

Systematics of *Baeostethus chiltoni*, a subantarctic liparocephaline (Coleoptera: Staphylinidae: Aleocharinae): a Pangean relic or a more recent immigrant?

Richard A. B. Leschen¹, Mark S. Bullians², Bernard Michaux³, and Kee-Jeong Ahn⁴

Abstract The placement of *Leptusa chiltoni* is restored to its original status as sole member of the genus *Baeostethus*. *Baeostethus chiltoni* is a subantarctic intertidal species that is present on the shores of Auckland, Antipodes, and Campbell islands. *Baeostethus* is concluded to be a member of Liparocephalini based on the absence of seta v on the adult mentum, several setae distributed only on the mesal surface and apex of the galea, and contiguous mesocoxal cavities. The phylogenetic relationships of Liparocephalini are investigated in the context of a previous study and *Baeostethus* is shown to be a sister taxon to *Liparocephalus* based on 12 synapomorphies (nine are unique). The majority of Liparocephalini are distributed along the coasts of the northern Pacific rim, some 9000 km away from *B. chiltoni*. Most are apterous, and with *Baeostethus* as a relatively derived member of the group, it is difficult to reconcile the biogeographic pattern based on a dispersal event from the northern Pacific to the Campbell Plateau. We argue that the trans-Pacific pattern in Liparocephalini is due to an older contiguous distribution along the coastal margins of Pangea. The data are supported by an alternative area cladogram derived from a rerooted tree, congruence with a Pacific rim pattern seen in intertidal Aegalitinae (Salpingidae), and the distribution and phylogeny of terrestrial Gymnusini (Aleocharinae).

Keywords islands; natural history; cladistics; vicariance biogeography; outgroup; *Baeostethus*; *Leptusa*; Campbell Plateau

INTRODUCTION

“As for the wildlife, well the way we see it in those days it was a source of food. There was a lot we could have told scientists in those days if they had got us to collect for them and told us what to look for. We did occasionally take an interest in nature when there was time.” (J. Timms, c. 1912, in Kerr & Judd 1978, p. 40.)

For early maritime visitors to New Zealand’s subantarctic, like J. Timms (Kerr & Judd 1978), natural history, though viewed as secondary, was rich, plentiful, and mysterious. Today’s scientists recognise that the spectacular flora and fauna of the world’s subantarctic islands are unique (Chown et al. 1998) and, despite the extensive biotic inventories for some subantarctic archipelagos (e.g., Gressitt & Wise 1971), the origin of these organisms remains

¹Landcare Research, Private Bag 92 170, 120 Mt Albert Road, Auckland, New Zealand. Email: LeschenR@landcare.cri.nz

²44 McBreen Avenue, Northcote, Auckland, New Zealand.

³Private Bag, Kaukapakapa, New Zealand.

⁴Department of Biology, Chungnam National University, Daejeon City, 305–764, Korea.

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unknown. The subantarctic flora and fauna are a mixture of endemics and taxa related to the closest continental areas (Morrone 1998). Here, we report for the first time phylogenetic evidence for a geographic connection with the Northern Hemisphere in a flightless insect, the staphylinid beetle *Baeostethus chiltoni* Broun (= *Leptusa chiltoni* (Broun)) recorded previously from the Antipodes and Campbell islands (Steel 1964; Marris 2000).

During a recent expedition to Campbell Island to survey the beetle fauna, larvae and adults of the intertidal species *B. chiltoni* (Fig. 1) were collected; this prompted a critical evaluation of its taxonomy. In this paper we re-establish its placement in the monotypic genus *Baeostethus* and determine its phylogenetic position in the Aleocharinae. We subject structural homologies to a cladistic analysis to determine the relationships of *B. chiltoni* in the aleocharine staphylinid tribe Liparocephalini (Ahn & Ashe 1996) and redescribe the larva and adult based on new morphological data derived from the phylogenetic analysis.

Campbell Island is the most southerly island of the Campbell Plateau which includes four additional island groups: Antipodes, Auckland, Bounty, and Snares islands. The insect faunas of some of the smaller island groups are well known, but those of the Auckland and Snares islands remain incomplete and require further study. Despite this lack of information, it is clear from the known number of endemic species and genera that the Campbell Plateau is a special place, and its fauna deserves further investigation. Though the taxonomy of some beetle families is reasonably complete for the area (e.g., Carabidae and Curculionidae), there is only one group where published phylogenies can be used to elucidate biogeographic relationships of Campbell Plateau beetles to those of other regions (Klimaszewski 1979; Ashe 2000a). Most hypotheses for Campbell Plateau insects suggest a strong biogeographic link with New Zealand (e.g., Kuschel 1964; Gressitt & Wise 1971). A phylogeny for *Baeostethus* and its relatives, therefore, would provide a significant step for interpreting the origin of the fauna of the Campbell Islands arthropod fauna and testing hypotheses about the insular nature of the world's subantarctic islands (Morrone 1998).

TAXONOMIC STATUS OF *BAEOSTETHUS*

Since the description by Broun (1909), *Baeostethus* remained a separate and monotypic genus until it was placed by Pace (1989) into the homalotine genus *Leptusa* Kraatz 1856 in the subgenus *Halmaeusia* Kiesenwetter 1877. *Halmaeusia*, which is endemic to subantarctic islands, includes another two described species: *L. antarctica* (Kiesenwetter), the type species from Auckland, Campbell, and Macquarie islands, and *L. atriceps* (Waterhouse) from Falkland, Kerguelen, and South Georgia islands. From the complete list of synonymies reported by Pace (1989), *L. antarctica* was previously included in *Antarctophytosus* Enderlein 1909, *Halmaeusia*, and *Sipalia* Fauvel 1877, while *L. atriceps* was included in *Antarctophytosus*, *Paraphytosus* Cameron 1917, *Phytosus* Curtis 1838, and *Austromalota* Bréthes 1925.

