RECONSTRUCTED PHYLOGENY AND RECLASSIFICATION OF THE GENERA OF DONACIINAE (COLEOPTERA: CHRYSOMELIDAE).

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ABSTRACT

Based on phylogenetic analysis of genera of Donaciinae, three tribes of Donaciinae are recognized: Plateumarini, new tribe, Donaciini Kirby and Haemoniini Chen. All described genus- and species-group taxa are placed within this tribal classification, except Donacia microcephala *Daniel and Daniel (uncertain generic assignment in Donaciini) and* Neohaemonia voronovae *Medvedev (uncertain generic assignment in Haemoniini).* Poecilocera *Schaeffer is removed from synonymy with* Sominella *Jacobson and includes a single Nearctic species,* P. harrisii *(LeConte).* Prodonacia *Chen and* Donaciocrioceris *Pic (both monobasic) are newly placed as junior subjective synonyms of* Donaciasta *Fairmaire.* Donacia *(*Donaciomima*) Medvedev is removed from synonymy with* Donacia, *and is recognized as a valid subgenus, including most species hitherto placed in* Donacia s. str. *(i.e., 22 Nearctic and 52 Palaearctic species). The fossil genus* Hemidonacia *Haupt is placed as junior subjective synonym of* Donacia *(*Cyphogaster*) Goecke;* Eodonacia *Haupt is placed as junior subjective synonym of* Donacia *(*s. str.*) Fabricius.* Donaciella *Reitter is elevated to generic status, with the Nearctic species* Donacia pubicollis *Suffrian and Palaearctic species* Donacia clavipes *Fabricius,* Donacia cinera *Herbst, and* Donacia tomentosa *Ahrens transferred to this genus.* Donacia reticulata *Gyllenhal and* D. kraatzi *Weise are transferred to* Sominella *from* Donacia, *and* Pseudodonacia *and* Plateumaroides *(both based on* D. kraatzi*) are removed from synonymy with* Donacia *and transferred to synonymy with* Sominella.

Among Palaearctic D. *(*Donaciomima*) species,* D. fukiensis *Goecke is placed as junior subjective synonym of* Donacia clavareaui *Jacobson, and* D. ochroleuca *Weise and* D. flavidula *Reitter are placed as junior subjective synonyms of* D. fennica *Paykull.* Donacia *(*Cyphogaster*)* tuberfrons *Goecke is placed as a junior subjective synonym of* D. transversicollis *Fairmaire, which is assigned to this subgenus.* Donacia *(*Donacia*)* clarki *Monrós and* D. indica *Clark are placed as junior subjective synonyms of* D. recticollis *Jacoby.* Haemonia piligera *Weise and* Haemonia incostata *Pic are placed as junior subjective synonyms of* Macroplea pubipennis *(Reuter).*

Relationship of sagroid subfamilies (Sagrinae + Criocerinae + Donaciinae) was examined to select an outgroup of Donaciinae. Criocerinae were found to show more synapomorphies in common with Donaciinae, and neither Criocerinae nor Donaciinae could be directly derived from Sagrinae. Despite lack of clarity of relationship, altered polarity of certain characters did not affect reconstruction of relationships of genera of Donaciinae.

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TABLE OF CONTENTS

INTRODUCTION

Donaciinae, among the Chrysomelidae, is a relatively small group of aquatic beetles comprised of fewer than 160 species, but most of the world fauna has been confused taxonomically. Numerous faunistic treatments provide means of identification of regional faunas (*e.g.*, Gruev and Tomov 1984, Kimoto 1983, Hatch 1971, Mohr 1966, Gressitt and Kimoto 1961, Schaeffer 1925, and many others). No genus has been monographed in its entirety except *Plateumaris* Thomson (Askevold, in prep. a), *Donaciasta* Fairmaire (Askevold, in prep. d) and *Neohaemonia* Székessy (Askevold 1988); *Donaciasta* was incompletely treated by Monrós (1958) and Jolivet (1972), and *Donacia* (*Cyphogaster*) Goecke was treated by Goecke (1934, 1935, 1936, 1944).

The subfamily has not been monographed broadly at the genus level because authors of regional treatments have accepted existing classifications. Perhaps the closest attempt to propose a phylogeny of donaciines was by Goecke (1960b); no empirical basis was provided, and it was based essentially on his existing classification (Goecke 1960a). Failure to question existing classifications in catalogues has led to taxonomic confusion and incorrect generic assignment, as for *Donaciasta*. This acceptance has also led to ill-founded zoogeographic analysis (*e.g.* Borowiec 1984). *Donacia* Fabricius has appeared first in most catalogues and probably has been inferred to be most primitive among donaciines; Monrós (1959) alone placed *Plateumaris* first (*i.e.* most primitive), an arrangement reversed by Jolivet (1970).

The present study grew from research to monograph *Plateumaris* and to assess the limits and phylogenetic position of that genus. It became an attempt to revise the generic assignment of as many of the described Donaciinae as possible, to analyze relationships of the genera, and to develop a new classification of donaciines. Most members of the subfamily have been examined, several genera monographed (Askevold 1988, in prep. a,d), some taxonomic problems among members of *Donacia* were resolved (Askevold 1987a, b), fossils were studied (Askevold 1990) and the relationship of donaciines to their host plants was analyzed (Askevold, in prep. b). Results and reclassification presented here represent the collective product of these interrelated and interdependent efforts.

MATERIALS AND METHODS

Materials

All New World and most Old World taxa of Donaciinae were studied. Old World taxa examined are listed within the section on reclassification of genera. New World taxa examined, as now reclassified, are listed elsewhere (Askevold, in prep. c). Specimens were personally collected, borrowed, or exchanged from 85 collections and museums, a list of which is given elsewhere (Askevold in prep. a). This revision is based on study of 111 specimens of *Poecilocera harrisii* (LeConte), 48 specimens of *Donaciella pubicollis* (Suffrian), more than 42,000 specimens of the other described and undescribed Nearctic species of Donaciinae, and more than 4,000 specimens of 79 Old World taxa of Donaciinae (excluding 16, names of which are placed in synonymy). I have not examined specimens of 21 Palaearctic taxa which remain unknown to me (these indicated as such in section on reclassification of genera).

The following sagrines were examined: *Atalasis sagroides* Lacordaire, *Ametalla atenodera* Lacordaire, *Ametalla spinolae* Hope, *Megamerus femoralis* Lea, *Mecynodera coxalgica* Boisduval, *Carpophagus banksiae* McLeay, *Polyoptilus erichsoni* Germar, *Diaphanops westermanni* Boheman, and various Oriental and Afrotropical species of *Sagra* Fabricius. I referred also to unpublished data of Mann and Crowson (in prep.) on genitalia of sagrines.

A number of criocerine species in the genera *Lema, Oulema, Lilioceris* and *Crioceris* were examined for general structure, and some of these were examined also for male genitalic structures. I relied principally on the figures of male genitalia of Criocerinae presented in White (in prep.) to infer widespread presence of characters among criocerines. Other than members of Sagrinae and Criocerinae, I have studied many other Chrysomelidae and perhaps some statements (hypotheses or observations) I make take their study into account, though not explicitly.

Methods

A general comment about wording should be made, in view of the general truth observed by Ball (1977) that many phrases in literature of systematic biology are grammatically incorrect. Therefore, the reader is advised that certain phrases should be understood to have a specific meaning. In particular, the use of phrases such as "*Atalasis* Lacordaire is most similar to *Plateumaris*", should be understood to mean "Specimens of members of *Atalasis* are more similar to specimens of members of *Plateumaris* ". Similarly, with regard to sex of specimens, when I state "Endophallus of *Plateumaris aurifer* with... ", this should be understood to mean "Endophallus of male specimens of *P. aurifer* with... ". In other words, I write as though I am discussing taxa, but this should be understood to mean that I am discussing specimens of members of those taxa. I do not use these phrases uniformly; sometimes I use the "correct" form for variation. However, in general, I use the "incorrect" forms because I find the correct forms lengthy and cumbersome.

Techniques and drawings.— The technique used for study of genitalia was that given by Askevold (1988:367) and discussed at length by Askevold (in prep. a) and is not repeated in detail here.

Drawings and figures were made using a Wild M5 dissecting microscope with the aid of a camera lucida.

Philosophy of classification.— An important component of systematics is the observation that nested sets of derived character states form the basis of classification, only in the cladistic school of systematics. A classification based upon reconstruction of phylogeny is ostensibly more stable because there exists only one true pattern of evolution; the classification that most accurately mirrors this pattern should be least altered by future treatments, and addition of new data and/or taxa. From such stability can arise reproducible results, and particularly, predictability about other components of the biota upon which other sciences draw and rely.

Schools of systematics do not agree entirely on how or to what degree classification should be a reflection of evolutionary relationships. Strict cladism dictates development of a strict hierarchical classification from which a phylogeny can be derived directly. However, the evolutionary systematics school diverges from cladistics on this point, attempting to draw evolutionary divergence into the classification as well (Bock 1974). That is, cladistic classifications allow only holophyletic and monophyletic taxa, while evolutionary classifications accept paraphyletic taxa as valid (Ashlock 1974, Cronquist 1987) because characters are differentially weighted as to their significance in the evolution of organisms (Mayr 1974). Thus, an evolutionary classification can reflect aspects of evolutionary phenomena or important structural innovations that are responsible for radiation in a group of organisms, while a strictly cladistic classification reflects only pattern of phyletic relationship.

While I ascribe to cladistic methods of phylogenetic analysis, I am also forced to accept a non-cladistic philosophy relating to derivation of classifications, at least among donaciines at the supra-generic level. Hull's (1979:437) simple assessment sums up my conclusions, that "the cladists' rules for classifying are simple enough, but that the resulting classifications are not." Disney (1989) observed that "Paraphyletic taxa... are avoided on principle, but in practise one is always confronted by 'residual paraphyletic groups'."

Thus, I have accepted paraphyletic groups in the Donaciinae, partly because I am not able to resolve the relationships of all genera, or because some clades are not well defined. I do so because such a tribal classification is more useful in conveying information about the state of knowledge of the evolution of Donaciinae than is the lack of a tribal classification. This tribal classification also allows statements about the successive grades donaciines have achieved with respect to host plant use (Askevold, in prep. b). Such statements would be confused by a more complicated higher classification. I suspect similar treatments in other groups of Chrysomelidae would result once they are analyzed, because much of evolution proceeds in grades of adaptation (see Erwin 1981, for example). It is my opinion that no strictly cladistic classification for most groups of chrysomelids could be manageable at this time, and donaciines are no exception.

Methods of phylogenetic reconstruction.— Phylogenetic reconstruction was carried out according to the principles of Hennig (1965,1966), which have been discussed at length by many authors (*e.g.* Kavanaugh 1972; Ashlock 1974; DeJong 1980; Wiley 1981). These methods are simply the process of searching for characters, by comparison among a number of related taxa, that one would consider useful for cladistic analysis (phylogenetic reconstruction). Such characters should be shared-derived, or synapomorphies.

I used two methods of reconstructing phylogenies (*i.e.* manual and computer-aided), and eventually selected a compromised result that was consistent both with certain *a priori* views about donaciine evolution, and to some extent with general parsimony; I did not take exception to Neff's (1986) advocating of *a priori* weighting as Sharkey (1989) did. Initially, I used a manual method based on first selecting principal characters that I thought were significant to partially resolve a tree and then added the remaining characters to resolve more fully this tree to support groupings. PAUP [Phylogenetic Analysis Using Parsimony, Version 2.4.1 (Swofford, 1985)] was used to test these reconstructions, and to demonstrate alternate character distributions on trees.

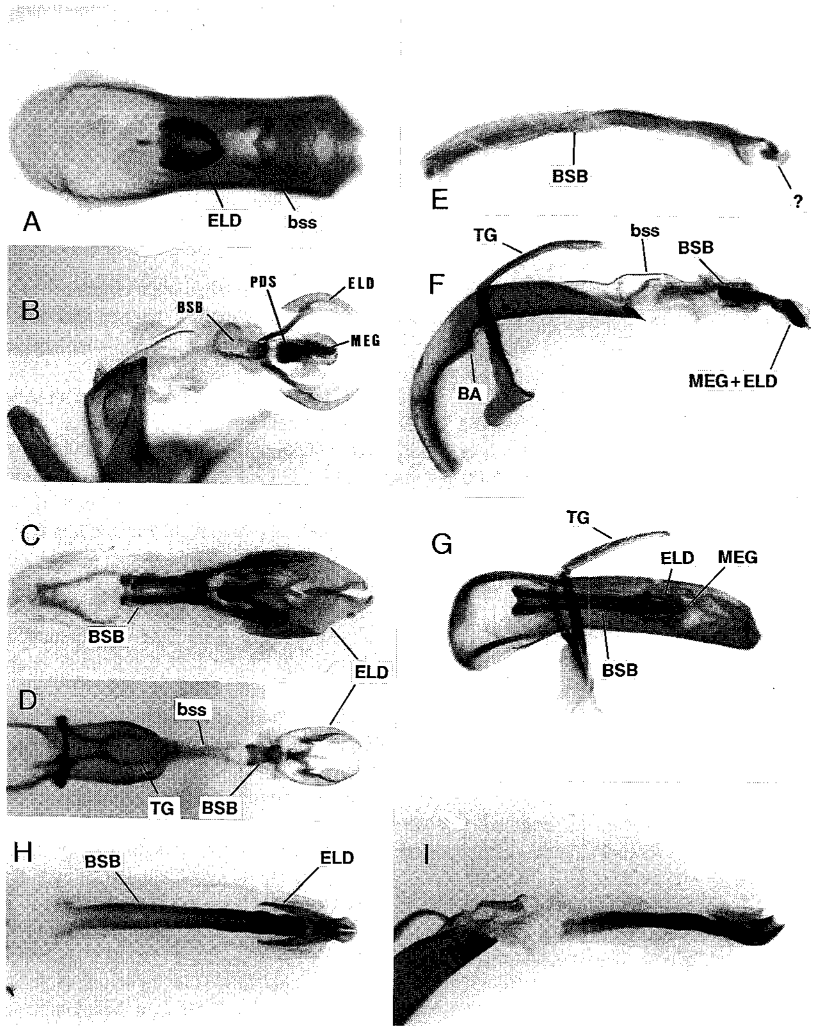
STRUCTURES USED IN CLASSIFICATION OF DONACIINAE

Elsewhere, I presented discussion of structures that are important in classification of donaciines (Askevold, in prep. a). I present here only some cursory remarks about endophallic structure in donaciines. Readers are referred to this reference for detailed information about endophallic structure in particular. In the character analysis, below, I give details about other structures as they pertain to reconstruction of phylogeny.

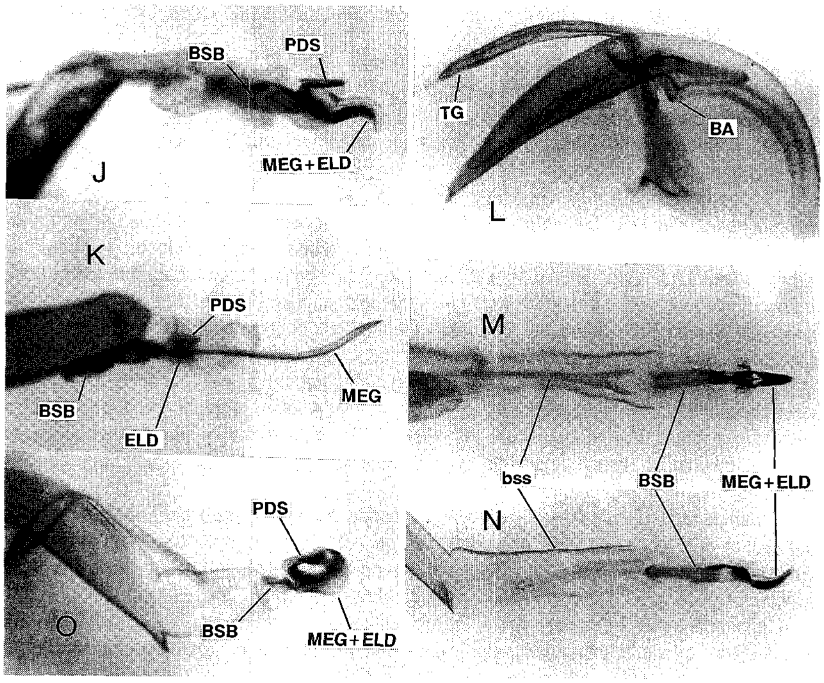
The endophallus consists of a several sclerites which are similar in arrangement among the sagroid subfamilies (*i.e.* the Sagrinae + Criocerinae + Donaciinae). I homologize them among genera of Donaciinae at least, though I am not fully convinced that all sclerites found in similar positions on the endophallus of sagrines and criocerines, are homologous with those found in donaciines. The important endophallic sclerites I use are assigned the following codens by which they are hereafter referred to in the text: BSB (basal supporting block), ELD (endophallic lateral digit), PDS (paired dorsal sclerite) and MEG (median ejaculatory guide) (see Photographs A-O). The BSB is a basal sclerite with which the remaining apical endophallic sclerites articulate (*i.e.* basal with respect to the apical sclerites; all sclerites are apical, except for those involved with sac-retracting - bss, Phots. A, M).

RECONSTRUCTED PHYLOGENY OF WORLD GENERA OF DONACIINAE

Reconstruction of relationships of donaciine genera proceeded, of necessity, along two lines of analysis. Character analysis requires understanding of out-group relationship. Some authors, such as Crowson (1945), have been rather explicit and have stated that certain sagrine genera are probably most closely related to donaciines. Others, such as Schmitt (1985a,b, 1988), have not made use of explicit out-group criteria in examining relationships among sagroid subfamilies. Therefore, the question of out-group to Donaciinae has not been examined critically. This problem is the first examined below because analysis of relationships of donaciine genera may depend upon the out-group



PHOTOGRAPHS A-I: Photographs of male genitalia of Sagrinae and Donaciinae. **A.** Dorsal aspect of median lobe of *Atalasis sagroides* Lacordaire, with endophallus in repose. **B.** Dorsal aspect of everted endophallus of *Plateumaris flavipes* (Kirby). **C.** Dorsal aspect of *Plateumaris robusta* (Schaeffer). *D.* Dorsal aspect of apex of median lobe, tegmen and everted endophallus of *Plateumaris neomexicana* (Schaeffer). **E.** Lateral aspect of endophallus of *Poecilocera harrisii* (LeConte). **F.** Lateral aspect of median lobe, tegmen and everted endophallus of *Donacia* (*Donaciomima*) *magnifica* LeConte. **G.** Dorsal aspect of median lobe and tegmen of *Sominella macrocnemia* (Fisch. v. Waldheim), with endophallus in repose. **H, I.** Dorsal and lateral aspects, respectively, of *Donacia* (*Donaciomima*) *hirticollis* Kirby. BA = subbasal angulation of median lobe; BSB = basal supporting block; ELD = endophallic lateral digit; MEG = median ejaculatory guide; PDS = paired dorsal sclerites; TG = tegmen.



PHOTOGRAPHS J-O: Photographs of male genitalia of Donaciinae. **J.** Lateral aspect of endophallus of *Donacia* (*Donaciomima*) *tuberculifrons* Schaeffer. **K.** Lateral aspect of endophallus of *Donaciasta perrieri* (Fairmaire). **L.** Lateral aspect of median lobe and tegmen of *Donacia* (*Donacia*) *cincticornis* Newman with endophallus in repose. **M, N.** Dorsal and lateral aspect, respectively, of endophallus of *Donacia cincticornis*. **O.** Lateral aspect of apex of median lobe and tegmen of *Macroplea pubipennis* (Reuter), with endophallus everted. BA = subbasal angulation of median lobe; BSB = basal supporting block; ELD = endophallic lateral digit; MEG = median ejaculatory guide; PDS = paired dorsal sclerites; TG = tegmen.

selected.

I develop hypotheses about sagroid subfamily (*i.e.* Sagrinae + Criocerinae + Donaciinae) relationships, which I use as a basis for determining polarity of characters. All characters considered for reconstruction of relationships are examined below, whether I find them useful as synapomorphies or not, and at what taxonomic level. I begin with the character analysis, proceeding to analysis of subfamily relationships, then to relationships of donaciine genera and problems in their classification.

Character analysis

Characters used in analysis of phylogenetic relationships of genera are coded in two ways. The plesiomorphic state is coded as 0, and states in a transformation series are coded as 1,2,3, in progressively derived apomorphic states. Some characters that have independently-derived apomorphic states (*e.g.* tegmen, ovipositor, tibial spurs, host plants) are divided into component characters (*e.g.* 24a-b, 27a-c, 30a-b). Character states and their polarities are summarized in accompanying tables: Tables 1 and 2 for sagroid relationships; and Tables 3 and 4 for donaciine generic relationships.

Character 1. Ligula of labium.— (see Askevold, 1988, Figs. 43-44). Two states: plesiomorphic, ligula membranous and bilobed; apomorphic, ligula not membranous, not bilobed.

Among members of Sagrinae and some other apparently primitive groups, (*e.g. Syneta* Dejean, *Orsodacne* Latreille, Aulacoscelinae and Megalopodinae) the ligula is bilobed and membranous (Crowson 1945), while in those of Donaciinae and Criocerinae this is not so. The derived, non-membranous, non-bilobed state could be considered synapomorphic for Criocerinae + Donaciinae, though Schmitt (1985a,b) did not consider this possibility. It is more parsimonious to consider a single, rather than parallel, reduction of ligular lobes among closely related groups, so it is arguable that the state found in criocerines and donaciines is synapomorphic. The derived state should be considered a reduction from the plesiomorphic state, and therefore could have occurred independently in many lineages, as appears to be so among other chrysomelid groups.

Tentatively I consider ligular form synapomorphic for the Donaciinae. On the basis of the hypothesis that donaciines are derived directly from a sagrine lineage, and not from a common ancestor of Criocerinae + Donaciinae, the non-bilobed ligula must be considered independently derived in criocerines.

Character 2. Tibial spurs.— Three states: plesiomorphic, all tibiae with two articulated spurs; apomorphic, only pro- and mesotibia with one articulated spur each, metatibia without articulated spur; apomorphic, all spurs lost.

Presence of two articulated spurs on all tibiae is probably the ground plan state in Chrysomelidae, retained in a few groups such as Megalopodinae, some *Syneta* (Synetinae) and certain Eumolpinae (*Hornius* Fairmaire, *Stenomela* Erichson). Three states are recognized in sagroids: criocerines retain the 2-2-2 state (some taxa with reduction) (Schmitt 1985a,b), while donaciines are 1-1-0 and sagrines have no articulated spurs [*i.e.* Sagrinae as defined by Seeno and Wilcox (1982), not as by Crowson (1945)].

If criocerines and donaciines are derived from sagrines, then they too should lack tibial spurs, by implication of Dollo's Law, and so this character presents a difficult problem in logic. It is unlikely that criocerines and donaciines re-evolved spurs. It is easier to consider that the reduced state, 1-1-0, is derived from the 2-2-2 state of an ancestor common to donaciines and criocerines, while sagrines independently lost tibial spurs subsequent to divergence from the remaining crioceriform lineage early in sagroid evolution. I have no explanation of this problem, in view of other characters that suggest alternate hypotheses of sagroid relationships, and I postulate tentatively that the 1-1-0 state is synapomorphic for donaciines.

Character 3. Larval spiracular hooks.— Three states: plesiomorphic, spiracular hooks on eighth abdominal segment absent; apomorphic 1, spiracular hooks present; apomorphic 2, spiracular hooks elongate.

Spiracles of the eighth abdominal segment of larvae with hooks are unique to donaciines. In members of *D.* (*Donacia*) and *D.* (*Cyphogaster*) these hooks are much more elongate than in other taxa; their state in *Donaciasta* is unknown. I hypothesize that greatly elongate hooks are synapomorphic for these two subgenera of *Donacia*, and that their length is related to use of host plants, the Nymphaeaceae. Larvae of *Donaciasta* also may be associated with Nymphaeaceae and therefore may have similar hook length.

Character 4. BSB of endophallus.— (Photographs A-O). Two states: plesiomorphic, BSB absent; apomorphic, BSB present. This structure was discussed in detail by Askevold (in prep a.).

In the sagrines examined, no sclerite resembling a BSB was found. Criocerines examined possess a BSB or a BSB-like sclerite. Figures of male genitalia of criocerines (White, in prep.), and those examined, show a structure that is similar to that of donaciines. I infer this occurs in all criocerines. Therefore, it is tempting to consider presence of a BSB as synapomorphic at least for Criocerinae + Donaciinae, and possibly for all sagroids.

Character 5. ELD of endophallus.— (Photographs A-O). Three states: plesiomorphic, ELDs absent; apomorphic 1, ELDs present, moveable, basally articulated with BSB, and easily distinguishable (Phot. A-D); apomorphic 2, ELDs contiguous at least apically (Phot. G), usually from base to apex, enclosing the MEG (Phot. E, J-O).

This character was discussed in detail by Askevold (in prep. a). Among sagrines and criocerines examined, in particular specimens of *Atalasis*, two sclerites that resemble the ELDs of *Plateumaris* are visible. Thus I hypothesize that the state possessed by *Plateumaris*, with ELDs separate and articulating, is plesiomorphic. In most other donaciines the ELDs are at least apically contiguous, and are generally contiguous from base to apex, enclosing the MEG. The contiguous state I hypothesize is synapomorphic for all members of Donaciini + Haemoniini. I could not interpret the state in *Poecilocera harrisii* because I was not able to homologize all endophallic sclerites with those of other genera.

Character 6. Basal angulation of median lobe.— (Photographs F, L). Two states: plesiomorphic, basal angulation of median lobe absent; apomorphic 1, basal angulation present (Phots. F, L); apomorphic 2, basal angulation lost.

In sagrines, *Plateumaris* and *Poecilocera* the median lobe does not have an angulation subbasally, and this state is hypothesized as plesiomorphic. Among Criocerinae and most Donaciini (except *Donaciasta* and some members of *Sominella* Jacobson) and Haemoniini, a basal angulation is present; its absence from *Donaciasta* and some members of *Sominella* is hypothesized as a secondary loss. If criocerines were considered an out-group, then absence of this structure in donaciines would have to be considered apomorphic. *Plateumaris* and *Poecilocera* then could be considered sister taxa on the basis of shared loss, with two species of *Sominella*, *Donaciasta*, and Sagrinae independently having lost this structure. However, shape and prominence of the angulation in criocerines is very different from that of donaciines, and I conclude they are derived independently.

Character 7. Underside of median lobe.— Two states: plesiomorphic states, surface of underside of median lobe smooth, or more commonly, striate; apomorphic, underside of median lobe with longitudinal furrow or flattened.

The apomorphic state is present only in members of *Donacia s.str.* and *D.* (*Cyphogaster*) [except *D.* (*Donaciomima*) *tuberculifrons* Schaeffer], and is hypothesized as synapomorphic for these two subgenera of *Donacia*.

Character 8. Elytral apex.— (see Askevold, in prep a, Figs. 9-13 and 1988, Figs. 34-35). Three states: plesiomorphic, apex of elytron rounded; apomorphic 1, elytral apex truncate; apomorphic 2, elytral apex with large spine at outer angle.

The elytral apex of most sagroids and *Plateumaris* is rounded. That of *Sominella reticulata* Gyllenhal, *Donacia microcephala* and members of *Donaciella* is also rounded, which I consider reversals. *Poecilocera* and most

Donaciini have truncate elytra, or with some slight modification, while Haemoniini are characterized by truncate elytra with an apical spine. The truncate condition I hypothesize is synapomorphic for *Poecilocera* + Donaciini + Haemoniini.

Character 9. Sutural interval of elytron.— (see Askevold, in prep. a, Figs. 10-13). Two states: plesiomorphic, sutural interval of elytron narrowed subapically, the inner and outer beads convergent and exposing an explanate lower sutural margin; apomorphic, inner and outer beads convergent only at apex, lower sutural margin only narrowly exposed.

The state hypothesized as plesiomorphic is present in *Plateumaris* and *Poecilocera*; it is also present in most sagrines (*cf.* Table 2), as well as a few criocerines, and is certainly a sagroid ground plan character. Monrós (1959) stated that this character is also present in *Donaciocrioceris dentatus* Pic (here transferred to *Donaciasta*), but the elytral apex in this species is not different from other members of *Donaciasta* and other Donaciini.

Character 10. Mandibular teeth.— (Figs. 8-10, see also Askevold, 1988, Figs. 45-46). Four states: plesiomorphic, mandible apically with single tooth, outer margin curved uniformly; apomorphic 1, mandible with two apical teeth, profile slender, apical teeth approximate, no prominent occlusal edge, the outer margin forming uniform curve; apomorphic 2, apical profile slightly explanate, the ventral apical tooth displaced from apex, forming short cutting edge, and outer margin rounded or slightly angulate; apomorphic 3, apical teeth more dramatically divergent and forming a long, finely serrate occlusal cutting edge, and outer margin distinctly angulate.

Sagrines (and cerambycids and bruchids) have only a single blunt or acute apical tooth and the mandible is sickle-like in shape. Among criocerines, most taxa examined possess a mandible which is distinctly bidentate apically, like that of donaciines (a few are tridentate). The mandible of criocerines is somewhat more robust, and less sickle-shaped than is found in *Plateumaris* and *Poecilocera*. It is tempting to consider the bidentate state synapomorphic for Criocerinae + Donaciinae. However, on the basis of selection of Sagrinae (*Atalasis*) as out-group, the bidentate mandible must be considered independently derived in criocerines. Similarly, the more complex, tridentate mandible found in many other chrysomelids is also independently derived.

In specimens of *Plateumaris* and *Poecilocera*, the apical teeth are slender, and the lateral surface is uniformly rounded; in the Donaciini and Haemoniini the apical teeth are at least slightly divergent. The ventral tooth is shorter and somewhat displaced basad, forming at least a short cutting occlusal edge. The mandible, therefore, is not so slender in profile, and rounded or a little angulate externally. I hypothesize that this state is synapomorphic for Donaciini + Haemoniini. In members of *D.* (*Donacia*) and *D.* (*Cyphogaster*), the apex is explanate, the ventral tooth markedly displaced ventrally and basad forming a prominent, serrate cutting edge; the outer margin in these taxa is prominently angulate. I hypothesize that this condition is synapomorphic for these two subgenera of *Donacia.*

One could consider several independent characters as comprising this series, but I think they are integrated as a single functional system that is related to host plant type and ovipositional behaviour. This is especially true of those members which are Nymphaeaceae-associated [*i.e.*, *Donacia s.str.* and *D.* (*Cyphogaster*)] Females of these species cut a hole in the leaf surface (floating) and lower the abdomen through this hole to oviposit. It seems a mandible of this shape, and with a serrate occlusal edge, would be effective in cutting a hole in a flat surface. Leaves of Nymphaeaceae are thick, and a long occlusal edge would be necessary in order to puncture the leaf.

