Abstract
Palorinae, new subfamily, type genus Palorus Mulsant, is proposed to include Ulomotypus plus nine other genera from outside New Zealand. The subfamily is described and its relationships discussed, the closest other subfamily being Tenebrioninae. Ulomotypus is redescribed in detail. Aphtora is briefly diagnosed and is found to be a primitive member of the Tenebrioninae which cannot be assigned to a known tribe. Demtrius is also briefly diagnosed and is found to be a member of the tribe Titaenini, subfamily Tenebrioninae.

Key words: Phylogeny, biogeography, New Zealand.

Introduction
In the Fauna of New Zealand volume on Tenebrionidae (Watt 1992), the three genera discussed here could not be placed taxonomically. Demtrius Broun was left in an uncertain position, while Aphtora Bates and Ulomotypus Broun were placed doubtfully in the tribe Ulomini (subfamily Tenebrioninae) following an opinion by Doyen (1985) that these genera might be the most primitive members of the tribe, although Doyen considered it more likely that the resemblances to Ulomini are convergent. He also noted that Ulomotypus lacks the transverse bridge of the tentorium and that the aedeagus is inverted, characters which Matthews (2003) listed as being two of the principal recognition features of the Palorus genus-group of Halstead (1967). In the present paper the three monotypic genera in question are discussed and opinions offered as to their positions in the family Tenebrionidae, but only Ulomotypus is redescribed in detail.

When attempting to propose a new subfamily for the Palorus group Matthews (2003) did not conform to the correct procedure for establishing a family-group name as set out in the Rules of Nomenclature (A. F. Newton, pers. comm.). It was not specifically stated that Palorinae is a new name, and no type genus was designated. These oversights are corrected here and the name Palorinae must therefore date from the present paper, not Matthews (2003).

Materials and Methods
Material was examined from the New Zealand Arthropod Collection (Auckland, NZAC) and label data were collated from the Auckland War Memorial Museum (AMNZ), Lincoln University Insect Collection (LUNZ), and the John Nunn Insect Collection (Dunedin, JNIC). Internal structures were cleared in boiling 10% KOH solution. For the dates, synonymies and type data relating to the New Zealand genera discussed here, see Watt (1992). Two-letter codes on labels and for New Zealand distributions follow Crosby et al. (1998).

Taxonomy
Subfamily Palorinae, new subfamily
Type genus: Palorus Mulsant

Description. Labrum prominent, subquadrate, with short, wide toral arms which have no extensions. Antennomeres usually cylindrical and compressed, often with a weak 5-segmented club, with simple sensilla only. Eyes usually small and rounded (transverse and emarginate in Ulomotypus). Mandibles bidentate, molar surface smooth or with coarse ridges. Laciniae unarmed. Distal maxillary palpomeres subparallel. Bridge of tentorium absent.

Pronotum often with lateral longitudinal grooves or depressions. Procoxal cavities externally closed, internally closed except in Ulomotypus. Mesocoxal cavities closed by ventrites only, except in Platycotylus where there is a gap, but mesepimeron not reaching cavity. Metendosternite without laminae. Elytra with 9 striae (rarely 10) and scutellar striole, epipleura complete to apices. Scutellum transverse. Wings fully developed, with complete normal tenebrionid venation in Ulomotypus and Platycotylus, in other genera anal venation is reduced and radial cell is absent, apical membrane long except in Ulomotypus, no medial fleck.
Legs not fossorial, tarsal formula 5-5-4 or (Pseudeba, Eutermicola) 4-4-4, basal tarsomeres short, tarsomeres cylindrical, with only sparse setae.

Abdomen with visible membranes between last 3 ventrites, defensive gland sacs usually present, not pleated, without common volume, but absent in Eutermicola and Ulomotypus. Edge of last ventrite grooved to receive epipleural edges. Ovipositor more or less shortened, coxites without lobation, gonostyles present or absent, sometimes claw-like. Female tract without bursa or accessory gland, usually with a large anterior sausage-shaped spermatheca separated by a constriction from vagina, to which a small tubular accessory gland may be attached, but in Ulomotypus spermatheca consisting of a very long fine tube distally coiled into a ball. Aedeagus inverted, with tapering apical piece, basal piece normally much shorter than apical but in Ulomotypus the 2 are subequal in length, alae at least in Ulomotypus present as extensions of parameres. Males of most genera with dense fields of small pits on internal surface of at least one abdominal ventrite.