Why *Baeostethus* was placed into *Leptusa* (*Halmaeusia*) by Pace (1989) is uncertain because there are obvious adult characters that separate the two genera from each other (e.g., compare illustrations in Jeannel (1940) with those in Steel (1964), and see list of characters below). Pace's (1989) action may have been based on the ambiguous taxonomy of subantarctic members of *Leptusa* that existed prior to his revision of the genus. For example, Moore (1956) treated *Antarctophytosus* as distinct (*Paraphytosus* and *Austromalota* are listed as synonymies) while Steel (1964) listed *Antarctophytosus* as a synonym of *Halmaeusia* (this synonymy was erroneously attributed to Pace (1989) by Ahn & Ashe (1996)). Catalysed by the disorderly taxonomy, Pace (1989) may have also been misled by anecdotal biological data published on these species. While some specimens of subantarctic *Leptusa* have been collected from the intertidal zone (Cameron 1917; Jeannel 1940; Steel 1964), most are encountered in terrestrial habitats and this is true for our observations of species present on

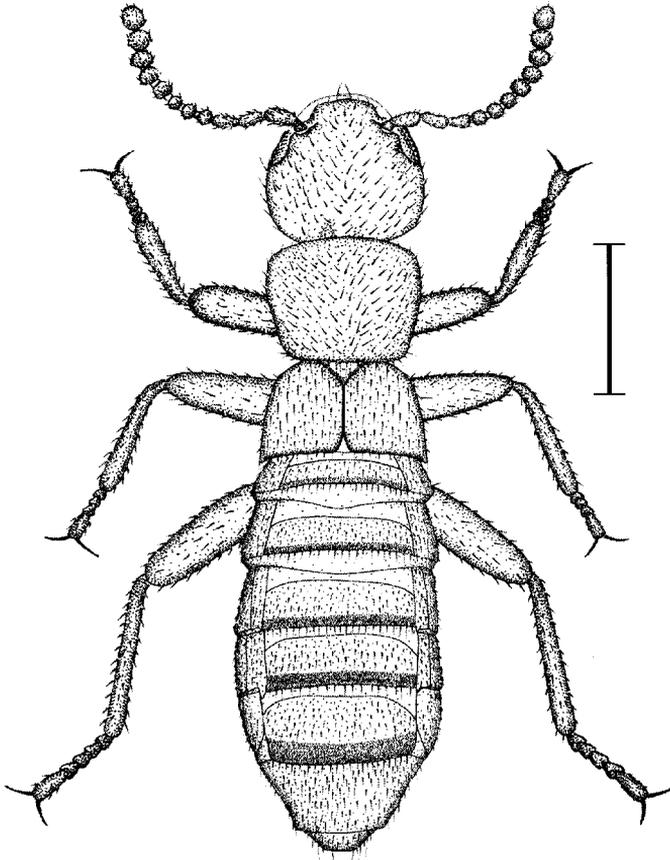


Fig. 1 Dorsal habitus of *Baeostethus chiltoni*. Scale bar = 1 mm.

Campbell and Auckland islands; they are strictly terrestrial, only coming into contact with intertidal areas where their leaf litter habitat is present just above the high tide mark or where leaf litter has fallen to these intertidal areas due to slumping. It is also possible that the distinguishing characters of *Baeostethus* and *Leptusa* were not critically evaluated by Pace. For example, in the first couplet of his key to the subgenera, Pace (1989) stated that the tarsal claws are as long as the last segment of tarsi on all the subantarctic taxa. This observation is incorrect, and in *Halmaeus* and *Baeostethus* the claws are shorter than the terminal tarsomere, but depending on the orientation of the specimen the true lengths of the structures may appear to vary significantly.

Baeostethus was placed in the Homalotini (=Bolitocharini) (group Phytosi, now referred to as Phytosini) by Fenyés (1920, see Ahn & Ashe 1996), a diverse and heterogeneous group having a tarsal formula of 4-4-5 as well as three key characters (Ashe 1992, p. 339): denticles present on the molar region of the mandible, medial setae close or contiguous on the

prementum, and a narrow medial pseudopore field on the prementum. This placement of *Baeostethus* was followed by Chamberlin & Ferris (1929), Bernhauer & Scheerpeltz (1926), and Moore (1956). Recent studies of intertidal aleocharines showed Phytosini to be a polyphyletic group (see Ahn & Ashe 1996). Steel (1964) suggested a strong resemblance of *Baeostethus* to *Liparocephalus* Mäklin 1853, though the former genus was not included in the study on Liparocephalini by Ahn & Ashe (1996) because of Pace's synonymy of *Baeostethus* with *Leptusa*. *Baeostethus* shares several characters with this tribe, specifically seta v absent from the adult mentum, a synapomorphy for the group as defined by Ahn & Ashe (1996), as well as several setae distributed only on the mesal surface and apex of the galea and contiguous mesocoxal cavities. Other characters that *Baeostethus* shares with members of Liparocephalini that are not present in *Leptusa* and members of Homalotini are as follows (Ashe 2000b): body densely covered with very fine, short setae; elytra very short and hind wings absent; labial palps with 2 palpomeres (palpomeres 1 and 2 fused); ligula of prementum long, slender and entire at apex; one medial seta present on prementum; mandibles without denticles in ventral molar area; metasternum greatly shortened; middle coxae contiguous. Note that in some homalotines, and particularly *Leptusa* (*Halmaeus*), the metasternum is short and the hind wings are absent, which are part of a suite of characters associated with the loss of flight capability (Thayer 1992). Also, *Leptusa* lacks a well-developed prostheca which is present on the adult mandible of *Baeostethus* and remaining Liparocephalini.