Character 11. Hypomeral pubescence.— (see Askevold, 1988, Figs. 23, 27, and in prep. a, Figs. 14-17). Four states: plesiomorphic, pubescence above procoxa absent, hypomeron glabrous above sternal-hypomeral suture; apomorphic 1, sparse setae present; apomorphic 2, prominent quadrate pubescent area present above procoxa, may occupy entire hypomeron, but generally only half; apomorphic 3, hypomeral pubescence lost.

Askevold (1988:393, 407) discussed the hypothesized adaptive significance of supracoxal pubescence among Donaciinae, and presented a simplified transformation series of absence as plesiomorphic, and presence as derived, with *Macroplea* as having secondarily lost this pubescence. However, *Poecilocera harrisii*, *Sominella macrocnemia* (Fisch. v. Waldheim), and *S. reticulata* possess some sparse, inconspicuous pubescence that could be considered intermediate between complete absence in *Plateumaris* and *S. longicornis* (Jacoby) and other Donaciini and Haemoniini. I have found no single synapomorphy to define *Sominella* as a monophyletic unit; tentatively, I group the four species together in *Sominella* on the basis of gross similarity, and exclusion from other Donaciini, but note that alternative equally parsimonious explanations are possible (*cf.* Table 4, and Figs. 16-18).

Character 12. Clypeal length.— (Figs. 1-3; see also Askevold, 1988, Figs. 38-39). Two states: plesiomorphic, clypeus short; apomorphic, clypeus elongate. The clypeal length in donaciines is typically short, such that the mandibular articulation is proximal to the antennal bases. In *Donaciasta* the clypeus is elongate, the clypeogenal suture longer; in *Neohaemonia* mandibular insertion is slightly removed from the antennal bases, but in *Macroplea* it is much like that of *Donaciasta*. I hypothesize the derived state to have arisen independently in *Donaciasta* and Haemoniini.

Character 13. Clypeal depression.— (Fig. 3). Two states: plesiomorphic, surface of clypeus flat or somewhat convex; apomorphic, clypeus with triangular or ⊥-shaped depression. The derived state occurs only in members of *Donaciasta* (most specimens), in which there is a shallow transverse furrow just above the clypeolabral suture.

Character 14. Pygidial shape, ♀♀.— (Fig. 6). Two states: plesiomorphic, pygidium apically broadly rounded or emarginate, more or less quadrate in overall shape; apomorphic, pygidial apex acute or narrowly rounded, more or less triangular and elongate in overall shape. The pygidium of female donaciines is typically rounded or emarginate apically (extensive homoplasy in states), and in overall shape the tergum is rather quadrate. In members of *D.* (*Donacia*) and *D.* (*Cyphogaster*), the pygidium is elongated, in overall shape much longer than broad, and with apex acute or narrowly rounded. This state is considered synapomorphic for these two subgenera of *Donacia*.

Character 15. Dorsal colour.— Two states: plesiomorphic, metallic in colour; apomorphic, metallic pigmentation lost or reduced, colour therefore piceous, rufous, or testaceous.

Donaciines are typically brightly metallic in colour, dorsally and ventrally. A few species of *Plateumaris* may be piceous or testaceous, as are several *D.* (*Donaciomima*) Medvedev, but in most of these taxa only some specimens lack metallic colour, while most or many are typically metallic. In many *Donacia* exclusive of *D.* (*Donaciomima*), specimens are entirely rufous or testaceous, or they may have a slight metallic luster, while some are entirely metallic (*e.g. D.*

crassipes Fabricius, *D. ozensis* Nakane, *D. proxima* Kirby), or are largely metallic with some reduction of metallic colour [*e.g.* many *D.* (*Cyphogaster*)].

Haemoniini are typified by lack of metallic colour, for which the state is considered synapomorphic as a consequence of development of a fully aquatic life history (Askevold 1988). Loss of colour in other groups, including several *D.* (*Donaciomima*) and most other *Donacia* should be considered independently achieved; Members of *Donaciasta* virtually completely lack metallic colouration, save a faint lustre; they are otherwise rufous (*e.g. D. goeckei*) or piceous (*D. perrieri*) in colour ventrally and dorsally (but head black in *D. assama*). I note that this character correlates with others to support grouping of *Donaciasta* + Haemoniini as sister taxa, and include it as synapomorphic for this grouping.

Character 16. Abdominal tubercles ♂♂.— Two states: plesiomorphic, males without pair of glabrous tubercles medially on basal abdominal sternum; apomorphic, with pair of small glabrous tubercles medially on basal abdominal sternum.

Males of *D.* (*Cyphogaster*) possess a pair of small, glabrous tubercles medially on the basal abdominal sternum. These structures are unique to the subgenus *D.* (*Cyphogaster*), with the exception of *D.* (*Donaciomima*) *dentata* Hoppe. In this latter species the tubercles probably are derived independently; Goecke (1934) suggested that they are not homologous, but the possibility that they are cannot be discounted, for the subgenus *Donaciomima* may be paraphyletic.

Character 17. Tarsal claw segment.— (see Askevold, 1988, Fig. 31). Two states: plesiomorphic, length of claw-bearing segment shorter; apomorphic, claw-bearing segment elongate. Askevold (1988) discussed this character, and considered the elongate claw segment as synapomorphic for Haemoniini.

Character 18. Ovipositor, subapical setae.— (see Askevold, in prep a, Figs. 237-239). Two states: plesiomorphic, setae on sternum and tergum VIII; apomorphic, setae of sternum and tergum VIII absent.

Taxa with a sclerotized ovipositor also lack the fine setae present in other groups of donaciines (see next character). Loss of setae from these segments is considered to have occurred independently in *Plateumaris* and *Donaciella* Reitter, but it is synapomorphic for each of these genera. It seems that taxa which oviposit within plant tissue, as members of *Plateumaris* at least, appear to do, would not need sensory setae on the ovipositor surface because they would tend to be abraded anyway.

Character 19. Ovipositor sclerotized.— (see Askevold, in prep. a, Figs. 237-239). Two states: plesiomorphic, tergum and sternum VIII pliable, not sclerotized markedly, and truncate apically; apomorphic, tergum and sternum VIII prominently sclerotized and apically acute, sternum VIII often with serrate apical margins.

Members of *Plateumaris* possess the most heavily sclerotized ovipositor. Two species of *Donaciella*, the Nearctic species, *D. pubicollis*, and the Palaearctic species, *D. clavipes* (Fabricius), possess an ovipositor that is similar to that of *Plateumaris*. Two other species of *Donaciella*, *D. cinerea* (Herbst) and *D. tomentosa* (Ahrens), have the ventral valve acute, and more heavily sclerotized than is usual among *Donacia*. I consider the state possessed by *Plateumaris* as synapomorphic for the genus, and the state found in *Donaciella* as independently derived. The less developed state in the species of *Donaciella* is probably intermediate between the plesiomorphic state and the more highly derived state found in the other two members of the genus.

Character 20. Ovipositor valve length.— (see Askevold, in prep a, Figs. 237-239). Two states: plesiomorphic, dorsal valve (tergum VIII) and ventral valve (sternum VIII) of equal length; apomorphic, ventral valve longer than dorsal valve.

Donaciines, as well as other sagroids, normally have the tergum and sternum VIII of an equal length, and not functioning as discussed in the previous character (#19). The elongate ventral valve (sternum VIII) is clearly a derived character state.

Character 21. Mesosternal width.— (Fig. 5). Two states: plesiomorphic, mesosternum narrow between mesocoxae; apomorphic, mesosternum, especially of female specimens, broad between mesocoxae, wider than half the mesocoxal diameter.

The mesosternum of sagroids is typically narrow, and this state is retained by most donaciines. Members of *D.* (*Donacia*) and *D.* (*Cyphogaster*), especially females, possess a broad mesosternum; therefore these insects are broader across the humerus than is typical of other donaciines. This broader body form occurs similarly in a number of taxa of *D.* (*Donaciomima*) and in *Donaciasta*, but very prominently so in members of *D.* (*Donacia*) and *D.* (*Cyphogaster*). In general, it seems the species that live on plants with floating leaves are broader in body shape, and have a broader mesosternal process, but among species of *D.* (*Donaciomima*) there is considerable variation. However, the species of the former two subgenera of *Donacia* are typically so prominently widened that I consider the extreme state they possess as synapomorphic for members of those two subgenera.

Character 22. Metafemoral tooth.— Two states: plesiomorphic, metafemoral tooth present; apomorphic, metafemoral tooth absent.

Most sagrines, and donaciines, have an acute tooth on the metafemur, and this is certainly a ground plan state. Few criocerines possess a femoral tooth. Males of *Poecilocera*, some species of *D.* (*Donaciomima*), and most species of *D.* (*Donacia*) and *D.* (*Cyphogaster*), possess a second, shorter tooth more proximally placed. A number of taxa have lost the tooth independently, *e.g.* some members of *Plateumaris*, or the tooth is small or absent in some specimens of some species. Loss of metafemoral tooth is associated generally with decrease of metafemoral diameter. All members of the Haemoniini lack the metafemoral tooth, and therefore have very slender metafemora; this state is considered synapomorphic for the tribe Haemoniini. Similarly, species of *Donaciella* lack a tooth (and have slender metafemora), though some specimens of *D. clavipes* possess a small tooth; tentatively I consider the state in *Donaciella* as synapomorphic for members of the genus.

Character 23. Pronotal punctures.— Three states: plesiomorphic, punctation of pronotal disc fine or absent; apomorphic 1, pronotal disc more or less uniformly coarsely punctate; apomorphic 2, pronotal punctation diminished or lost completely.

Pronotal punctation is a variable character state among donaciines, and evidently it is subject to considerable homoplasy. Members of *Plateumaris* show a range of prominence of punctation, while all *Sominella*, *Donaciasta* and most *D.* (*Donaciomima*) are prominently punctate. Pronotal punctation in most *Donaciella* is concealed by pubescence, though punctation is somewhat finer. Coarse punctation could be considered independently derived in the various groups of Donaciini (*i.e.*, at least three times). Alternatively, it is more parsimonious to consider that coarse punctation is synapomorphic for Donaciini + Haemoniini, and that such punctation was lost no more than twice [not counting a few otherwise typical members of *D.* (*Donaciomima*)], perhaps once as synapomorphic for the Haemoniini, and once in the other two subgenera of *Donacia*. Members of *D.* (*Donacia*) and *D.* (*Cyphogaster*) show no coarse punctation that is uniformly distributed in a way that typifies other Donaciini. Largely on the basis of character correlation, lack of coarse punctation in *D.* (*Donacia*) and *D.* (*Cyphogaster*) is hypothesized as synapomorphic for these two sugenera. Askevold (1988) discussed punctation in Haemoniini, and suggested that diminished punctation probably was independent in the various groups of Haemoniini; whether independently lost or acquired by the taxa of Haemoniini that do or do not possess pronotal punctation requires the same degree of homoplasy. Thus, I consider the state of diminished punctation as synapomorphic for the Haemoniini, with subsequent independent additional reduction among other members of the tribe.

Character 24. Frontal and ocular grooves.— (Figs 1-4; see also Schmitt, 1985a, Fig. 41, 1985b, Fig. 10). Three states: plesiomorphic, frontal grooves absent; apomorphic (24a), frontal grooves complete, with grooves deep and connected with ocular grooves; apomorphic (24b), grooves mesad of eyes somewhat to well developed, extending behind eyes. I consider the term frontal grooves in a more restricted sense than have other authors, as detailed below.

Frontal (24a) and ocular grooves (24b) are, in my opinion, two separate structures. The former are actually deeply incised frontoclypeal suture, forming ^-shaped grooves. The latter are entirely unrelated grooves located mesad of the eyes and are usually \ /-shaped or exceptionally V-shaped. In some exceptional groups, such as *Sagra*, the frontal and ocular grooves meet at their apices, forming X-shaped furrows.

Schmitt (1985a,b, 1988) hypothesized that the members of Criocerinae and Sagrinae are sister taxa on the basis of the single character of presence of crossed frontal grooves (Character 24a). He noted that such complete grooves are not typical of all Sagrinae, but that they are typical of Criocerinae. However, he interpreted the character as synapomorphic for the two groups, stating that frontal grooves are absent from members of Donaciinae and the bruchids. However, many donaciines possess the lower, frontoclypeal half, and to some extent also the upper, ocular part of these grooves. Donaciines merely lack the X-shaped complete furrows and have prominent antennal calli (as do some sagrines that lack the X-shaped part).

Most genera of sagrines do not have ocular and frontoclypeal grooves typical of *Sagra*. In fact, of sagrines examined (Table 2), *Sagra* alone possesses complete frontal grooves, and *Carpophagus* MacLeay has short ocular grooves. Therefore I think a reassessment of this character is needed. The frontal and ocular grooves may indeed be derived, but cannot be synapomorphic for Sagrinae + Criocerinae exclusively, as Schmitt (1985a,b, 1988) suggested.

The lower, frontal portion of these grooves occurs in many sagroids, including many donaciines except some more highly derived taxa, despite contrary claims (*e.g.* Schmitt 1985a,b). Some of the more highly derived donaciines have slightly developed frontoclypeal grooves, but they are found in many taxa and should be considered part of the ground plan of donaciines.

The upper, or ocular grooves, are structures that vary in development among sagrines and criocerines (Table 2). At best, frontoclypeal and ocular grooves could be considered part of the ground plan of sagroids, or even variously derived within sagroids, but not of use in resolving relationships at the subfamily level.

In Donaciinae the ocular grooves are indicated by an indistinct glabrous line or shallow furrow. However, in *Donaciasta*, there is a more prominent furrow that extends from near the antennal callus to behind the eyes, much like in some criocerines, and is unique to this genus, among donaciines. The furrow may be homologous with the ocular grooves, but because it is unique among donaciines I must consider it a redevelopment of a groove similar to the ground-plan state, and therefore synapomorphic for the genus (character 24b).

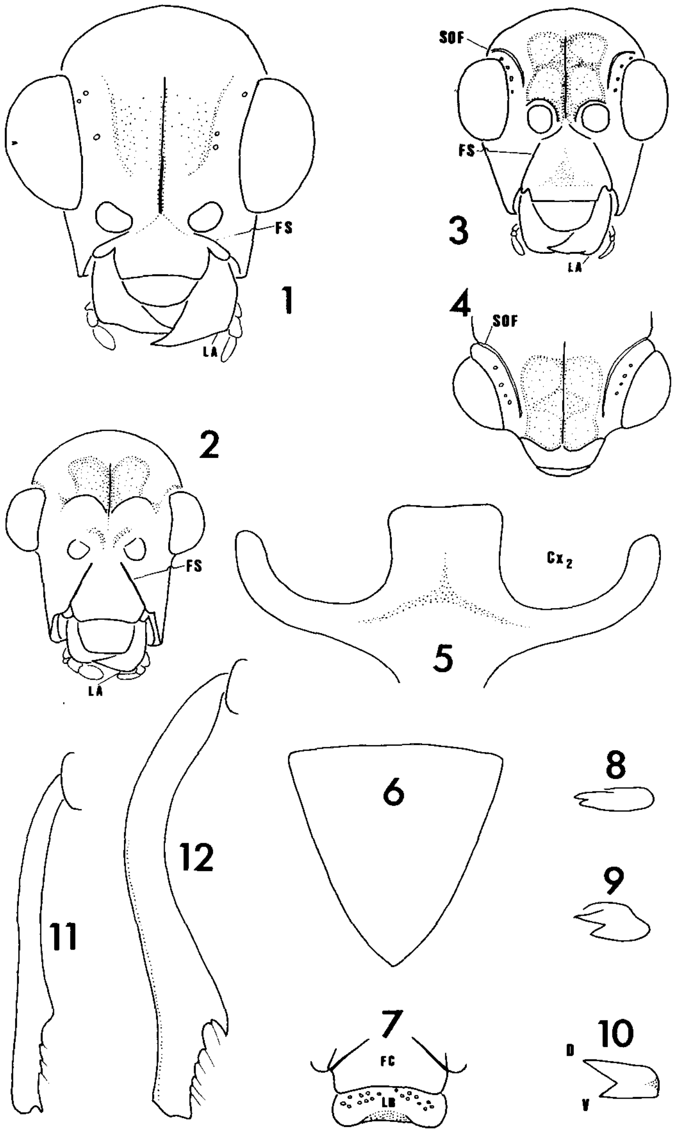
Character 25. Egg bursters.— Two states: plesiomorphic, egg bursters present in first instar larvae; apomorphic, egg bursters lost.

Cox (1988) reviewed the occurrence of egg bursters in the Chrysomeloidea, stating that Donaciinae examined lack them; however, only larvae of *D. (Donaciomima) semicuprea* Panzer and *D. (Donaciomima) bicolor* Zschach were examined. Cox (1988, p. 415) suggested that absence of egg bursters in the donaciines "may be correlated with the specialized extrachorion of the eggs." He supposed that first instar larvae must bite through the chorion in order to ingest bacteria that are contained in the extrachorion (*i.e.*, the gelatinous matrix into which Donaciini and Haemoniini oviposit). This loss correlates well with most Haemoniini and Donaciini, which oviposit under water in a gelatinous matrix. However, females of *Plateumaris* (but *Poecilocera* and *Sominella* oviposition behaviour unknown) do not oviposit in this way, and so their larvae may not achieve bacterial transmission in this way. While sagrines have not been investigated for egg bursters, criocerines do possess them, and oviposit on foliage. Primitive donaciines (*i.e. Plateumaris*) also oviposit on foliage (or insert their eggs into plant tissue), as opposed to under water in extrachorion. Thus I question whether primitive donaciines have egg bursters, namely *Plateumaris*, possibly *Poecilocera* and even *Sominella*. If so, then egg bursters should be found in the same location as in criocerines and bruchids (*i.e.*, on abdominal segment 1, dorsad of spiracle). Thus, I hypothesize tentatively that lack of eggbursters in donaciines is synapomorphic for Donaciini + Haemoniini. This interpretation is consistent with other characters that define the same grouping of genera, and with the historical scenario I have constructed summarizing the evolution of Donaciinae.

Character 26. Oviposition glands.— Two states: plesiomorphic, paired glands opening into common oviduct absent or not modified; apomorphic, sac-like glands, hypothesized to produce a gelatinous extrachorion, present.

Mann and Crowson (1983a) found that "gelatinous glands" are absent from females of *Plateumaris sericea* (Linnaeus) [(as *P. discolor* (Panzer)], but present in those of *D. (Donacia) crassipes*. These scanty data are hardly sufficient, but I observe that they are consistent with other characters, notably ovipositor and mandibular structure, egg bursters, oviposition behaviour, and host plants. Lack of such a gland is tentatively considered plesiomorphic, and I predict that most, if not all, Donaciini and Haemoniini should have them.

In another publication, Mann and Crowson (1983b) refered to "vaginal pouches", which were described as occurring in what seems to be the same position as their "gelatinous glands" (Mann and Crowson 1983a). They (Mann and Crowson 1983b) thought that these "pouches" are organs of symbiont transmission, though this may not preclude production of an ovipositional matrix. Their claim that vaginal pouches are absent from Donaciinae (Mann and Crowson 1983b) is contradicted by their recognition of "gelatinous glands" (Mann and Crowson 1983a) if the organs in question are in fact the same. Further, Stammer (1935) investigated symbiont transmission in donaciines, and found that "Mitteldarmblindsäcke" (four blind sacs of midgut, at junction of mid- and foreguts) of larvae harbour the bacteria, and that in the adult beetles bacteria are restricted to swellings of Malpighian tubules of females. At present, for want



FIGURES 1-12: 1. Frontal aspect of head of *Donacia hypoleuca* Lacordaire. **2.** Frontal aspect of head of *Macroplea pubipennis* (Reuter). **3.** Frontal aspect of head of *Donaciasta luridiventris* (Lacordaire). **4.** Dorsal aspect of head of *Donaciasta luridiventris.* **5.** Mesosternum of *Donacia cincticornis* Newman. **6.** Pygium of female of *Donacia cincticornis* **7.** Frontal aspect of frontoclypeus and labrum of *Sominella kraatzi* (Weise). **8.** Apical aspect of left mandible of *Plateumaris rufa* (Say). **9.** Apical aspect of left mandible of *Poecilocera harrisii* (LeConte). **10.** Apical aspect of left mandible of *Donacia cincticornis.* **11.** Lateral aspect of metatibia of female of *Sominella macrocnemia* (Fisch. v. Wald.). **12.** Lateral aspect of left metatibia of male of *Sominella macrocnemia.* Cx_2 = mesocoxa; D = dorsal apical tooth of mandible; FC = frontoclypeus; FS = frontoclypeal suture; LA = lateral angulation of mandible; LB = labrum; SOF = supraocular furrow; V = ventral apical tooth of mandible. Scale bar = 1.0 mm for Figs. 1-10, 0.5 mm for Figs. 11 and 12.

of more complete data, I postulate the above character sequence of absence = plesiomorphic, and presence = apomorphic. I observe that if this interpretation is correct, this character would be consistent with several other characters that I have suggested are integrated and related to other structures, general behaviour and host plant associations.

Character 27. Host plants.— Four states: plesiomorphic, hosts principally Cyperaceae; apomorphic 27a, hosts Gramineae; apomorphic 27b, hosts Nymphaeaceae; apomorphic 27c, hosts principally Zosteraceae and Haloragaceae. Each of the states, a, b and c, I postulate are derived host associations relative to the plesiomorphic association with vertical-emergent plants; each represents an independent shift to plant taxa in the same (Gramineae, for example) or another type (Nymphaeaceae, Zosteraceae) of growth form.

Based on study of host plant associations, I have postulated that host plant growth form is an important feature in the evolution of donaciines (Askevold, in prep. b). I postulated that donaciines are primitively associated with plants the leaves of which are vertical in growth form and emergent from the water, occurring along water body margins; *Plateumaris*, *Poecilocera* and most *D. (Donaciomima)* use these plants (mostly Cyperaceae). Also using vertical plants, are *Donaciella* (Gramineae); I hypothesize use of grasses as synapomorphic for the genus *Donaciella.*

Members of *D. (Donacia)* and *D. (Cyphogaster)* are restricted to floating plants, exclusively to the Nymphaeaceae. I consider tentatively use of pond lilies and related genera as synapomorphic for these two subgenera, and uses by some *D. (Donaciomima)* as independently derived associations.

Members of *Donaciasta* also appear to be restricted to floating plants, on the basis of two host records, from *Potamogeton* (Bertrand 1965) and "*Nymphaea* and *Trapa natans*" (Askevold, in prep. d). The Haemoniini are restricted to the Zosteraceae (with some records from Haloragaceae) (Askevold 1988).

Host plant data are useful in the ecological definition of certain genera and subgenera, but are not useful in grouping of genera, with the possible exception of state 27c, hosts of the Zosteraceae and Haloragaceae. In an ecological and adaptive sense, taxa using these plants conceivably are derived from an intermediate group, state 27b. That is, the floating-leaf category could be considered phylogenetically and adaptively intermediate between the vertical and submerged plants. Such a progression in donaciine phylogeny is supported by the character of colour loss (character 15) that is shared by Haemoniini, *Donaciasta* and many *D. (Donacia)* and *D. (Cyphogaster)*, and a few *D. (Donaciomima)*.

Character 28. Metatibia ventrally explanate.— (Figs. 11-12). Two states: plesiomorphic, metatibia ventrally with at most prominent denticles; apomorphic, metatibia ventrally prominently carinate or explanate, producing a large tooth in many males. Some species of *Donacia* (especially *s.str.*) have prominent denticles ventrally on the metatibia, as do some species of *D. (Donaciomima)*. Otherwise, donaciines have no modification of the tibial underside except in two species of *Sominella*: *S. longicornis* and *S. macrocnemia*, especially males, have prominently carinate metatibiae, varying from having an explanate carina to a prominent tooth about midlength. I consider this structure synapomorphic for this species pair.

Character 29. Ratio of antennomeres 3:4.— Two states: plesiomorphic, antennomere 3 shorter than antennomere 4; apomorphic, antennomere 3 as long as or longer than 4.

Typically among donaciines, antennomere 3 is much shorter than 4. However, some specimens of *Poecilocera*, most specimens of *Sominella longicornis* and *S. macrocnemia*, and many specimens of *S. reticulata* and *S. kraatzi* have antennomere 3 as long as or longer than 4. The derived state is considered synapomorphic for at least *S. macrocnemia* + *S. longicornis*, and possibly independently derived in some specimens of other taxa. PAUP analysis selected character 29 as synapomorphic for Donaciinae exclusive of *Plateumaris*, with reversal at the node connecting the remaining Donaciini + Haemoniini, but I find such an explanation unsatisfactory. Rather, I must consider the state occurring homoplastically in at least *Poecilocera*, and possibly in *S. reticulata* and *S. kraatzi* also. However, it could also be argued that this character is synapomorphic for all four species of *Sominella*, but this would require homoplasy in some other characters that I weight more heavily.

Character 30. Form of tegmen.— (Photographs B, D, F, L, O). I consider two independent characters of this structure, divided into characters 30a and 30b. Four states: plesiomorphic, parameres complete, forming a ring around the median lobe, with dorsal cap robust (Phots. B, D); apomorphic 1 (30a), dorsal cap slender, of more or less uniform width and thickness (Phots. F, O); apomorphic 2 (30a) dorsal cap slender, but uniformly broadened (Phot. L); apomorphic (30b), dorsal cap portion absent.

Within donaciines, *Plateumaris* and *Poecilocera* have a robust dorsal cap similar to that of sagrines, and this is undoubtedly the plesiomorphic state. Donaciini and Haemoniini have a slender and thin dorsal cap, while in *D.* (*Donacia*) and *D.* (*Cyphogaster*) the cap is wide, but thin. I consider the slender state synapomorphic for Donaciini + Haemoniini, and the widened state synapomorphic for the two subgenera of *D.* (*Donacia*).

Sagroids exclusive of Criocerinae possess a complete tegmen. Criocerines appear to have lost the dorsal cap portion (30b), leaving only a V-shaped ventral strut portion, much like in Alticinae and Galerucinae. I consider the reduced tegmen synapomorphic for the Criocerinae.

Character 31. Form of epipleuron.— Two states: plesiomorphic, epipleuron more or less angulate from humerus to near apex; apomorphic, epipleuron flattened or rounded, not more prominent than the outer interval.

Most donaciines possess an angulate epipleuron, which is elevated and more prominent than the flat outer interval. Several groups possess a flattened epipleuron, for which the state appears to be synapomorphic. Members of *Donaciella*, *D. microcephala* Daniel and Daniel, *D.* (*Donacia*) and *D.* (*Cyphogaster*) possess this state, as do a few species of *D.* (*Donaciomima*) and *S. kraatzi*. The degree to which the epipleuron is flat varies within these groups, so I cannot consider the character synapomorphic for these groups together, even though character 32 (eye size) is consistent with such a grouping.

Character 32. Eye size.— (Fig. 1). Two states: plesiomorphic, eyes small and round; apomorphic, eyes large and oval or round. Most donaciines have eyes rather small in relation to overall head size or length of occiput.

Several groups in Donaciini have very prominent, large eyes, and it is tempting to consider the state synapomorphic for these groups: *Donaciella*, *D. microcephala*, *D.* (*Donacia*) and *D.* (*Cyphogaster*), and a few unrelated species of *D.* (*Donaciomima*). Rather, I choose to consider the state synapomorphic for *D.*

(*Donacia*) + *D.* (*Cyphogaster*), and as an independent synapomorphy for *Donaciella.*

Character 33. Male abdominal apex.— Two states: plesiomorphic, basal sternum and apical sternum without medial depression in males; apomorphic, abdominal apex and basal sternum with broad depression in males.

All male donaciines are recognized by adominal depressions medially on the basal sternite, and apically on the apical sternite. The same condition occurs in some sagrines (Table 2), but not among criocerines I examined. I consider presence of this depression synapomorphic for Donaciinae + *Atalasis* and perhaps some other sagrines.

Character 34. Pronotal lateral margin.— Two states: plesiomorphic, pronotum laterally margined; apomorphic, lateral margin absent.

All sagroids lack a lateral margin of the pronotum, whereas most Coleoptera possess a lateral margin. While the character is therefore one of loss, it could be considered synapomorphic for the sagroid subfamilies. Lack of this margin also occurs in widely unrelated chrysomelids: some Galerucinae (*e.g. Cyclotrypema* Blake), many Eumolpinae (*e.g.* most, if not all, Adoxini), Orsodacninae, Zeugophorinae and Megalopodinae; the latter three are generally considered relatively primitive groups.

Character 35. MEG.— Two states: plesiomorphic, ejaculatory duct (flagellum) slender, unmodified; apomorphic, flagellum shortened, not exceeding the median lobe in length, more heavily sclerotized and sheathed with membrane.

Many chrysomelids possess an elongate flagellar structure that protrudes from the median lobe; it is sclerotized, but is not part of an internal sac complex as in donaciines. In sagroids examined, the ejaculatory duct is not elongate, but forms part of a sclerotized complex on the internal sac apex. This ground plan seems to characterize sagroids, as far as I can ascertain, and I consider this state synapomorphic for the sagroid subfamilies.

Character 36. Basal sac sclerites.— (Photographs D, F, I, M, N). Two states: plesiomorphic, basal sac sclerites absent or slightly developed; apomorphic, basal sac sclerites well developed as a sac-retracting mechanism (*cf.* Askevold in prep. a, Figs. 4-6 and discussion).

I am not familiar with detailed internal sac structure in chrysomeloids other than those I have examined (sagroids and bruchids). However, the median lobe of many chrysomelids seems to possess apical structures about the orifice, that appear much like those of sagroids (internal sac in repose). In sagroids, when the internal sac is everted, these structures can be seen as basal sclerites on the sac, an elongate one dorsally, and one or more on each side which I interpret as functioning to facilitate sac retraction. Bruchids appear not to possess such sclerites (*cf.* Borowiec 1987), and so I suggest that presence of basal sac-folding sclerites is synapomorphic for the sagroids (not including bruchids).

Character 37. Pubescence of scutellum.— Two states: plesiomorphic, scutellum pubescent; apomorphic, scutellum glabrous.

Most sagrines possess a pubescent scutellum (see Table 2), as do all donaciines, while criocerines (at least most) have a glabrous scutellum. Two explanations are possible: either the pubescent scutellum is part of the ground plan of sagroids, and it is lost from some sagrines and the criocerines; or the pubescent scutellum is derived within sagroids, and synapomorphic for Donaciinae + some other sagrines. Partly on the basis of the common = primitive criterion (*i.e.*, widespread among sagroids), I conclude that it is a ground plan character, lost from criocerines and a few sagrines. Also it is more reasonable to infer that a few groups lost pubescence, rather than requiring multiple independent derivations of pubescence among sagroids.