**Included genera.** Palorus Mulsant and Platycotylus Olliff (widespread in Old World), Ulomina Baudi (= Coelopalus Blair) and Palorinus Blair (Oriental Region), Prolabrus Fairmaire and Astalbus Fairmaire (Madagascar), Pseudeba Blackburn, Austropalorus Halstead and Eutermicola Lea (northern Australia), and Ulomotypus Broun (New Zealand). There is also a highly distinctive undescribed genus in India (A. Slipinski, pers. com.).

**Relationships of Palorinae**

The key characters in the above description are the absence of the tentorial bridge, subquadrate labrum with short, broad unbranched tormal arms, simple antennal sensilla, an outer groove on the last abdominal ventrite, inverted aedeagus, alae of aedeagus formed as extensions of parameres, internal pits on the male ventrites, and single coiled bursa-derived spermatheca (in Ulomotypus).

Absence of the tentorial bridge is considered to be a lagrine feature (Doyen et al. 1990). Among the Australian lagriines examined the bridge is absent in Lagriini and Choerodini. However, in the tenebrionoid branch it also is absent in the Leiochridini and Scaphidemini of the Diaperinae, as well as in Palorinae.

A subquadrate or elongate labrum is considered to be a primitive character in the family (Doyen & Tschinkel 1982) and it is also a typical feature of Lagriinae and Phrenapatinae (lagrioid branch), but it recurs in Zolodininae (pimelioid branch), and Toxicini, Bolitophagini, Ulomini and Opatrinae of the tenebrionoid branch. However, in many of these groups including Ulomini, the tormal arms have extensions at their internal ends angled forward and/or backward. The particular configuration of the labrum in all Palorinae examined, which is subquadrate with short unbranched tormal arms (Fig. 3, t), recurs only in the Phrenapatinae and Bolitophagini.

The simple antennal sensilla are another primitive feature found throughout the lagrioid and pimelioid branches, and in many plesiotypic tenebrionoids (Toxicini, Bolitophagini, primitive Tenebrioninae, and Opatrinae). Among other things, the simple sensilla immediately separate Palorinae from Ulomini, with which they have been confused. True Ulomini have prominent placoid sensoria on the antennae (Doyen 1985).

The groove along the outer edge of the last ventrite (Fig. 4, g) is a plesiomorphic character first noted by Doyen and Tschinkel (1982) and is universally present in all Lagriinae, Phrenapatinae, Zolodininae and Pimeliinae. Until now, it was thought to be absent in the tenebrionoid branch, where the edge of the last ventrite is rounded or squared, not grooved. A grooved ventrite in Palorinae and Aphtora (see below) is a primitive character in these taxa, which are members of the tenebrionoid branch.

The inverted aedeagus is a striking apomorphy of Palorinae. While occasional aedeagal inversion is seen in some groups such as Coelometopinae, a consistently inverted aedeagus has been a characteristic of the pimelioid branch alone until now (Zolodininae and Pimeliinae). In Palorinae the aedeagus is always inverted in every taxon examined for this feature (which has been overlooked until recently because it needs to be noted before the aedeagus is extracted). The actual structure of the aedeagus, with tapering parameres and usually a small basal piece, is also similar to that of some Pimeliinae. However, Pimeliinae (and Zolodininae) have what appears to be a primary absence of defensive glands, as shown by the central (‘tentyroid’) hinging of the abdominal ventrites,
and for this reason alone it would quite impossible to associate Palorinae with the pimelioids. An inverted aedeagus may have evolved early in the history of Tenebrionidae, even before defensive glands, but it can hardly be considered to be an ancestral condition in the family as a whole.

The aedeagus of *Ulomotypus* has alae which are extensions of the parameres (Fig. 4, a). In all palorines previously examined alae appeared to be absent, but it is possible that they were overlooked because of the small size of the aedeagus. In Lagriinae and Phrenapatinae the alae are absent or, if present, are separate sclerites articulated with the parameres by a membrane. The presence of alae as extensions of the parameres means that the aedeagus of *Ulomotypus*, and by implication all Palorinae, is not lagrioid. The abdominal pits of the male, first noted by Halstead (1967), have not yet been found in any other tenebrionids. However, they can be overlooked because they generally do not show externally. It is necessary to clear the abdomen and examine the ventrites by transmitted light. The pits will then show up clearly as circles of light. They open externally by way of minute canals (Halstead 1967). In *Ulomotypus*, which is extraordinarily large for a palorine, the pits are represented externally as shallow depressions covering the entire ventrum of the abdomen. In other genera of Palorinae it is generally only one or two ventrites which have pits (undetectable externally). The function of these pits is unknown.