In the cladistic analysis that follows, we add *Baeostethus* to the original data matrix of Ahn & Ashe (1996) and place it properly in Liparocephalini to determine its phylogenetic relationships to other members of the tribe.

PHYLOGENETIC ANALYSIS

Methods

We repeated the cladistic analysis of Ahn & Ashe (1996), consisting of 70 characters (21 larval and 49 adult), to which we add the data for *B. chiltoni* to the data matrix as follows: 0011001510 3120000201 0020001002 1121110101 0101011011 1001002001 0000000000. Eight characters were parsimony-uninformative (14, 22, 52, 53, 56, 61, 64, 65) and no new character states were identified in this study. The ingroup consisted of 18 species of the following genera (known distribution of each genus is provided): *Amblopusa* Casey 1893 (3 spp., Asia and North America), *Baeostethus* (1 sp., Campbell Plateau), *Diaulota* Casey 1893 (8 spp., Asia, Mexico, and North America), *Liparocephalus* (3 spp., Asia and North America), *Paramblopusa* Ahn & Ashe 1996 (1 sp., Asia and North America), and *Salinomex* Moore & Legener 1977 (2 spp., Mexico). *Heterota* Mulsant & Rey 1873, *Phytosus*, and *Leptusa* were included as outgroups.

The data were coded and entered into MacClade version 3 (Maddison & Maddison 1992) and analysed using PAUP* Version 4.0b3a for Macintosh (Swofford 2000). The settings used in PAUP* for heuristic tree searches included a random addition sequence with steepest descent; character states were treated as unordered. Branch support was determined by Bremer support (Bremer 1988), which measures the number of steps a clade will dissolve as tree length is increased, using Autodecay 3.0 (Ericksson & Wikström 1995) and by bootstrap (Felsenstein 1985; Sanderson 1995) and jackknife analyses (see Farris et al. 1996) with 100 replications each with simple addition sequences. Tree rooting and polarity of character states was determined by selecting outgroup taxa in PAUP*. To further resolve relationships and find consistency for character congruence in these trees, successive approximations character weighting (SAW; Farris 1969; Carpenter 1988, 1994), an *a posteriori* weighting

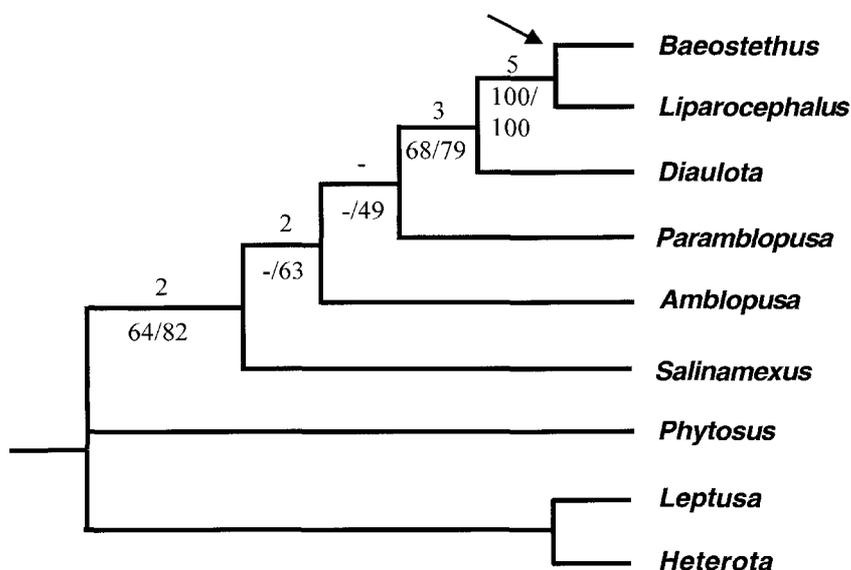


Fig. 2 Cladogram of the genera of Liparocephalini produced by successive approximations character weighting and rooted with *Heterota*, *Leptusa*, and *Phytosus*. Alternative rooting is indicated by the arrow. Bremer support is above the branch and bootstrap/jackknife values are below the branch.

method, was performed on the resulting trees (weights were set at 10 and based on the consistency index with analyses truncated). Ambiguous characters were optimised using standard ACCTRAN and DELTRAN optimisations (Maddison et al. 1984).

RESULTS

A total of 54 trees resulted from the phylogenetic analysis (tree length = 162, consistency index = 0.70, retention index = 0.81). SAW resulted in eight trees by two iterations. These trees are identical with those derived by Ahn & Ashe (1996) with *Baeostethus* placed as sister taxon to *Liparocephalus* (Bremer support = 5, bootstrap value = 100, jackknife value = 100). Analysed partitions of larval and adult data were also consistent with Ahn & Ashe (1996). The strict consensus of the SAW trees with the species terminals collapsed to genera is provided in Fig. 2 (relevant support values are indicated at each node). Characters that support the *Baeostethus*–*Liparocephalus* clade are as follows (unique characters indicated by an asterisk (*)) and larval characters indicated by an L): labrum with more than 50 setae (C9-1*), mandible straight (C12-1*), mandibles symmetrical, each bearing a median tooth (C13-2*), elytra wider than long (C35-1, present in some species of *Diaulota*), tarsal setae spatulate (C38-1*), abdominal tergites not impressed (C44-1*), ratio of length of sensory appendage to length of first flagellomere less than 1.0 (C50-1*L, coded as missing for many terminals), ratio of length of pedicel to length of scape more than 1.9 (C54-1*L, present in some species of *Diaulota* and coded as missing for many terminals), presence of two spines on the anterolateral margin of labium (C60-1*L, coded as missing for many terminals). Additional

characters that support this sister relationship are as follows: head length to width ratio less than 1.0 (C1-0, ACCTRAN), shape of scape longer than wide (C51-1L, DELTRAN), mandible with large serrations between the apex and median tooth (C57-2L, DELTRAN).

