031012000 012020201 000001002 0122010001 0010001100 012002201   Brochspronomeas esokii 1031012000 012020002 01-2011000 0010001100 112002201   Dyserrita problematica 1031012002 0222102000 007227000 00120701100 112002201   Dyserrita problematica 1031012022 020200000 012072100 0102070110 11200221   Masaria chinesis 1000101001 00210001 001207010 0777777 12011201   Masaria chinesis 1001010001 00211011 011001100 112002201 Masaria chinesis 102010201   Masaria ch	Cypha discolaes	1000100220	0032204112	000300-010	0000001100	012002201
Immunity functions 1000101220 000122021 000101200 01100101 011002101 011001100 012002201 Name Nam Name Name	Cypha longicornis Holobus flaviaornis	1000100220	0032202112	000300-010	0000202100	0111111111
Orgent minin 1000101210 0032124212 000301001 0100001700 011002201   Trichogesnins frosti 0000102220 00131-3-212 000000-000 0010001100 012002201   Amacanopora manaasensis 1031012000 010000100 012002201 Amacanopora manaasensis 1031012000 010000100 012002201   Brachypronomeae esakti 1031012000 0100000002 0-2011000 0110001100 012002201   Bryothimsa minuta 103103000 0100000002 1-2011000 0110001100 012002201   Dyscrita problematica 103102223 201200200 07207101 010107100 0727777   Lautae merphyi 103102220 2000000000 002011001 0110001100 12202201   Masuria chienensis 1000101001 0021131101 00110001100 012002201   Myllaena brevicennis 1030102220 000000000 002011001 0110001010 12202201   Myllaena brevicennis 1030102220 0002000000 002011010 012002201   Myllaena brevicennis 102010200 0021220200	Oligota inflata	1000101220	0031214212	000300-010	010001200	011002201
Orgent pissuinia 1001012220 0013-3-212 000001000 012-001102 07201201   Amaconopora lescheni 1030102000 0100000002 0002010001 0110001100 012002201   Bryohimsa catalinae 1031102000 0100000002 01-2011000 0100001100 012002201   Bryohimsa catalinae 103102000 010000002 01-2011000 0010001100 012002201   Bryohimsa catalinae 1030102000 010000002 01-2011000 0010001100 012002201   Bryohimsa catalinae 103010207 0727277701 010101100 0127001201   Masuria chinensis 1000103001 0021203111 01-101000 010001100 012002201   Myllaena breicomis 1030102220 000000000 0002011001 0010001102 01201101   Myllaena gracificomis 1030102220 000000000 0022010101 011000100 012002201   Myllaena gracificomis 1030102220 000000000 0022011001 011000100 012002201   Myllaena gracificomis 1030102200 002120000 0021000100	Oligota musillima	1000101210	0032204212	0003010010	0100001200	011002201
Interposition Display and the second se	Trichonsenius frosti	0000101210	0031214212	0003010010	0100001:00	022011201
International attransi 100012000 000000000 000000000 000000000 000000100 0100000000   Brachypronomae cakii 1031102000 012200000 01-1021000 001001100 012002201   Bryothmas catalance 103103000 0100000002 01-2011000 001001100 012002201   Bryothmas catalance 10310200 0100000002 01-2011000 001001100 012002201   Dimonomera indica 1000002020 002212000 0072027001 001001100 12202201   Masuria chinensis 1000103001 001211311 01-101000 0010001100 12202201   Myllaena brevicornis 1030102220 000000000 0002011001 001001102 122011101   Myllaena frecina 102010300 0112120201 007200-001 001001102 12201201   Nagromaea dericennis 1030102222 022102201 002200-001 0010001101 12002201   Prilomina torrenum 1030102222 2022102201 002200-001 0010001101 12002201   Prilomina torrenum 1030102200 02213040	Amazonopora laschani	1030102220	0013 3 212	000000 000	002 011102	012002201
Antemporo influenza Display constraints Display constraints Display constraints Display constraints   Bryothmusa minuta 103110200 0122300002 01-2011000 001001100 012002201   Bryothmusa minuta 103010300 0100000002 01-2011000 001001100 012002201   Dimonmere indica 1030102223 2012002000 0075021000 000075100 07277727   Lautaca murphyi 103102027 772277701 01-1011001 001001100 12002201   Masuria chinensis 1000101001 021113101 000101000 0010001102 12012101   Myllaena breviconis 1030102220 000000000 0002011001 001001102 12011101   Myllaena breviconis 1030102220 000000000 002210-001 0010001102 12011201   Napromaea difetana 102010200 02120200 07200-001 0010001101 12002201   Philomita torrentum 1031102200 0021303201 001100-000 0110001101 12002201   Proomaea constrata 1020102000 021303201 00110000 <th>Amazonopora manausonsis</th> <th>1030102000</th> <th>0100000002</th> <th>0002010001</th> <th>0010001100</th> <th>012002201</th>	Amazonopora manausonsis	1030102000	0100000002	0002010001	0010001100	012002201