It is the female tract of *Ulomotypus* which casts the most doubt over the lagrioid relationship theory advanced by Matthews (2003). In known lagrioids there is a bursa copulatrix (e.g. Lagriini, Phrenapatinae) or, if the bursa is replaced by a spermatheca, the latter consists of multiple tubules (e.g. Adeliini). The same is true in the pimelioid branch and occasionally in the Toxicini of the tenebrionid branch. Only in most Tenebrioninae (e.g. Bolitophagini, Tenebrionini, Heleini, Ullomini, etc.) and in Opatrinae do we see a single tightly coiled spermatheca without a bursa as in *Ulomotypus* (Fig. 5, sp). Seeing this was unexpected, considering that all other palorines examined have a large sausage-shaped structure which was interpreted as a bursa, since in some palorines a separate apparent spermatheca emerges from this structure (see Fig. 8 sp in Doyen *et al.* 1990). It appears now that the sausage-shaped structure is a spermatheca, perhaps a simplification of the original coiled organ, and that therefore a true bursa is not present in the group.

*Ulomotypus* is by far the largest of all the known Palorinae, the others not exceeding 4 mm in length, and as such it differs from the others in a number of characters which prove to be size-related. In particular, the eyes which are entire and round or oval in the other palorine genera, are transverse and emarginate in *Ulomotypus*. The wing venation is fully developed and like that of most other tenebrionids, whereas in all the other palorine genera except *Platycotylus* the venation is reduced and the apical membrane elongate. The aedeagus, universally with a much reduced basal piece in all other known Palorinae (see figures in Halstead 1967), has in *Ulomotypus* a more normal basal piece which is subequal in length to the apical piece.

The absence of defensive glands in *Ulomotypus* is secondary, since most palorines retain them. Internally open procoxal cavities are a unique feature of *Ulomotypus* among the palorines, but this is a plesiomorphy which recurs among several other groups of tenebrionids, notably the basal pimelioids, tenebrionoids and lagrioids, and so it has little phylogenetic significance but can be useful for diagnostic purposes.

**Biogeography of Palorinae**

The present distribution of the Palorinae provides us with clues as to its probable age. Considering only the endemic genera listed above (that is, not considering *Palorus* and *Platycotylus* which appear to have dispersed widely), we are left with a distribution which takes in Madagascar, India with south-east Asia, northern Australia and New Zealand. These areas correspond to eastern Gondwana, which may be thought of as the ancestral area, and which began to break up 140 Ma ago with the departure of India and terranes now forming part of south-east Asia. New Zealand broke away from Gondwana + 80 Ma ago. The latter date would be the minimum age for Palorinae, with the former date a more likely one. The apparent absence of the group in the Americas is puzzling, since Australia retained a connection with South America via Antarctica until about 50 Ma ago, and the presence of Palorinae in New Zealand seems to suggest past occurrence in the
south of Gondwana where it could have moved into South America. The most likely explanation is that Palorinae do in fact occur in South America but have not yet been recognized. Because of their unremarkable ‘ulomine’ appearance their relationships can easily be overlooked.

**Redescription of Ulomotypus Broun**

Form subparallel, strongly convex, surfaces shining, glabrous, smooth, entirely black except in teneral individuals. Total length 10.1 – 13.2 mm, width 4.1 – 4.9 mm.

**Head.** Clypeus deeply angularly emarginate. Eyes moderately transverse, anteriorly shallowly emarginate. Antennae (Fig. 2) short, with segments 1 – 6 subparallel, 5 – 11 gradually widening, with sparse long bristles, with simple sensilla in patches on outer surfaces of last 5 segments. Labrum (Fig. 3) prominent, subquadrate, with broad tormal arms which have no extensions. Mandibles apically bidentate, molar surfaces coarsely ridged. Laciniae unarmed. Tentorium without a complete bridge, with only basal portions present.

**Prothorax.** Pronotum evenly convex, fully margined, angles subquadrate, lateral margin thicker posteriorly. Prosternum moderately long before procoxae, process subparallel, evenly curved. Procoxal cavities closed externally, open internally.