REDESCRIPTION OF *BAEOSTETHUS* BROUN

Baeostethus Broun, 1909: 96

TYPE SPECIES: *Baeostethus chiltoni* Broun, 1909: 96 (by monotypy).

Adult (Fig. 1)

DIAGNOSIS: Labrum large, robust and more or less semicircular; serrations between apex and median tooth of mandible irregularly spaced; galea with spinules present; two medial setae present on labium; prosternum not acute posteriorly; apical lobe of paramere more or less diamond-shaped; basal bulb of spermatheca projected apically; spermathecal tube long and coiled.

DESCRIPTION: Length 3.91–5.00 mm (tip of abdomen to tip of head). With the characters of *Liparocephalus*. Colour dark red-brown, pubescent with relatively short microsetae more or less densely and uniformly distributed. Head lightly deflexed, length slightly wider than long. Eyes small, 0.3× length of head; with interfacetal setae. Antennomeres not all elongate as shown in Fig. 1. Infraorbital carina present to level of eyes. Labrum large, robust and more or less semicircular. Epipharynx with 13 large lateral pores on each side and scattered small medial pores. Mandibles slightly curved mesally; 3 well-developed teeth distally and 2 smaller teeth proximally between apex and median tooth; prosthema with 8 setae present laterally. Lacinia with a comb of 8 regularly separated spines; setae distributed on mesal surface. Galea with numerous setae present on mesal surface. Labium with twin median and distal pores; two medial setae present; lateral pseudopores absent. Mentum almost trapezoidal; lacking seta v; shallowly emarginate; apico-lateral margin without projecting knob. Pronotum with two long filiform setae present anterolaterally on each side. Mesosternal process absent. Metasternum greatly shortened; middle coxae contiguous. Elytron with 4 long filiform setae present, 2 on disk and 2 laterally. Abdomen broadest at segment VI or VII. Sternite VIII of male prolonged posteriorly as a broad lobe; in female very slightly prolonged. Aedeagus with median lobe more or less projected laterally; basal bulb projected apically. Spermatheca bipartite with short round bulb apically and a tubulate section distally that is approximately 3× length of bulb.

Late instar larva (Fig. 3)

DIAGNOSIS: Distribution of setae of head and pronotum incomplete (see Ahn 1997 for chaetotaxy of *Liparocephalus cordicollis* LeConte to which *Baeostethus* is compared).

DESCRIPTION: Length 4.00–5.10 mm (tip of abdomen to tip of head). With the characters of *Liparocephalus*. Antenna with article 1 with large campaniform sensillum. Head chaetotaxy complete with Fc2 present as a seta (not a campaniform sensilla) next to frontal suture; seta between E12 and Ed1 absent from laterodorsal area; ventral setae V13, L2, L3, and unnamed seta next to L3 absent. Labrum lacking 4 distinct setae; 2 campaniform sensillae present. Mandible with 3 serrations present on internal edge (the first is weakly developed), 6 present between middle tooth and base. Mala without branched setae. Labium with distinctly separated prementum and mentum; ligula short; prementum with 1 pair of campaniform sensillae. Pronotal chaetotaxy incomplete, lacking unnamed (secondary) setae. Mesonotal chaetotaxy mostly complete; lacking A5, A4, and Pg in membrane and P5 and unnamed setae present on sclerite. Abdominal tergites granulate, especially posterior segments; chaetotaxy of tergite I complete. Anal hooks large and sclerotised.

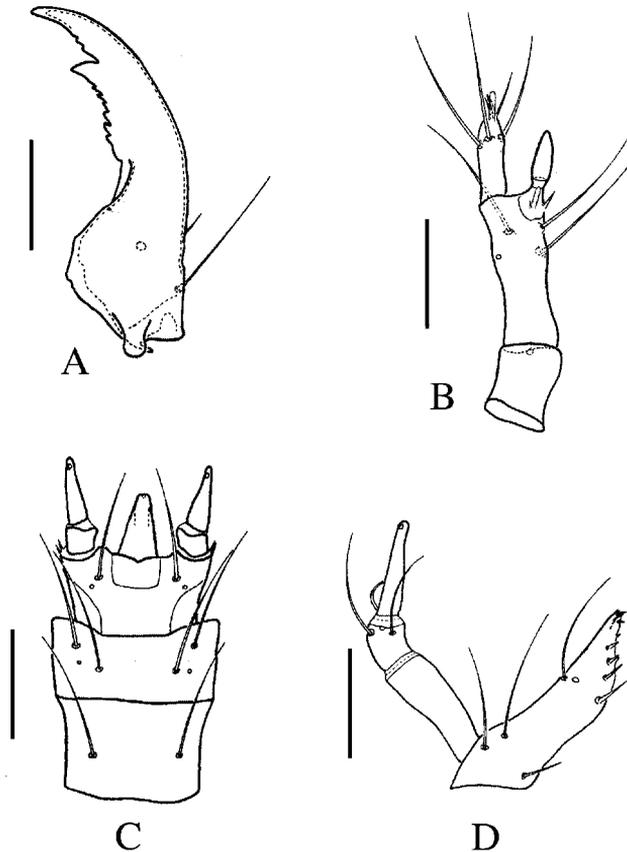


Fig. 3 Larval structures of *Baeostethus chiltoni*. **A**, Left mandible ventral view; **B**, Left antenna ventral view; **C**, Mentum ventral view; **D**, Left maxilla ventral view. Scale bars = 0.05 μm .