Data journalitation 100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0100000000 0010001100 012002201   Dimonomera indica 1000002020 00221020000 0027072001 001077100 07777777   Lauteea murphyi 1000103001 0012113111 01-1010000 0010001100 12002201   Masuria chinensis 1000103001 0012113111 00101000 0010001100 12002201   Myllaena brevicornis 1030102220 000000000 002011001 001001100 12002201   Nagromaca diricana 102010200 001210201 0010001100 12002201   Nagromaca diricana 102010200 002210201 00200-000 0010001101 12002201   Philomina torrentum 1030102222 202210201 072070100 072777777   Poromaca cargeensis 102010200 0221304101 01100-000 010001101 12002201   Promomaca cargeensis 102010200 0221303101<	Brachypronomaga asakii	1031102000	0100000002	01-1021000	0011001100	012002201
Bryothinas trianas 100000000 01000000000 01-2011000 0010001100 012002201   Dimonomera indica 103010222 2012002000 0075021000 0010001100 012002201   Dysacrite problematica 100000200 0022102000 0075021000 0010001100 012002201   Masuria chinensis 1000101001 0021113101 01-1011000 0010001100 012002201   Masuria chinensis 1030102220 000000000 0002011001 010001100 012002201   Myllaena previeornis 1030102220 000000000 0002011001 010001102 01201101   Myllaena previeornis 1030102220 001200200 00220000 007200-001 000000101 012002201   Napromeaa aleocharoides 102012202 0022102020 012021010 011072100 07777777   Polypea cardili 1031102000 0022102020 01200100 07777777 Polypea cardili 013102000 0022103201 00110001101 012002201   Pronomaea cariniventris 1020102000 0221303201 001100000 0100001101	Bruchypronomaeu esaku Brvothimusa catalinae	1030103000	0122300002	01-2011000	0010001100	012000201
Dimonomera indica 1030102223 2012002000 0075021000 0000701101 010001201   Dysacrita problematica 100000202 0022102000 00725021000 0010702100 07777777   Lautaca murphyi 1037102077 777277770 01-1011001 0077001107 012011201   Masuria chinensis 10001001 0021103111 01-1010000 0010001100 012002201   Myllaena previcornis 1030102220 000000000 0002011001 0010001102 012011101   Nopromaea africana 102010200 0012202000 007200-001 000000101 012002201   Philomina torrentum 103102222 022102020 007200-000 0100701100 07777777   Polyzea coralli 1031102000 002130202 01-2011000 0110001101 012002201   Pronomaea congoestis 102010200 0721303101 001100-000 010001101 012002201   Pronomaea congoestis 102010223 2022402200 0011010100 0100001101 012002201   Pronomaea congoestis 1020101223 2022402200	Bryothinusa minuta	1030103000	0100000002	01-2011000	0010001100	012002201
Dysacrita problematica 100000200 0022102000 0072077001 0010707100 07777777   Lautae numphyi 1037102027 ????27701 01-1011001 0072001107 012001107   Masuria chimesis 1000103001 0021103111 01-101000 0010001100 012002201   Masuria chimesis 103010220 000000000 0002011001 0010001102 012011101   Myllaena brevieornis 103010220 000000000 002201001 0100001102 01201101   Nopromaea aleocharoides 102010202 0012002000 007200-001 000000100 07777777   Polypea cardili 103102222 202210201 007200-000 010001101 012002201   Pronomaea cariniventris 102010200 002130301 001100-000 0100001201 012002201   Pronomaea congenesis 102010200 0021303201 001100000 0100001101 012002201   Preudominophilia suictat 1020101223 2022402200 0011010000 0100001101 012002201   Preudominophilia suictat 1020101223 2022402200	Dimonomera indica	1030102223	2012002000	00?5021000	0000?01101	010001201
Lataca murphyi 1037102077 777227701 01-1011001 0077001107 012011201   Masuria chinensis 1000103001 00211031111 01-1011000 001001100 01202201   Masuria ichinensis 1030102220 000000000 002011101 001001102 012012011   Myllaeng previsornis 1030102220 000000000 0002011001 0010001102 012012011   Nopromace africana 1020102020 001202000 007207-001 000001101 012002201   Philomina torrentum 1030102222 2022102201 007200-000 001077100 07777777   Portomace acriniventris 102010200 002130301 001100-000 010001101 012002201   Pronomace acriniventris 102010200 002130301 001100-000 0100001701 012002201   Pronomace acriniventris 102010200 022130301 001100-000 010001101 012002201   Pronomace acriniventris 102010223 202240200 0011020000 010001101 012002201   Pronomace acriniventris 1020101223 202240200	Dysacrita problematica	1000002020	0022102000	00?20??001	0010?0?100	0?????????