Character 38. Pubescence of humerus.— The character is not polarized and was not used for analysis of relationships of sagroid subfamilies, but states are detailed in Table 2 for sagrines, to which could be added Criocerinae without, and Donaciinae with, humeral pubescence. Humeral pubescence is probably also a ground plan character, variously lost from Criocerinae and sagrines, but retained by the aquatic donaciines, perhaps as part of their plastron system.

Relationship of donaciines to other sagroid subfamilies

The sagroid subfamilies.— Traditionally, the Sagrinae, Criocerinae and Donaciinae are placed close to one another in classifications (*e.g.* Seeno and Wilcox 1982, Monrós 1959). Schmitt (1985a,b, 1988, 1989) considered these three subfamilies as comprising a single, monophyletic group, but the matter is not resolved satisfactorily.

Schmitt (1985a,b, 1988) has been the only author to approach the problem of relationship by methods of phylogenetic systematics; his work is therefore the most satisfactory point at which to begin. Polarity of certain synapomorphic characters and therefore inclusiveness of taxa by such synapomorphies, might be affected by choice of hypothesis about out-group. The hypothesis selected was that donaciines are derived from a lineage of sagrines, and that criocerines are independently derived from sagrines.

A discussion of donaciine generic relationships must first establish that the general hypothesis of progression of character states in donaciines is valid despite ambiguities about relationships of sagroid subfamilies. That is, reversal of polarity of the relatively few characters because of out-group choice does not alter relationships of donaciine genera significantly.

Some authors have considered Bruchidae to belong among the sagroids (*e.g.* Mann and Crowson 1981, 1983b, 1983c, Crowson 1960). Chen (1986) included the Bruchidae in this group (named the Crioceridae). Monrós (1959, Fig. 1, p. 20) used the term Crioceriformes for the grouping of these three subfamilies, but including also the Bruchidae as sister group to the Sagrinae. Schmitt (1989) considered that bruchids belong within Chrysomelidae, probably as sister group to the "Crioceriformes" + "Cryptostomes" (Cassidinae + Hispinae), largely on the basis of presence of bifid tarsal setae.

Bruchids have an internal sac structure and retraction musculature that bears little resemblance to any other sagroids I have examined (based on figures in Kingsolver 1970 and Borowiec 1987). I considered certain bruchid characteristics, but I find that these do not have much bearing either on relationships of sagroid subfamilies or on phylogeny of donaciine genera for the purpose of analyzing character polarity in sagroids.

Problematic characters and outgroup to Donaciinae.— Certain characters discussed above, some of which were used by Schmitt (1985a,b) to reconstruct the relationship among the Sagrinae, Criocerinae and Donaciinae, are problematic. These characters are: (1), ligular lobes; (2), tibial spurs; (4), BSB of endophallus; (6), basal angle of median lobe; (10), mandibular teeth; and (24), frontal grooves. Each of these characters is considered above, to rationalize sagroid subfamily relationships and selection of out-group. Character states are summarized in Tables 1 and 2.

Definition of an out-group to donaciines is problematic. If one were to echo Crowson's (1945) view that Sagrinae are a stem-group, then only one or a few genera of sagrines should be considered valid for proximal out-group purposes.

Table 1. Comparison of males of *Erebia mackinleyensis* and *E. magdalena* adult males using measurements and character index values.

Character	**Species**													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon		Alberta to New Mexico		Alberta		Montana		Utah		Colorado		Colorado (south) & New Mexico	
	n=39		n=167		n=28		n=6		n=20		n=95		n=18	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.7	22.8-28.9	25.1	21.4-28.9	23.8	21.4-26.1	24.9	24.2-25.8	25.7	21.9-27.7	25.3	21.9-28.9	25.1	23.5-27.9
-white scale index	0.33	0-10	1.5	0-26	4.6	0-26	7.2	2-16	3.3	0-24	0.18	0-10	0.33	0-3
-white hair index	3.2	0-38	2.1	0-35	1.7	0-10	10.5	2-22	5.5	5.5-35	1.1	0-20	1.8	0-14
Hindwing														
-length (mm)	21.5	18.2-23.8	20.9	17.7-23.5	19.9	17.7-21.7	20.7	19.8-21.4	21.2	18.2-23.3	21.1	18.2-23.5	20.8	19.1-22.6
-white scale index	0.03	0-1	3.6	0-48	8.7	0-48	13.5	0-38	1.5	0-12	1.8	0-32	3.9	0-42
-white hair index	1.3	0-28	1.7	0-46	1.0	1-10	11.0	0-33	0.35	0-5	1.2	0-27	4.2	0-46
Wing markings														
-mesial band index	2.5	1-3	1.7	1-3	1	1	1	1	1	1	1.1	1-3	1.2	1-2
-dorsal rust patch	1.7	1-5	1	1	1	1	1	1	1	1	1	1	1	1
-ventral rust patch	3.2	1-6	1.02	1-3	1	1	1.5	1-3	1	1	1	1	1	1
Antennal club														
-color index	3.6	1-8	5.9	4-8	6.4	5-7	7.0	5-8	6.4	4-8	5.6	5-8	6.1	5-8

TABLE 1. CHARACTERS USED TO ASSESS PHYLOGENETIC RELATIONSHIP OF SAGROID SUBFAMILIES.

		TAXA							
CHARACTERS**		CRIOCERINAE		**SAGRINAE		*ATALASIS*		DONACIINAE	
(1-30 from Table 3)		state	code	state	code	state	code	state	code
1.	Ligular lobes	absent	1	GP- present	0	present	0	absent	1
2.	Tibial spurs	GP- 2-2-2	0	0-0-0	A	0-0-0	A	1-1-0	B
4.	BSB	present ?	1	absent	0	absent	0	present	1
5.	ELD	present ?	1	abs./pres.	0/1	present	1	present	1
6.	Med. lobe angulation	present	1	GP- absent	0	absent	0	abs./pres.	0/1
9.	El. suture explanate	no (yes)	1/0	GP- yes/no	0/1	yes	0	yes/no	0/1
10.	Mandibular teeth	bidentate	1	GP- unidentate	0	unidentate	0	bidentate	1
24a.	Frontoclypeal groove	present	1	GP- present	1	present	1	present	1
30b.	Tegmen, dorsal cap	reduced	1	GP- no	0	no	0	no	0
33.	♂♂ Sexual characters	no	1	GP- yes/no	0/1	yes	0	yes	0
34.	Pn. lat. margin	absent	1	GP- absent	1	absent	1	absent	1
35.	MEG	present	1	abs./pres.	0/1	present	1	present	1
36.	Basal sac sclerites	present	1	GP- present	1	present	1	present	1
37.	Scutellum pubescent	no	1	GP- yes/no	0/1	yes	0	yes	0
38.	Humeral pubescence	GP- no	*	GP- yes/no	*	no	*	yes	*

** Characters 30b to 37 are presented here for subfamilial level character assessment; for details of Sagrinae genera, see Table 2, for Donaciinae see Table 3. A and B = separate reductions from ground plan state. GP- = probable groundplan state. * = polarity undetermined.

Corrected table added after publication. Inserted here by KWW, 2010.

Table 2. Comparison of *Erebia mackinleyensis* and *E. magdalena* adult females using measurements and character index values.

Character	Species													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon		Alberta to New Mexico		Alberta		Montana		Utah		Colorado		Colorado (south) & New Mexico	
	n=15		n=75		n=20		n=3		n=4		n=42		n=6	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.8	23.5-28.2	25.3	22.1-28.0	25.0	22.1-27.7	25.5	24.9-26.3	25.4	23.7-26.3	25.3	22.4-28.0	26.5	24.5-27.5
-white scale index	4.9	0-39	20.6	0-200	46.4	3-200	49.3	21-105	6.7	4-13	9.7	0-30	5.5	0-14
-white hair index	18.8	0-52	68.5	1-218	66.5	2-150	84	49-137	33	17-68	74.9	1-218	46	0-111
Hindwing														
-length (mm)	21.5	19.1-22.8	21.0	17.2-23.3	20.5	17.2-22.8	21.4	19.8-22.6	20.8	19.8-21.4	21.1	18.2-23.3	21.9	20.0-23.3
-white scale index	3.9	0-23	31.8	0-135	59.6	6-135	53.7	25-97	6.0	0-14	17.9	0-93	41.8	0-97
-white hair index	4.5	0-24	73.5	0-258	51.8	0-153	168.3	139-216	9.7	1-29	8.5	0-258	63.8	0-147
Wing markings														
-mesial band index	2.9	2-3	1.8	1-3	1	1	1	1	1	1	2.4	1-3	2	2
-dorsal rust patch	5.4	1-6	1.2	1-6	1.05	1-2	4	3-6	1.25	1-2	1.09	1-5	1	1
-ventral rust patch	5.0	1-6	1.1	1-5	1	1	1.7	1-3	1.25	1-2	1.09	1-5	1	1
Antennal club														
-color index	2.7	2-4	6.1	5-8	6.8	6-8	6.0	5-8	7	7	5.7	5-7	6.0	5-7

TABLE 2. ASSESSMENT OF SOME PHYLOGENETIC CHARACTER STATES OF SAGRINAE.

		TAXA*							
Characters		*Diap*	*Carp*	*Poly*	*Mega*	*Mecy*	*Sagr*	*Amet*	*Atal*
4.	ELD	?	?	-	-	?	NH	NH	1
5.	BSB	?	?	-	-	?	NH	NH	0
9.	Elytral suture	0	1	0	0	0	0	1	0
24.	Ocular groove	no	yes(I)	no	no	no	yes	no	no
30b.	Tegmen	0(?)	0(?)	0(?)	0(?)	0(?)	0	0	0
33.	♂ ♂ Sexual characters	?	?	1	1	?	1	1	1
34.	Pronotal lateral margin	1	1	1	1	1	1	1	1
35.	MEG	?	?	-	-	?	1	NH	1
36.	Basal sac sclerites	?	?	?	?	?	1	1	1
37.	Scutellum pubescent	yes	yes	yes	yes	yes	no	yes	yes
38.	Humeral pubescence	yes	yes	no	no	no	no	yes	no

Characters stated as yes/no are not polarized.

I= character more or less present, but incomplete in development.

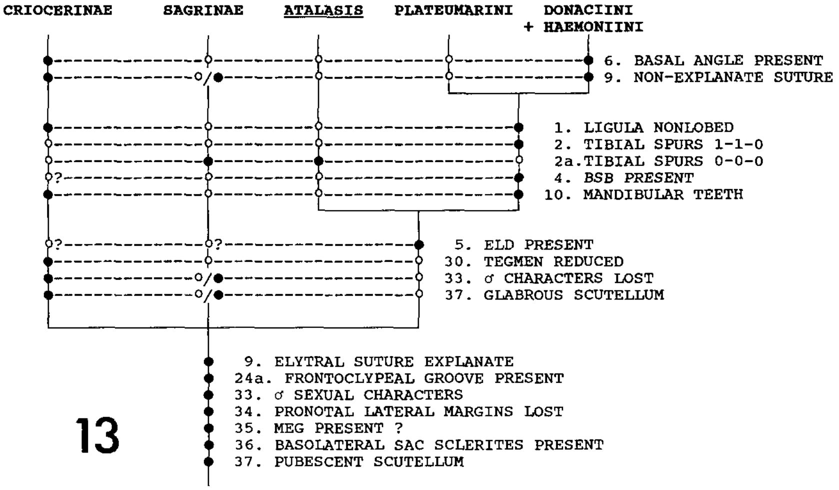
? = state unknown because no male specimens examined, or structure not identified (*Polyoptilus* and *Megamerus*).

- = internal sac without sclerites.

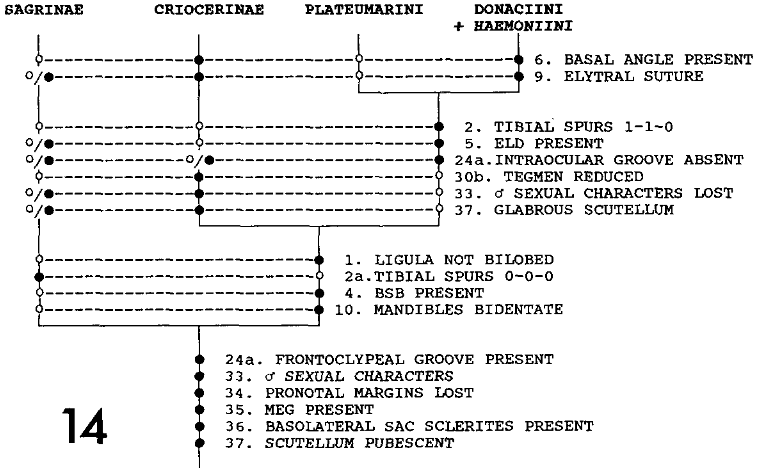
NH = sac sclerite not homologized.

*Names of taxa: *Amet* = *Ametalla; Atal* = *Atalasis; Carp* = *Carpophagus; Diap* = *Diaphanops; Mecy* = *Mecynodera; Mega* = *Megamerus; Poly* = *Polyoptilus; Sagr* = *Sagra.*

Corrected table added after publication. Inserted here by KWW, 2010.



13



14

FIGURES 13, 14. Cladograms illustrating hypotheses of phylogenetic relationship of Donaciinae to Criocerinae and Sagrinae. Apomorphic states indicated on diagrams. ●= apomorphic character states; O= plesiomorphic character states. **13, Hypothesis 1.** The genus *Atalasis* is assumed to be the sister taxon to Donaciinae if apomorphic states in characters 1,4,6 and 10 in Criocerinae are considered independently derived. **14, Hypothesis 2.** The Criocerinae is assumed to be the sister taxon to Donaciinae because characters 1, 4 and 10 could be considered synapomorphic for the grouping Criocerinae + Donaciinae. This hypothesis requires reversal of character 6 in Plateumarini and most Sagrinae, or homoplasy of 6 between Donaciini and Criocerinae. Reduction of character 2 is more easily derived from the criocerine type than from the sagrine type.

Using Sagrinae as a whole might be misleading, for character state polarity would be ambiguous for the most part. The same could be said of the Criocerinae, if they were also derived from Sagrinae independently of Donaciinae. The principal purpose of this discussion is to rationalize use of *Atalasis* as closest out-group to Donaciinae. My preliminary view of relationships among the three sagroid subfamilies was that among *Atalasis*, the rest of Sagrinae, and Criocerinae, *Atalasis* possesses more derived character states in common with Donaciinae and should therefore be considered the closest out-group.

Results of analysis of sagroid groups (Figures 13, 14) using PAUP varied according to which out-group was defined. If either Criocerinae or *Atalasis* was defined as hypothetical out-group, PAUP presented *Atalasis* as sister taxon to Donaciinae because fewer character transformations were required **within** Donaciinae than among the three groups. However, if an additional hypothetical out-group (*i.e.* the remainder of Sagrinae) was defined, then PAUP selected Criocerinae as sister taxon to Donaciinae, based partly on a number of shared loss characters, or losses in Donaciinae from the plesiomorphic state in Criocerinae.

Several characters suggest that Criocerinae is indeed the sister group to Donaciinae: tibial spurs, mandibular teeth, ligular lobes, median lobe angulation and possibly certain endophallic sclerites. Other characters suggest a group of sagrines is the sister taxon: male sexual characters, pubescent scutellum and elytral humerus, toothed metafemora, and elytral suture explanate (at least primitively). However, none of these characters can be considered shared-derived (at least at this taxonomic level) because they constitute part of the ground plan of the sagroids, from which many character states can be derived.

The possible character state distributions, and relationships of sagroids, are presented in Figures 13 and 14. I am not satisfied that sagroid relationships are well resolved, but select sagrines as out-group as the hypothesis to proceed with. *However, I note that characters the polarity of which would be reversed by selection of criocerines as out-group would not alter the general donaciine generic relationships.*

RECLASSIFICATION OF GENERA OF DONACIINAE

This section comprises two parts. First, I discuss aspects of the hypothesis of reconstructed phylogeny of donaciine genera (Fig. 15), especially as relevant to their classification. Following, I summarize my ideas about higher classification of Donaciinae by means of a brief treatment of each tribe and its included genera. Both Old and New World supraspecific taxa are included: tribes, genera and subgenera are characterized and diagnosed; and genera and subgenera are keyed (Old and New World taxa separately). Analysis of the Haemoniini was examined previously (Askevold 1988), and is condensed here.

The classification of Donaciinae proposed herein is provisional. Clearly, problems at both generic and tribal levels persist because of lack of resolution of relationships (Figs. 15-18), subjectivity of character assessment, and perhaps also because I am reluctant to recognize multiple monobasic genera. These problems require a classification of donaciines that is not strictly phylogenetic. Therefore, the appertaining principles adopted are clarified briefly in the context of a discussion about the phylogeny.

Paraphyletic tribes

For tribal classification, it is clearly desirable to recognize only monophyletic taxa (Donoghue and Cantino 1988). However, among the tribes of Donaciinae, this is possible only for Haemoniini. To adhere strictly to cladistic classification, I would have to follow either a complicated and cumbersome arrangement, or none at all. Lack of a tribal classification would hinder discussion of such aspects as host plant relationship. I regard the reconstructed phylogeny as not fully resolved and consider that the classification derived from it justifiably is not fully resolved either.

The relationship of *Plateumaris* and *Poecilocera* is based largely on symplesiomorphy; additional characters may show them to be sister taxa, but there is no particular reason to expect this. I group them here on the basis of symplesiomorphy, structurally and in host plant use. Thus the Plateumarini constitutes a paraphyletic, grade-based taxon. *Poecilocera* could be placed in Donaciini just as readily on the basis of host relations because many taxa in Donaciini are associated with the same plants as are Plateumarini. However, it bears greater resemblance to *Plateumaris*, albeit plesiomorphically, and I am more comfortable with this assignment at this time.

The tribe Donaciini is a broad mixture of structurally generalized to specialized groups, and would be holophyletic only if Haemoniini were not recognized as a distinct tribe. As I discuss elsewhere (Askevold, in prep. b), the Donaciini consists ecologically of members that are generalized in host plant use [*i.e. Sominella*, most *D.* (*Donaciomima*)], as well as of lineages that have become highly specialized in host plant use [*i.e. Donacia* (*Cyphogaster*), *D.* (*Donacia*) and *Donaciasta*]. The former are mostly taxa that are structurally more generalized and most similar to the donaciine ground plan exmplified by *Plateumaris*; the latter are both structurally and ecologically specialized groups. The Donaciini is therefore a stem-group from which several lineages succeeded in attaining greater specialization.

One of these lineages is the Haemoniini which, as is supported by several characters (Table 3 and Fig. 15), is the sister taxon to *Donaciasta* of Donaciini. Haemoniini consists of members that are profoundly different from other lineages of donaciines, both ecologically and structurally (Askevold 1988), and I am reluctant to reject this group as a useful monophyletic taxon.

For Plateumarini and Donaciini then, two paraphyletic taxa are recognized. There is an inherent danger that such groups will be treated as monophyletic by subsequent investigators (Donoghue and Cantino 1988), but this classification should be recognized for what it represents: a provisional one that could be a staging-point for subsequent investigations. Many published classifications in chrysomelids have no apparent structural basis. Available classifications of almost all chrysomelid groups therefore must be regarded as fully unsubstantiated and effectively uninvestigated. The classification of Donaciinae proposed here is a solution to certain problems but creates others; however, it puts Donaciinae on a better foundation than is available for other subfamilies of chrysomelids. My classification can be reexamined and modified in the future as it becomes supplemented by additional and new kinds of data, both biochemical and structural.

TABLE 3. MATRIX OF CHARACTER STATES USED IN PHYLOGENETIC RECONSTRUCTION OF GENERA OF DONACIINAE.

		TAXA*											
	Characters	*SAGR*	*CRIO*	*Plat*	*Poec*	*Somi*	*Donl*	*"Don" micr*	*Dona (Dim)*	*Dona (Don)*	*Dona (Cyp)*	*Dont*	*HAEM*
1.	Labial ligula	0	1	1	1	1	1	1	1	1	1	1	1
2.	Tibial spurs	0	0	1	1	1	1	1	1	1	1	1	1
3.	Larval hooks	0	0	1	1	1	1	?	2	2	1	?	1
4.	BSB	0(-1?)	1	1	1	1	1	1	1	1	1	1	1
5.	ELD	1	1	1	1	2	2	2	2	2	2	2	2
6.	M.L. basal angle	0	1	0	0	0-1	1	1	1	1	1	0(R)	1
7.	M.L.furrowed	0	0	0	0	0	0	0	1	1	0	0	0
8.	Elytral apex	0	0	0	1	1	1	0(R)	1	1	1	1	2
9.	Sut. interval	0-1	0-1	0	0	1	1	1	1	1	1	1	1
10.	Mandib. teeth	0	1	1	1	2	2	1(R)	3	3	2	2	2
11.	Hypom. pubesc.	0	0	0	1	0-2	2	2	2	2	2	2	2[1]-3
12	Clypeus length	NA	NA	0	0	0	0	0	0	0	0	1	1[1]
13.	Clyp. depress.	NA	NA	0	0	0	0	0	0	0	0	1	0
14.	♀♀ pygidium	0	0	0	0	0	0	0	1	1	0	0	0
15.	Dorsal colour	0	0	0(1)	0	0	0	1	0-1	0-1	0(1)	1	1
16.	Abd .tubercles	0	0	0	0	0	0	0	0	1	0(1)	0	0
17.	Claw segment	0	0	0	0	0	0	0	0	0	0	0	1
18.	Ovipos. setae	NA	NA	1	0	0	1	0	0	0	0	0	0
19.	Ovipos. scler.	0	0	1	0	0	1	0	0	0	0	0	0
20.	Valve length	NA	NA	1	0	0	1	0	0	0	0	0	0

(continued on next page)

Table 3 (continued)

Characters	TAXA*											
	SAGR	*CRIO*	*Plat*	*Poec*	*Somi*	*Donl*	*"Don" micr*	*Dona (Dim)*	*Dona (Don)*	*Dona (Cyp)*	*Dont*	*HAEM*
21. Mesost. width	0	0	0	0	0	0	0(1)	1	1	0(1)	0(1)	0
22. Metafem. tooth	0	1(0)	0(1)	0	0	1(0)	0(1)	0(1)	0(1)	0(1)	0	1
23. Pronot. punct.	NA	NA	0	0	1	1	1	2	2	1	1	1
24. Ocular grooves	0(1)	0(1)	0	0	0	0	0	0	0	0	1	0
25. Egg bursters	NA	NA	0(?)	0(?)	1(?)	1(?)	1(?)	1(?)	1(?)	1	1(?)	1(?)
26. Ovipos. gland	NA	NA	0	0(?)	1(?)	1(?)	1(?)	1	1(?)	1	1(?)	1(?)
27a Hosts	NA	NA	0	0	0(?)	1	?	0	0	0	0	0
27b. Hosts	NA	NA	0	0	0(?)	0	?	1	1	0(1,2)	1,2	2
28. Metatibia expl.	0	0	0	0	0(1)	0	0	0	0	0	0	0
29. Antenn. 3:4	0	0	0	0(1)	1	0	0	0	0	0	0	0
30a. Tegmen	0	0	0	0	1	1	1	2	2	1	1	1
31. Elytral epipl.	0	NA	0	0	0-1	1	1	1	1	0(1)	0	0
32. Eyes large	NA	NA	0	0	0	1	1	1	1	0(1)	0	0

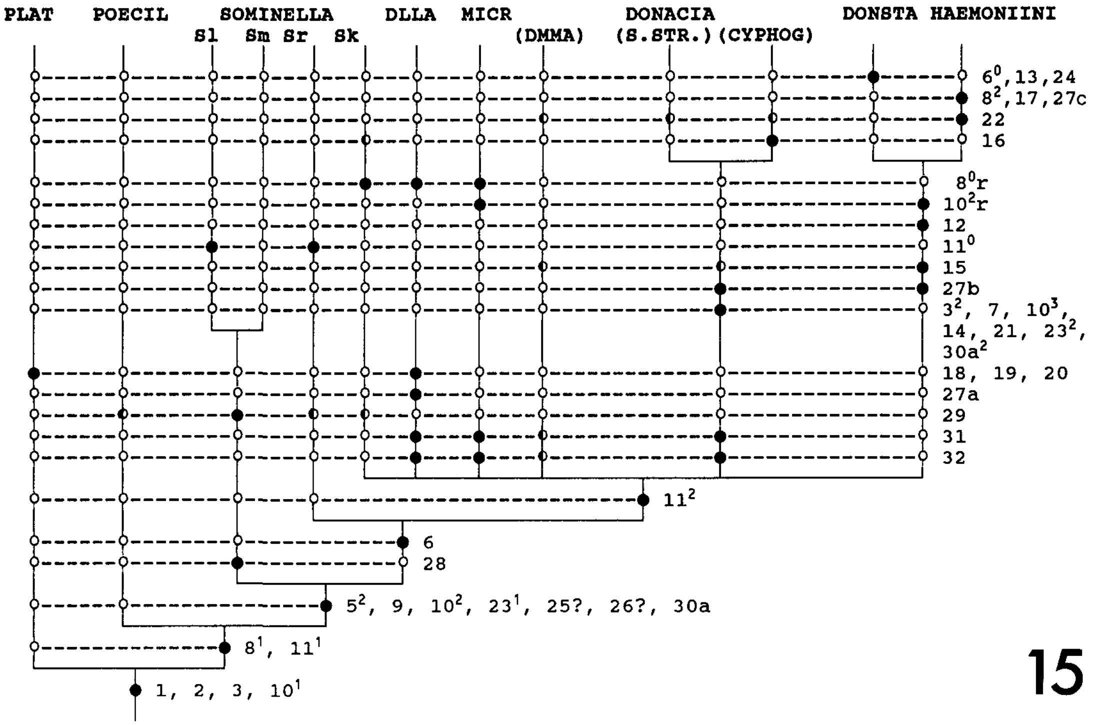
1 = state unknown in *Neohaemonia voronovae* Medvedev (for character 6). ? = state unknown.

R = postulated reversal to plesiotypic state, 0 or 1.

NA = character not assessed, not relevent to analysis.

(1) or (0) = some members possess state in parentheses, = homoplasy.

*Names of taxa: CRIO = Criocerinae; "Don" micr = "Donacia" microcephala; Dona (Cyp) = Donacia (Cyphogaster); Dona (Dim) = Donacia (Donaciomima); Dona (DDon) = Donacia (Donacia); Donl = Donaciella; Dont = Donaciasta; HAEM = Haemoniini; Plat = Plateumanis; Poec = Poecilocera; and SAGR = Sagrinae.



15

FIGURE 15. Reconstructed phylogeny of genera and some taxa of Donaciinae not assigned to genus. PLAT = *Plateumaris;* POECIL = *Poecilocera*; Sl = *Sominella longicornis*; Sm = *Sominella macrocnemia*; Sr = *Sominella reticulata*; Sk = *Sominella kraatzi*; DLLA = *Donaciella*; MICR = "*Donacia*" *microcephala*; DMMA = *D.* (*Donaciomima*); CYPHOG = *Donacia* (*Cyphogaster*); DONSTA = *Donaciasta*. ● = apomorphic character states; O= plesiomorphic character states; half-circles = specimens (or taxa) with both states occurring in that taxon; r = reversal.

Paraphyletic genera and subgenera

Donacia s.str. is probably paraphyletic because I have no synapomorphy for the group; the grouping of this subgenus and *D.* (*Cyphogaster*) is clearly defined, but without a synapomorphy for the nominate subgenus I cannot rule out the possibility that *D.* (*Cyphogaster*) could have arisen from some group within *D.* (*Donacia*). Similarly, *D.* (*Donaciomima*) is very likely a paraphyletic group from which the major lineage of the other two subgenera could have diverged ecologically and structurally, and become specialized to Nymphaeaceae-hosts. Among these subgenera, *D.* (*Cyphogaster*) alone is defined by a synapomorphy.

That these paraphyletic relationships exist is virtually a certainty for, as Disney (1989) observed, residual paraphyletic groups remain when the rank of a subset of species within a genus is raised to the generic (or subgeneric) level. The remainder, which belong in the group bearing the original genus name, cannot be defined by a synapomorphy. As long as relationships and limits of these groups remain confused, I am inclined to accept a relatively *status quo* approach rather than to elevate all apparently defined lineages to generic status.

The problem of *Sominella*, also a paraphyletic group, is discussed below. According to strict criteria of monophyly, *Sominella* would remain, consisting of two species, *S. longicornis* and *S. macrocnemia*; *S. kraatzi* and *S. reticulata* should be assigned to their own genera: *Pseudodonacia* Reitter and a new genus, respectively. However, this approach seems simply inappropriate for species which are not significantly unique from others.

Problems in classification of some genera

The reconstructed phylogeny of donaciine genera is partly clearly resolved. Some groupings, like the Haemoniini (see Askevold 1988) and the pair of subgenera *D.* (*Donacia*) and *D.* (*Cyphogaster*), are defined by many synapomorphies. The relationship of Haemoniini to *Donaciasta* is supported by at least one structural character (#12) as well as by host plant association (#27); an additional character (#15), loss of dorsal colour, supports this arrangement.

No synapomorphy was found for taxa grouped in *D.* (*Donaciomima*) and *Sominella*. Both groups are recognized on the basis of general similarity of included members. *Donacia microcephala* and *Neohaemonia voronovae* Medvedev also remain of uncertain relationship within Donaciini and Haemoniini, respectively. The relationships I have not been able to resolve satisfactorily are discussed in greater detail, below.

Problem of phylogeny and classification of Sominella.— On the basis of characters examined, no single primary synapomorphy was found for the group to which four species are here assigned, *Sominella*, except perhaps character 29 (antennomere 3:4 ratio). Even if character 29 was considered a primary synapomorphy, this arrangement would require homoplasy in characters 11 and 6. The species here placed in *Sominella* have a general facies that suggests their combination into one genus: occiput not constricted behind eye (or only slightly), eye therefore not protruding, elongate antenna, femora coarsely and closely punctured, vertexal calli at most slight, elytron sparsely but coarsely rugose. I cannot consider confidently any of these characters as synapomorphic.