COMMENTS: *Baeostethus chiltoni* can be distinguished from remaining members of Liparocephalini by the combination of characters provided in the diagnoses and from *Liparocephalus* by the characters provided in the diagnoses and descriptions. There is presently one species in *Baeostethus* endemic to the Campbell Plateau and present in the rocky intertidal areas of Antipodes, Auckland, and Campbell islands (Steel 1964; Marris 2000; P. Hammond pers. comm.).

MATERIAL EXAMINED: (all specimens deposited in the New Zealand Collection of Arthropods, Landcare Research, except those with the acronym CNUIC, Chungnam National University Insect Collection): New Zealand. Antipodes I., Reef Pt, 31 Jan 1969, G. Kuschel, intertidal (14 adults); Campbell I., Venus Cove, 12 Mar 2000, M. Bullians, E. Edwards, R. Leschen, intertidal, SUB 053, 52°32'S, 169°08'E (1 larva, 1 adult); same, but 14 Mar 2000, SUB 069 (17 larvae, 8 adults); same, but Beeman Pt, 15 Mar 2000, SUB 072, 52°32'S, 169°08'E (2 larvae, 4 adults, CNUIC).

NATURAL HISTORY AND DISTRIBUTION

Coleoptera make up a significant portion of the insect fauna of the intertidal zone (Doyen 1976), and the highest number of species belongs to the family Staphylinidae. In the subantarctic the staphylinids are dominated by at least 20 species from the subfamilies Omaliinae (4 genera) and Aleocharinae (3 genera), though individual species and their taxonomic status have not been studied in detail (Hammond 2000; Johnston et al. 2001). Liparocephalini, with the exception of *Baeostethus*, are northern circum-Pacific with species found from southern Korea, northward to Russia, Japan, Alaska, and south to Baja California (Ahn & Ashe 1996; Ahn & Maruyama 2000). All known members of the tribe, which is composed of 6 genera and 22 species, are flightless except for *Salinamexus*, and inhabit rocky intertidal areas. Most members of the tribe except *Liparocephalus* and *Diaulota* are nocturnal (Jones 1968; Topp & Ring 1988; Ahn 1996, 1997).

Baeostethus chiltoni is restricted to a small band of habitat of loose pebbles proximal to the moving tide and it is likely that this species is not exposed to climatic conditions that may affect populations of terrestrial subantarctic species (French & Smith 1985; Danks 1999). Most specimens were captured beneath larger stones where they were spotted after close inspection of the rock surfaces; the red-brown bodies of adults and light coloured bodies of larvae are similar to the colour of their background. This area of loose stones is also inhabited by many other invertebrates including small starfish, mites, molluscs, crabs, and numerous Collembola of one species. Lack of material in larval and adult guts suggests that *B. chiltoni* is a predator that may preally digest its food, possibly feeding on the Collembola that congregate in large numbers in association with the beetle. Specimens of larvae and adults submerged in salt water formed a layer of air on the surface of their bodies.

ORIGIN AND BIOGEOGRAPHY OF *BAEOSTETHUS*

One way to examine biogeographic patterns is to replace terminal taxa with their areas of distribution, producing an area cladogram that is used to elucidate historical relationships of areas (Morrone & Carpenter 1994). The consensus area cladogram is based on the substitution of areas (derived from Ahn & Ashe 1996) for taxa in Fig. 2 (Fig. 4A). In this analysis, Mexico (Sonora) is the out-area and the Campbell Plateau occupies a relatively derived position on the cladogram. The Campbell Plateau is related as a sister-area to northern Pacific rim regions. One hypothesis to explain the occurrence of *Baeostethus* on the Campbell Plateau is that the distribution of this genus resulted from a chance dispersal event by an ancestor from the northern Pacific rim at some time after significant evolution and differentiation within Liparocephalini. While this ancestral taxon evolved into the monotypic genus *Baeostethus* on the Campbell Plateau, it differentiated into a number of species on the coasts of North America and Japan. We reject this hypothesis because, while aptery (loss of hind wings) could evolve repeatedly as it does in other insect lineages (e.g., Thayer 1992), in this case it is unparsimonious to assume that each genus (or species) has evolved wing loss independently from others. Based on the cladogram (Fig. 2), aptery evolved prior to the origin of the ancestor of *Baeostethus* and *Liparocephalus*, four steps after the divergence of flight-capable *Salinamexus* from the remaining liparocephalines. Moreover, if aptery did evolve repeatedly in Liparocephalini, there is no way to identify where losses or gains of wings have occurred as all but *Salinamexus* are apterous. Chance dispersal of a flightless intertidal ancestor over 9000 km of ocean is not feasible.

The asymmetric distribution of species diversity with a high number of Holarctic species is inconsistent with a derived Laurasia-Gondwana split. Given that Liparocephalini may have had a widespread Pangean distribution, we would have to accept an early Mesozoic origin