Masuria chinensis 1000103001 0012103111 01-1010000 0010001100 012002201   Masuria lochi 100010101 0021113101 001010000 0010001100 012002201   Masuria lochi 1000102220 000000000 0002011001 0010001102 012012210   Myllaena previcernis 1030102220 000000000 002211001 0010001102 01201101   Mylaena gracilleornis 1020102020 0012120200 002200-001 0000001101 012002201   Philomina torrentum 1030102222 022102201 07200-000 001072100 07??????   Ponomaca congeensis 1020102000 022133201 001100-000 0100001701 012002201   Pronomaca congeensis 1020102232 2022402200 011010000 0100001101 012002201   Pseudominiphilia multeatrat 1020101223 2022402200 001102000 010001101 012002201   Pseudominiphilia multeatrat 1020101223 2022402200 001102000 010001101 012002201   Pseudominiphilia multeatrat 1020101223 2022402200	Lautaea murphyi	103?1020??	?????????01	01-1011001	00??00110?	012011201
Masuria locbli 1000101001 0021113101 000101000 0010001100 012002201   Myllaena previcornis 1030102220 000000000 0002011001 0010001102 012011101   Nagrena cariicornis 1030102220 000000000 0002011001 0010001102 01201101   Nopromaca africana 1020103000 001120200 007207-000 700701101 012002201   Philomina torrentum 1030102222 2022102201 007200-000 001077100 07777777   Porpea coralli 103102200 072103010 01100-000 010001101 012002201   Pronomaca congeensis 1020102000 072130310 01100-000 010001101 012002201   Preudomniophilla multiserrata 1020101223 2022402200 0011010000 010001101 012002201   Pseudomniophilla sulcata 1020101223 2022402200 0011021000 011001101 012002201   Rothium ashlocki 1031101000 003220020 001021100 011001110 012002201   Rothium ashlocki 1031102000 0022100122	Masuria chinensis	1000103001	0012103111	01-1010000	0010001100	012002201
Myllaena brevicornis 1030102220 000000000 0002011001 0010001102 012011011   Myllaena graciicornis 1030102220 00000000 0002011001 0010001102 01201101   Nopromaea africana 1020102020 0011202000 007200-001 000000101 012002201   Nopromaea aleocharoides 102010200 0022102202 01-2011000 0011707100 07777777   Polypea coralli 1031102000 0022102202 01-2011000 011007100 077777777   Pronomaea congoensis 1020102000 0221303101 001100-000 0100001701 012002201   Pronomaea congoensis 1020102000 022402200 0011010000 0100001101 012002201   Pseudomiophilia multerrata 1020101223 2022402200 0011001000 0100001101 012002201   Rothium ashlocki 1031101000 032202022 0001021000 011001110 012002201   Rothium runsi 1031102000 002210022 001021000 011001110 012001201   Rothium anglidiani 1031102000 0022100220	Masuria loebli	1000101001	0021113101	0001010000	0010001100	012002201
M_filaena gracilicornis 1030102220 000000000 00020110101 001001102 012011011   Nopromaca africana 1020103000 0011113200 0071077000 0700701101 012002201   Nopromaca africana 1020102020 0012202000 0000001101 012002201   Philomina torrentum 1030102222 2022102201 007200-000 0011707100 077777777   Pronomaca cariniventris 1020102000 0021304101 001100-000 0100001701 012002201   Pronomace oristrat 1020102000 021303201 001100-000 0100001701 012002201   Pseudominphilia multiserrata 1020101223 2022402200 0011010000 0100001101 012002201   Pseudominphilia unidentata 1020101223 2022402200 0011010010 012002201   Rothium ashioki 1031101000 0032200202 0011020100 01100110 012002201   Rothium giulianii 1031102000 0022100102 07107707 0011001110 012001201   Rothium giulianii 1031102000 0022100102 007107000 00	Myllaena brevicornis	1030102220	0000000000	0002011001	0010001102	012011101
Nopromaça africana1020103000001111320000710720000720701101012002201Nopromaça algocharoides1020102020012202000007200-001000001101012002201Philomina torrentum103110222220221022010021000001170710007777777Polypea coralli10311020000021020201-2011000001170710007777777Pronomaca cariniventris10201020000021303201001100-000010001701012002201Pronomaca rostrata1020101223202240220000110100-000010001101012002201Pseudomniophilia nutiferrata102010122320224022000011010000010001101012002201Pseudomniophilia nutiferrata10201012232022402200001101000010001101012002201Rothium ashlocki1031101000003220020200010210000011001110012002201Rothium giulianii1031102000002210012200010210000011001110012001201Rothium giulianii1031102000002210012200710770070011001110012001201Rothium sinderisis1031102000002210012200710770070011001110012001201Rothium sindieniis103102000002210012200710770070011001110012002201Rothium sindieniis1001002130022100122001001000000001100022002201Rothium sindieniis1000102000022002201001001000000001100022002201Meochara curuda100001020002201200001001100<	Myllaena gracilicornis	1030102220	0000000000	0002011001	0010001102	012011101
Nopromace decoharoides 1020102020 0012202000 00200-001 0000001101 012002201   Philomina torrentum 1030102222 2022102201 007200-000 0011707100 07??????   Poromace acriniventris 1020102000 0021304101 001100-000 0100001101 012002201   Pronomace acriniventris 1020102000 0021303201 001100-000 0100001701 012002201   Pronomace rostrata 1020101223 2022402200 001101000 0100001101 012002201   Pseudomniophilia multiserrata 1020101223 2022402200 0011010000 0100001101 012002201   Pseudomniophilia multiserrata 1020101223 2022402200 0011010000 0100001101 012002201   Rothium estina 1031101000 0032200202 0001021000 0011001110 012002201   Rothium giulianii 1031102000 0022100102 001021001 0011001110 012001201   Rothium sonorensis 1031102000 0022100102 001010100 010001100 12002201   Rothium sonorensis 1031002000	Nopromaea africana	1020103000	0011113200	00?10??000	0?00?01101	012002201