Other characters constitute a confusing array of plesiomorphic and apomorphic characters: characters suggesting inclusion in the rest of Donaciini (elytral apex, median lobe angulation, hypomeral pubescence) by some taxa, but others retaining or reverting to plesiomorphic states. The elytral apex of these species varies: narrowly truncate in *S. longicornis*, toothed and emarginate in *S. macrocnemia*, produced into a narrowly rounded apex in *S. kraatzi*, and typical of

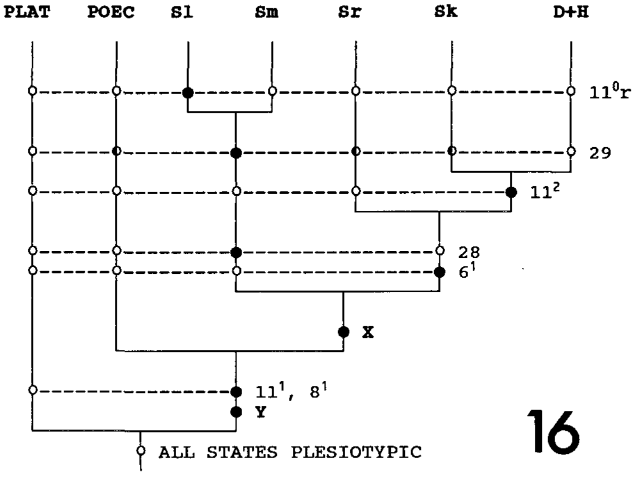
TABLE 4. DETAILS OF CHARACTER STATE DISTRIBUTION OF SOME HOMOPLASTIC CHARACTERS IN DONACIINAE.

			TAXA*				
CHARACTERS	*Plat.*	*Poec.*	*Sominella*				DONA+
			long.	*macr.*	*reti.*	*kraatzi*	HEM
6. Median lobe angulation	0	0	0	0	1	1	1
11. Hypomeral pubescence	0	1(0)=1	0	1	1(0)=1	2	2(1)=2
28. Metatibial explanation	0	0	1	1	0	0	0
29. Antennomeres 3:4	0	0(1)=0	1	1	1(0)=1	1(0)=1	0

Characters and their states are taken from Table 3, with specific states in species of "*Sominella*" inserted.

See discussion of characters for analysis of polarity. Value in parentheses (e.g. 1(0)=1) = some specimens of that taxon, or some taxa in the group, have on alternate character state, and "=1" or "=2" indicates subsequent decisions about polarity.

*Names of Taxa: DONA = DONACIINI; HAEM = HAEMONIINI; *long* = *S. longicornis; macr* = *S. macrocnemia; Plat* = *Plateumaris; Poec* = *Poecilocera; reti* = *S. reticulata.*



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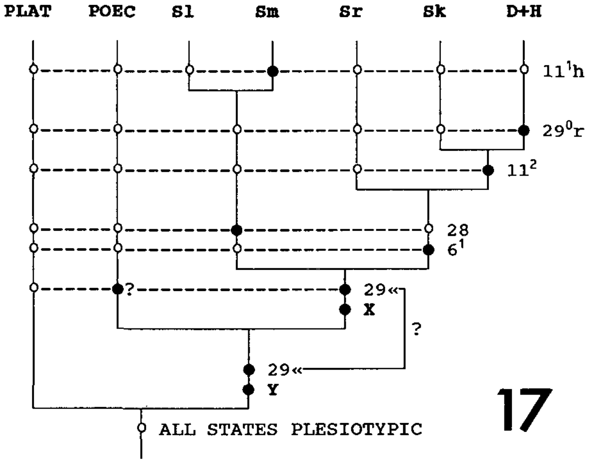

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FIGURES 16, 17: Possible relationships of members here assigned to *Sominella* to remaining Donaciini. X and Y indicate apomorphies defining these clades (see Fig. 15). **16, Hypothesis 1.** In this hypothesis, *S. reticulata* and *Poecilocera harrisii* are assumed to possess the derived state of character 11. Character 29 is selected by PAUP analysis to be derived at branch Y, and reversed on the D+H branch. **17, Hypothesis 2.** In this hypothesis, *S. reticulata* and *Poecilocera harrisii* are assumed to possess the plesiomorphic state of character 11. PAUP analysis did not select possible monophyly of *Sominella* based on 29 because of additional tree length caused by greater required homoplasy in characters 11 and 6; 29 was selected by PAUP analysis to be derived at branch Y (or X if *P. harrisii* does not possess 29), and reversed at the D+H branch.

● = apomorphic states, O= plesiomorphic states, and half-circles = specimens with both states occurring in this taxon. PLAT= *Plateumaris*; POEC= *Poecilocera*; Sl= *Sominella longicornis*; Sm= *Sominella macrocnemia*; Sr= *Sominella reticulata*; Sk= *Sominella kraatzi*; D+H= rest of Donaciini + Haemoniini; r= postulated reversal to plesiomorphic state, O; h= postulated homoplastic occurrence of derived state, 1.

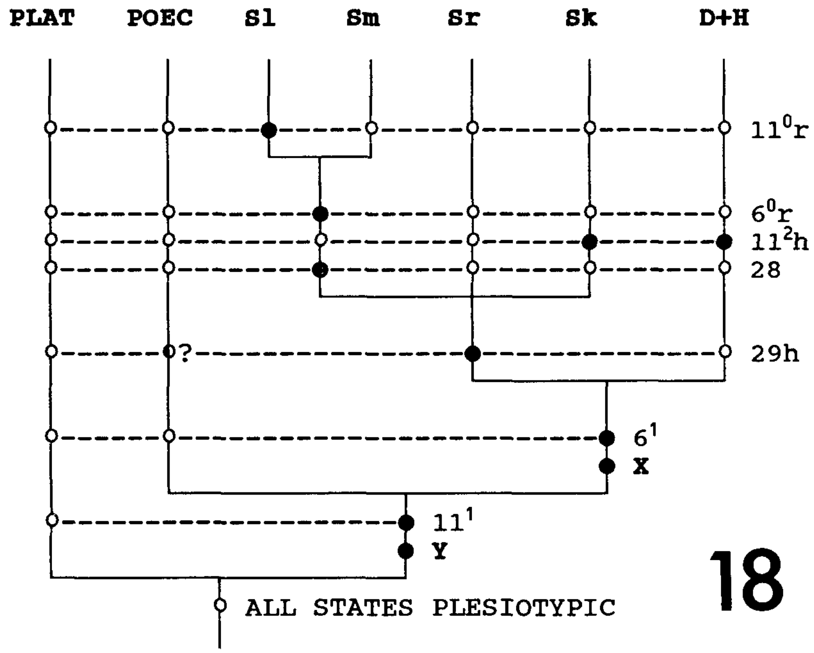

FIGURE 18. Possible relationship of members here assigned to *Sominella* to remaining Donaciini. **Hypothesis 3.** The derived state of character 11 is assumed to be possessed by *P. harrisii* and *S. reticulata*. PAUP analysis did not select possible monophyly of *Sominella* based on character 29 because of additional tree length caused by greater required homoplasy in characters 11 and 6. For explanation of abbreviations *etc*, see Figure 17.

Donaciini in *S. reticulata*. Median lobe and hypomeral characters are detailed in Table 4 and Figures 16-18.

There is no satisfactory resolution for the purposes of classifying these taxa. I am reluctant to erect a new monobasic genus to accommodate *S. reticulata*, while *Pseudodonacia* Reitter is available for *S. kraatzi*. Therefore I expand *Sominella* to include four species that are similar in general facies, and that can be excluded from other genera in Donaciini. Therefore, the genus constitutes a paraphyletic group as now defined by phylogenetic reconstruction.

Placement of Donacia microcephala Daniel and Daniel.— *Donacia microcephala* is known from the Middle East only. I examined a series of specimens from Iran. Specimens of *D. microcephala* possess most character states of Donaciini, with the notable exception of mandibular structure: the mandibles are slender in width and profile and each possesses only a single apical tooth, a reduction from the state typical of Donaciini. Specimens of the Nearctic *D.* (*Donaciomima*) *pubescens* LeConte are similar to those of *D. microcephala* in being totally pubescent dorsally; additionally, specimens of both species have rounded elytral apex, flat epipleuron, and are testaceous in colour. The species of *Donaciella* are similar to these two species in the flattened epipleuron, most species with rounded elytral apex, and dorsal pubescence in some species. Most species of *D.* (*Donacia*) and *D.* (*Cyphogaster*) have extremely dense ventral pubescence, through which the fine punctures are not visible; this is also so for *D. microcephala* and a few species of *D.* (*Donaciomima*). *Donaciella* and *D.* (*Donacia*) and *D.* (*Cyphogaster*) are similar to *D. microcephala* in size of eyes and general lack or slight development of antennal and vertexal calli. There was no single character that I considered convincing evidence for inclusion in any of the generic taxa of Donaciini as they are currently defined, though *D. microcephala* has several characters that suggest inclusion in *Donaciella*. I am reluctant to erect a monobasic genus because relationships are not resolved adequately.

Problem of placement of Neohaemonia voronovae Medvedev.— I have not examined specimens of this species. Askevold (1988) suggested it does not belong in any described genus, but the problem remains unresolved.

Treatment of tribes and genera

Details of reclassification of Donaciinae as proposed herein, based on phylogenetic analysis of the genera, are treated below. Jolivet (1970:1) listed all suprageneric names based on *Donacia* Fabricius; these are not relisted here but authorship of Donaciinae, and therefore Donaciini, is attributable to Kirby by implication of ICZN (1985) Articles 33b(ii), 43(a) and 36(a) bearing on the matter of family-group name authorship. Below, each tribe is diagnosed and included generic names are listed. Generic names for fossils proposed by Haupt (1956) are incorporated on the basis of my interpretation of their original descriptions and as suggested by Askevold (1990). Type species designations are stated for all genus-group taxa and are verified or corrected by me *by reference to original literature*.

For each genus and/or subgenus I list the Old World species that I assign to them. *The Palaearctic taxa listed are those of which I have examined specimens.*

To conserve space, *I do not present full bibliographic citation for all Old World species* (references are not given); I give date of original description, but most bibliographic details can be found in Jolivet (1970) and Borowiec (1984). I give full bibliographic information only for taxa described after Jolivet (1970), for taxa involved with new synonymies proposed here, and for those about which I report type specimen data (which indicates that I have examined these types). New World species are to be listed separately (Askevold, in prep. c).

DONACIINAE KIRBY, 1837

DONACIADAE KIRBY, 1837:22

TRIBE PLATEUMARINI, NEW TRIBE

Type genus.— *Plateumaris* Thomson, 1859.

Diagnosis.— Sutural margin of elytron explanate apically, inner sutural bead sinuate far from apex and joined to outer bead, and elytral apex rounded in most species; hypomeron of pronotum glabrous (or with few scattered setae); mandible with apical teeth approximate, lacking serrulate occlusal edge; median lobe without basal angulation, tegmen robust and tapered. Hosts typically Cyperaceae, but also a few other emergent plant types.

Plateumaris Thomson, 1859

Plateumaris Thomson (1859:154). Type species *Donacia nigra* Fabricius (1792), by original designation.

Juliusina Reitter (1920:41). Type species *Prionus braccatus* Scopoli (1772), designation by Monrós (1959).

Euplateumaris Iablokoff-Khnzorian (1966:121). Type species *Leptura sericea* Linnaeus, 1758, by original designation.

Donacocia Gistel (1857:12). Type species *Donacocia aenea* Gistel (1857:12), by monotypy. Application for suppression submitted to ICZN.

Juliusiana Mohr (1966: 108). Unjustified emendation.

The genus was monographed by Askevold (in prep. a) recognizing 26 species: 9 Old World, and 17 New World. Taxonomic details provided there are not repeated here.

Poecilocera Schaeffer, 1919. NEW STATUS

Poecilocera Schaeffer (1919:307), Type species *Donacia harrisii* LeConte, 1851, by monotypy.

Donacia (Poecilocera) Schaeffer (1919:307, 1925:120).

Sominella, *ex parte*: Goecke (1931, 1960a:10), Jolivet (1970:61), Wilcox (1975:3), Borowiec (1984:454).

Sominaella: Monrós and Bechyné (1956:1121). unjustified emendation

Plateumaris (*Sominaella*), *ex parte*: Monrós (1959:94,107). unjustified emendation

Etymology.— Not stated by Schaeffer. The name could be based on the Greek *poecil*, meaning variegated or coloured, and *keras*, meaning horns (or antennae) (Jaeger 1955). This may be the meaning Schaeffer intended, but such characters are not at all distinctive among donaciines.

Diagnosis.— Elytral apex emarginate or truncate, sutural interval narrowed before apex, lower margin explanate; pronotum with pubescence of anterior lateral parts of prosternum extended slightly and sparsely onto hypomeron; latter otherwise entirely glabrous; apical teeth of mandibles approximate; mesosternal process narrow between mesocoxae; eyes small, vertex not raised; median lobe without basal angulation, tegmen robust and tapered; ovipositor with ventral and dorsal valves of equal length, and with subapical surface finely setose.

Taxonomic history.— The name *Poecilocera* first was proposed for a subgenus of *Donacia* (*sensu lato*) by Schaeffer (1919) to accommodate a single Nearctic species, *Donacia harrisii* LeConte. As Schaeffer observed, this species possesses character states similar to *Plateumaris*, but also to *Donacia*. The name *Plateumaris* had not yet achieved common use as a genus name among North American coleopterists when Schaeffer revised the Nearctic Donaciinae (1919, 1925). Thus, *Poecilocera* subsequently was not recognized as a genus either. Goecke (1931) was the first and last author to examine the generic assignment of *Donacia harrisii*, and transferred it to the genus *Sominella* on the basis of gross similarity and antennomere proportion. Marx (1957) followed Schaeffer (1925) and considered *Poecilocera* a subgenus of *Donacia*, while Monrós (1959) considered *Sominella* (including *D. harrisii*) a subgenus of *Plateumaris*. Recent authors (*i.e.* Jolivet 1970, Borowiec 1984), retained genus status of *Sominella*, with *D. harrisii* placed in it, according to Goecke's (1931) arrangement.

Discussion of genus status.— Adult specimens of *Poecilocera* are characterized primarily by plesiomorphic character states: small eyes, undeveloped vertexal calli, lack of pubescence on pronotal hypomeron, rounded elytral apices (or apex depressed, and therefore appearing emarginate), robust, tapering tegmen, lack of subbasal angulation of median lobe, teeth of mandibles approximate, and mesosternal process narrow.

Adult specimens of *Sominella* also share most of these plesiomorphic states, but shape of elytral apex and hypomeral pubescence vary; the tegmen is slender, and mandible with apical teeth a little divergent. These character states are derived in relation to states possessed by *Poecilocera* (and *Plateumaris*), and are shared with other genera of Donaciini and the Haemoniini.

Additionally, specimens of *P. harrisii* have a slightly developed hypomeral pubescent area, which I consider a state intermediate between that shown by *Plateumaris* and most of the Donaciini and Haemoniini. Among the species placed in *Sominella*, a variety of states occur; specimens of *S. longicornis* lack hypomeral pubescence; those of *S. reticulata* have only a very few inconspicuous setae and could be equally considered as lacking, or having poorly developed, hypomeral pubescence; specimens of *S. macrocnemia* are much like those of *P. harrisii* in this character, while those of *S. kraatzi* have hypomeral pubescence fully developed, as in other Donaciini. I argued (Askevold 1988) that this character may have been important in donaciine evolution, its presence being apomorphic (but lost independently in the ancestor to *Macroplea*).

Goecke's (1931) observation that *Sominella* species (*i.e.*, *S. macrocnemia* and *S. longicornis*) are convincingly similar to *P. harrisii* is true. General similarity in body form and appearance would lead to the conclusion that they are congeneric: small eyes, antennomere 3 equal to or longer than 4, coarse but sparse transverse rugae on elytra, and apical teeth of mandibles approximate in *Poecilocera*, only a little divergent in *Sominella*. Specimens of *S. longicornis* have the apical sutural interval somewhat narrowed, similar to that of *P. harrisii* and members of *Plateumaris*, but this is not shared by *S. macrocnemia* or the two other species I tentatively place in the genus.

Character states possessed by members of *Sominella* therefore constitute a mosaic of plesiomorphic and apomorphic states. Apomorphic states suggest placement in Donaciini + Haemoniini, while the plesiomorphic states are shared with the Plateumarini. Plesiomorphies cannot be used to reconstruct relationships (Hennig 1966, Kavanaugh 1972), so despite substantial similarity of *P. harrisii* to members of *Sominella*, I cannot consider them contribal or congeneric. Therefore, I remove *P. harrisii* from *Sominella* and place it in a monobasic genus, for which the name *Poecilocera* was made available by Schaeffer (1919). I redescribe its single included member, below.

Poecilocera harrisii (LeConte 1851:316) NEW COMBINATION
Figures 19, 20, Phot. E.

Donacia harrisii LeConte (1851:316).
Donacia harrisii: Crotch (1873:20), Leng (1891:172).
Donacia harrisi: Jacoby and Clavareau (1904:8), Clavareau (1913:21), Wilcox (1954:372).
Donacia (*Poecilocera*) *harrisi*: Schaeffer (1919:308, 1925:120), Marx (1957:196).
Sominella harrisi: Goecke (1931:159), Jolivet (1970:61), Wilcox (1975:3), Borowiec (1984:454).
Plateumaris (*Sominaella*) *harrisi*: Monrós (1959:107).

Type specimen.— LECTOTYPE ♀, MCZ Type #4244. LeConte stated he had a male and female, and therefore had at leat two specimens before him. The single, remaining specimen found in the LeConte collection is here designated: "[pink disc] ♀, Type #4244 [red], D. Harrisii *Lec.* / LECTOTYPE ♀ Donacia harrisii LeConte design. I.S. Askevold 1990 [red]".

Type locality.— The LeConte pink disc indicates "Middle States, N.Y.", although LeConte states "Penn. rarissime".

Etymology.— Evidently named after T.W. Harris, from whom LeConte states he obtained the specimen under the manuscript name *D. inermis* Harris.

Taxonomic history.— *Poecilocera harrisii* has been long recognized by authors, there being no taxon with which to confuse it, although the *Donacia harrisi* [*sic*] that Blatchley (1910) recognized was described subsequently by Schaeffer (1925) as *D.* (*Plateumaris*) *diversa*. *Donacia harrisii* became emended to *D. harrisi*, it seems first by Jacoby and Clavareau (1904), and has been spelled as such since. Schaeffer recognized that *D. harrisii* was unusual among North American donaciines, and erected the subgenus (*Poecilocera*) to accommodate it. Goecke (1931) then moved it to the genus *Sominella* Jacobson because of antennomere proportions, and there it has remained in treatments by European authors, but has been assigned to *Donacia* by most American authors.

Diagnosis.— Elytral apex emarginate or truncate, sutural interval narrowed before apex, lower margin explanate; eyes small, vertex not raised, apical teeth of mandibles approximate; pronotum with pubescence of anterior lateral parts of prosternum extended slightly and sparsely onto hypomeron, latter otherwise entirely glabrous; elytra and disc of pronotum transversely rugose; mesosternal process narrow; metafemur extremely robust, almost hemispherical, ventral margin of metafemur of ♂ and metatibia of both sexes with denticles; colour above coppery, below entirely dark to entirely reddish; elytron of some specimens with epipleuron and/or suture narrowly reddish.

Description.— **Length.** Males: 6.90 - 7.74 mm, females: 8.23 - 8.64 mm

Colour. Coppery brown dorsally, similar ventrally, but with abdomen, pygidium, antennae and tarsi of most specimens fulvous.

Pronotum. Pubescence of prosternum extended only slightly onto area of hypomeron, of few scattered setae; anterolateral and posterolateral tubercles of tactile setae of most specimens fulvous; disc of moderate to fine punctures and punctulae confluent over much of disc in form of transverse rugae, like elytra but denser; disc of some specimens partly microreticulate in areas of diminished punctation.

Head. Eyes small, round; occiput hardly constricted, eyes therefore not markedly protruded, temporal area very short behind eyes and oblique to axis of head; mandibles with apical teeth approximate, of subequal length, mandibles therefore slender in apical and lateral views; antennae entirely reddish, antennomere 3 equal to or slightly greater than length of 4.

Legs. Metafemur metallic in apical half or more, reddish basally, tibia and tarsus reddish. Metafemur of male specimens with two subapical ventral spines and most specimens with several large denticles along ventral margin, that of female specimens without these; ventral margin of metafemur straight, dorsally curved, therefore in appearance almost hemispherical; metatibia conspicuously denticulate along ventral margin in both sexes, meso- and metatibia of both sexes without tibial tubercle, mesotibia of both sexes with small mucro, about same size as that of protibia.

Elytra. Coppery brown; strial punctures united transversely by strigations over most of the surface, these rather uniformly transverse except in areas of antemedial and postmedial depressions; intervening strial intervals more or less uniformly and densely punctulate; apex truncate, that concavely depressed, therefore in appearance slightly emarginate; epipleuron slightly reddish in most specimens; sutural interval indistinctly delimited except near apex, beads developed only toward apex, inner sutural bead in contact with outer lateral bead of sutural interval some distance from apex, lower sutural margin exposed, that reddish fulvous.

Males. Pygidium broadly emarginate; tegmen broad, robust; median lobe without subbasal angulation; BSB of endophallus extremely long, about half as long as median lobe; basal

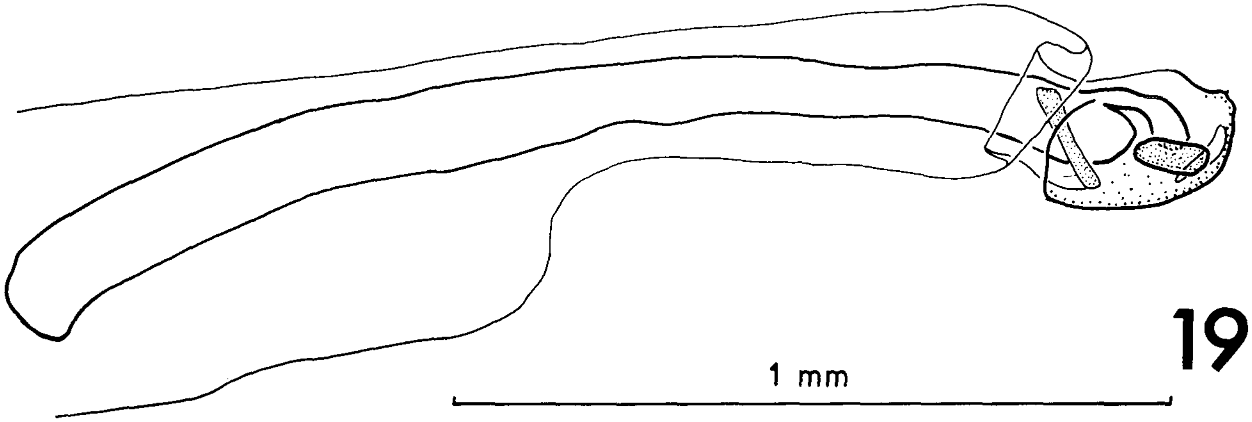

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FIGURE 19. Lateral aspect of endophallus of *Poecilocera harrisii* (LeConte).

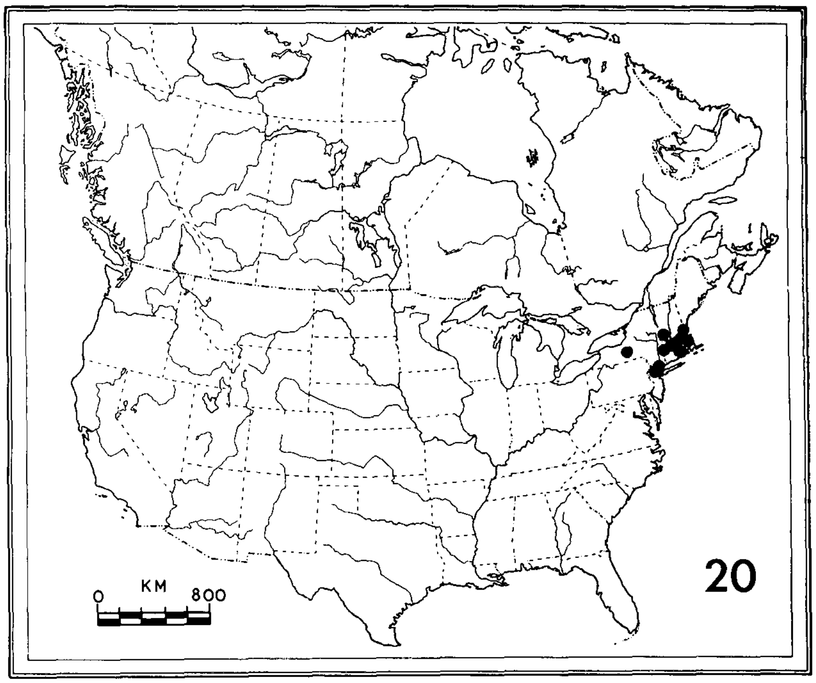

FIGURE 20. Known distribution in North America of *Poecilocera harrisii* (LeConte), based on specimens examined, and on published records (Schaeffer 1925). Each dot represents one collection record, or a group of very close records.

abdominal sternum flat, not impressed.

Females. Pygidium broadly emarginate; dorsal and ventral valves of ovipositor of equal length, both setose around apical area; apical sternum broadly truncate.

Sexual dimorphism.— Specimens of *P. harrisii* sexually dimorphic in size, armature of metafemur, and shape of apical abdominal sternum.

Variation.— Labrum, clypeus and antennal calli vary from fulvous to colour of rest of head; pro- to metasternum and anterior margin of pronotum fulvous in some specimens, in some specimens entire venter dark.

Natural history.— Few host records accompanied pinned specimens, but some collected by C.A. Frost indicate that *P. harrisii* occurs on sedges (probably *Carex* and *Scirpus* species). *Carex* was reported by Schaeffer (1925) according to collections made by Frost. Dates of collection are typically May to July. Judging by these data, the species probably overwinters in the adult stage, as do the species of *Plateumaris* and many *Donacia*, especially of the subgenus *Donaciomima*.

Distribution.— (Fig. 20). The known distribution is only from northern New Jersey to southern New Hampshire and Maine, mostly in areas close to the Atlantic coast.

Specimens examined.— 111 males and females, plus holotype.

UNITED STATES. CONNECTICUT: Fairfield Co.: Wilton, vi.24.1930 (AMNH 1); New London Co./Windham Co.: Pachaug State Forest, vi.29.47 (PMY 1). MASSACHUSSETTS: Berkshire Co.: Sheffield, vi.21.30 (MCZ 1); Essex Co.: Plum Isl., vi.12.1932 (MCZ 2); Middlesex Co.: Arlington, June.27.1897 (MCZ 1); Boston, no date (MCZ 1); Framingham, v.29 (USNM 1), 21.v.11 (UAE 1, MCZ 2, UMMA 2), vii.8.1917 (CAS 1), v.19.12 (UMMA 2); Natick, vi.8.46 (NMDC 1), vi.10.1926 (CAS 2), vi.18.49 (CAS 1), vi.16.1949 (CAS 1, USNM 1, UCR 2), vi.20.1950, "on sedge (or grass) in wet meadow" (OSUC 2), vi.20.50, "coll'd on heads of a sedge" (MCZ 1), vi.20.50 (UMMA 2); Sherborn, 28.vi.24 (CNC 1), vi.20.1931 (NMDC 1), vi.28.24 (USNM 3, ISAC 2), vii.1927 (USNM 4), vii.5 (USNM 1), 29.vi.24 (UAE 1, MCZ 2), v.16.09 (MCZ 1, UANH 2), vi.27.15 (UAE 1), vii.4.1924 (MCZ 1), vi.16.1923 (MCZ 1), vii.2.17 (UMMA 1), vi.22.15 (UMMA 1); Sudbury, vi.15.19 (MCZ 1), July.10.1892 (MCZ 1); Tyngsboro, 7.4.97 (MCZ 3), no date (MCZ 3). Norfolk Co.: Dover, II.22 (USNM 1); Wellesley, June.11.'95 (MCZ 1); Suffolk Co.: Winchendon, vi.28 (CMP 1); Worchester Co.: Berlin, vi.23.1937 (MCZ 2, OKS 1), vi.25.1937 (MCZ 2), 6.18.40 (UMMA 2), vi.26.1937 (CAS 1), vii.1.1935 (USNM 2, FMNH 1), vi.13.15 (UMMA 1), vii.1.1937 (CAS 7); Southboro, vi.22.24 (MCZ 2); Locality not found: Mt. Tom, Jy.73 (MCZ 2), no date (MCZ 2); Miscellaneous: "Mass." no dates (WEEM 1, CAS 1). MICHIGAN: Wayne Co.: Detroit (ex Schaeffer 1925). NEW HAMPSHIRE: Rockingham Co.: Dover, vii.7.1934 (UNH 1); Exeter, vi.23.24 (MCZ 2); Strafford Co.: Milton, June.26-7.'09 (MCZ 1). NEW JERSEY: Morris Co.: Boonton, vi.12.01 (USNM 1); Miscellaneous: "N.J." no dates (MCZ 4). NEW YORK: Delaware Co.: Hamden [ex Schaeffer 1925, but stated as a locality in Pennsylvania; Rockland Co.: Suffern, no date (CUCC 1); Tompkins Co.: McLean, no date (USNM 1); Miscellaneous: "N.Y." no date (USNM 1). VERMONT: Bennington Co.: East Dorset, vi.4.1957 (CVCC 1), June.11/15.1935 (CVCC 1, ISAC 1). MISCELLANEOUS SPECIMENS: "Drac." 6.18.91 (MCZ 4); no data (FMNH 2). Schaeffer (1925) also gives Michigan and Pennsylvania, but I have not seen these specimens. The locality given for Pennsylvania was not found in Pennsylvania, but in New York, and I suppose this was an error by Schaeffer.

TRIBE DONACIINI Kirby (1837)

Type genus.— *Donacia* Fabricius (1775).

Diagnosis.— Sutural margin of elytron more or less straight to apex, beads in contact only at extreme apex, apex truncate in most species; hypomeron with broad pubescent area in most species; mandible with apical teeth slightly to markedly divergent with occlusal edge long, serrulate; median lobe with basal angulation in most species, tegmen thin and slender in most species. Hosts various, including most aquatic vascular plants.

Sominella Jacobson, 1908

Sominella Jacobson (1908:622). Type species *Donacia macrocnemia* Fischer v. Waldheim (1824), by original designation.

Pseudodonacia Reitter (1920:27). Type species *Donacia kraatzi* Weise (1882), by monotypy. **NEW SYNONYMY**

Plateumaroides Khnzorian (1962:116). Type species *Plateumaroides fastuosa* Khnzorian (1962), (= *Donacia kraatzi* Weise, 1882), by monotypy. **NEW SYNONYMY**

Pseudodonacia: Iablokoff-Khnzorian (1968:262).

Pseudonacia Jolivet (1970:9). unjustified emendation

Sominaella Monrós and Bechyné (1956:1121). unjustified emendation

Etymology.— Jacobson named this genus after O. Somina.