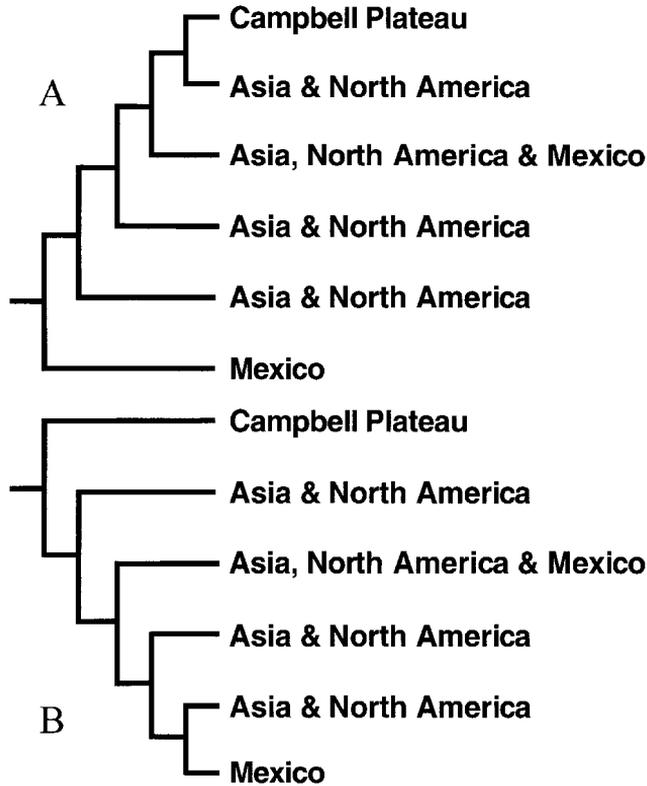


Fig. 4 Alternative area cladograms for Liparocephalini. **A**, Area cladogram derived from the cladogram in Fig. 2; **B**, Area cladogram derived by rerooting the tree at *Baeostethus*.

and extinction of all other taxa confined to Gondwana. A simpler explanation is that the split was basal and cladogenesis occurred afterward, mainly in the Northern Hemisphere.

Having evaluated the dispersal and vicariant hypotheses based on the area cladogram (Fig. 4A), we were compelled to re-examine the assumptions behind the cladistic analysis. In particular, we focused attention on the way in which the cladogram was rooted to see if alternative roots would produce trees consistent with the expected vicariant pattern that there was a Gondwana-Laurasian split at the base of the tree. In the original analysis rooting was achieved by designating three outgroups *a priori*. Using outgroups to root trees is a standard technique (Nixon & Carpenter 1993) and those chosen were the most suitable based on present knowledge. Nevertheless, the phylogeny of higher Aleocharinae is far from settled (see Ashe 1998) and it is possible that the outgroups chosen by Ahn & Ashe (1996) may be incorrect. Also, *Baeostethus* has one of the highest number of adult autapomorphies (8 compared with the ingroup mean which is 2.4) which may be more consistent with a basal position within Liparocephalini. Based on these data we placed the root at *Baeostethus*, making this taxon the basal-most member of Liparocephalini (see Fig. 2).

An area cladogram based on the rerooted tree that excludes the outgroup taxa (Fig. 4B) shows the Holarctic regions as one group that is sister area to the Campbell Plateau. This hypothesis implies that the evolution of the Liparocephalini can be traced back to ancestors widespread along the coasts of Pangea. The initial vicariant event involved the splitting of Pangea into Gondwana and Laurasia at about 150–135 Ma. While considerable evolution and differentiation occurred in Northern Hemisphere taxa, the *Baeostethus* lineage of the Campbell Plateau appears to have remained phylogenetically conservative. We consider this hypothesis provisional because the placement of *Baeostethus* is enigmatic (probably due to the high number of autapomorphies that define the taxon) and because hind wings and flight capability are implied to have re-evolved in *Salinamexus*.

Congruency of distribution with other organisms is a standard test for choosing between biogeographic hypotheses, and the unusual distribution of Liparocephalini is not unique in Coleoptera. A similar distribution is seen in the intertidal subfamily Aegalitinae (Salpingidae), a group containing two flightless genera, one found on the Pacific shores of North America, Russia, and Japan, and the other present on the shores of Antipodes, Auckland, Bounty, Campbell, Chatham, Snares, and Stewart islands (Spilman 1967; Emberson 1998; Marris 2000 pers. comm.). The distribution is also matched by the aleocharine tribe Gymnusini, a terrestrial group which has its most primitive member present in Auckland Islands and is sister taxon to the rest of the group which is widespread in the Holarctic (Hammond 1975; Klimaszewski 1979); a phylogenetic relationship supported in two of parsimonious trees produced by Ashe (2000a). Moreover, the phylogeny and biogeographic distribution of taxa of gymnusines are completely congruent with relationships for Liparocephalini shown in Fig. 4B, supporting the rerooted cladogram.

Distributional evidence supports the possibility of a long biological history of *Baeostethus* on the Campbell Plateau. The Campbell Plateau is a continental fragment adjacent to the South Island, New Zealand. The Plateau was originally part of west Gondwana before rifting away at 80 Ma (McAdoo & Laxon 1997). Early Tertiary quartzose sediments show that parts of this rifted continental fragment were still above sea level and *Nothofagus* forests grew prior to Pliocene glaciations (Dettman et al. 1990). Provided that some of parts of this plateau remained above sea level, the subantarctic islands of New Zealand represent eroded remnants of a more extensive landmass providing refugia for plants and animals, including suitable intertidal habitats for Liparocephalini. Presence of a liparocephaline ancestor on the Gondwanan shoreline is consistent with the fossil record for staphylinids which includes members of the tachyporine group which includes Aleocharinae in the Jurassic (Carpenter 1992).

New characters for resolving the relationships of Liparocephalini are necessary. Moreover, additional phylogenies for species distributed on the Campbell Plateau and other regions are necessary to confirm that some of these taxa are members of widespread Pangean lineages that were somehow lost in time and confined to New Zealand's subantarctic archipelagos.