Philomina torrentum 103012222 2222102201 007200-000 0010707100 0777777   Polypea coralli 1031102000 0022102202 01-2011000 0011070100 0777777   Pronomaea cariniventris 1020102000 0021303201 001100-000 0100001101 012002201   Pronomaea congoensis 1020102000 0721303101 001100-000 0100001101 012002201   Prenomaea rostrata 1020101223 2022402200 0011010000 0100001101 012002201   Pseudomniophilia sulcata 1020101223 2022402200 001102000 010001101 012002201   Rothium giulanii 103110200 0032202020 001021000 0011001110 012002201   Rothium giulanii 1031102000 0022100102 001221001 011001110 10201201   Rothium giulanii 1031102000 0022100102 00121001 0011001110 12002201   Rothium giulanii 1031102000 0022100102 00122101 011001110 12001201   Rothium sonorensis 1031102000 0022100102 0120210	Nopromaea aleocharoides	1020102020	0012202000	00?200-001	0000001101	012002201
Polypeq coralli1031102000002210220201-2011000001170710007??????Pronomaca cariniventris10201020000721303101001100-0000100001101012002201Pronomaca congoensis10201020000721303101001100-0000100001201012002201Presudomniophilia multiserrata1020101223202240220000110100000100001101012002201Pseudomniophilia sulcata102010122320224022000011020000100001101012002201Rothium ashlocki103110100003220020200010210000011001101012002201Rothium giulianii10311020000221001020010210000011001110012002201Rothium sonorensis10311020000022100102012021010011001110012001201Stylpaplus rufus10311020000022100102012021000011001110012001201Stylpaplus rufus100100021002230220200100101000100001100022002201Aleochara sulcicollis10000020130022103101010000000000001100022002201Aleochara sulcicollis1001030000100000011-200-00000000110002202201Halorkadinus aequalis10010130000100000010120220101202201Aleochara sulcicollis10000300001100200000000110002202201Aleochara sulcicollis100003000011002001000002110002202201Aleochara sulcicollis100003000011002001000002110002202201Aleochara sulcicollis <th>Philomina torrentum</th> <th>1030102222</th> <th>2022102201</th> <th>00?200-000</th> <th>0010?0?100</th> <th>0????????</th>	Philomina torrentum	1030102222	2022102201	00?200-000	0010?0?100	0????????
Pronomaea cariniventris 1020102000 0021304101 001100-000 0100001101 012002201   Pronomaea congoensis 1020102000 0021303201 001100-000 0100001701 012002201   Pronomaea rostrata 1020101223 2022402200 001100-000 0100001101 012002201   Pseudomniophilia unidentata 1020101223 2022402200 0011010000 0100001101 012002201   Resudomniophilia unidentata 1020101223 2022402200 001101000 011000110 012002201   Rothum exnsi 1031101000 0032200202 0001021000 0011001110 012002201   Rothum giuliani 1031102000 002210012 0001021001 0011001110 012002201   Rothum giuliani 1031102000 0022100120 007107:007 0011001110 012001201   Rothum suiterits 100100021 003220220 007101000 011000110 012002201   Rothum suiterits 100210300 0012210012 007107:000 0010001100 012002201   Rothum suiterits 1002010300 001022000	Polypea coralli	1031102000	0022102202	01-2011000	0011?0?100	0????????
Pronomaea congoensis 1020102000 0?21303101 001100-000 0100001701 012002201   Pronomaea rostrata 102010200 0021303201 001100-000 0100001701 012002201   Pseudomniophilia sulcata 1020101223 2022402200 001101000 0100001101 012002201   Pseudomniophilia sulcata 1020101223 2022402200 0011021000 0100001101 012002201   Rothium ashlocki 1031101000 0032200202 0001021000 0011001110 012002201   Rothium guidanii 1031102000 0022100102 0071077007 0011001110 012002201   Rothium guidanii 1031102000 0022100102 01-2021001 0011001110 012002201   Rothium sonorensis 1031102000 002210022 0071077007 0011001110 012002201   Stylopalpus rafus 100100021 0032202200 0071010000 010001100 022002201   Aleochara sulcicollis 100000201 002210310 0010020100 000001100 022002201   Aleochara sulcicollis 100010300 010000001	Pronomaea cariniventris	1020102000	0021304101	001100-000	0100001101	012002201
Pronomaca rostrata 1020102000 0021303201 001100-000 0100001701 012002201   Pseudomniophilia multiserrata 1020101223 2022402200 0011010000 0100001101 012002201   Pseudomniophilia unidentata 1020101223 2022402200 0011010000 0100001101 012002201   Rothium ashlocki 1031101000 0032200202 0001021000 0011001110 012002201   Rothium evansi 1031102000 0022100102 0001021001 0011001110 012002201   Rothium pallidus 1031102000 0022100102 001021001 0011001110 012002201   Rothium pallidus 1031102000 0022100102 01-2021001 0011001110 012002201   Stylopalpus rufus 101010021 0032202200 007107000 0010001100 012002201   Aleochara curtula 1000002013 0022103101 001002000 000001100 02202201   Aleochara sulcicollis 1000103000 010000001 01-2010000 000021100 02202201   Aleochara sulcicollis 1000103000 0100000001 <th>Pronomaea congoensis</th> <th>1020102000</th> <th>0?21303101</th> <th>001100-000</th> <th>0100001?01</th> <th>012002201</th>	Pronomaea congoensis	1020102000	0?21303101	001100-000	0100001?01	012002201
Pseudomniophilia multiserrata1020101223202240220000110100000100001101012002201Pseudomniophilia sulcata102010122320224022000011020000100001101012002201Rothium ashlocki1031101000003220020200010210000011001110012002201Rothium evansi1031101000003220020200010210000011001110012002201Rothium gluilamii1031102000002210012200010210000011001110012002201Rothium gluidanii10311020000022100122007107:0070011001110012001201Rothium gluidas10311020000022100102007107:0070011001110012001201Rothium gluidas10311020000022100102007107:0070011001110012001201Rothium sonorensis10301000001120032202200007107:0000010001100012002201Stylopalpus rufus10010100010022002201007107:0000000001100022002201Aleochara curtula1000002030022103101007107:000000000110002202201Aleochara sulcicollis1000103000010000000101-200-00000002110002202201Halorhadinus aequalis10110300000000000101-200-000000020110001202201Phytosus spirifer100003000011002001001100001000000110002202201Phytosus spirifer10000030000120020000011010001000000110002202201Phytosus spirifer100000300000110020000010100010020	Pronomaea rostrata	1020102000	0021303201	001100-000	0100001?01	012002201