Diagnosis.— No single synapomorphy, really suffices to define the genus. Members here assigned to *Sominella* share a general facies: most specimens with antennomere 3 as long as or longer than 4, most specimens with elytra sparsely and coarsely rugose, with interspaces finely punctulate. Other character states, of hypomeral pubescence, metatibial tooth, shape of elytral apex, and density and coarseness of pronotal punctation are various.

Included taxa (examined by me).—

S. kraatzi (Weise, 1882), **NEW COMBINATION**

Plateumaroides fastuosa Khnzorian, 1962. Synonymy with *Donacia kraatzi* was suspected by Iablokoff-Khnzorian (1968:262), and was listed, probably correctly, as a synonym by Borowiec (1984).

S. longicornis (Jacoby, 1890:84, plate I). Jacoby indicated "a few specimens"; two specimens were found in MCZ, and are here designated. Lectotype ♂, MCZ #8452: "Chang Yang A.E. Pratt. Coll. June 1888 / 1st Jacoby Coll. / TYPE [pink] / Type 8453 [red] / D. longicornis Jac. Type [blue] / LECTOTYPE ♂ Donacia longicornis Jacoby design. I.S. Askevold '90 [red]. Paralectotype ♀: "Chang Yang A.E. Pratt. Coll. June 1888 / 1st Jacoby Coll. / TYPE [pink] / PARALECTOTYPE ♀ Donacia longicornis Jacoby [red]".

S. macrocnemia (Fischer von Waldheim, 1824).
Plateumaris excisipennis Jacobson, 1894.

S. reticulata (Gyllenhal, 1817) **NEW COMBINATION**
Donacia appendiculata Ahrens, 1810 (not *Donacia appendiculata* Panzer, 1794, now in *Macroplea*; *cf.* Silfverberg, 1977:93).

Transfer of the two species, *Donacia kraatzi* and *Donacia reticulata* to *Sominella* is a compromise in classification which is discussed above.

I do not present further details about the included species here. Adults are easily identified using publications and the key to genera presented here. *Sominella reticulata* is identified easily using Mohr (1966); *S. kraatzi* is a distinctive species, one of rather few donaciines occurring in the area of the Black Sea, and the description given by Weise (1882), comments by Reitter (1920:27-28) and description of *Plateumaroides fastuosa* Khnzorian (1962) are adequate for identification; the two remaining species, *S. longicornis* and *S. macrocnemia*, are separable using the characters presented by Gressitt and Kimoto (1961), and more detailed discussion of the genus by Goecke (1931).

Donaciella Reitter, 1920. NEW STATUS

Donaciella Reitter (1920:38). Type species *Donacia tomentosa* Ahrens (1810), designation by Monrós (1959:94)

Donacia (*Donaciella*) Reitter 1920:38.

Donacia (*Donaciella*): Chûjô (1951:48), Müller (1949-53:259), Mohr (1966:107), Gruev and Tomov (1984:62).

Etymology.— Diminutive form of *Donacia*.

Diagnosis.— The species transferred to this genus have in common a general, slender facies, and characters as listed and discussed in the character analysis and used in the key to genera. Principally, members of the genus have a slender mesosternal process between the mesocoxae, elongate body and elytra, slender femora with absent or reduced metafemoral tooth, most members have well-sclerotized, acute, glabrous valves of the ovipositor (sternum VIII and tergum VIII) and the species are associated with grasses as host plants, principally *Phragmites*.

Taxonomic history.— *Donaciella* has been recognized as a subgenus by most authors since Reitter (1920) proposed the name to include two species with integument pubescent. Monrós (1959:107) and Jolivet (1970:9) placed the name *Donaciella* in synonymy with *Donacia s.str.* Other authors, cited above, used *Donaciella* as a subgenus of *Donacia*. Schaeffer (1925:120) realized that *D. pubicollis*, a Nearctic species, is similar in certain respects to *D. clavipes*, which is not pubescent dorsally; curiously, he made no comparison with the two pubescent Palaearctic species.

Donaciella is here elevated to genus status, and expanded to include four species, on the basis of monophyly and structural and ecological specialization of these included members.

Included Palaearctic taxa (examined by me).—

Donaciella clavipes (Fabricius, 1793). **NEW COMBINATION**
Donaciella cinerea (Herbst, 1784). **NEW COMBINATION**
Donaciella tomentosa (Ahrens, 1810). **NEW COMBINATION**

More detailed treatment of the single Nearctic species is given here of which I present taxonomic details, a brief description and outline its geographical distribution. The Palaearctic species are separable using keys provided by the authors cited.

Donaciella pubicollis (Suffrian, 1872). NEW COMBINATION
Fig. 21

Donacia pubicollis Suffrian, 1872:21. (not Crotch 1873).

Donacia pubicollis Crotch 1873:21. (not Suffrian 1872). Synonymized with *D. pubicollis* Suffrian by Marx (1957:247).

Donacia pubicollis:Leng 1891:165, Blatchley 1910:1100, Schaeffer 1925:119, Wilcox 1954:372, Marx 1957:247.

Type specimen.— The types of neither Suffrian nor Crotch were examined. No specimens that could be identified as types of Crotch's species were found in the MCZ in 1990. For this species, however, there is no doubt of assignment. The Suffrian type should be preserved in Berlin or Halle (MLU).

Type locality.— "Illinois".

Etymology.-- The specific epithet is in obvious reference to the finely pubescent pronotal disc.

Taxonomic history.— Crotch (1873) did not cite Suffrian (1872) as authority of *D. pubicollis*, and evidently thought it to be undescribed, and aptly named it *D. pubicollis*. Indeed, this is not at all surprising, in view of the possibility that Crotch may not have been aware of Suffrian's (1872) publication. Most authors since Crotch have listed Crotch as the author of *D. pubicollis*, without considering the possibility of inadvertent homonomy (*i.e.* Leng 1891,Blatchley 1910, Jacoby and Clavareau 1904, Clavareau 1913, Schaeffer 1925, Wilcox 1954, Jolivet 1970). I believe this to be so because Crotch specifically stated "*D. pubicollis* sp. n." (1873:21); interestingly enough, Crotch described *D. texana* on the following page, and that species has been recognized by authors since, but these same authors (except Marx, 1957) failed to recognize that "sp. n." applied to *D. pubicollis* probably indicated that Crotch was unaware of Suffrian's species by the same name. Be that as it may, it is obvious that there is a case of homonymy, and that Suffrian's name has priority.

Schaeffer (1925) recognized that *D. pubicollis* is similar in body form to the Palaearctic species *D. clavipes*, but did not mention *D. tomentosa* or *D. cinerea*, which bear an even greater resemblance. Reitter (1920) placed both *D. tomentosa* and *D. cinerea* together, constituting a new subgenus of *Donacia*, but the taxon has not been recognized consistently since, even by European authors.

Diagnosis.— large, elongate, coppery in colour; pronotum entirely finely pubescent; appendages slender, metafemora toothless, not clavate; mesosternal process narrow between mesocoxae; elytral disc coarsely reticulately wrinkled, apex rounded, apical punctures coarse, entirely confused, epipleuron rounded from base to apex; females with ventral valve of ovipositor sclerotized and apex acute.

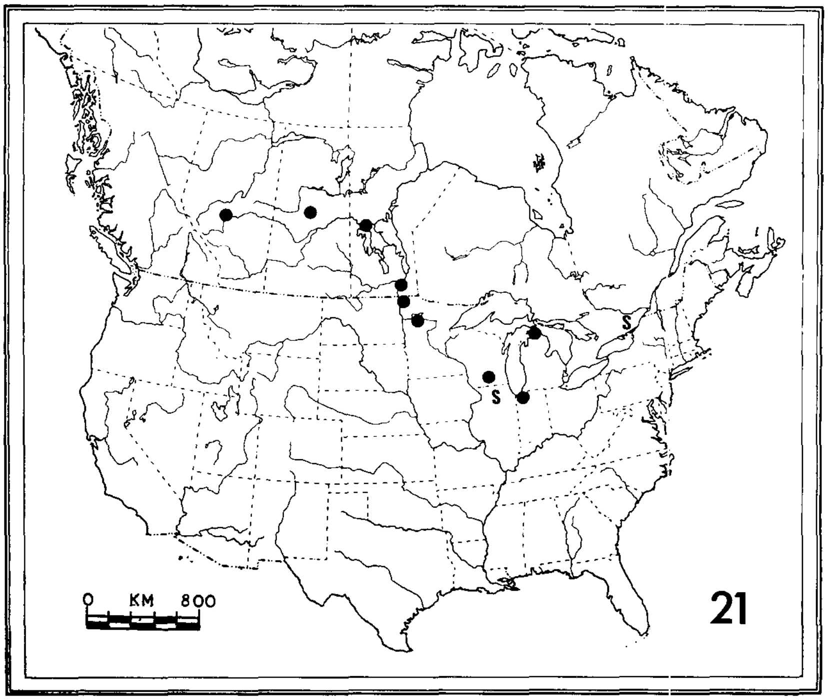

FIGURE 21. Known distribution in North America of *Donaciella pubicollis* (Suffrian), based on specimens examined, and on published records (Schaeffer 1925, Marx 1957). Each dot represents one collection record, or a group of very close records; S = state or provincial record.

Host.— *Phragmites; Nymphaea* reported, but most likely an adventitious record.

Distribution.— (Fig. 21). *Donaciella pubicollis* is known to occur narrowly from northern Indiana west to Alberta, exclusive of the prairies. The known distribution to date has included northernmost Indiana to Itasca State Park, Minnesota (Marx 1957, Schaeffer 1925).

Specimens examined.— 48 males and females.

CANADA: ALBERTA: Sturgeon River at Lac Sainte Anne, 53°90.43' N., 114°90.20' W., 1-3.vi.1982, "ex emergence traps", J.S. Richardson (ISAC 2). MANITOBA: Cedar Lake, July.5,12,26.1936, C.T. Parsons (MCZ 5), July.1936, Brues (MCZ 1); Winnipeg, June.24.1951, DH Groves (CNC 1). SASKATCHEWAN: Timber Bay, E. Montreal Lake, 1.vii.1985, C & A v.Nidek (ISAC 1). ONTARIO: "E. Ont.", Entomol. Branch (CNC 1, CAS 1, CMNH 1). UNITED STATES: ILLINOIS: Cook Co., Evanston, July 20 1900 (*ex* Marx 1957:249), county record, no date (MCZ 2); "Ill." (MCZ 11, CAS 1), "N. Ill." (CAS 1, ROM 1, UANH 1). INDIANA: Lake Co., Pine, May (*ex* Schaeffer 1925:120), Laporte Co., Laporte, no date (CMNH 2); Locality not found: Hessville, vii.1.12, AB Wolcott (FMNH 1). MICHIGAN: Cheboygan Co., Douglas Lake (*ex* Hoffman, 1940). MINNESOTA: Clearwater Co., Itasca State Park, 6.17.57, ex Phragmites (SCSU 2, ISAC 2), 6.14.1920, SA Graham (UMMZ 2, UASM 1, FMNH 5, CAS 1); Kittson Co., [county record], no date, OW Oestland (DEFW 1). WISCONSIN: Dane Co., (county record), April (*ex* Schaeffer 1925:120).

Donacia (*Donaciomima*) Medvedev, 1973. NEW STATUS

Plateumaris (*Donaciomima*) Medvedev (1973:876). Type species *Donacia clavareaui* Jacobson (1906), by original designation.

Etymology.— Diminutive form of *Donacia*.

Taxonomic history.— Medvedev (1973) apparently created this name as a subgenus of *Plateumaris* and based it on *Donacia clavreaui* Jacobson, though this is not clear from arrangement of taxa in that publication. Possibly he misidentified the type species as a species of *Plateumaris*, but I have examined the type (see below), and the species is similar to *D. simplex* Fabricius and *D. vulgaris* Zschach. Authors have not recognized *D. clavareaui*, and have recognized instead *D. fukiensis* Goecke (here synonymized). Borowiec (1984) synonymized the names *Donaciomima* and *Donacia s.str.*

Donaciomima is here removed from synonymy and accorded status as a subgenus of *Donacia*, because the included members cannot be assigned to either of the other subgenera of *Donacia*. To deny these subgenera status would be to deny that they include members that form a clearly defined, monophyletic group, and that are clearly defined ecologically (host plant use).

Diagnosis.— No single synapomorphy defines this subgenus. Most species share a general facies, but exceptions to all character states exist: most members have a coarsely punctate pronotum, the punctures confluent to form transverse rugae in many members, the spaces between the punctures alutaceous in many members, elytra of most members rugose, to rugulose, epipleuron of most members raised and sharply defined; most species are entirely metallic in colour, above and below, with metallic or dark appendages (but this varies greatly).

Included Palaearctic taxa (examined by me).—

D. aequidorsis Jacobson, 1894.
D. antiqua Kunze, 1818.
D. apricans Lacordaire, 1845.
D. aquatica Linnaeus, 1758.
D. aureocincta J. Sahlberg, 1921.
D. bactriana Weise, 1887.
D. bicolor Zschach, 1788.
D. bicoloricornis Chen, 1941.
D. brevicornis Ahrens, 1810.
D. brevitarsis Thomson, 1884.
D. clavareaui Jacobson (1906:311). Holotype ♂ MNHN: "Kjachta Siberie par Götzelmann [Clavareau's handwriting] / Donacia Clavareaui *TYPE* Jacob. [Clavareau's handwriting] / TYPE [red, added by N. Berti] / Museum Paris Coll. H. Clavareau 1932 / Donacia clavareaui Jac. ♂ typ. G. Jacobson det."
    D. fukiensis Goecke (1944:9). No type specimens of Goecke's species were examined, but *D. fukiensis* is a well known species in Japan, which are no different from specimens I have examined from China, and these are no different from the type of *D. clavareaui* Jacobson. **NEW SYNONMY**
D. delagrangei Pic (1896:35). Holotype ♀, MNHN: "Asie-Min. Anatolie *CD*. 1888 / type [written on underside of pink disc] / Donacia Delagrangei Pic [handwritten] / communique la returner [handwritten] / Goecke vidit. / HOLOTYPE ♀ [red] / vidit 1984 I.S. Askevold".
D. dentata Hoppe, 1795.
D. fennica Paykull (1800:70)
    D. ochroleuca Weise (1912:76). Holotype ♂, ZMHB: "Sibir or. Ertl / ♂ / TYPUS [orange] / Zool. Mus. Berlin / ochroleuca m." I added the label

"HOLOTYPE ♂ Donacia ochroleuca Weise [red]} and "Donacia fennica Paykull ♂ det. I.S. Askevold 1989". **NEW SYNONYMY**

D. flavidula Reitter (1913:124). This name has been placed in synonymy of *D. ochroleuca* by authors, and is therefore transferred. **NEW SYNONYMY**

D. flemola Goecke, 1944.
D. frontalis Jacoby (1893:261). Syntype BMNH. No further data recorded.
D. gracilicornis Jacobson, 1899.
D. gracilipes Jacoby (1885:191). Lectotype ♀ MCZ #8485, by present designation: "Japan Lewis / 1st Jacoby Coll. / Type 8485 [red] / LECTOTYPE ♀ Donacia gracilipes Jacoby design. IS Askevold 1990 [red]", and paralectotype ♀ "Japan Lewis / 1st Jacoby Coll. / PARALECTOTYPE ♀ Donacia gracilipes [red]". A syntype specimen is also labelled as type, BMNH (further data not recorded).
D. hirtihumeralis Komiya and Kobuta, 1987:41.
D. hiurai Kimoto, 1983:11.
D. impressa Paykull, 1799.
D. jacobsoni Semenov and Reichardt, 1927.
D. jacobsoniana Shavrov, 1946.
D. japana Chûjô and Goecke, 1956.
D. katsurai Kimoto, 1981:24.
D. kweilina Chen, 1941. [This reference missed by Jolivet, 1970]. Two paratypes examined (ISAC).
D. malinowskyi Ahrens, 1810.
D. marginata Hoppe, 1795.
D. mistshenkoi Jacobson, 1910.
D. nitidior (Nakane, 1963).
D. obscura Gyllenhal, 1813.
D. polita Kunze, 1818.
D. semenowi Jacobson (1907:5). Holotype ♂, MNHN: "Zaïdam (Thibet) Kozlow 1895 G. Jacobson / Donacia Semenovi *TYPE* Jacob. / Donacia ♂ semenovi Jac. typ G. Jacobson det. / TYPE [pink] / Museum Paris Coll. H. Clavareau 1932 / vidit 1984 I.S. Askevold".
D. semicuprea Panzer, 1796.
D. simplex Fabricius, 1775.
D. sparganii Ahrens, 1810.
D. springeri Müller, 1916.
D. thalassina Germar, 1811.
D. versicolorea Brahm, 1790.
D. vulgaris Zschach, 1788.

Taxa unknown to me.— *D. breviuscula* Jacobson, 1899, *D. fedtschenkoae* Jacobson, 1899, *D. freyi* Goecke, 1940, *D. galaica* Baguena, 1959, *D. humilis* Weise, 1912, *D. intermedia* Jacobson, 1899, *D. kirgizkaisaka* Jacobson, 1910, *D. knipowitschi* Jacobson, 1927, *D. koenigi* Jacobson, 1899, *D. mannerheimi* Lacordaire, 1845, *D. mediohirsuta* Chen, 1941, and *D. tschitscherini* Semenow, 1895 (= 12 taxa).

Donacia (*Donacia*) Fabricius, 1775

Donacia (*Donacia*) Fabricius (1775:195). Type species *Donacia crassipes* Fabricius (1775), designation by Curtis (1834), not Chapuis (1874).

Eodonacia Haupt (1956:54). Type species *Eodonacia goeckei* Haupt (1956), by original designation. Askevold (1990) presented reasons for synonymization of this name. **NEW SYNONYMY**

Etymology.— Based on the Greek *Donax*, for reed, reeds or other aquatic plants being host plants for the majority of species.

Taxonomic history and synonymies.— *Donacia* is the oldest genus-group name in the subfamily, which is based on this name. Most members of the subfamily were described in *Donacia*, which has gradually become restricted in composition. It is unfortunate that Curtis (1834) selected *Donacia crassipes* as type species, for the group of species to which *D. crassipes* belongs is a much smaller group of species in the genus. With resurrection of *D.* (*Donaciomima*) to subgenus status, the subgenus *Donacia* (*Donacia*) becomes restricted to a small group of 10 Nearctic species and five Old World species (one undescribed).

Diagnosis.— Species of this subgenus are recognized by their large and broad size (most members), with mesosternum broad, pygidium of females elongate and pointed (rounded apically in some species, but shape at least elongate), elytra partly to entirely rufous (most species) and tending toward diminished rugosity (most species), occiput of head with at least a pair of small rufous spots (most species), varying to entirely rufous, pronotum of most species rufous, underside with extremely dense pubescence, the punctation not visible, mandibles with prominent lateral angulation and widely splayed apical teeth (Figs. 1, 10), and median lobe with underside flat or sulcate.

Included Old World taxa (examined by me).—

D. crassipes Fabricius, 1775.

Donacia sp. nov., from Botswana.

D. ozensis Nakane, 1954.

D. recticollis Jacoby (1893:261). Syntypes (# not recorded), one labelled as holotype (sex not recorded), BMNH, Berhampur, India (and three possible syntypes also labelled simply "Berhampur", MCZ).

> *D. indica* Clark (1866:1, not Melsheimer 1847). Holotype ♀, BMNH. The specimen is a composite. Elytra, pterothorax and abdomen undoubtedly represent the authentic type, but the prothorax and head belong to a specimen of *Sominella reticulata*. Nonetheless, Clark described the species from this composite specimen and drew particular attention to the curious green nature of the head and thorax, strongly contrasting with the testaceous elytra [as did Jacoby (1908:11)]. The body and elytra of the specimen agree fully with the type of *D. recticollis*, which is a large species with flavous elytra. **NEW SYNONYMY**
>
> *D. clarki* Monrós (1959:115) (replacement name for *D. indica* Clark), **NEW SYNONYMY**

Taxon unknown to me.— *D. ussuriensis* Medvedev.

Donacia (*Cyphogaster*) Goecke, 1934.

Donacia (*Cyphogaster*) Goecke (1934:219). Type species *Donacia provostii* Fairmaire (1885), designation by Chen (1941).

Hemidonacia Haupt (1956:60). Type species *Hemidonacia insolita* Haupt (1956) by monotypy. Askevold (1990) presented reasons for synonymization of this name. **NEW SYNONYMY**

Etymology.— Not stated by Goecke; it appears to be based on the Greek *kyphos*, meaning bent or humb-backed, and *gaster*, or abdomen, but I do not know what this should be in reference to.

Taxonomic history.— The subgenus was erected by Goecke (1934) for most of the species listed below, and has been recognized in catalogues [Monrós (1959), Jolivet (1970), Borowiec (1984)] and faunistic treatments [Gressitt and Kimoto (1961), Chûjô (1951), Kimoto (1983)] as a subgenus since.

Diagnosis.— Members of this subgenus are recognized by the same characters of *Donacia s.str.*, but most members have elytra more uniformly dark or metallic. The only character that defines the subgenus is a pair of small, glabrous, raised tubercles about midlength, medially, on the basal abdominal sternum of male specimens (though *D.* (*Donaciomima*) *dentata* has a similar structure).

Included taxa (examined by me).—

D. australasiae Blackburn (1892:235). Holotype ♂, BMNH. Additional data not recorded.

D. delesserti Guérin-Méneville (1844:258). Type, BMNH. Additional data not recorded. Taxonomic status not evaluated, but I cannot determine consistent differences from *D. javana.*

D. inopinata Goecke, 1944.

D. javana Wiedemann, 1821.

D. lenzi Schönfeld (1888:33). Holotype ♂, SMF (Frankfurt): "Hiogo Jap. L. [white with black trim] / coll. v. Schönfeldt [white] / TYPUS [red with black trim] / Lenzi Schönf [white with black trim] / vidit 1984 I.S. Askevold".

D. papuana Gressitt (1971:607). Paratype ♀, BPBM. Additional data not recorded.

D. provostii Fairmaire (1885:LXIV). Holotype ♀, MNHN. Additional data not recorded.

D. transversicollis Fairmaire (1887:135) (new subgenus combination). Holotype ♀, MNHN. Fairmaire's type keys to *D. tuberfrons* Goecke, in the key to species of *D.* (*Cyphogaster*) presented by Goecke (1934:217), and agrees in detail with paratypes of *D. tuberfrons* examined.

D. tuberfrons Goecke (1934:221). Four paratypes, MNHN, examined. Additional data not recorded. **NEW SYNONYMY**

Taxon unknown to me.— *D. yuasi* Nakane, 1963.

Donaciasta Fairmaire, 1901

Donaciasta Fairmaire (1901b:233) (replacement name). Type species *Donacilla perrieri* Fairmaire (1901a), by ICZN (1985) Art. 67h.

Donacilla Fairmaire (1901a:127) (not Lamarck, 1818). Type species *Donacilla perrieri* Fairmaire (1901a), by monotypy.

Donaciocrioceris Pic (1936:10). Type species *Donaciocrioceris dentatus* Pic (1936), by monotypy. **NEW SYNONYMY**

Prodonacia Chen (1966:144). Type species *Prodonacia shishona* Chen (1966), by monotypy. **NEW SYNONYMY**

Etymology.— Unknown, probably merely a diminutive of *Donacia*, based on the Latin *donax*, a reed.

Taxonomic history.— *Donaciasta* is not well known taxonomically despite recent treatments, by Monrós (1958) and Jolivet (1972), both of whom described additional species but did not examine types of other described African and Madagascan donaciines. On examination of types of described species I find that African species hitherto placed in *Donacia* belong in *Donaciasta.* Taxonomic treatment is in progress (Askevold in prep. d); I list the revised synonymies below because of reassignment of species to this genus.

Borowiec (1984) synonymized the names *Prodonacia shishona* Chen and *Donacia vietnamensis* Gressitt and Kimoto (both species described from ♂♂), and the names *Prodonacia* Chen and *Donacia* Fabricius. The description of *Donacia assama* Goecke was based on a single female (holotype ♀, BMNH). On the basis of non-sexually dimorphic characters, the types of *Prodonacia shishona* and *Donacia vietnamensis* are conspecific with the type of *Donacia assama*. *Donacia assama* is the senior and valid name of the species. Specimens of this species possess the majority of characters that are typical of *Donaciasta*, and I transfer this species to *Donaciasta*.

Elytral structure of *Donaciocrioceris dentatus* Pic was interpreted incorrectly by Monrós (1959), who claimed that its elytral apex is like that of *Plateumaris* (*i.e.* like Fig. 9, Askevold, in prep. a). This is not so; the elytral apex is typical of Donaciini. This species is odd in other respects, however: in head and body shape it is similar to *Plateumaris*; in tarsal claw structure it is similar to certain criocerines that have connate claws (hence the name Pic created). It is highly autapomorphic and therefore it is not surprising that a genus was erected for it; however, it possesses the synapomorphies of *Donaciasta* as well, and is phylogenetically in an intermediate position in the genus (Askevold, in prep. b) (reflected by position in list of taxa, below).

Diagnosis.— Specimens of *Donaciasta* are recognized by the coarsely punctured pronotal disc (except *D. dentata*), presence of proepimeral pubescence, lack of tactile seta of anterolateral tubercles; mandible articulation remote from antennal bases (not especially in *D. assama*), the clypeus therefore somewhat elongate; colour of most species not metallic like most other Donaciinae, dorsum rufous, testaceous or piceous, and with at most a metallic luster; elytra of most members with supernumerary punctures in some intervals, and interval 8 at least a little costate (especially ♀♀); males with median lobe lacking subbasal angulation, tegmen slender, of uniform width and thickness from base to apex; legs and antennae at most partially infuscate.

Donaciasta is the only donaciine genus that occurs in Madagascar and tropical Africa, with the exception of a single, undescribed species of *Donacia* (*Donacia*) known from Botswana. Species are associated with the plants *Potamogeton*, *Trapa natans* L. and possibly *Nymphaea*, as indicated by the few available host records.

Included taxa.—[revised synonymies and details about type specimens examined are given by Askevold (prep. d), and are not repeated here].

D. assama (Goecke) (1936:224), **NEW COMBINATION**
    Prodonacia shishona Chen (1966:144, 146). **NEW SYNONYMY**
    Donacia vietnamensis Kimoto and Gressitt (1979:202). Placed in synonymy with *Prodonacia shishona* by Borowiec (1984). **NEW SYNONYMY**
D. dentata (Pic, 1936:10), **NEW COMBINATION**
D. perrieri (Fairmaire, 1901a).
D. luridiventris (Lacordaire, 1845).
D. abortiva (Fairmaire, 1899:27), **NEW COMBINATION**
    Donaciasta minuta Pic, 1936.
    Donacia madecassa Pic, 1944.
    Donacia notaticollis Pic, 1944.
D. goeckei Monrós, 1958.
    Donaciasta quioca Monrós. 1958.
    Donaciasta capensis Monrós, 1958.

Donaciasta garambana Jolivet, 1972.
Donaciasta monrosi Jolivet, 1972.

Taxon of uncertain placement within Donaciini.—
Donacia microcephala Daniel and Daniel (1904:89).
Donacia testaceipes Pic (1908:52). Holotype ♂, MNHN: "Adana [handwritten] / Type [handwritten] / Museum Paris Coll. M. Pic / HOLOTYPE [red] / testaceipes Pic [handwritten] / Lesne vidit (1926) / vidit 1984 I.S. Askevold".

TRIBE HAEMONIINI CHEN (1941)

Type genus.— *Haemonia* Dejean (1821).

Diagnosis.— Dorsum testaceous; legs almost entirely testaceous, metafemur edentate, slender, tarsi with apical tarsomere elongate, tarsomeres with reduced ventral pubescence; elytron apically with spine at outer angle (most species); hypomeron with pubescent area above coxa (lost in *Macroplea*, character state in *N. voronovae* unknown); mandible with apical teeth divergent, in form of serrate occlusal edge; median lobe with basal angulation, tegmen slender. Hosts Zosteraceae and Haloragaceae.

Macroplea Samouelle, 1819

Macroplea Samouelle (1819:211). Type species *Donacia zosterae* Fabricius (1801), designation by Curtis (1830) [Monrós (1959:102) stated that Barber and Bridwell (1940) designated the type species, but Curtis (1830) had already done so, as Barber and Bridwell (1940) had stated].

Apelma Billberg (1820:53). Type species *Donacia zosterae* Fabricius (1801), designation by Barber and Bridwell (1940).

Haemonia Dejean (1821:114). Type species *Donacia zosterae* Fabricius (1801), designation by Thomson (1859:154) [Monrós (1959:102) stated that Barber and Bridwell (1940) designated the type species, but Thomson (1859) had already done so].

Included taxa (examined by me).—
M. appendiculata (Panzer, 1794)
Donacia zosterae Fabricius, 1801
M. japana (Jacoby, 1885)
M. mutica (Fabricius, 1792)
M. pubipennis (Reuter, 1875)
Haemonia piligera Weise (1889:576). **NEW SYNONYMY**
Haemonia incostata Pic (1907:100). Holotype ♂, MNHN: "Ost-Turkestan, Aksu 1067 m, 5.1903 Coll. Hauser / type [handwritten] / Haemonia incostata Pic [handwritten]". This synonymy was suggested previously by Hellén (1937), but was not adopted by later authors. I have not found any differences among specimens of *M. piligera* from Turkestan (also collected by Hauser) and *M. pubipennis* from Finland, including genitalic structure. **NEW SYNONYMY**

Neohaemonia Székessy, 1941

Neohaemonia Székessy (1941:148). Type species *Haemonia nigricornis* Kirby (1837), by original designation.

Five species are known in this genus, which was treated in full by Askevold (1988); members are listed by Askevold (in prep. c).

Incertae sedis in Haemoniini.— *Neohaemonia voronovae* Medvedev (1977).

Nomen incertae sedis in Donaciinae.— *Arundinarius* Voet (1806:31). This name has been placed in synonymy with *Donacia* by previous authors. Most likely, the name would have included species now assigned to *Donaciomima*, most of the species of which are reed plant-associated (the origin of the name). Silfverberg (pers. comm. 27.6.1985) assured me that this work of Voet (1806) should be considered rejected because he did not adhere to the principle of binominality (using names inconsistently as binomials and trinomials) (ICZN 1985, Art. 11c (iii).