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REFERENCES

- Ahn, K. J. 1996: A review of *Diaulota* Casey (Coleoptera: Staphylinidae: Aleocharinae), with description of a new species and known larvae. *The Coleopterists Bulletin* 50: 270–290.
- Ahn, K. J. 1997: A review of *Liparocephalus* Mäklin (Coleoptera: Staphylinidae: Aleocharinae) with descriptions of larvae. *Pan-Pacific Entomologist* 73: 79–92.
- Ahn, K. J.; Ashe, J. S. 1996: Phylogeny of the intertidal aleocharine tribe Liparocephalini (Coleoptera: Staphylinidae). *Systematic Entomology* 21: 99–114.
- Ahn, K. J.; Maruyama, M. 2000: *Paramblopusa eoa*, a new intertidal species (Coleoptera: Staphylinidae: Aleocharinae) from Kuril Islands. *The Coleopterists Bulletin* 54: 359–364.
- Ashe, J. S. 1992: Phylogeny and revision of genera of the subtribe Bolitocharina (Coleoptera: Staphylinidae: Aleocharinae). *The University of Kansas Science Bulletin* 10: 335–406.
- Ashe, J. S. 1998: Aleocharinae. In: Maddison, D. R. ed. Tree of life. Published on the WWW at <http://phylogeny.arizona.edu>
- Ashe, J. S. 2000a: Mouthpart structure of *Stylogymnusa subantarctica* Hammond, 1975 (Coleoptera: Staphylinidae: Aleocharinae) with a reanalysis of the phylogenetic position of the genus. *Zoological Journal of the Linnean Society* 130: 471–498.
- Ashe, J. S.; 2000b: Aleocharinae, Staphylinidae. In: Arnett, R.; Thomas, M. ed. Beetles of the United States. Gainesville, Sandhill Press. Pp. 272–418.
- Bernhauer, M.; Scheerpeltz, O. 1926: Coleopterorum catalogus. Pars 82, Staphylinidae VI. Berlin, W. Junk. Pp. 499–988.
- Bremer K. 1988: The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795–803.
- Bréthes, J. 1925: Un coléoptère et un diptère nouveaux de la Georgie du Sud. *Communications Museo Nacional Historia Naturale Bernardino Rivadavia* 2: 169–173.
- Broun, T. 1909: Descriptions of Coleoptera from the subantarctic islands of New Zealand; with remarks on the affinities of the genera. In: Chilton, C. ed. The subantarctic islands of New Zealand. Wellington, Philosophical Society of Canterbury. Pp. 78–123.
- Cameron, M. 1917: Description of a new genus of Staphylinidae. *Entomologists Monthly Magazine* 53: 125.
- Carpenter, F. M. 1992: Treatise on invertebrate paleontology. Part R. Arthropoda 4. Vol. 4: Superclass Hexapoda. Lawrence, The University of Kansas and The Geological Society of America. 655 p.
- Carpenter, J. M. 1988: Choosing among multiple equally parsimonious cladograms. *Cladistics* 4: 291–296.
- Carpenter, J. M. 1994: Successive weighting, reliability and evidence. *Cladistics* 10: 215–220.
- Casey, T. L. 1893: Coleopterological notices V. *Annals of New York Academy of Science* 7: 281–606.
- Chamberlin, J. C.; Ferris, G. F. 1929: On *Liparocephalus* and allied genera (Coleoptera: Staphylinidae). *Pan-Pacific Entomologist* 5: 137–162.
- Chown, S. L.; Gremmen, N. J. M.; Gaston, K. J. 1998: Ecological biogeography of southern ocean islands: species-area relationships, human impacts, and conservation. *American Naturalist* 152: 562–575.
- Curtis, J. 1838: British entomology, being illustrations and descriptions of the genera of insects found in Great Britain and Ireland; containing coloured figures from nature of the most rare and beautiful species, and in many instances of the plants upon which they are found. Coleoptera, V. London, L. Reeve & Co. Pl. 1–15.
- Danks, H. V. 1999: Life cycles in polar arthropods—flexible or programmed? *European Journal of Entomology* 96: 83–102.
- Dettmann, M. E.; Pocknall, D. T.; Romero, E. J.; del Carmen Zamalao, M. 1990: *Nothofagidites* Erdtman ex Potonié, 1960: a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* Bl. (Southern Beech). *New Zealand Geological Survey Paleontological Bulletin* 60: 1–79.
- Doyen, J. T. 1976: Marine beetles (Coleoptera excluding Staphylinidae). In: Cheng L. ed. Marine insects. Amsterdam, North Holland Publishing Company. Pp. 497–519.
- Emberson, R. M. 1998: The beetle (Coleoptera) fauna of Chatham Islands. *New Zealand Entomologist* 21: 25–64.