Pseudomniophilia sulcata1020101223202240220000110200000100001101012002201Pseudomniophilia unidentata102010122320224022000011010000010001101012002201Rothium ashlocki1031101000003220020200010210000011001110012002201Rothium sani1031102000002210012200010210010011001110012002201Rothium giulianii1031102000002210012200710720070011001110012001201Rothium giulianii1031102000002210012200710720070011001110012001201Rothium sonorensis103110200000221001220071010000010001100012001201Stylpadpus rufus10101002100322022020010010000100001100012002201Aleochara curtula100001220002230220200100101000000001100022002201Aleochara sulcicollis100010300001000000101-201000000000110002202201Aleochara sulcicollis100010300001000000101-200-0000000201100012022201Aleochara sulcicollis100010300001000000101-200-0000000201100012022201Aleochara sulcicollis100010300001000000101-200-0000000201100012022201Aleochara sulcicollis100010300001000000101-200-0000000201100012022201Aleochara sulcicollis1000103000011002001001000000000201100012022201Aleochara sulcicollis100003000011002001001000000	Pseudomniophilia multiserrata	1020101223	2022402200	0011010000	0100001101	012002201
Pseudomniophilia unidentata1020101223202240220000110100000100001101012002201Rothium ashlocki1031101000003220020200010210000011001110012002201Rothium evansi1031102000002210010200010210010011001110012002201Rothium giulianii1031102000002210010200010210010011001110012001201Rothium sonorensis1031102000002210010201-2021010011001110012001201Stylopalpus rufus101010021003220220000?107?000010001100012002201Tomoxelia nairobiensis1020103000001121310000?10??00002000011010???????Aleochara sulcicollis1000002013002210310100102000000000110002202201Aleochara sulcicollis10010300001000000101-2010000000002110002202201Jiglotta mersa100010300001000000101-200-0000000201100012022201Jiglotta mersa1000003000011002001001110001012002201Jiglotta mersa10000030000110020010011100010020010001202201Atheta crassicornis100000300001200200000111000100202010002202201Atheta rassicornis100000300001200200001011000100000110002202201Atheta rassicornis1000003000012002000010110001000020110002202201Atheta rassicornis100000300001200200001011000000000110002202201Do	Pseudomniophilia sulcata	1020101223	2022402200	0011020000	0100001101	012002201
Rothium ashtocki103110100000322022200010210000011001110012002201Rothium evansi103110100000322022200010210010011001110012002201Rothium giulianii1031102000002210010200010210010011001110012001201Rothium sonorensis1031102000002210010201-20210010011001110012001201Rothium sonorensis1031102000002210010201-20210010011001110012001201Rothium sonorensis1001100021003220220000710770000700001100012002201Tomoxelia nairobiensis1020103000001121310000710770000700001100022002201Aleochara curtula10000021300221031010100200000000001100022002201Aleochara sulcicollis10010300001000000101-2010000000001100022022201Halorhadinus aequalis10101030000000020010220210000000010100012022201Halorhadinus aequalis10000300001100200100200-0000000201100012022201Atheta crassicornis1000003000012102200011110001000001100022002201Oxypoda longipes10000030000121022000010101001000001100022002201Homalota plana1000003000001100200000201000000001100022002201Leptusa lombarda10000020000302201001200220102202201Homalota plana10000030000011002100012002201012002201Invasila canalicula	Pseudomniophilia unidentata	1020101223	2022402200	0011010000	0100001101	012002201
Rothium evansi103110100000322002000010210000011001110012002201Rothium guilianii1031102000002210010200010210010011001110012001201Rothium pallidus10311020000022100202007107?00?0011001110012001201Rothium sonorensis1031102000002210010201-20210010011001110012001201Stylpalpus rufus1001010021003220220000710100000100001100012002201Aleochara curtula1000001220002230220200100101000000001100022002201Aleochara sulcicollis1000103000010000000101-2010000000001100022002201Aleochara sulcicollis1001030000000020010202010000000001100022002201Halorhadinus aequalis10101030000000020010202010000000001100012022201Jiglotta mersa100010300000110020010012000000000110001202201Phytosus spinifer10000030000111002001001110001000001100022102201Ontomalata opaca100000300001210220000101110001000001100022002201Calodera_riparia100000300000112020000010110000000001100022002201Leptusa lambarda1000002000001020000010110000000001100022002201Drusila candiculata1000003000001200200000101100000000001100012002201Drusila candiculata100000300000120020000010110000000001100012002	Rothium ashlocki	1031101000	0032200202	0001021000	0011001110	012002201