Key to Genera and Subgenera of New World Donaciinae

1 Prothorax of most specimens with broad, finely pubescent area above procoxa, disc of some specimens conspicuously pubescent also; sutural interval of elytron with inner and outer beads convergent only at apex, in form of a short apical carina in some specimens, lower sutural margin narrow, not explanate; eyes of most specimens set off from vertex by distinct sulcus, vertex of many specimens with two distinct calli; median lobe sub-basally with distinct angulation, tegmen thin and slender, and of uniform width 3

1' Prothorax without conspicuous broad pubescent area above procoxae (but *cf. Plateumaris aurifer*); sutural interval of elytron with sutural bead sinuate, and convergent with inner bead some distance from apex (sutural bead sinuate), exposing the lower, internal, explanate margin of elytron; vertex of head more or less flat in most specimens; median lobe sub-basally without angulation, tegmen robust, tapering apically.....2

2 (1') Apex of elytron broadly rounded; antennomere 3 shorter than 4; metatibia and metafemur not denticulate on underside, metafemur untoothed or with only one tooth; underside metallic or not, but not largely rufous, except for all or apex of abdominal sterna, reddish; females with strongly sclerotized, acute ovipositor, in some specimens distinctly serrate, dorsal valve shorter than ventral valve.................... ....*Plateumaris* Thomson, p. 634

2' Apex of elytron truncate or emarginate; antennomere 3 as long as or longer than 4; metatibia and metafemur (especially males) distinctly denticulate on underside, metafemur of males with both a subapical ventral and a ventromesal tooth, females with only subapical ventral tooth; underside largely rufous; ovipositor of females not strongly sclerotized or acute, dorsal and ventral valves of equal length.................. ....*Poecilocera* Schaeffer, p. 634

3 (1) Outer apical angle of elytron with distinct spine; metafemur slender and untoothed, apical tarsomere elongate, about as long as preceding tarsomeres combined; legs, thorax, and elytron pale brown, most of underside, tarsi, scutellum, antenna, strial punctures, and head (except vertex of many specimens), black.............*Neohaemonia* Székessy, p. 648

3' Outer apical angle of elytron not toothed; metafemur of most specimens distinctly clavate, most specimens with 1 or 2 subapical ventral teeth, apical tarsomere much shorter than preceding tarsomeres combined; colour not as above, most specimens dorsally metallic, not entirely pale brown 4

4 (3') Pronotal disc distinctly and finely pubescent AND legs entirely rufous, at most with indistinct infuscation; metafemur without distinct subapical tooth below; epipleuron of elytron rounded, not angulate; elytral apex broadly rounded, apical punctation close, entirely confused; female with acute, sclerotized ovipositor; host *Phragmites* ....*Donaciella* Reitter, p. 640

4' Pronotal disc glabrous, if pubescent then elytral apex truncate or elytra pubescent also; legs rufous to entirely metallic, metafemur of most specimens with one or more subapical teeth; epipleuron of elytron rounded or distinctly angulate; elytral apex truncated, with obtuse to acute outer angle, punctures of striae finer, more widely spaced, and more or less regular in arrangement apically; hosts other than *Phragmites* 5

5 (4') Occiput of most specimens with two reddish spots, in many specimens spots expanded over entire occiput; legs (except *D. proxima*) with no more than dorsum of metafemur darkened; pronotal disc without coarse punctures, but many specimens with very fine transverse to irregular rugae, OR surface granulate, alutaceous, OR smooth and shiny between punctures; mesosternal process, especially in females, broad between the mesocoxae, at least half as broad as diameter of mesocoxal cavities; ventral punctation obscured by dense pubescence; pygidium of most females more or less elongately triangular, apically acute or narrowly rounded; host Nymphaeaceae.......*Donacia* (*Donacia*) Fabricius, p. 644

5' Head more or less unicolourous, not reddish in most specimens; legs entirely dark to entirely red, but not with only dorsum of metafemur dark; pronotal disc with coarse punctures, punctures typically contiguous to confluent laterally to form coarse to moderate rugae (except 2 pubescent species and *D. caerulea*-Group); mesosternal process no more than half diameter of mesocoxal cavities; ventral coarse punctation visible, at most obscured by pubescence (except *D. cuprea*); pygidium of females broadly rounded or emarginate, not elongate; hosts mostly Cyperaceae, Sparganiaceae, Zosteraceae, and Nymphaeaceae ....*Donacia* (*Donaciomima*) Medvedev, p. 642

Key to Tribes, Genera and Subgenera of Old World Donaciinae

1 Elytron with outer apical angle prolonged as spine; if only with obtuse or acute angulation, then elytra and pronotum with conspicuous sparse, long setae; apical tarsomere elongate, as long as basal 3 together, and tarsus with markedly reduced pubescence; elytra, pronotum and legs testaceous or brownish, with black strial punctures (most taxa); hosts Zosteraceae and Haloragaceae ....

HAEMONIINI 2

1' Elytron with outer apical angle not markedly produced, but truncate, rounded, or emarginate, pubescent or not; apical tarsomere shorter than remaining articles together, tarsi typically with dense and plush pubescence below; elytra and pronotum typically metallic, but colour various; host plants various 3

2 (1) Pronotal disc without individually distinct punctures; elytron with strial punctures black; geographical range from Europe to Japan............................*Macroplea* Samouelle, p. 648

2' Pronotal disc with individually distinct punctures; elytron with strial punctures not black; known only from Lake Ugii-Nur, Ara-Khankai Aimak, Mongolia; generic assignment not established.................*Neohaemonia voronovae* Medvedev

3 (1') Elytron with inner bead of sutural interval sinuate distinctly before apex, joined with outer bead as single bead, explanate sutural margin below exposed; pronotal hypomeron without broad pubescent area above procoxa; median lobe without subasal angulation, and tegmen robust and tapered; ovipositor of females acute and markedly sclerotized, serrate in most species, and with acute apex; (*Plateumaris* Thomson, single Palaearctic genus) .............PLATEUMARINI, p. 633

3' Elytron with beads of sutural interval in contact near apex only, or obscured, interval more or less uniformly wide to near apex, and explanate margin not broadly exposed; pronotal hypomeron typically broadly pubescent above procoxa; median lobe with or without prominent subbasal angulation (cannot be seen if uncleared!), tegmen typically slender, more or less parallel-sided, not thick; ovipositor of most female specimens not acute and markedly sclerotized..... ......DONACIINI.. 4

4 (3') Specimens from Madagascar or Africa south of 15° North latitude 5

4' Specimens not from tropical Africa or Madagascar.................. 6

5 (4) Pronotum with anterolateral tactile seta absent; elytron with interval 8 slightly to markedly costate, some intervals with unordered punctation; frons and vertex with calli distinct and largely glabrous (Fig. 3,4); metatibia not markedly carinate or denticulate below; punctures of pronotal disc, if individally distinct, not confluent to form irregular rugae. Geographical distribution: Senegal to Uganda, south to South Africa, and Madagascar .... *Donaciasta* Fairmaire, p. 646

5' Pronotum with anterolateral tactile seta prominent, of normal length; elytron with interval 8 not costate, intervals without punctation; frons and vertex uniformly pubescent, without distinct calli; metatibia markedly explanate and denticulate below; punctures of pronotal disc not individually distinct, the disc irregularly rugose. Geographical distribution: Botswana ....*Donacia* (*Donacia*) sp., undescribed

6 (4') Pronotum and elytra uniformly pubescent, like head and underside; mesosternal process slender between mesocoxa;

elytral epipleuron flat, or rounded and slightly raised, at most angulate at extreme base by humerus 7

6' Pronotum and elytra pubescent or not; mesosternal process typically broader, as much as half or more width of mesocoxae (especially ♀♀); epipleuron prominently angulate in most taxa from below humerus to near apex 8

7 (6) Body dorsally and ventrally bronzish or bright pale green; mandible distinctly and broadly bidentate apically; metafemur rather slender, hardly clavate, in most specimens edentate; female ovipositor of most species with acute, sclerotized ventral valve; hosts typically Gramineae. Geographical distribution: more northern Palaearctic region . ... *Donaciella* Reitter (part), p. 640

7' Entire body dorsally and ventrally testaceous, pronotal disc at most broadly darkened in middle; mandibles unidentate, therefore slender and sickle shaped; metafemur toothed; female ovipositor blunt, not sclerotized; host plant unknown. Geographical distribution: Middle East. Generic assignment undetermined... .... *Donacia microcephala* Daniel and Daniel

8 (6') Labrum with apex broadly and deeply emarginate (Fig. 7).......... 9

8' Labrum with apex broadly rounded (Fig. 1) 11

9 (8) Pronotal disc of most specimens with fine, short pubescence; metafemur without subapical ventral tooth; pronotum wider across posterior margin than across anterior margin; elytral apex narrow and rounded. Geographical distribution: southwestern Caucasus.............. *Sominella kraatzi* (Weise)

9' Pronotal disc without distinct setae; metafemur of most specimens with subapical tooth, legs largely rufous; pronotum of most specimens wider across anterior margin than across posterior margin; elytral apex various, most specimens with apex broadly truncate. Geographical distribution: almost Transpalaearctic, including Caucasus 10

10 (9') Elytron with epipleuron flat or slightly rounded from behind humerus to near apex; dorsum pale metallic green or bronzish .... *Donaciella clavipes* (Fabricius)

10' Elytron with epipleuron angulate from behind humerus to near apex; dorsum with colour various, testaceous or brown, very dark green, or pale green (or with elytron laterally reddish).... .... *Donacia* (*Donaciomima*) Medvedev (part), p. 642

11 (8') Pronotal disc more or less uniformly coarsely punctured (most taxa), and intervening spaces alutaceous or not; elytral disc typically coarsely rugose, and generally metallic in colour; female pygidium rounded or emarginate apically, similar to that of male in length; mandibular teeth not especially prominently divergent apically, and outer margin typically more or less uniformly arcuate; head of uniform colour, metallic to piceous; epipleuron typically raised and angulate along upper edge adjacent to outermost stria; hosts Cyperaceae, Zosteraceae, Nymphaeaceae and Trapaceae 12

11' Pronotal disc at most punctulate, shiny or alutaceous and smooth, or finely rugulose; elytral disc largely smooth and shiny, and punctulate, with few coarse rugae; elytra metallic, testaceous or brown in colour, then with or without metallic lustre; female pygidium prolonged and more or less triangular, acute or narrowly rounded at apex, very different from males; mandibular teeth very prominently explanate and divergent, lower tooth directed ventrally and inwards, in form of a broad, cutting edge; head typically with pair of small red spots behind eyes on occiput, or head partially to completely red; epipleuron typically rounded or flat, at most angulate near humerus; hosts Nymphaeaceae....................................14

12 (11) Pronotum with anterolateral tactile seta prominent, of normal length; dorsum entirely metallic; underside metallic, legs and antenna largely metallic, some specimens with ventral half of femora rufous; antennae densely and uniformly pubescent. Geographical distribution: Europe to Japan, some in China. Hosts various. 13

12' Pronotum with anterolateral tactile seta absent; dorsum except head brown or testaceous, at most somewhat piceous with pale metallic tinge; underside, antenna and legs largely rufous; antenna sparsely pubescent basally. Known only from three localities in southeast Asia. Host plant unknown, probably Trapaceae, Zosteraceae, or Nymphaeaceae............. ....*Donaciasta assama* (Goecke)

13 (12) Pronotal hypomeron without dense patch of pubescence above coxa (sparse setae in *S. macrocnemia* and *S. reticulata*), hypomeron very coarsely rugose longitudinally; elytral apex various, narrow and rounded, toothed at inner apical angle, some specimens also at outer angles, or narrowly truncate; specimens of two Oriental species with metatibia explanate to prominently toothed ventrally (Figs. 11, 12); elytral disc typically shiny, punctulate or not, but most specimens not coarsely and densely rugose; vertex of head flat or depressed, without pair of calli; antennomere 3 typically long, in most specimens with article 3 as long as or longer than 4 ....*Sominella* Jacobson (part), p. 639

13' Pronotal hypomeron typically with pubescent patch above coxa in most specimens, and hypomeron generally not so coarsely rugose; elytral apex generally broadly truncate, and disc generally densely rugose, shiny in some; metatibia at most denticulate along ventral margin; most specimens with calli of vertex convex to prominently raised; antennomere 3 not as long as 4 ....*Donacia* (*Donaciomima*) Medvedev (part), p. 642

14 (11') Male specimens without pair of small shiny tubercles on abdomen. Geographical distribution: Europe to Japan, and northern India......*Donacia* (*Donacia*) Fabricius (part), p. 644

14' Male specimens with pair of small glabrous tubercles at middle of basal abdominal sternum. Geographical distribution: Japan to S.E. Asia, including Nepal, India and Sri Lanka, Java, Singapore, Mindanao, New Guinea, and northern Australia.....*Donacia* (*Cyphogaster*) Goecke, p. 645

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INDEX TO NAMES OF TAXA

(Junior synonyms in italics)

FAMILY GROUP TAXA

GENERA AND SUBGENERA

SPECIES AND SUBSPECIES

CLASSFICATION, RELATIONSHIPS, LIFE HISTORY, AND EVOLUTION OF *EREBIA MAGDALENA* STRECKER (LEPIDOPTERA: SATYRIDAE)

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ABSTRACT

Several populations of Erebia magdalena *Strecker were discovered in Alberta and British Columbia, Canada, all within a limited geographic area. Specimens from the Rocky Mountain states and the sister species* E. mackinleyensis *Gunder from Alaska and Yukon Territory were compared with the newly discovered populations. Principal Component Analysis showed little evidence of introgression of the Alberta populations with populations of* E. mackinleyensis. *Populations of* E. magdalena *from the Rocky Mountain states clustered near and overlapped with the Alberta populations. Discriminant analysis demonstrated a clinal shift in character states within* E. magdalena *which were separate from those of* E. mackinleyensis. *These permitted recognition of different populations. Egg and larval characteristics show similarity between* Erebia magdalena *and* E. mackinleyensis. *Observable differences occur between the* E. magdalena/mackinleyensis *species pair eggs and larvae, and those of* E. fasciata *Butler.* Erebia magdalena saxicola *new subspecies is described. Type locality is Adams Lookout, Wilmore Wilderness Park (43 km southeast of Grande Cache), Alberta.* Erebia magdalena *females oviposit on rocks. Larval development appears univoltine with late instar larvae overwintering. Larvae feed on a variety of grasses.* Erebia magdalena *appears to have evolved from a common ancestor with* E. mackinleyensis *during a pre Wisconsinan glacial period. Subsequent dispersal and isolation resulted in fragmentation and subspeciation. In Alberta* E. magdalena *appears derived from ancestral populations formerly located in the Montana front ranges during the last glacial stage.*

INTRODUCTION

Erebia magdalena Strecker was known to inhabit high mountain boulder fields and talus slopes in alpine scree of northern New Mexico, Colorado, Wyoming, Utah, and southern Montana (Ferris and Brown, 1980). Inaccessibility and remoteness have limited collection of this species in many parts of its range. Its discovery in Alberta and adjacent British Columbia raises some interesting questions. What are the affinities of these populations with other populations of *E. magdalena* and those of its seemingly close relative *E. mackinleyensis* Gunder? Why has this butterfly species not been found in the mountain areas between Wilmore Wilderness Park (near Grande Cache), Alberta and Carbon County, southern Montana? Is it a relic of pre- or post- Wisconsinan dispersal? To attempt to answer these questions, populations of *E. magdalena* are compared with each other and with populations of *E. mackinleyensis.* Aspects of life history are included as further characterization.

MATERIAL AND METHODS

Material

Study material included: 242 adults, eggs, egg shells, larvae, 1 pupa, and photographic material of life stages of *Erebia magdalena*; 54 adults, eggs, egg shells and larvae of *E. mackinleyensis*; and and eggs, egg shells and larvae of *Erebia fasciata*.

The following codens designate collections cited in this paper. Names of curators or owners of private collections are in parentheses following the address of each collection.

ALME	Allyn Museum of Entomology, 3701 Bay Shore Road, Sarasota, Florida 33580. (L.D. Miller).
AMNH	American Museum of Natural History, Central Park West at 79 Street, New York, New York 10024. (F.H. Rindge).
AVER	Avery Collection, Hinton, Alberta. (K. Avery).
CNC	Canadian National Collection, Biosystematics Research Institute, Ottawa, Ontario, K1A 0C6. (J.D. Lafontaine).
HILC	Hilchie Collection, Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3. (G. J. Hilchie).
INHS	Illinois Natural History Survey, 172 Natural Resources Building, Urbana, Illinois 61800. (K.C. McGiffen).
PIKE	Pike Collection, Department of Biology, University of Calgary, Calgary, Alberta T2N 1N4 (E. M. Pike).
PRES	Preston Collection, Lawrence Kansas. (J. & F. Preston).
SHEP	Shepard Collection, Sproule Cr. Road, Nelson, B.C. (J. Shepard).
SPER	Sperling Collection, Department of Ecology and Systematics, Cornell University, Ithaca, New York, 14853. (F. A. H. Sperling).
UASM	University of Alberta, Strickland Museum, Edmonton, Alberta, T6G 2E3. (D. Shpeley).
USNM	United States National Museum, Smithsonian Institution, Washington, D.C. 20560. (R.K. Robbins).
YOUN	Young Collection, 256 Clear Falls Circle, Eagle River, Alaska 99577. (M. E. Young)

Methods

Several populations of *E. magdalena* were examined critically for similarities and differences to assist in recognizing species and subspecies boundaries. Characters used in the analysis include scale pattern and color, on the wings and antennae, measurements, structure of male genitalia and structure of the egg. Data generated from the study was examined statistically.

Measurements.— Specimens were examined using a Wild M5 microscope equipped with an ocular micrometer. Wing length measurements were made from base to margin at R4 for the forewing and from base to margin at M3 on the hindwing. Larval head capsule widths were measured frontally at the widest point. Egg capsules were measured for length (apex to base) and width (widest point).

Scale pattern and color.— Wing scale and hair counts were made on limited regions of the fore and hindwings. On the forewing the area was delimited by the veins R4 and R5 and the wing margin. On the hindwing the area was delimited by the veins M1 and M2 and the wing margin.

Medial band on the hind wing was indexed as three character states: present and clearly defined; present but faint and indistinctly defined; and absent. The presence and extent of pattern exhibited by rust coloured scales was indexed as five character states (only three listed): no rust scales; a few scattered scales; large well defined patch. Variation of pigmentation of the antennal club was indexed as seven character states dependent on colour and pattern of light and dark areas. Indexing of the antennal club did not use color patterns of the covering scales as these were badly abraded on many specimens. Index values were polarized to reflect recognized taxa, with low numbers assigned to *E. magdalena* and higher numbers to *E. mackinleyensis*

Male genitalia.— Male genitalia were studied by removing the terminal segments of the abdomen and placing them in hot 10% KOH solution until soft. Illustrations were made with the aid of a camera lucida on a Wild M5 microscope. Then genitalia and terminal segments of the abdomen were placed in glycerol in a microvial which was pinned through its cork beneath the specimen of origin.

Egg and larval structures .— Egg and larval structures were examined and photographed with the aid of a Zeiss Tessovar light microscope and Cambridge Stereoscan 250 and 100 Electron Scanning Microscopes.

Chromosome study.— Butterflies were brought to the lab alive, frozen at -20°C and stored until chromosome fixing. Frozen testes were dissected and fixed in 95% ethanol:acetic acid (3:1). Testes were Fuelgen stained, squashed in 50% acetic acid and preserved in Euparol.

Life history study.— Caged females were given substrate choices (rocks, lichens, grasses, willow twigs and leaves) on which to oviposit. Eggs were collected for rearing and taxonomic study. Larvae initially were given a choice of food until the food preference was determined. Larvae were reared to maturity in petri dishes, lined with absorbent toweling, and supplied with fresh leaves daily. Incubators were used to control environmental conditions for part of the rearing.

Statistical analysis.— Data obtained were subjected to Principal Component Analysis, Discriminant Analysis and Cluster Analysis for evaluation of variance and relationship between populations and individuals. Statistical manipulations were made with the Michigan Interactive Data Analysis System (MIDAS) on the Amdhal Computer at the University of Alberta.

The data were pooled to provide population samples of adequate size for statistical analysis. Small samples that could not be pooled were excluded from the initial analysis, then compared with the results on an individual basis.

CHARACTER ANALYSIS

Characters for species and subspecies designation in *Erebia* species are based on structural differences in genitalia, chromosome number, wing venation, wing shape, differences in maculation and scale types (Warren, 1936). Lesser levels of difference in maculation pattern with geographic isolation serve as criteria for subspecies discrimination.

Warren (1936) commented "There is obviously little possibility of showing variation" in reference to the uniform black colour of *E. magdalena*. This results in placing more emphasis on character states which do show variation.

TABLE 1. CHARACTERS USED TO ASSESS PHYLOGENETIC RELATIONSHIP OF SAGROID SUBFAMILIES.

						TAXA					
CHARACTERS**			CRIOCERINAE			**SAGRINAE		*ATALASIS*		DONACIINAE	
(1-30 from Table 3)			state	code		state	code	state	code	state	code
1.	Ligular lobes		absent	1	GP-	present	0	present	0	absent	1
2.	Tibial spurs	GP-	2-2-2	0		0-0-0	A	0-0-0	A	1-1-0	B
4.	BSB		present ?	1		absent	0	absent	0	present	1
5.	ELD		present ?	1		abs./pres.	0/1	present	1	present	1
6.	Med. lobe angulation		present	1	GP-	absent	0	absent	0	abs./pres.	0/1
9.	El. suture explanate		no (yes)	1/0	GP-	yes/no	0/1	yes	0	yes/no	0/1
10.	Mandibular teeth		bidentate	1	GP-	unidentate	0	unidentate	0	bidentate	1
24a.	Frontoclypeal groove		present	1	GP-	present	1	present	1	present	1
30b.	Tegmen, dorsal cap		reduced	1	GP-	no	0	no	0	no	0
33.	♂ ♂ Sexual characters		no	1	GP-	yes/no	0/1	yes	0	yes	0
34.	Pn. lat. margin		absent	1	GP-	absent	1	absent	1	absent	1
35.	MEG		present	1		abs./pres.	0/1	present	1	present	1
36.	Basal sac sclerites		present	1	GP-	present	1	present	1	present	1
37.	Scutellum pubescent		no	1	GP-	yes/no	0/1	yes	0	yes	0
38.	Humeral pubescence	GP-	no	*	GP-	yes/no	*	no	*	yes	*

** Characters 30b to 37 are presented here for subfamilial level character assessment; for details of Sagrinae genera, see Table 2, for Donaciinae see Table 3. A and B = separate reductions from ground plan state. GP- = probable groundplan state. * = polarity undetermined.

Table 1. Comparison of males of *Erebia mackinleyensis* and *E. magdalena* adult males using measurements and character index values.

Character	**Species**													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon		Alberta to New Mexico		Alberta		Montana		Utah		Colorado		Colorado (south) & New Mexico	
	n=39		n=167		n=28		n=6		n=20		n=95		n=18	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.7	22.8-28.9	25.1	21.4-28.9	23.8	21.4-26.1	24.9	24.2-25.8	25.7	21.9-27.7	25.3	21.9-28.9	25.1	23.5-27.9
-white scale index	0.33	0-10	1.5	0-26	4.6	0-26	7.2	2-16	3.3	0-24	0.18	0-10	0.33	0-3
-white hair index	3.2	0-38	2.1	0-35	1.7	0-10	10.5	2-22	5.5	5.5-35	1.1	0-20	1.8	0-14
Hindwing														
-length (mm)	21.5	18.2-23.8	20.9	17.7-23.5	19.9	17.7-21.7	20.7	19.8-21.4	21.2	18.2-23.3	21.1	18.2-23.5	20.8	19.1-22.6
-white scale index	0.03	0-1	3.6	0-48	8.7	0-48	13.5	0-38	1.5	0-12	1.8	0-32	3.9	0-42
-white hair index	1.3	0-28	1.7	0-46	1.0	1-10	11.0	0-33	0.35	0-5	1.2	0-27	4.2	0-46
Wing markings														
-mesial band index	2.5	1-3	1.7	1-3	1	1	1	1	1	1	1.1	1-3	1.2	1-2
-dorsal rust patch	1.7	1-5	1	1	1	1	1	1	1	1	1	1	1	1
-ventral rust patch	3.2	1-6	1.02	1-3	1	1	1.5	1-3	1	1	1	1	1	1
Antennal club														
-color index	3.6	1-8	5.9	4-8	6.4	5-7	7.0	5-8	6.4	4-8	5.6	5-8	6.1	5-8

Corrected table added after publication. Inserted here by KWW, 2010.

Table 2. Comparison of *Erebia mackinleyensis* and *E. magdalena* adult females using measurements and character index values.

Character	**Species**													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon		Alberta to New Mexico		Alberta		Montana		Utah		Colorado		Colorado (south) & New Mexico	
	n=15		n=75		n=20		n=3		n=4		n=42		n=6	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.8	23.5-28.2	25.3	22.1-28.0	25.0	22.1-27.7	25.5	24.9-26.3	25.4	23.7-26.3	25.3	22.4-28.0	26.5	24.5-27.5
-white scale index	4.9	0-39	20.6	0-200	46.4	3-200	49.3	21-105	6.7	4-13	9.7	0-30	5.5	0-14
-white hair index	18.8	0-52	68.5	1-218	66.5	2-150	84	49-137	33	17-68	74.9	1-218	46	0-111
Hindwing														
-length (mm)	21.5	19.1-22.8	21.0	17.2-23.3	20.5	17.2-22.8	21.4	19.8-22.6	20.8	19.8-21.4	21.1	18.2-23.3	21.9	20.0-23.3
-white scale index	3.9	0-23	31.8	0-135	59.6	6-135	53.7	25-97	6.0	0-14	17.9	0-93	41.8	0-97
-white hair index	4.5	0-24	73.5	0-258	51.8	0-153	168.3	139-216	9.7	1-29	8.5	0-258	63.8	0-147
Wing markings														
-mesial band index	2.9	2-3	1.8	1-3	1	1	1	1	1	1	2.4	1-3	2	2
-dorsal rust patch	5.4	1-6	1.2	1-6	1.05	1-2	4	3-6	1.25	1-2	1.09	1-5	1	1
-ventral rust patch	5.0	1-6	1.1	1-5	1	1	1.7	1-3	1.25	1-2	1.09	1-5	1	1
Antennal club														
-color index	2.7	2-4	6.1	5-8	6.8	6-8	6.0	5-8	7	7	5.7	5-7	6.0	5-7

Corrected table added after publication. Inserted here by KWW, 2010.

TABLE 2. ASSESSMENT OF SOME PHYLOGENETIC CHARACTER STATES OF SAGRINAE.

	TAXA*							
Characters	*Diap*	*Carp*	*Poly*	*Mega*	*Mecy*	*Sagr*	*Amet*	*Atal*
4. ELD	?	?	-	-	?	NH	NH	1
5. BSB	?	?	-	-	?	NH	NH	0
9. Elytral suture	0	1	0	0	0	0	1	0
24. Ocular groove	no	yes(I)	no	no	no	yes	no	no
30b. Tegmen	0(?)	0(?)	0(?)	0(?)	0(?)	0	0	0
33. ♂ ♂ Sexual characters	?	?	1	1	?	1	1	1
34. Pronotal lateral margin	1	1	1	1	1	1	1	1
35. MEG	?	?	-	-	?	1	NH	1
36. Basal sac sclerites	?	?	?	?	?	1	1	1
37. Scutellum pubescent	yes	yes	yes	yes	yes	no	yes	yes
38. Humeral pubescence	yes	yes	no	no	no	no	yes	no

Characters stated as yes/no are not polarized.

I= character more or less present, but incomplete in development.

? = state unknown because no male specimens examined, or structure not identified (*Polyoptilus* and *Megamerus*).

\- = internal sac without sclerites.

NH = sac sclerite not homologized.

*Names of taxa: *Amet* = *Ametalla; Atal* = *Atalasis; Carp* = *Carpophagus; Diap* = *Diaphanops; Mecy* = *Mecynodera; Mega* = *Megamerus; Poly* = *Polyoptilus; Sagr* = *Sagra.*

External Features

Erebia magdalena is one of the plainest butterfly species in North America, with adults uniformly black to dark brown. Other colours and patterns are absent from most specimens. Data on populations sampled are presented in Tables 1 and 2. Few females have a reddish flush (6.7%, n=75), with one population (Montana, Beartooth Plateau) in which all females examined (n=3) and one of the males (n=5) were marked. Ventral maculations are slightly developed to obsolete with considerable variation between localities. Most females from Colorado (80%, n=45) are banded (Figure 43) while females from Alberta, Montana, Utah, New Mexico (n=20, 3, 4, 4) were unbanded. Most males lack ventral banding. Degree of coverage by scattered white hairs and scales on the ventral wing surface varies markedly. When present in quantity the white scales and hairs dusted the ventral apex of the forewing and were more evenly distributed on the hind wing. In females from Colorado these scales enhance the banding pattern on the hind wing but do not do so on females from Alberta. Markings on the antennal club vary, but on average it has a dark piceous half partially bisected by a longitudinal strip lighter in colour. The remaining half of the club is paler on many adults. Scales obscure the boundaries of the markings (Figure 41).

Data for the Principal Component Analysis were placed in the following groups for comparative purposes (males, females):

E. magdalena

CANADA. Alberta, (Mount Hamell 11, 4; Adams Look Out 17, 15; Dore River, B.C. 0, 1). U.S.A. Montana (Beartooth Plateau of Montana and Wyoming 6, 3). Utah (Summit, Duchesne and Uintah Counties 20, 4). Colorado, northern (Larimer, Grand, Gilpin and Boulder Counties 42, 18). Loveland Pass, (central Colorado 40, 13). Colorado, southern (Gunnison, Park, Hinsdale, La Plata, Custer, *etc.* Counties 27, 14). New Mexico (Taos County 4, 3).