**Pterothorax.** Mesoventrite strongly stepped. Mesocoxal cavities nearly closed by meeting of meso- and metaventrites, leaving a narrow gap where trochantin is visible, mesepimeron not reaching cavities. Metendosternite without laminae. Elytra with 9 striae and scutellary striaule, striae closely punctate, intervals flat, epipleura complete to apices. Wings fully developed, with small apical membrane containing diffuse flecks, with complete, unmodified basic tenebrionid venation, without medial fleck.

**Legs.** Pro- and mesocoxae globose, metacoxae transverse. Meso- and metatrochanters with tufts of long setae. Metafemora of female with dense setae on posterior face, absent in male. All tibiae strongly expanded apically, protibia with 2 outer apical teeth, outer edges of pro- and mesotibiae serrate, not toothed. Metatibia with inner basal tooth in both sexes. All tibiae with two apical spurs of which the outer on protibia is large and curved. Tarsomeres 5-5-4, subparallel and cylindrical, preapical ones relatively compressed, apical one longer (Fig. 1), with sparse bristles.

**Abdomen.** Membrane visible between last 3 ventrites. Outer edge of last visible ventrite dorsally grooved (Fig. 4, g). Male only with very dense, deep pits pockmarking entire surfaces of all ventrites, more evident on inside (Fig. 4, p). Aedeagus (Fig. 4) inverted, basal and apical pieces subequal in length, parameres tapering, alae (Fig. 4, a) formed as extensions of parameres, basal piece deeply split on morphological dorsal (actual ventral) surface. Ovipositor (Fig. 5) extremely reduced, without gonostyles, with paraprocts rotated distad. Female tract without bursa, with

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**Figs 1–3. Ulomotypus laevigatus Broun. 1, Metatarsus; 2, Antenna, underside; 3, Labrum. t, tormal arm. Scale line 0.5 mm.**

**Fig. 4. Ulomotypus laevigatus. Apex of male abdomen in dorsal view, tergites 6 and 7 removed, with aedeagus extruded in natural orientation. Right: aedeagus in ventral (morphological dorsal) view. a, alae; g, groove along edge of last visible ventrite; p, pits on inside of ventrites. Scale line 1 mm.**
bursa-derived spermatheca consisting of a stem and ball made up of an extremely long, probably unbranched coiled tubule (Fig. 5, sp).

**Included species.** *U. laevigatus* Broun.


**Aphrora Bates**

**Diagnosis.** Form oblong-oval, moderately convex. Total length 4.2 – 5.1 mm. Eyes suboval, weakly emarginate. Labrum largely concealed under clypeus, moderately transverse, tormal arms short and wide, without extensions. Antennae short with weak 3-segmented club, with simple sensilla only. Mandibles apically bidentate, mola coarsely ridged. Distal maxillary palpomere subparallel. Lacinia unarmed. Bridge of tentorium present, strongly arched. Procoxal cavities externally closed, internally open. Mesocoxal cavities almost closed by ventrites, meseptira not reaching them. Elytra with 9 striae and scutellary striole, epipleura complete to apices. Wings fully developed, with complete venation but radial cell reduced, apical membrane making up about 1/3 of wing length, medial fleck absent. Metendosternite without laminae. Legs with tibiae somewhat expanded apically, tarsi 5-5-4, tarsomeres cylindrical with sparse setae. Abdomen with membrane visible between last 3 ventrites, outer edge of last ventrite grooved. Defensive glands absent. Aedeagus not inverted, with relatively long

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**Fig. 5.** *Ulomotypus laevigatus.* Ovipositor and female tract. *ag,* accessory gland (broken off); *cx,* unlobed coxa of ovipositor; *ov,* oviduct; *pp,* rotated paraproct of ovipositor; *sp,* spermatheca. Scale line 1 mm.

**Fig. 6.** *Ulomotypus laevigatus,* female. Scale line 1 mm.
basal piece, with thin-walled alae formed as extensions of middle part of parameres. Ovipositor greatly reduced, coxites without lobation, without gonostyles, paraprocts rotated distad. Female tract without bursa, with very long and delicate spermathecal tubule distally coiled into a ball.