- Enderlein, G. 1909: Die Insekten des Antarktischen Gebeites. In: von Drygalski, E. ed. Deutsche Südpolar-Expedition. Vol. 10. Chapter 9, Book 4. Zoologie. Berlin, Georg Reimer. Pp. 361–518.
- Ericksson, T.; Wikström, N. 1995: Autodecay (version 3.0). (Program distributed by the first author.) Stockholm, Department of Botany, Stockholm University.
- Farris, J. S. 1969: A successive approximations approach to character weighting. *Systematic Zoology* 18: 374–385.
- Farris, J. S.; Albert, V. A.; Källersjö, M.; Lipscombe, D.; Kluge, A. G. 1996: Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99–124.
- Fauvel, A. 1877: Les staphylinides de l'Australie et de la Polynésie. *Annali Civico di Storia Naturale di Genova* 10: 168–298.
- Felsenstein, J. 1985: Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Fenyés, A. 1920: Coleoptera. Fam. Staphylinidae, Subfam. Aleocharinae. Genera Insectorum, Fascicule 173b. Brussels. Pp. 111–414.
- French, D. D.; Smith, V. R. 1985: A comparison between northern and southern tundras and related ecosystems. *Polar Biology* 5: 5–21.
- Gressitt, J. L.; Wise, K. A. J. 1971: Entomology of the Aucklands and other islands south of New Zealand: introduction. *Pacific Insects Monograph* 27: 1–45.
- Hammond, P. M. 1975: The phylogeny of a remarkable new genus and species of gymnosine staphylinid (Coleoptera) from the Auckland Islands. *Journal of Entomology (B)* 44: 153–173.
- Hammond, P. M. 2000: Coastal Staphylinidae (rove beetles) in the British Isles, with special reference to saltmarshes. In: Sherwood, B. R.; Gardiner, B. G.; Harris, T. ed. British saltmarshes. London, The Linnean Society of London. Pp. 247–302.
- Jeannel, R. 1940: Coléoptères. In: Croisière du Bougainville aux îles australes françaises. *Mémoires du Muséum National d'Histoire Naturelle* 14: 64–201.
- Johnston, P.; Leschen, R. A. B.; Stephenson, S. 2001: Subantarctic fungi, slime moulds and beetles. Published on the WWW at http://www.landcare.cri.nz/science/biodiversity/antarctic/subant_home.htm
- Jones, T. W. 1968: The zonal distribution of three species of Staphylinidae in the rocky intertidal zone in California (Coleoptera: Staphylinidae). *Pan-Pacific Entomologist* 44: 203–210.
- Kerr, I. S.; Judd, N. 1978: Marlborough whalers at Campbell Island 1909–1916. A narrative based on the recollections of J. Timms. Wellington, Department of Lands and Survey. 75 p.
- Kiesenwetter, H.; Kirsch T. 1877: Die Käferfauna der Auckland-Inseln, nach Herrn Krones Sammlungen beschrieben. *Deutsch Entomologische Zeitschrift* 21: 153–174.
- Klimaszewski, J. 1979: A revision of the Gymnosini and Deinopsini of the world (Coleoptera: Staphylinidae, Aleocharinae). *Agriculture Canada Monograph* 25: 1–169.
- Kraatz, G. 1856: Naturgeschichte den Insecten Deutschlands. Abteilung 1, Coleoptera, Vol. 2, Staphylinii. Berlin, Nicolai. 376 p.
- Kuschel, G. 1964: Insects of Campbell Island. Coleoptera: Curculionidae of the subantarctic islands of New Zealand. *Pacific Island Monograph* 7: 416–493.
- Maddison, W. P.; Maddison, D. R. 1992: MacClade, version 3: analysis of phylogeny and character evolution (manual). Sunderland, Sinauer. 398 p.
- Maddison, W. P.; Donoghue, M. J.; Maddison, D. R. 1984: Outgroup analysis and parsimony. *Systematic Zoology* 33: 83–103.
- Mäklin, F. G. 1853: Description of new taxa. In: Mannerheim, C. Dritter Nachtrag der Aleutischen. *Bulletin de la Société Impériale des Naturalistes de Moscou* 26: 95–269.
- Marris, J. W. M. 2000: The beetle fauna (Coleoptera) fauna of the Antipodes Islands, with comments on the impact of mice; and an annotated checklist of the insect and arachnid fauna. *Journal of the Royal Society of New Zealand* 30: 169–195.
- McAdoo, D. C.; Laxon, S. 1997: Antarctic tectonics: constraints from an ERS-1 satellite marine gravity field. *Science* 276: 556–560.
- Moore, I. 1956: A revision of the Pacific Coast Phytosi with a review of the foreign genera (Coleoptera: Staphylinidae). *Transactions of the San Diego Society of Natural History* 7: 103–152.
- Moore, I.; Legener, E. F. 1977: A report on some intertidal Staphylinidae from Sonora, Mexico with four new genera (Coleoptera). *Pacific Insects* 7: 459–471.
- Morrone, J. J. 1998: On Uvardy's insular antarctica province: a test from weevils (Coleoptera: Curculionidae). *Journal of Biogeography* 25: 947–955.

- Morrone, J. J.; Carpenter, J. 1994: In search of a method for cladistic biogeography: an empirical comparison of component analysis, Brooks parsimony analysis, and three-area statements. *Cladistics* 10: 99–153.
- Mulsant, M. E.; Rey, C. 1873: Histoire naturelle de coléoptères de France. Brévipennes. Aléochariens [Branches 1–5]. Paris, Deyrolle Fils. 155 p.
- Nixon, K. C.; Carpenter, J. 1993: On outgroups. *Cladistics* 9: 413–426.
- Pace, R. 1989: Monographia del genere *Leptusa* Kraatz (Coleoptera, Staphylinidae). *Memorie del Museo Civico di Storia Naturale di Verona* 8: 1–307.
- Sanderson, M. J. 1995: Objections to bootstrapping phylogenies: a critique. *Systematic Biology* 44: 299–320.
- Spilman, T. J. 1967: The heteromorous intertidal beetles (Coleoptera: Salpingidae: Aegialitinae). *Pacific Insects* 9: 1–21.
- Steel, W. O. 1964: Insects of Campbell Island. Coleoptera: Staphylinidae. *Pacific Insects Monographs* 7: 340–375.
- Swofford, D. L. 2000: Phylogenetic Analysis Using Parsimony (PAUP[®]), version 4 (manual). Sunderland, Sinauer. 128 p.
- Thayer, M. K. 1992: Discovery of sexual dimorphism in Staphylinidae (Coleoptera): “*Omalium*” *flavidum*, and a discussion of wing dimorphism in insects. *Journal of the New York Entomological Society* 100: 540–573.
- Topp, W.; Ring, R. A. 1988: Adaptations of Coleoptera to the marine environment. II. Observation on rove beetles (Staphylinidae) from rocky shores. *Canadian Journal of Zoology* 66: 2469–2474.