Rothium gulitanii1031102000002210010200010210010011001110012001201Rothium sonorensis1031102000002210010201-20210010011001110012001201Stylopalpus rufus1010100021003220220000710720000010001100012002201Tomoxelia nairobiensis10201300000112131000071072000020000110107777727Aleochara curtula100000220100223022020010010100000001100022002201Aleochara sulcicollis100010300001000000101-2010000000001100022002201Halorhadinus aequalis101010300000000200102202100000000110002202201Halorhadinus aequalis100010300001000000101-200-00000002110001202201Phytosus spinifer1000003000011002001001110001012002201Phytosus spinifer100000300001210200001101001001202201Oxypoda longipes10000012200012002000001011000022002201Homalota opaca1000002000001100200100101100000201100022002201Homalota plana10000020000011003002000201100022002201Homalota plana100000200000110020010101110001000001100012002201Leptusa lombarda1000003000001100200101-1110001000001100012002201Jyras laticellis1000003100012002000011010000000001100012002201Jyras laticellis10000031000120000020	Rothium evansi	1031101000	0032200202	0001021000	0011001110	012002201
Rothium patitaits1031102000002210020200710770070011001110012001201Bothium sonorensis1031102000002210010201-20210010011001110012001201Stylopalpus rufus101010021003220220000710100000100001100012002201Tomoxelia nairobiensis10201030000011213100007107?000070000110107??????Aleochara curtula10000012000223022020010101000000001100022002201Aleochara sulcicollis100010300001000000101-20100000000021100022022201Halorhadinus aequalis101013000000002001022021000000000201100012022201Diglotta mersa1000103000011002001001110001012022201Atheta crassicornis10000020000011002001001110001002002201Oxypoda longipes10000030000120220000010110001002201201Calodera_riparia10000030000010020000010110001002201201Calodera_riparia100000200000110030020020100100000110002202201Leptusa lombarda10000020000010020000010110001000001100022002201Zyras laticollis100000200000302242010111100010000001100022002201Zyras laticollis1000002000030224201011110001000001100012002201Leptusa lombarda100000200003022420101111000100000110012002201Zyras laticollis100000200003002201	Rothium giulianii	1031102000	0022100102	0001021001	0011001110	012001201
Rotinian Sondrenkis10311020000022101020122021010011001110012001201Stylopalpus rufus1010100021003220220000?10100000100001100012002201Tomoxelia nairobiensis102010300000121310000?10??0000700001100022002201Aleochara curtula1000001220002230220200100101000000001100022002201Aleochara sulcicollis1000002013002210310100100200000000001100022022201Amblopusa alaskana100103000010000000101-20100000000201100022022201Halorhadinus aequalis101010300001000000101-200-0000000201100012022201Phytosus spinifer1000003000001100200100200-0000000201100012022201Phytosus spinifer10000030000110020010011110001000001100022102201Portomalota opaca10000030000120020000110100010000201100022002201Caledera_riparia10000030000011003002002010001000001100012002201Leptusa lombarda1000002000001100210001-2010000000001100012002201Zyras laticollis1000003100002021300101-11100010000001100012002201Leptusa lombarda1000003100002021300101-11100010000001100012002201Leptusa lombarda100000310001200200001-2010000000001100012002201Leptusa lombarda100000310001200000201-2010000000001100	Rothium gamanagia	1031102000	0022100202	00/10//00/	0011001110	012001201
Stylopaptix rupts10101000210032202000071010000010001100012002201Tomoxelia nairobiensis10201030000011213100002107?00002000110107??????Aleochara curtula1000001220002230220200100101000000001100022002201Aleochara sulcicollis1000002013002210310100100200000000001100022002201Amblopusa alaskana1000103000010000000101-20100000000201100022022201Halorhadinus aequalis10101030000000002001022020100000000201100012022201Diglotta mersa100010300001100200100200-0000000201100012022201Atheta crassicornis10000030000110020010011110001000001100022102201Pontomalota opaca10000030000121022000011010010000201100022002201Calodera_riparia100004200001200200000101100010000201100022002201Leptusa lombarda1000002000001100210001-20100000000201100012002201Leptusa lombarda100000200000302242010111100010000001100022002201Zyras laticollis100000310001200220101-2010000000001100012002201Leptusa loriba bicolor10000310001000000201-2010000000001100112002211Hoplandria laeviventris10000031000120020000011010000000001100112002211Horadicia laeviventris10000032000022103100001101000000000	Rotnium sonorensis	1031102000	0022100102	01-2021001	0011001110	012001201
Tomoxelia harbotensis10201030000011231000071077000077077777Aleochara curtula10000122000223022020010010100000001100022002201Aleochara sulcicollis10000020130022103101001002000000000110002202201Amblopusa alaskana10010300001000000101-201000000000110002202201Halorhadinus aequalis10101030000000020010220201000000000201100012022201Diglotta mersa100010300001000000101-200-0000000201100012022201Atheta crassicornis100000200000110020010011110001000001100022102201Pontomalota opaca10000030000121020000101110001000001100022002201Calodera_riparia10000030000011003002000201001000001100022002201Homalota plana1000002000001100200101-2010000000001100012002201Leptusa lombarda1000002000001100210001-2010000000001100012002201Zyras laticollis1000002000030224201011110001000001100012002201Zyras laticollis100000310001200200101-2010000000001100112002211Hoplandria laeviventris100000310001200000201-2010000000001100112002211Hoplandria laeviventris10000020000311142000011010000000001100112002211Hoplandria laeviventris10000020000221031000110100000000001100012002201 </th <th>Stylopalpus rujus</th> <th>1010100021</th> <th>0032202200</th> <th>00/1010000</th> <th>0100001100</th> <th>012002201</th>	Stylopalpus rujus	1010100021	0032202200	00/1010000	0100001100	012002201