**Comments.** The above combination of characters does not correspond to that of any known group of Tenebrionidae. Many features resemble *Ulomotypus* (tormal arms, mandibles, maxillae, procoxal cavities, elytra, wings, metendosternite, legs, last ventrite, absent defensive glands, and female structures), but there are differences in the tentorium, aedeagal orientation, and absence of ventral pits of the male. There is some resemblance to Phrenapatinae in the eyes, tormal arms of labrum (but not shape of latter), antennae, molar surfaces of mandibles, maxillae, tentorium, wings, metendosternite, legs, grooved last ventrite, ovipositor, and absent defensive glands, but these are mostly plesiomorphies or possible convergences and *Aphthora* does not display any of the apomorphies of Phrenapatinae, notably the tridentate mandibles, absence of a scutellary stirole, or types of mesoscoanal closure described by Doyen and Lawrence (1979). More importantly, Phrenapatinae have a lageniine type of female tract, that is, a large bursa with a simple tubular spermathecum-accessory gland emerging from around the middle of the tract, whereas *Aphthora* has a typical tenebrionine tract exactly as in *Ulomotypus* (Fig. 5). The ovipositor is also as in *Ulomotypus*, but ovipositor structure in tenebrionids relates to the medium in which the female oviposits, rotten wood in this case, and it is rarely of phylogenetic significance.

In discussing the larva of *Aphthora*, Watt (1974) saw some similarities to Diaperini (‘Platydemini’) as well as Ulomini, but in the adults examined here the only such similarities are believed to be symplesiomorphies.

*Aphthora* is clearly a basal member of the tenebrionine branch in the company of Palorinae and primitive Tenebrioninae, but one which does not exactly fit into any known tribe. Probably a new tribe of Tenebrioninae is indicated, but this is not a step which should be taken now without further study. As a tribe it would be difficult to define because of the small number of apomorphies.

**Included species.** *A. rufipes* Bates.

Matthews: Tenebrionidae Palorinae


Demtrius Broun

Diagnosis. Form elongate, subparallel, prothorax narrower than hind body, rectangular, fully margined. Total length 5.0 – 6.0 mm. Eyes transverse, deeply emarginate. Labrum strongly transverse, largely concealed under clypeus, tormal arms basal in position with posteriorly directed medial extensions. Antennae gradually expanding to apices, not clubbed, apical segment reduced, with simple sensilla only. Mandibles bidentate, mola finely striate. Apical maxillary palpomere securiform, lacinia armed with a slender uncus. Procoxal cavities closed externally, open internally. Mesocoxal cavities open, although only slightly so with mesepimeron only partially extending toward coxal cavity. Elytra with 9 striae and scutellary striole, epimera abruptly abbreviated before apices. Wings with complete venation, with medial fleck. Metendosternite with laminae. Legs slender, tarsi 5-5-4, tarsomers not expanded. Abdomen with membranes visible between last 3 ventrites, edge of last ventrite not grooved. A pair of large defensive gland reservoirs present, aedeagus not inverted, alae present as extensions of basal part of parameres. Female not seen.

Comments. The above combination of characters corresponds to that of the tribe Titaenini, subfamily Tenebrioninae, and there can be no doubt that this is where Demtrius belongs, only one character being atypical: metendosternite with laminae. The armed lacinia is shared among the Titaenini with Pseudhelops Guérin, but not the other genera. The abbreviated elytral epipleura are particularly diagnostic of Titaenini, and the parallel form with a porrect head is similar to that of Leaus Matthews and Lawrence (here transferred to Titaenini) although the procoxae are not as strongly approximated as in the latter genus and there are
many other minor differences.

Titaenini is an Austral Gondwanan tribe which is also represented in the New Zealand region by *Artystona* Bates, *Partystone* Watt, *Cerodolus* Sharp and *Pseudhelops* Guérin, in Australia by *Titaena* Erichson and *Leaus* Matthews and Lawrence, and in New Caledonia by *Callismilax* Bates.

**Included species.** *D. carinulatus* Broun.

**Material examined.** North Island (all records NZAC except where noted). **RI,** 1, Oraukura Gorge, Taihape, 14 Oct 1954?, under loose bark of dead white pine, R. M. Bull Collection. **South Island.** **BR,** 1, L. Rotoroa, 1200', 2 or 3 Jan 1939, E. S. Gourlay. **CO,** 1, Woodside, Taieri, 28-10-23, C. E. Clarke (AMNZ), 1, same but 11-11-28 (AMNZ). **NN,** 1, Mt Robert, Nelson (Rotoiti), 2000', 2 Nov 1958, J. I. Townsend, R. M. Bull Collection; 1, Mt Robert, 610 m, 2 Nov. '58, J. C. Townsend; 1, L. Rotoiti, 25 Dec 1976, J. T. Nunn (JNIC); 1, same label data but J. I. Townsend collection (JNIC). **SD,** 2, Tahakopa, Catlins, 17-3-20 (AMNZ); 1, same but not dated.

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**References**