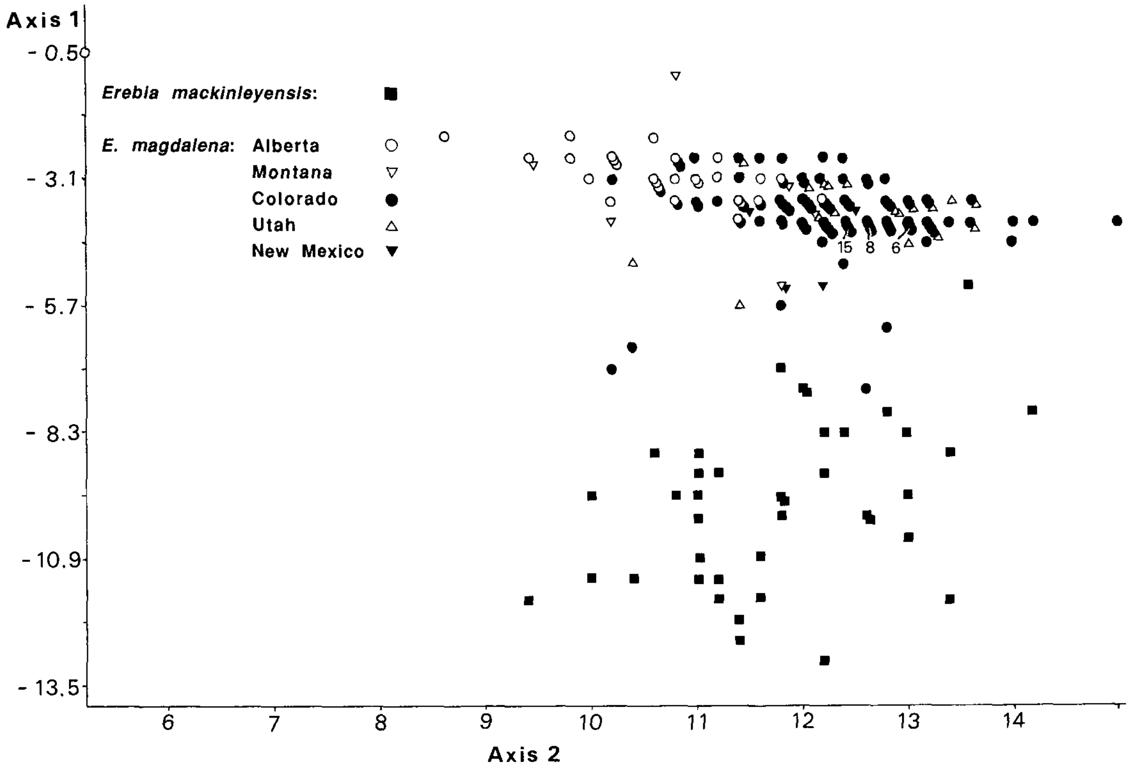
E. mackinleyensis

CANADA. Yukon (Dempster Highway 37, 11). U.S.A. Alaska (2, 4)

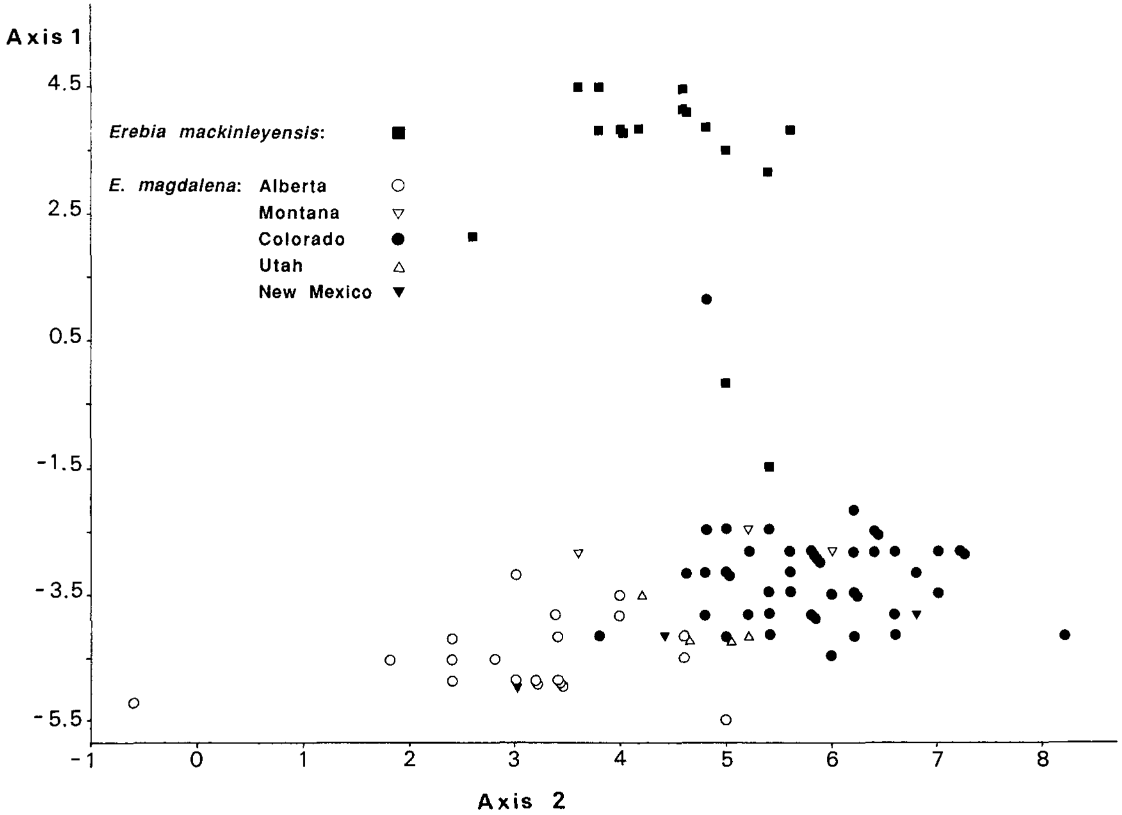
Results from Principal Component Analysis of the various populations support the idea that *E. magdalena* and *E. mackinleyensis* are separate and recognizable entities as shown in Graphs A and B. Tables 1 and 2 list the mean values for variables used in the analysis and their range of variation expressed by length, or indexed value. Populations of *E. magdalena* show a trend (Graphs A and B: Tables 1 and 2): data points cluster but are skewed geographically. Northern (Alberta) specimens appear as one end of a cline, with intermediate individuals forming a blend zone with southern (Colorado) specimens. Albeit the Montana sample is small, the specimens examined tend to be somewhat intermediate in placement, along with specimens from Utah. It is clear that these populations belong together; it is also clear that there are recognizable differences between the populations. Discriminant Analysis and Cluster Analysis exhibited similar results.

Male Genitalia

Males of *E. magdalena* (Figures 31–36) are very similar in genitalic structure to males of *E. mackinleyensis* (Figures 37 and 38). Spination of the claspers (Figures 32b-36b) is along the outer margin. In males of *E. mackinleyensis* (Figures 37b-38b) the spines are expanded onto the inner face. Warren (1981) reports the dorsal parts of the uncus and brachia are on a smaller



Graph A. Principal Component Analysis of adult females of *Erebia mackinleyensis* and several populations of *E. magdalena* from Alberta, Montana, Colorado, Utah and New Mexico. (Re-plotted from computer printout.)



Graph B. Principal Component Analysis of adult males of *Erebia mackinleyensis* and several populations of *E. magdalena* from Alberta, Montana, Colorado, Utah and New Mexico. (Re-plotted from computer printout.) Numbers refer to numbers of individuals whose scores fall on one plotting point.

scale in *E. mackinleyensis*. Variation in shape and size of parts of the male genitalia of *E. magdalena* as shown in Figures 32–36 (male claspers) indicate that size and shape do not discriminate these species reliably.

Conclusions

Erebia mackinleyensis and *E. magdalena* have been considered as conspecfic subspecies (*e.g.*, Ehrlich and Ehrlich 1961, Howe 1975). The distinct appearance of the adults, structural differences in male genitalia and vicariance strongly suggest separate gene pools. Until genetic compatibility is determined, I accept Warren's (1981) decision in recognition of *Erebia magdalena* and *Erebia mackinleyensis* as distinct species. Further I suggest that they are sister species.

Based on phenetic differences and geographical disjunction, the populations of *Erebia magdalena* form two identifiable groups. These groups deserve subspecific recognition, with the names that are given them serving as convenient designations for use by systematists and others. Although some individuals reject the formal recognition of a subspecies category, I accept the position taken by Willis (1967): "... if a subspecies reflects to some degree the actual pattern of variation, as well as being convenient 'handles' for reference, their value seems sufficient to justify their recognition".

TAXONOMIC TREATMENT

Erebia magdalena Species Group

Similarities in structure of the male genitalia place *Erebia magdalena* and *E. mackinleyensis* in a group with *E. fasciata* Butler, *E. semo* Grüm-Grschimailo and *E. erinnyn* Warren (Warren 1936,1981). The *magdalena* group is subdivided on the presence or absence of male androconial scales. *Erebia magdalena, mackinleyensis, semo* and *erinnyn* are included in the subgroup which possesses androconia (*erinnyn* is assumed by Warren to have androconia). Reduction of the

Table 3. Comparison of larval head capsule width, and egg diameter and length for *Erebia magdalena, E. mackinleyensis* and *E. fasciata.*

Stadia	**Species**							
	E. m. mag.		*E. m. sax.*		*E. mack.*		*E. fasc.*	
Egg dia.	1.23		1.22±0.07		1.10±0.09		1.03±0.05	
lgth.	1.36	n=3	1.45±0.07	n=25	1.28±0.05	n=11	1.27±0.08	n=11
Instar								
1st	0.74	n=3	0.81±0.02	n=25	0.74±0.03	n=13	0.69±0.03	n=12
2nd			1.18±0.04	n= 4	1.05±0.04	n=19	0.99±0.04	n=16
3rd			1.55±0.02	n= 5	1.51±0.07	n=19	1.41±0.05	n=36
4th	2.15	n=2	2.19±0.04	n=10	2.13	n= 3	2.00±0.06	n= 5
5th	3.15	n=2	3.00±0.10	n=10	3.00	n= 1	2.79	n= 3

Units are in mm, error limit is ± one standard deviation Abbreviations used: diam. = diameter; *E. m. mag.* = *E. m. magdalena; E. m. sax* = *E. m. saxicola; E. m. mack.* = *E. mackinleyensis; E. fasc.* = *E. fasciata.*

mesal banding pattern helps to unify the subgroup. The uniform black color of *E. magdalena* in both sexes differentiates the species from *E. mackinleyensis* and *E. erinnyn*. *Erebia erinnyn* is Asian while *E. mackinleyensis* is North American.

Erebia fasciata Butler 1868
(Figures 51 and 52, Table 3)

Eggs and larvae were examined and compared with immatures of *Erebia mackinleyensis* and *E. magdalena* .

Material Examined.—

Immatures. CANADA. Yukon; Dempster Highway, 14 eggs and egg shells, 11 first larvae, 4 second instar larvae, 38 third instar larvae, 4 fourth instar larvae, 3 fifth instar larvae and associated exuviae (HILC).

Erebia mackinleyensis Gunder 1932
Figures 37, 38, 40 and 44 - 50, Tables 1, 2 and 3)

Recognition.— Most adults are easily recognized by reddish wing patches to well marked bands on the wings. Geographic locality in Alaska and Yukon Territory further assists in identification.

Description.—

Adults (Figures 37, 38, 40 and 44). Form, shape and general appearance are similar to *E. magdalena* as mentioned by Gunder's original description (1932). Data are summarized in Tables 1 and 2. Maculations are more prevalent in both sexes. Most females (91%, n=15) display a conspicious rust patch on the forewing (Figure 44) or at least scattered rust scales. Males show the same marking but at a lower frequency (74% n=39). Both sexes have a ventral mesial band on the hind wing (males 97%, n=39; females 100%, n=15). Few white hairs and scales are present on either sex. The antennal club is different from *E. magdalena* in that it tends to be testaceous to two-toned yellow (Figure 40). A few *E. mackinleyensis* adults had darker antennal clubs (7.5%, n= 39 males, 0%, n=15 females) resembling those of *E. magdalena*.

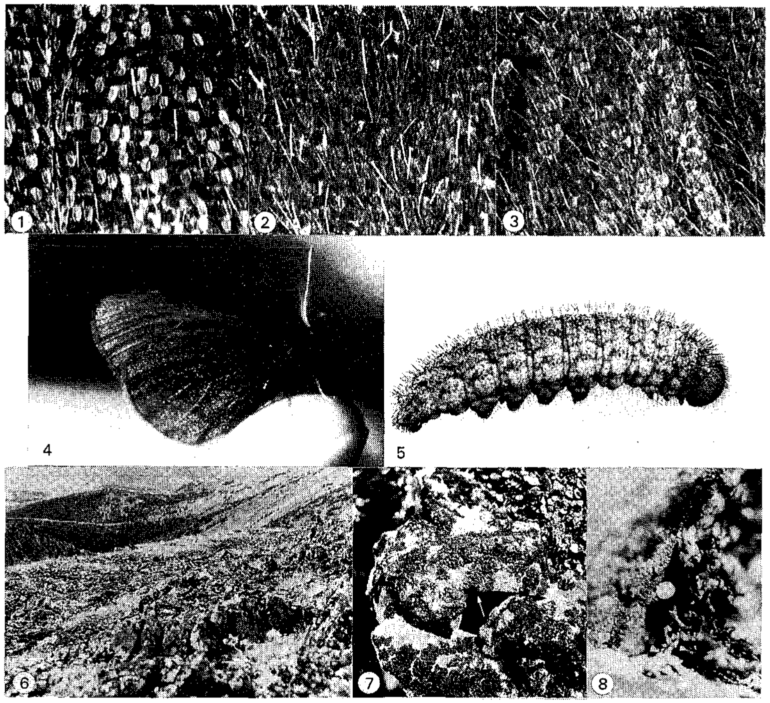
Male genitalia are similar to those of *E. magdalena* The spination on the uncus is expanded onto the inner surface (Figures 37 and 38).

Larvae (Figures 46–50, Table 3). Larvae were indistinguishable from those of *E. magdalena* but differed from those of *E. fasciata*. *Erebia fasciata* larvae were similar in body appearance structurally but differed in maculation pattern and first instar larvae (Figure 52) showed differences in the sculpture pattern of the head capsule. Measurements of head capsule are summarized in Table 3.

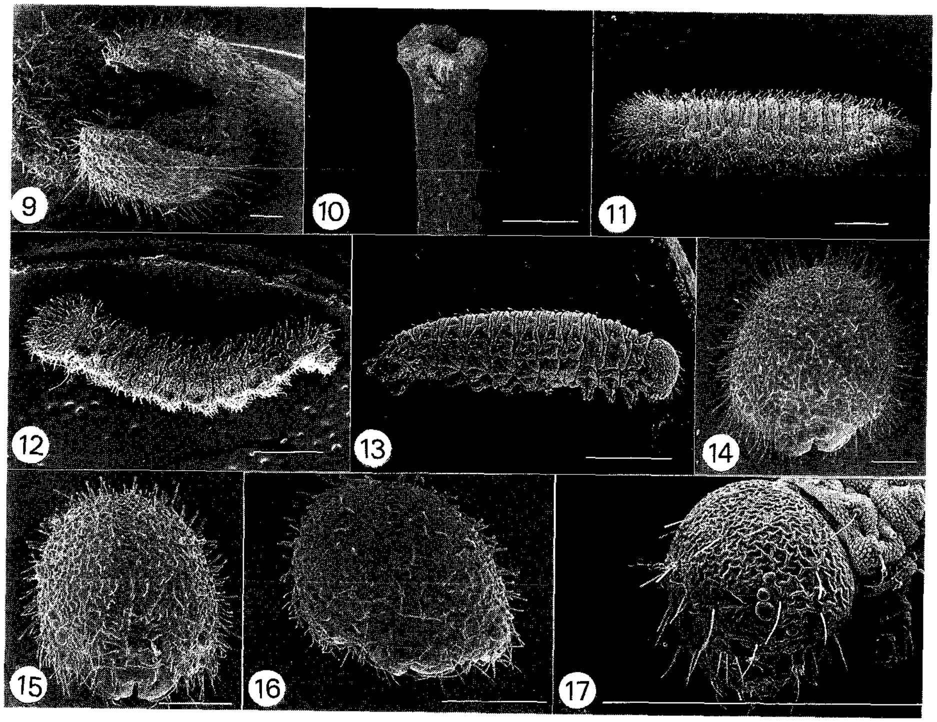
Egg (Figure 45). Sculpture and shape are very similar to that seen in eggs of *E. magdalena*, length 1.10 mm, diameter 1.28 mm, (n= 11). The area around the micropyle appears different; (compare Figures 24 and 45). The basic ground plan pattern is similar but differs in the number of micropyle holes (the differences could be due to individual variation). For comparative purposes the micropyle region of a third species of the *magdalena* group was examined, *E. fasciata* (Figure 51). On the eggs of this species the micropyle region is very similar to that seen on the eggs of *E. mackinleyensis* with only slight symmetry differences of the openings.

Geographical Distribution.— *Erebia mackinleyensis* is known from alpine tundra rock pile habitat in Alaska and Yukon Territory. The southern range limits in the mountain regions have not been documented.

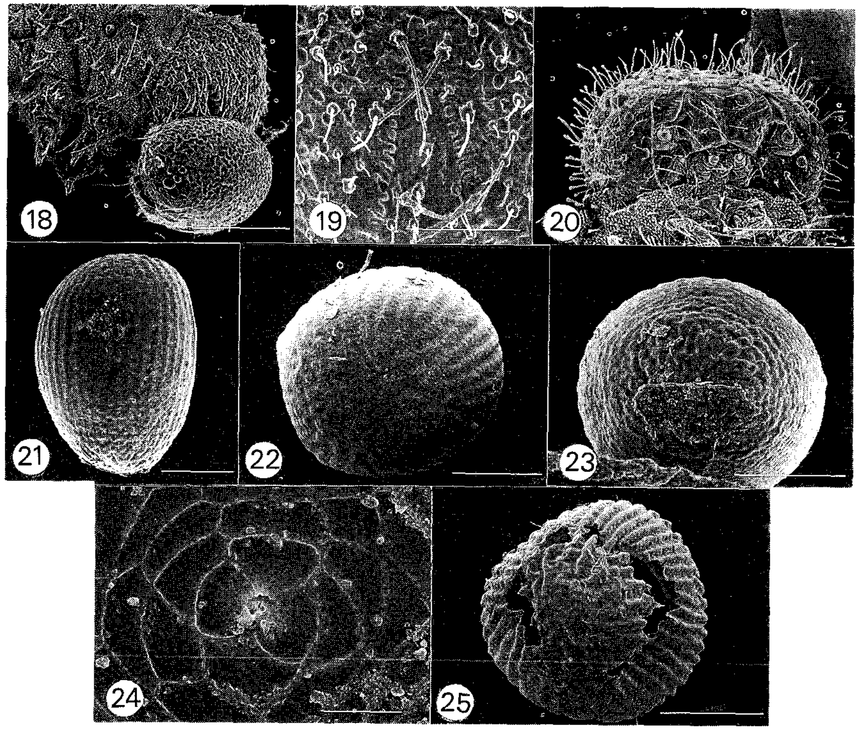
Chorological Affinities.— *Erebia mackinleyensis* occurs in areas inhabitated by other species of *Erebia*. *Erebia fasciata* is often found in close proximity. Ferris *et. al.* (1983) report on the occurrence of *E. erinnyn* in North America but the butterfly prefers low elevation moist meadow habitat and thus is not in contact with populations of, *E. magdalena* .



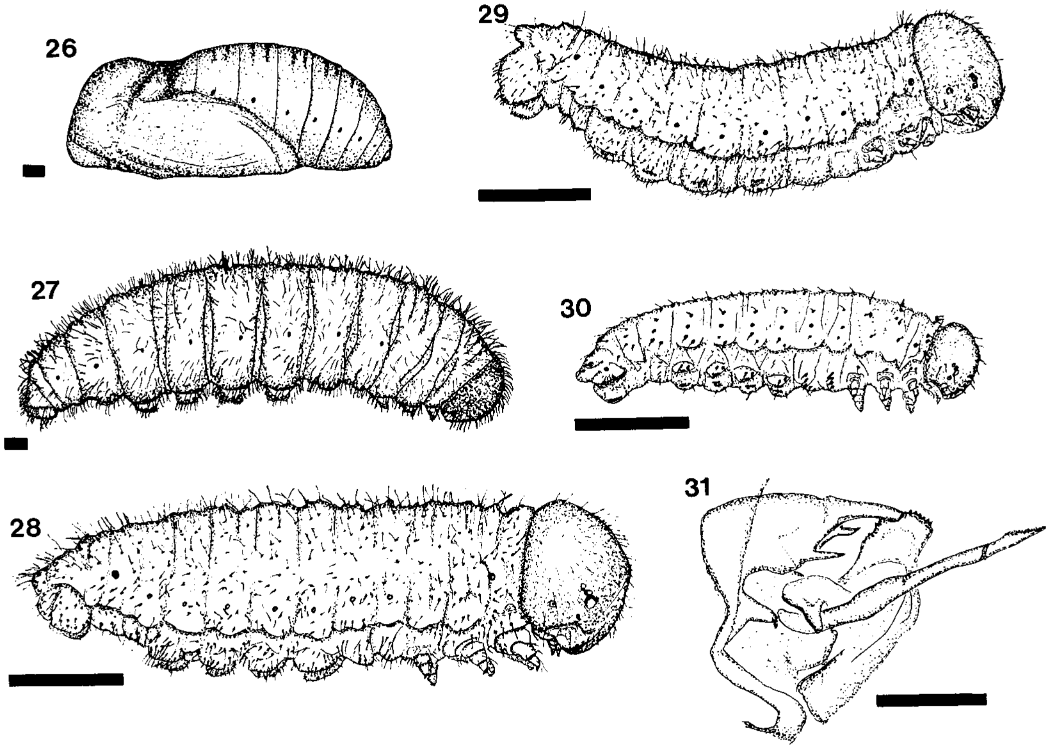
Figures 1-8. Fig. 1. White scales and hairs on ventral forewing surface of *E. magdalena saxicola* female. Fig. 2. White hairs on ventral hindwing surface of *E. m. saxicola* male. Fig. 3. Dark scales and hairs on ventral forewing surface of *E. m. magdalena* female. Fig. 4. Adult female of *E. m. saxicola*; note dusting of white on the wings. Fig. 5. Fifth instar larvae of *E. m. saxicola*. Fig. 6. View of type locality, Adams Lookout, Wilmore Wilderness Park, boulder field near top of mountain, interspersed with patches of vegetation. Fig. 7. Natural oviposition side, egg deposited under edge of rock near arrow. Fig. 8. Egg on underside of rock in Fig. 7.



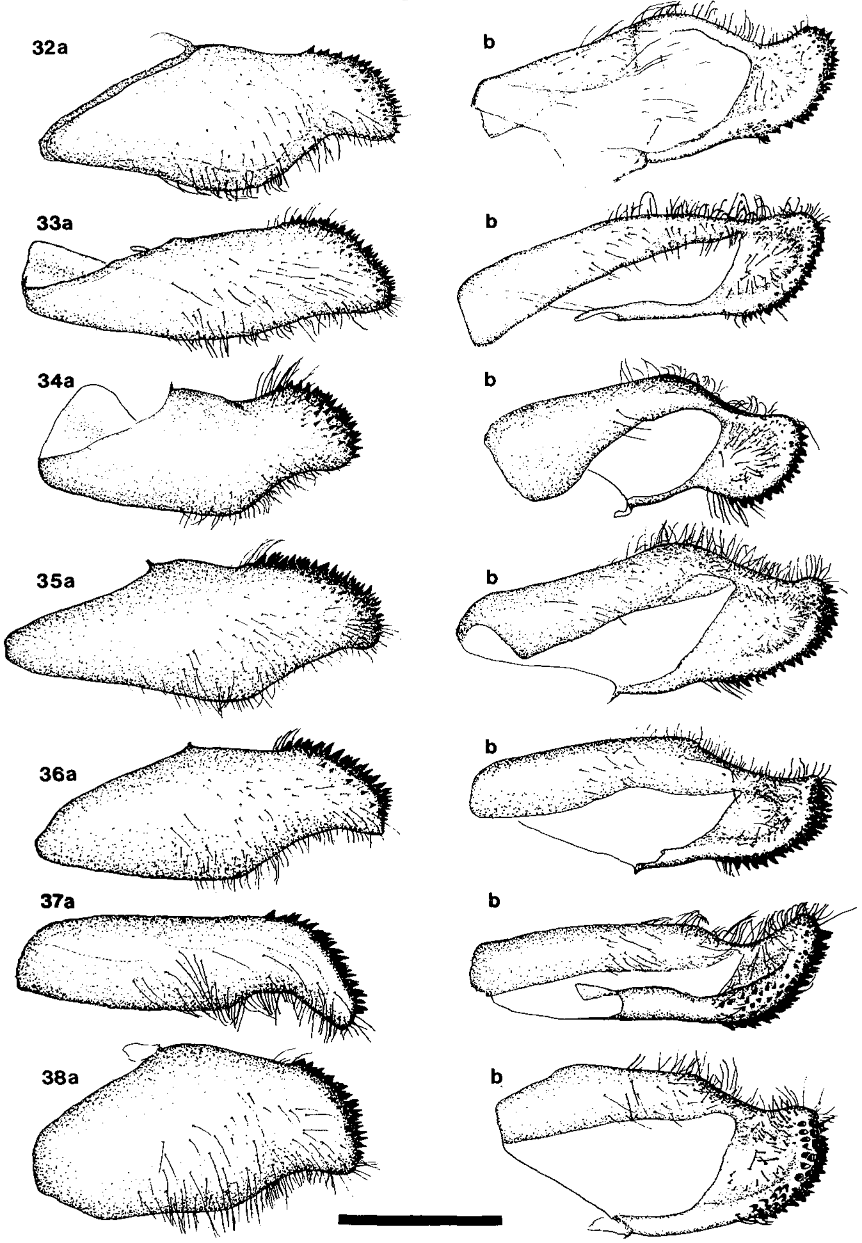
Figures 9-17. Scanning electron micrographs of *E. magdalena saxicola*. Scale line = 1 mm unless specified otherwise. Fig. 9. Cast cuticle from fifth instar larva. Fig. 10. Tip of fifth instar larval body hair; scale = 50 mm Fig. 11. Third instar larva. Fig. 12. Second instar larva. Fig. 13. First instar larva. Fig. 14. Fourth larval instar head capsule. Fig. 15. Third larval instar head capsule. Fig. 16. Second larval instar head capsule. Fig. 17. First larval instar head capsule.



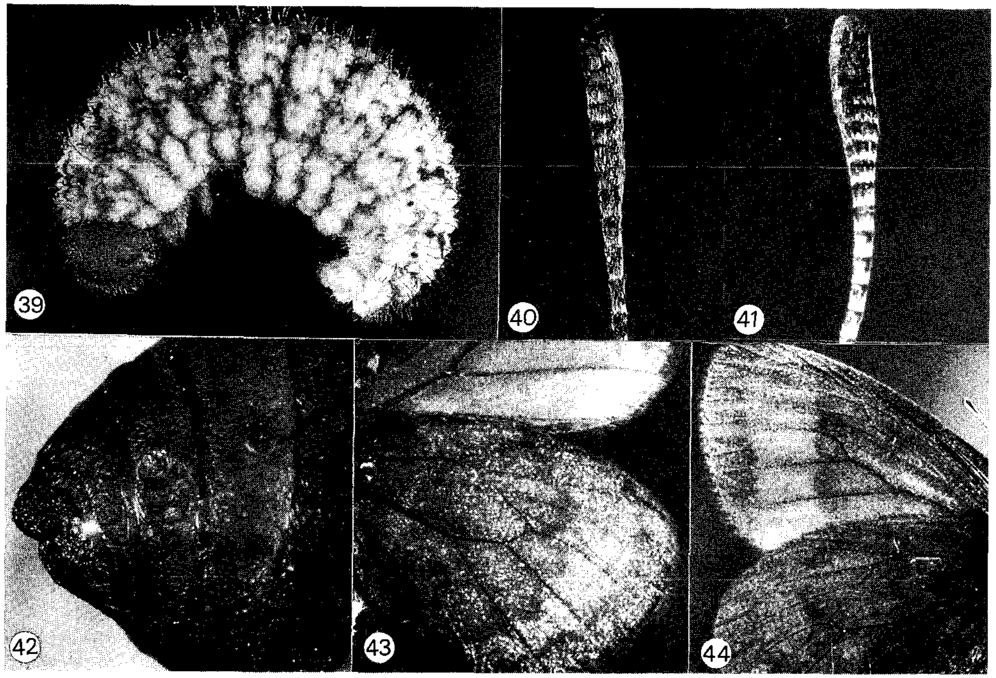
Figures 18-25. Scanning electron micrographs of *E. magdalena saxicola*. Scale line = 0.5 mm unless specified otherwise. Fig. 18. First instar molting to second instar larva. Fig. 19. Sutures on head of third instar larva. Fig. 20. Mouthparts of third instar larva. Fig. 21. Lateral view of egg. Fig. 22. Apical view of egg. Fig. 23. Basal portion of egg: note patch of adhesive material. Fig. 24. Micropyle on apex of egg; scale = 20 mm. Fig. 25. Egg after emergence of larva.



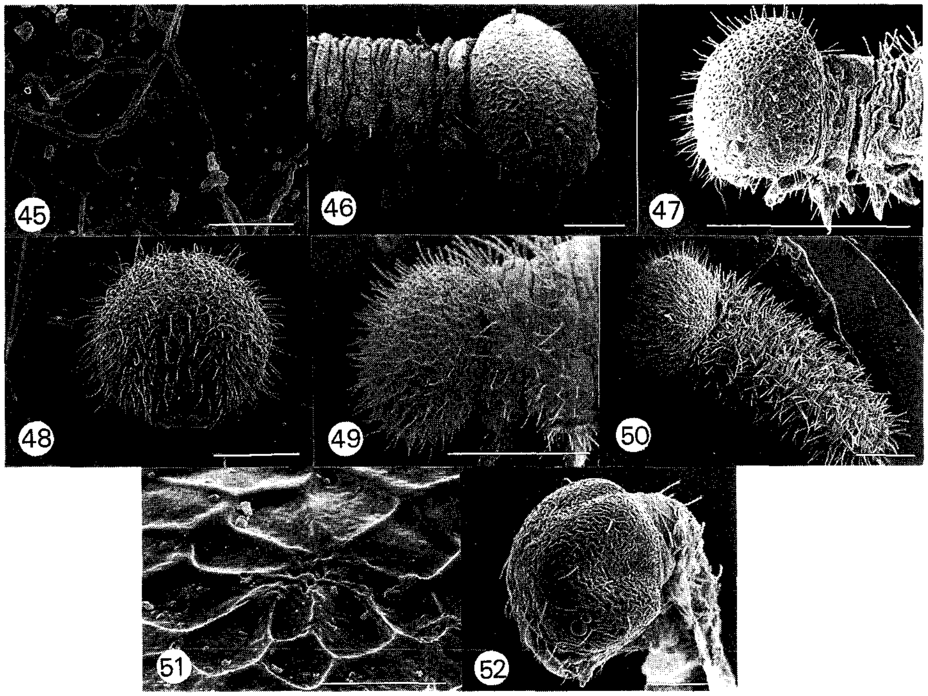
Figures 26-31. Line drawings of *E. magdalena saxicola*. Scale line = 1 mm. Fig. 26. Pupa. Fig. 27. Fifth instar larva. Fig. 28. Third instar larva. Fig. 29. Second instar larva. Fig. 30. First instar larva. Fig. 31. Male genitalia with left clasper removed.