Aleochara sulcicollis100000122000220220200100101000020001100022002201Aleochara sulcicollis100002013002210310100100200000000110002202201Halorhadinus aequalis10010300001000000101-20100000000101100012022201Diglotta mersa100010300001000000101-200-0000000201100012022201Phytosus spinifer10000030000011002001000200-0000000201100012022201Atheta crassicornis1000002000001100200100111100010000001100022102201Pontomalota opaca1000003000012102020000101100010000201100012102201Caldera_riparia1000004200001200200000101100010000201100022002201Homalota plana1000002000001100210001-20100000000201100012002201Drusilla canaliculata1000004000002021300101-2010000000001100012002201Zyras laticollis1000003100012002201011110001000001100012002201Myrmecocephalus arizonicus100000310001200000201-2010000000001100112002211Hoplandria laeviventris100000200003114200001101000000001100112002211Platandria mormonica10000020200221031000011010000000001100012002201	Loochara curtula	1020103000	0011213100	0010010100	0200001101	022002201
Ambinist10000020130012010110010000010010000010120020110002202201Amblopusa alaskana100010300001000000101-2010000000020110002202201Diglotta mersa1000103000010000000101-200-0000000201100012002201Phytosus spinifer10000020000011002001000200-0000000001100012022201Atheta crassicornis1000002000001100200100111100010000001100022102201Pontomalota opaca10000030000121020000010110001000020110002200201Caldera_riparia1000004200001200200000101100010000201100022002201Homalota plana1000003000001100210001-20100000000201100012002201Drusilla canaliculata1000004000002021300101-1110001000001100012002201Zyras laticollis100000310001200000201-2010000000001100012002201Bryobiota bicolor10000310001200000201-2010000000001100112002211Myrmecocephalus arizonicus100000310001200000201-20100000000001100112002211Hoplandria laeviventris10000220000311420000110100000000001100112002211Platandria mormonica10000220000221031000110100000000001100012002201	Aleochara sulcicollis	1000001220	0022302202	0010010100	0000001100	022002201
Initioplasic attastanti100010000001000000010120200000000101100012022011Halorhadinus aequalis10101030000000002001022010000000010100012022201Diglotta mersa1000103000011002001000200-0000000201100012022201Atheta crassicornis1000002000001100200100111100010000001100022102201Pontomalota opaca1000003000012102020000111100010000201100022001201Calodera_riparia1000004200001200200000101100010000201100022002201Homalota plana100000300000110030020002010010000001100012002201Leptusa lombarda1000002000001100210001-20100000000201100012002201Drusilla canaliculata100000200000302242010011110001000001100012002201Zyras laticollis100000310001200000201-2010000000001100012002201Myrmecocephalus arizonicus100003100012000002011010000000001100112002211Hoplandria laeviventris10000202000311142000011010000000001100112002201Platandria mormonica1000020200022103100011010000000001100012002201	Amblonusa alaskana	1000103000	010000001	01-2010000	0000201100	022002201
Initial departs101010300001000000101202201Diglotta mersa100010300001000000101-200-000000020110001202201Phytosus spinifer10000030000011002001000200-000000020110001202201Atheta crassicornis1000003000012110200001-10100000000001100022102201Pontomalota opaca100000120001200200000101100010000001100022002201Oxypoda longipes1000004200001200200000101100010000201100022002201Calodera_riparia1000003000001100300200020100010000001100012002201Homalota plana1000002000001100210001-20100000000201100012002201Drusilla canaliculata1000002000003022420100111100010000001100012002201Zyras laticollis100000310001200000201-2010000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris1000022000031142000011010000000001100112002201Platandria mormonica1000022000022103100011010000000001100012002201	Halorhadinus apaualis	1010103000	000000000000000000000000000000000000000	0202010000	0000201100	012022201
DescriptionInformationInformationInformationInformationPhytosus spinifer10000030000011002001000200-0000000201100012022201Atheta crassicornis10000030000121102000001-10100000000001100022102201Pontomalota opaca1000001200001200200000101100010000201100012102201Oxypoda longipes1000004200001200200000101100010000201100022002201Calodera_riparia1000003000001100300200020100010000001100012002201Homalota plana1000002000001100210001-20100000000201100012002201Leptusa lombarda1000004000002021300101-11100010000001100012002201Zyras laticollis1000002000003022420100111100010000001100012002201Bryobiota bicolor10000310001200000201-20100000000001100112002211Myrmecocephalus arizonicus10000020000311420000110100000000001100112002201Platandria mormonica1000022000022103100011010000000001100012002201	Diglotta mersa	1000103000	01000000001	01-200-000	0000201100	012022201
Atheta crassicornis100000200000110020010011110001000001100022102201Pontomalota opaca1000003000012110200001-10100000000001100012102201Oxypoda longipes1000001220001200200000101100010000201100022002201Calodera riparia1000004200001200200000101100000000201100022002201Homalota plana1000003000001100300200020100010000001100012002201Leptusa lombarda1000004000002021300101-20100000000201100012002201Drusilla canaliculata1000002000003022420100111100010000001100012002201Zyras laticollis100000310001000000201-20100000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000220000311142000011010000000001100012002201Platandria mormonica10000220000221031000011010000000001100012002201	Phytosus spinifer	1000003000	0011002001	000200-000	0000201100	012022201
Pontomalota opaca1000003000012110200001-010000000001100012102201Oxypoda longipes1000001220001200200000101100010000201100022001201Calodera riparia1000004200001200200000101100000000201100022002201Homalota plana1000003000001100300200020100010000001100012002201Leptusa lombarda1000002000001100210001-20100000000201100012002201Drusilla canaliculata1000004000002021300101-11100010000001100022002201Zyras laticollis100000310001000000201-2010000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000220000311142000011010000000001100012002201Platandria mormonica10000220000221031000011010000000001100012002201	Atheta crassicornis	1000002000	0011002001	0011110001	0000001100	022102201
Oxypoda longipes1000001220001200200000101100010000201100022001201Calodera_riparia100004200001200200000101100000000201100022002201Homalota plana100003000001100300200020100010000001100012002201Leptusa lombarda100004000002021300101-2010000000001100012002201Drusilla canaliculata100002000003022420100111100010000001100012002201Zyras laticollis10000310001000000201-2010000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000220000311142000011010000000001100012002201Platandria mormonica10000220000221031000011010000000001100012002201	Pontomalota opaca	1000003000	0121102000	01-1010000	0000001100	012102201
Calodera_riparia1000004200001200200000101100000000201100022002201Homalota plana1000003000001100300200020100010000001100012002201Leptusa lombarda1000002000001100210001-20100000000201100012002201Drusilla canaliculata1000002000003022420100111100010000001100022002201Zyras laticollis100000310001000000201-20100000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000220000311142000011010000000001100012002201Platandria mormonica10000220000221031000011010000000001100012002201	Oxypoda longipes	1000001220	0012002000	0010110001	0000201100	022001201
Homaloia plana1000003000001100300200020100010000001100012002201Leptusa lombarda1000002000001100210001-20100000000201100012002201Drusilla canaliculata1000004000002021300101-11100010000001100022002201Zyras laticollis100000310001000000201-20100000000001100012002201Bryobiota bicolor10000310001200000201-20100000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000220000311142000011010000000001100012002201Platandria mormonica10000220000221031000011010000000001100012002201	Calodera riparia	1000004200	0012002000	0010110000	0000201100	022002201
Leptusa lombarda1000002000001100210001-20100000000201100012002201Drusilla canaliculata1000004000002021300101-11100010000001100022002201Zyras laticollis1000002000003022420100111100010000001100012002201Bryobiota bicolor10000310001200000201-20100000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000220000311142000011010000000001100012002201Platandria mormonica10000220000221031000011010000000001100012002201	Homalota plana	1000003000	0011003002	0002010001	0000001100	012002201
Drusilla canaliculata1000004000002021300101-1110001000001100022002201Zyras laticollis10000200000302242010011110001000001100012002201Bryobiota bicolor10000310001000000201-2010000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000202000311142000011010000000001100012002201Platandria mormonica10000202000221031000011010000000001100012002201	Leptusa lombarda	1000002000	0011002100	01-2010000	0000201100	012002201
Zyras laticollis100000200000302242010011110001000001100012002201Bryobiota bicolor10000310001000000201-2010000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000202000311142000011010000000001100012002201Platandria mormonica10000202000221031000011010000000001100012002201	Drusilla canaliculata	1000004000	0020213001	01-1110001	0000001100	022002201
Bryobiota bicolor10000310001000000201-2010000000001100112002211Myrmecocephalus arizonicus1000031000120000020011010000000001100112002211Hoplandria laeviventris10000202000311142000011010000000001100012002201Platandria mormonica10000202000221031000011010000000001100012002201	Zyras laticollis	1000002000	0030224201	0011110001	0000001100	012002201
Myrmecocephalus arizonicus100003100012000002001101000000001100112002211Hoplandria laeviventris10000202000311142000011010000000001100012002201Platandria mormonica10000202000221031000011010000000001100012002201	Bryobiota bicolor	1000003100	010000002	01-2010000	0000001100	112002211
Hoplandria laeviventris100002020003111420000110100000000001100012002201Platandria mormonica100002020002210310000110100000000001100012002201	Myrmecocephalus arizonicus	1000003100	0120000002	0011010000	0000001100	112002211
Platandria mormonica 1000002020 0022103100 0011010000 0000001100 012002201	Hoplandria laeviventris	1000002020	0031114200	0011010000	0000001100	012002201
	Platandria mormonica	1000002020	0022103100	0011010000	0000001100	012002201

#### Acknowledgments

We thank the following individuals and institutions for their contribution of this project: V. Assing (Germany), M. Maruyama (National Science Museum, Tokyo), R. Pace (Verona, Italia), G. Rougemont (France), Institut Royal des Sciences Naturelles de Belgique, Bruxelles (ISNB, D. Drugmand), Field Museum of Natural History, Chicago (FMNH, A. F. Newton), Muséum d'Historie Naturelle, Genève (MHNG, G. Cuccodoro and I. Löbl), Natural History Museum, London (NHM, M. Brendell), Naturhistorisches Museum Wien, Wien (NMW, H. Schillhammer), Deutsches Entomologisches Institut (DEI, L. Zerche) and Humboldt-Universität Museum für Naturkunde, Berlin (HUMN, J. Frisch). They generously provided us with the opportunity to examine the collections including type series of species of the Myllaenini and Pronomaeini by arranging for the loan of specimens. This research was supported by Korea Research Foundation Grant KRF-2001-015-DP0469 to K.-J. Ahn and by National Science Foundation PEET Grants DEB 9521755 and DEB-9978110 to James S. Ashe.

#### 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.