Figures 32-38. Line drawings of the left clasper of male genitalia for *E. magdalena magdalena*, *E. m. saxicola* and *E. mackinleyensis*. Drawing **a**, view of outer surface, dorsal to the top of the page; drawing **b**, inner surface, dorsal side to bottom of page. Scale line = 1 mm. Fig. 32 *E. m. saxicola*, Adams Lookout. Fig. 33. *E. m. saxicola*, Adams Lookout. Fig. 34 *E. m. magdalena*, Utah. Fig. 35. *E. m. magdalena*, Maroon Pass, Colorado. Fig. 36. *E. m. magdalena*, Mount Audubon, Colorado. Fig. 37. *E. mackinleyensis*, Dempster Highway, km 131, Yukon. Fig. 38. *E. mackinleyensis*, Dempster Highway, Km 468, North West Territories.



Figures 39-44. Photographs of *E. magdalena magdalena*, *E. m. saxicola* and *E. mackinleyensis*. Fig. 39. Fifth instar larva of *E. m. magdalena*, reared from eggs collected at Wheeler Basin, Colorado by M. E. Young, 1973. Fig. 40. Left antennal club of *E. mackinleyensis*, *Dempster Highway, Yukon*. Fig. 41. Left antennal club of *E. m. saxicola* Adams Lookout, Alberta. Fig. 42. Abdomen of pupa of *E. m. saxicola*, reared from eggs from females collected at Adams Lookout, Alberta (adult emerged 1983, see Fig. 4.). Fig. 43. Ventral hind wing of female *E. m. magdalena*, showing enhanced banding pattern with white scales, Mount Kelso, Colorado. Fig. 44. Ventral forewing of female *E. mackinleyensis* with distinct rust patch, Dempster Highway, km 465, Yukon.



Figures 45-52. Eggs and reared larvae of *E. mackinleyensis* and *E. fasciata*. Eggs were collected by P. Ross from captive females, 1985, Dempster Highway, Yukon. Fig. 45. Egg micropyle of *E. mackinleyensis*. Scale line = 20 mm. Fig. 46. First instar larva of *E. mackinleyensis*. Scale line = 0.2 mm. Fig. 47. Second instar larva of *E. mackinleyensis*. Scale line = 1 mm. Fig. 48. Larval head capsule of third instar larva of *E. mackinleyensis*. Scale line = 1 mm. Fig. 49. Lateral view of third instar larvae of *E. mackinleyensis*. Scale line = 1 mm. Fig. 50. Dorsal view of third instar larvae of E. mackinleyensis. Fig. 51. Micropyle region on egg of *E. fasciata* Scale line = 20 µm. Fig. 52. Head of first instar of *E. fasciata*. 0.2 mm.

Phylogenetic Relationships.— The *E. magdalena /mackinleyensis* species pair exhibits many characters which unite them as sister species: structure of male genitalia; lack of maculations from most adults; when maculations are present, a similarity of design; and presence of andriconial scales in the males. Other related species are *E. erinnyn* (Siberia, except for the presumed Canadian record); and *E. fasciata.*

Material Examined.—

Adults (males, females). CANADA: Yukon; Dempster Highway, Km 154 to 156, 34, 10 (CNC, HILC, PIKE, PRES, SHEP, SPER). Dempster Highway, Km 465 to 468, 3, 1 (CNC). U.S.A.: Alaska; Atigun Gorge, north ridge, 2, 4 (SHEP).

Immatures. CANADA: Yukon; Dempster Highway, Eggs 20 eggs and egg shells, 17 first instar larvae,16 second instar larvae, 12 third instar larvae, 2 fourth instar larvae, 1 fifth instar larvae and associated exuviae (HILC).

Erebia magdalena Strecker 1880

(Figures 1 – 5, 8 – 36, 39 and 41 – 43, Tables 1 – 3)

Recognition.— This is perhaps the plainest butterfly species in North America, most specimens exhibiting a uniform dull black to dark brown color.

Description.—

Adults (Figures 1–4, 31–36, and 41). Wings dark blackish brown, population variations occur with some individuals exhibiting banding ventrally, and others developing a rust colored patch. See the discussion on character states under Character Analysis. Body similar color to the wings. Antennae annulated with gray white, club ferruginous above, black below (Figure 41).

Male genitalia as illustrated (Figures 31–36). Spination of uncus not expanded to inner surface as in *E. mackinleyensis* (Figures 37 and 38). Chromosome numbers reported by Maeki and Remington (1960) for *E. magdalena* from Gunnison County, Colorado were 10 large, 11 medium and 8 small for a sum of 29.

Immatures (Figures 5, 9–28, 39, 42; Table 3). Pupa (Figures 26 and 42). Alberta specimen (n=1); Length, 14 mm long. Head and thorax regions olive to dark green with abdomen medium brown tinged with green, without distinct markings, spines or hairs. Cremaster blunt, rounded (Figure 42), sculpturing on abdominal sclerites is a series of short longitudinal lines (Figure 42). Silk not observed. Colorado specimen; (from photo, YOUN) similar to Alberta specimen.

Larva, fifth instar (Figures 5 and 27). Alberta specimens (n=10); Integument with numerous blunt hairs (Figure 10). Head capsule dark brown, ground color of body green with black mottled maculations (Figure 5). Head capsule width 3.00 ± 0.10 mm. Colorado specimens (n=2); head capsule lighter brown, photo of larvae show light green ground colour, head capsule width 3.15 mm.

Larva, fourth instar. Alberta (n=10); Similar to fifth instars except smaller and with fewer hairs. Head capsule (Figure 14), width 2.19 ± 0.04 mm, n= 10. Colorado specimens (n=2); Ground colour cream in preserved specimens, head capsule width 2.15 mm.

Larva, third instar (Figures 11 and 28). Alberta specimens (n=5); similar to fourth instars, with reduced maculation and fewer hairs. Head capsule (Figure 15) width 1.55 ± 0.02 mm. Colorado specimens not seen.

Larva, second instar (Figures 12 and 29). Alberta specimens (n=4); hairs very few, no obvious maculations, ground color green. Head capsule, brown, lightly rugose (Figure 16) width 1.18 ± 0.04 mm. Colorado specimens not seen.

Larva, first instar (Figures 13 and 30). Alberta specimens (n=25); hairs very few, in discrete pattern. Ground color various from cream to light green with no dark maculations. Head capsule (Figure 17) with markedly rugose sculpture. Head width measurements 0.812 ± 0.018 mm. Colorado specimens (n=2); Similar ground colour, cream in preserved specimens, head capsule width 0.743 mm. Published illustration in Edwards [1888, collected by Mr. Bruce at Hall Valley, Mount Bullion (Edwards 1951)].

Egg (Figures 8, 21–25). Alberta specimens (n=25); ovoid with rounded ridges on sides (Figure 21). Top and bottom with rounded bumps (Figures 22 and 23). Micropile centered at apex (Figure 24). Color cream, darkened just before hatching. Length 1.45 ± 0.07 mm with diameter of 1.22 ± 0.07 mm. Bottom glued to substrate during oviposition (adhesive pad on bottom of egg, Figure 23). *Colorado specimens (n=3); Similar in appearance*, length 1.36 mm, diameter 1.23 mm. Published illustration in Edwards (1888).

Geographical Distribution.— *Erebia magdalena* is known from the high alpine meadows of northern New Mexico, through Colorado, Utah and Wyoming north to southern Montana, and west central Alberta and adjacent British Columbia.

Chorological Affinities.— Few other species of butterflies share the high mountain slopes with *E. magdalena*. Other species of *Erebia* may be found as strays in high mountain habitat, but none are closely related to *E. magdalena.*

Phylogenetic Relationships.— As indicated, *E. mackinleyensis* and *E. magdalena* appear to be sister species. *Erebia magdalena* populations show recognisable differences which can be attributed to subspeciation on isolated mountains. Taxa included are *E. m. magdalena* Strecker and *E. m. saxicola* new subspecies.

Erebia magdalena magdalena Strecker 1880
(Figures 3, 4 - 36, 39 and 43, Tables 1 - 3)

Recognition.— These butterflies are dark brown to black, with individuals in southern populations exhibiting mesial bands (predominantly in females) and occasionally with rust colored scales, but seldom developed as a distinct patch.

Description.—As described for *E. magdalena.*

Geographical Distribution (Figure 58).— *Erebia magdalena magdalena* is known from northern New Mexico, through Colorado, eastern Utah, north to Wyoming and southern Montana.

Chorological Affinities.— Few other high elevation butterflies are found in the same habitat. Some of these are *Oeneis melissa* (*O. m. lucilla* Barnes and McDunnough, in Colorado *O. m. beani* Elwes, in Montana and Wyoming). Other high elevation species are found in adjacent habitats of moist meadows such as *O. polixenes* (Fabricius), *O. taygete* Geyer and *Colias nastes streckeri* Grüm-Grschimailo. No other species of *Erebia* shares the high mountain habitat with *E. magdalena.*

Phylogenetic Relationships.— The very local isolated populations scattered over many mountains has facilatated population differentiation. The analysis of the different populations shows a clinal type relationship (Graphs A and B), with individual character states showing no clear trends. The greatest shift is shown with the Alberta population, described below as a separate subspecies.

Material Examined.—

Adults (males, females). U.S.A.: Colorado; Boulder County; Arapahoe Pass 1, 0 (USNM). Arapahoe Pass Trail 3, 0 (YOUN). Boulder 3, 2 (USNM). Mount Audubon 11, 3 (ALME, AMNH, CNC, USNM). Mount Navajo, ridge east of, 1, 2 (ALME, USNM). Navajo Peak, 1, 0 (USNM). Needles Eye Tunnel, Corona Pass 1, 2 (ALME, SHEP). Niwot Ridge, near Ward 1, 0 (CNC). Clear Creek County; Loveland Pass 40, 11 (ALME, INHS). Mount Kelso 0, 2 (PIKE, YOUN). Custer County; Hermit Pass 1, 0 (PRES). Grand County; Berthoud Pass 2, 0 (YOUN). Corona Pass 2, 0 (ALME). Wheeler Basin 0, 2 (YOUN). Gilpin County; Corona Pass 4, 0 (ALME, AMNH, PRES). Gunnison County; Copper Lake, above 1, 0 (USNM). Cumberland Pass 2, 0 (SHEP). East Maroon Pass 9, 1 (SPER). Yule Pass 0, 1 (SPER). Hinsdale County; Mount Umcompadre 0, 1 (SPER). La Plata County; Chicago Basin 1, 0 (AMNH). Larimer County; (Rocky Mountain National Park) 6, 3 (ALME, CNC, USNM). Longs Peak 3, 1 (ALME, AMNH). Peacock Lake 1, 1 (ALME). Specimen Mountain 2, 2 (ALME, USNM). Park County; 2, 0

(USNM). Hall Valley 9, 9 (ALME, USNM). Hoosier Pass 0, 1 (AMNH). Bullion Peak 1, 0 (USNM). Pennsylvania Mountain 0, 1 (ALME). Storm Peak 1, 0 (ALME). Montana: Carbon County; Beartooth Plateau 5, 3 (SHEP). New Mexico: Taos County; Wheeler Peak 4, 3 (INHS). Utah: 3, 0 (ALME, UASM). Summit and Duchesne Counties; Bald Mountain 8, 1 (ALME, PRES). Summit County; 1, 0 (ALME). Uintah County; Leidy Peak 8, 3 (ALME). Wyoming: Fremont County; 1, 0 (USNM).

Immatures. U.S.A.: Colorado: Boulder County; Corona Pass, Eggs 3 (shells), 1st instar 1 (UASM). Grand County; 1st instar 1, 4th instar 1, 4–5th instar (died in moult) 1, 5th instar 1, photographs of larvae and pupa (YOUN).

Erebia magdalena saxicola, NEW SUBSPECIES
(Figures 1, 2, 4, 5, 8 - 33 and 41, Tables 1 - 3)

Derivation Of Subspecific Epithet — The subspecies is named for its association with rocky habitat. All specimens were captured on a boulder field on top of a mountain. *Saxicola* from Latin means 'inhabits rocks'.

Type Material.— Holotype: male, Adams Lookout, Alberta Forestry Service, Wilmore Wilderness Park, Alberta, 1.viii.81, G.J. HILCHIE. Allotype: 24.vii.81, same locality data.

Paratypes: 27 males, 19 females, Adams Lookout, AFS, Wilmore Wilderness Park, Alberta, 4.vii.81, K. AVERY; 1.viii.81, G.J. HILCHIE; 11.vii.82, F.A.H. SPERLING; 12.vii.82, F.A.H. SPERLING; 12.vii.82, E.M. PIKE; 13.vii.82, E.M. PIKE; 24.vii.82, G.J. HILCHIE; 25.vii.82, G.J. HILCHIE; 29.vii.84, G.J. HILCHIE; Mount Hamell, 23.vii.84, K. AVERY; 25.vii.84, K. AVERY; 30.vii.84, K. AVERY; 26.vii.85, G.J. HILCHIE; 27.vii.85, G.J. HILCHIE; 28,vii.85, G. HILCHIE; Dore River, near McBride, British Columbia, 15.viii.84, D. L. THREATFUL.

Type material is deposited in the following institutions: holotype, allotype, and 6 paratypes, CNC; 4 paratypes, USNM; 6 paratypes, UASM; 5 paratypes, Alberta Provincial Museum, Edmonton; 8 paratypes, AVER; 10 paratypes, HILC; 5 paratypes, SPER; 2 paratypes, PIKE. 2 paratypes, SHEP.

Type Locality.— Adams Lookout, Alberta Forestry Service, Wilmore Wilderness Park, 43 km southeast of Grande Cache, Alberta, Canada.

Recognition.—This subspecies is distinguished from *Erebia magdalena magdalena* by the following features: males have scattered white hairs on the ventral surface of the wings; females have scattered white scales and hairs on the ventral surface of the wings (Figures 1, 2 and 4) with concentrations near the apex of the forewing, mesial wing bands absent; geographic range confined to Alberta and B.C.

Description.—

Adults (Figures 4, 31–33 and 41). Male: wings with ground color, dorsal and ventral dark brown to black without pattern, androconial scales present; forewing length 23.8 ± 1.2 mm[1], range 21.4–26.1 mm; hind wing length 19.9 ± 0.9 mm, range 17.7–21.7 mm, n=28; ventral surface of wings with scattered white hairs near apex of forewing and on central area of hind wing (Figure 2). Genitalia typical for *E. magdalena* as illustrated in Warren (1936, Plate 35, Figure 327 and 330). Claspers various in shape (Figures 32 and 33). Gnathos, uncus and aedeagus typical for *E. magdalena* (Figure 31).

Haploid chromosome number is 29 (mode number from counts).

Female: wings with color similar to male; forewing length 25.0 ± 1.4 mm, range 22.1–27.7 mm; hindwing length 20.5 ± 1.3 mm, range 17.2–22.8 mm, n=20; ventral surface of wings with white hairs near tip of forewing and on most of hindwing (Figure 1). Twelve of 16 females examined had from a few to hundreds of white or very pale scales near the tip of the forewing and on the central area and margins of the hindwing. Four females appeared to have their wings dusted with white scales when viewed at low magnification.

Immatures (Figures 5–30). As figured and previously described.

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[1] One standard deviation

Habitat.— *Erebia magdalena saxicola* inhabits alpine boulder fields (ca. 2200 to 3000 m), interspersed with patches of vegetation (Figure 6).

Geographic Distribution (Figure 58).— Known from Adams Lookout, (Wilmore Wilderness Park) and Mount Hamell in Alberta and in an adjacent area in British Columbia which are widely disjunct from the next nearest known populations, found in southern Montana.

Chorological Affinities .— *Erebia discoidalis* Butler, *E. epipsodea* Butler, and *E. disa* Thunberg overlap in range with *E. m. saxicola* None of these species share the high mountain habitat.

Phylogenetic Relationships.— *Erebia magdalena saxicola* is the sister group of *Erebia magdalena magdalena.*

Material Examined.— Type material only.

LIFE CYCLE AND BEHAVIOUR OF *EREBIA MAGDALENA SAXICOLA*

Behaviour of Adults

Males and females (about 1:1) are in the same flight area from July 4 to August 1. They fly over areas of rocks covered with the black lichens *Hypogymnia oroarctica* Krog., *Umbilicaria proboscidea* (L.) Schrad., *U. hyperborea* (Ach.) Hoffm., *Pseudephebe pubescens* (L.) Choisy, and the yellow crustose lichen *Rhizocarpon geographicum* (L.) DC. Rock areas are interspersed with patches of vegetation in the centers of polygon frost formations (Figure 6). Vegetation is high mountain alpine, with the ground cover dominated by *Dryas hookeriana* Juz., *Salix arctica* Pall. and *Silene acaulis* L. Other plant taxa are *Saxifraga oppositifolia* (L.), *Oxitropis podocarpa* A. Gray, *Cassiope tetragona* (L.), *Carex* spp. and various alpine grasses, *Festuca saximontana* Rydb. and *Poa alpina* (L.) (Porsild, 1974).

Erebia magdalena saxicola adults fly in association with many alpine butterfly species but only a few are found in the same habitat [*e.g., Boloria astarte* (Doubleday and Hewitson) and *Oeneis melissa* (Fabricius), see Table 4.]. Some of these species are near the limits of their ranges, *e.g., Boloria napaea alaskensis* (Holland) is at its southern limit and *Boloria alberta* (Edwards) at is at its northern known limit.

Adults fly in sunshine from about 1000 hr to 1730 hr. Females have a wandering flight over the rocks, periodically landing to bask or visit flowers. Males appear more directed in flight, and dark butterflies that pass near them are pursued with great vigor. These included female *E. magdalena*, other males, and males and females of *Oeneis melissa.*

Oviposition

Oviposition in the field occurs in areas of loose rock which are covered by black lichen. One female observed ovipositing backed down the side of a rock (Figure 7) and laid a single egg on the underside near an edge (egg shown on rock in Figure 8). Eggs laid in the field are not placed near plants.

Development

In the laboratory, females laid eggs on any substrate (rocks, cage, water container), preferring sides and lower surfaces. Oviposition normally occurred in the early morning, with some eggs being laid in late afternoon.

Table 4. List of butterflies collected at or near Adams Lookout, Alberta Forest service, Wilmore Wilderness Park, Alberta (1980-1983).

Species	Collection areas				
	Valley	Subalpine	Alpine [1]		
	willows, meadows	pine, fir, spruce	wet meadows	dry meadows	rocks, scree
Erynnis persius Scudder	++[2]				
Hesperia comma manitoba Scudder	+++	++			
Pyrgus centaurae freija Warren	++	+			+
Carterocephalus palaemon mandan Edw.	++				
Euchloe creusa Dbld.	+				
E. ausonides ausonides Lucas	+				
Anthocharis sara Lucas [3a]	+				
Colias meadii elis Strecker		+	+		
C. alexandra christina Edw.	+++	+			
C. nastes streckeri Gr. Gr.			+	+++	+
C. pelidne minisini Bean	+				
C. philodice philodice Godart	++				
C. interior interior Scudder	+				
Pieris napi oleracea Harris	+	+			
P. protodice occidentalis Reak.			+	++	+
Parnassius phoebus Fabricus [3a,b]		+++	++		
Papilio machaon L.	+				+
P. machaon X *zelicaon*					++
P. zelicaon Lucas	+				+
P. glaucus canadensis R. & J.	++	+			
Plebjus argyrognomon scudderii Edw.	++	+			
P. saepiolus amica Edw.	++				
P. aquilo megalo McD.	+	+	+	+	
Glausopsyche lygdamus Dbld.	+++	+			
Everes amyntula Boisduval	++				
Celastrina argiolus lucia Kby.	+	+			+
Lycaena phleas arethusa Dod.	+++	+	+	+	
L. cupreus snowi Edw.	+	+		+	
L. dorcas Kby.	++	+			
L. mariposa Reakirt	+				
Erebia disa mancinus Dbld.	+				
E. epipsodea epipsodea Butler	+++	+			
E. magdalena saxicola n.ssp.					+++

(continued on next page)

Table 4 (continued)

Species	Collection areas				
	Valley	Subalpine	Alpine [1]		
	willows, meadows	pine, fir, spruce	wet meadows	dry meadows	rocks, scree
Oeneis c. chryxus Dbld.	++	+++	+		
O. melissa beanii Elwes				+	+++
O. polixenes brucei Edw.				++	
O. taygete edwardsi dos Passos			+	+	
O. jutta chermocki Wyatt		+			
Boloria napaea alaskensis Holland				+++	+
Boloria epithore Edw.[3a]		+			
B. eunomia nichollae Barnes & Benjamin			+		
E. eunomia dawsoni B. & McD.	+++	++			
B. frigga saga Staudinger		+	+	+	
B. improba youngi Holland				++	
B. alberta Edw.					+
B. a. astarte Dbld.				+	++
B. titania grandis B. & McD.		+++	+		
B. freija freija Thunberg		+	+		
Speyeria mormonia eurynome Edw.		+	+	++	+
Phyciodes c. campestris Behr		++			
Euphydryas editha beani Skinner				+	
E. anicia anicia Dbld.		+++		+	
Nymphalis milberti Lat.	+	+	+	+	+
N. antiopa L.		+			
Vanessa cardui L.					+
Polygonia faunus rustica Edwards		+			

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[1]. Some species collected are migrants from lower elevations "hill topping".

[2]. Key to symbols: + uncommon (1-3 specimens); ++ common (4-10 specimens); +++ abundant (11+ specimens) Numbers are based on specimens collected during visits to the alpine habitat.

[3]. Additional species from nearby mountains: 3a. Horn Ridge; 3b. Mount Hamell).

Table 5. Rates of development for immatures of *Erebia magdalena saxicola.*

Stadia	Development Time (days/stadia)		Sample Size
	Minimum	Maximum	
egg	11	12	110[1]
first	4	6	75
second	8	36	31
third	14	68	18
fourth	22	90	11
fifth	99[2]	-	1
pupa	7	-	1

[1]. Numbers refer only to those individuals which matured and moulted to the next stadium.

[2]. Includes time while in diapause in an incubator (33 days below +4°C)

Larvae were reared in the laboratory. Development from egg to adult required a minimum of 165 days. Eggs and early instar larvae were maintained at 20–23°C. Development was rapid and mortality high. Table 5 summarizes rates of development

Fourth, and especially fifth instar larvae were slower in development than the first 3 instars. The surviving fifth instar larva pupated after a 99 day stadium including 63 days at 20–25°C and 33 days at +4 to -2°C. During cold treatment larvae were provided with food. One larva continued to feed at +4°C for a few days. Upon removal from the incubator fifth instar larvae were given fresh food. The larvae did not resume feeding (T=20°C, photo period natural short day). Larvae were returned to the incubator for five days at +4°C then brought out in another attempt to stimulate feeding. The temperature was raised to 25°C and they were placed under artificial photoperiod of 16 hours of light and 8 hours of dark. All larvae resumed feeding. Of the 11 reared to fifth instar and brought through the incubation process, 10 contracted a fungal infection and died, one pupated and emerged as an adult. In the molt from fifth instar to pupa, the head capsule splits (Figure 9) and is shed posteriorly with the rest of the larval cuticle. Pupal period at 25°C had a duration of 7 days (n=1) and a female emerged.

By comparison with the natural time span available for development with the rate of development in Table 5, I infer that larvae falcultatively overwinter in Alberta as second or third instar larvae with potential for diapause in any larval instar. Rates of development barring diapause are sufficient that the species should normally complete one generation per year, but two or three years may be required pending unfavourable climatic conditions.

Food Plants.— Larvae were fed grasses throughout rearing. First instar larvae were given a choice of black lichen, fleabane, willow, dandeleon, larkspur, lawngrass clippings, and barley. Larvae readily ate grass clippings and barley. The lawn clippings were a mixture of creeping fescue and Kentucky blue grass. Judging from the oviposition site and non-specificity of food grasses, larvae will eat most grasses of the alpine zone.

EVOLUTION OF *EREBIA MAGDALENA* STRECKER

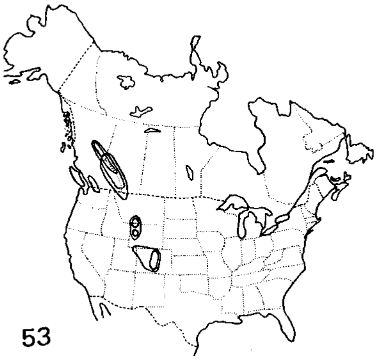
Erebia magdalena belongs to a group of Rocky Mountain arctic-alpine butterflies the components of which are distributed more or less discontinuously from Colorado to Alaska. *Erebia magdalena* is the southern sister-species of the Beringian *Erebia mackinleyensis*. This pair of vicars is likely the descendant of an ancestral arctic-alpine stock the range of which was interrupted by one of the pre-Wisconsinan glaciations, since it is unlikely that the surviving stocks would have differentiated to the species level in the time interval embraced by the Wisconsinan glacial stage plus the Holocene (See Whitehead, 1972:334-337, for a discussion of rates of speciation in insects).

Erebia magdalena/mackinleyensis stock dispersed into North America from Asia during one of the early glacials. Subsequent dispersal and isolation during glacial and interstadial periods caused speciation of *Erebia magdalena* and *Erebia mackinleyensis*.

Time of differentiation within *Erebia magdalena* could be comparatively recent, for the included taxa are very similar to one another. Two hypotheses have been proposed that would account for both the discontinuity in range between the two subspecies and their differentiation. Scudder (1979) proposed that the Alberta fauna has a southern affinity and dispersed northward from Wisconsinan-time refugia located south of the ice as the glacial ice melted and exposed the underlying soil. Subsequently, as the climate became more temperate, alpine stocks moved upward to suitable sites at higher altitude on the slopes of the Rockies, with consequent interruption of geographical ranges.

On the other hand, Pike (1980) proposed that various arctic-alpine stocks of butterflies of southern affinity survived the Wisconsinan glaciation on known nunataks and thus were isolated for an extended period of time from their counterparts which survived in suitable habitats south, or north of the ice. As a result of isolation, differentiation took place, at least to the subspecies level (see Kavanaugh (1979:39-40)), for discussion of rates of subspeciation in montane carabids). Although the geological evidence favoring existence of nunataks on the eastern slopes of the Rockies seems firm, and a few plants (Packer and Vitt 1974) exhibit distribution patterns consistent with survival in such areas (also proposed by Pike 1980, for two butterfly subspecies), I am not convinced that nunataks did serve as refugia for butterflies.

I have re-examined distribution data for alpine butterflies (Ferris and Brown 1980; Shepard, British Columbia butterfly distribution maps, pers. comm.; Bird *et. al.*, Alberta butterfly distribution maps, pers. com.; Ferris *et.al.*, 1983). Of the 12 taxa examined by Pike (1980), four are not restricted to above treeline (*E. editha beani, L. phleas arethusa, L. cupreus snowi*, and *B. e. nichollae*). The remaining eight may be considered true alpine/tundra insects. Mapping generalized ranges for each recognizable subspecies, six are distributed widely in the Alberta and British Columbia Rockies with some populations also in the Canadian coastal ranges and in the Rocky Mountain states of the United States (Figures 53 and 54), implying a refugium south of the ice. Two other species show a northern origin (Figure 55) with a distribution pattern extending along the mountains (personal collecting records show *B. improba* at several localities including, Alberta— Adams Lookout, Horn Ridge, British Columbia— Torrens River, Thunder Mountain and Pink Mountain) from the Yukon. This



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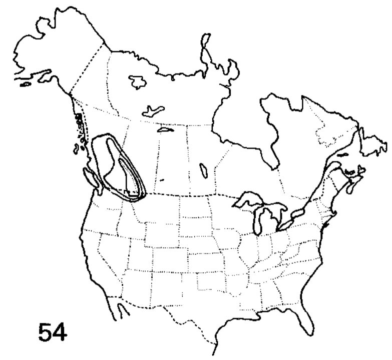

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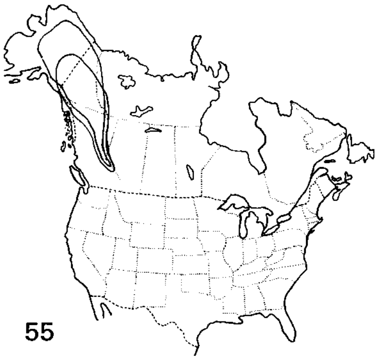

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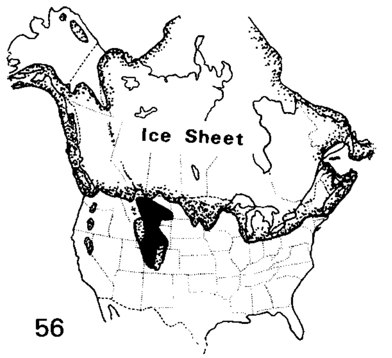

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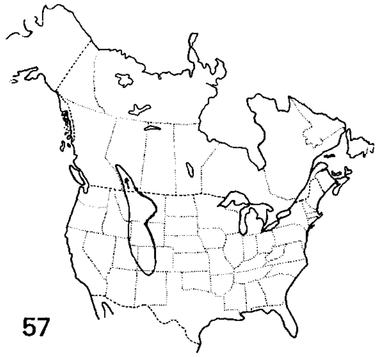

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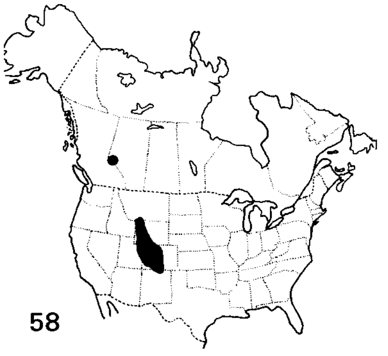

58

Figures 53-58. Butterfly distribution and proposed Pleistocene scenerio maps. Fig. 53. Generalized distribution for *Oeneis polixenes brucei*, *O. taygete edwardsii*, and *O. melissa beani*. Fig. 54. Generalized distribution for *Colias nastes streckeri*, *Boloria astarte astarte*, and *B. alberta*. Fig. 55. Generalized distribution for *Boloria improba youngi* and *B. napea alaskensis*. Fig. 56. Posible distribution of *Erebia magdalena ca*. 1700 B.P. with continuous range in a Wisconsinan refugium. Fig. 57. Dispersal and movement of *E. magdalena ca*. 1200 B.P. north along the foothill ranges following retreating ice sheets. Fig. 58. Present range of *E. magdalena* following climatic readjustments, extinctions and isolation with subspecies differentiation. (dot = *E. m. saxicola*, black area = *E. m. magdalena*).

differs from Pike's proposed interpretation: the range of the one disjunct (*B. improba*), actually extends along the mountains and the one supposed endemic (*B. eunomia*) is not actually a true alpine species but has a wide ranging lowland form, surrounding the highland form that occurs in the Mountain Park area (Cadomin, Alberta).

In terms of available biogeographic data there is no firm support of the hypothesis that a few butterfly species survived on nunataks in northwestern Alberta between the ice sheets. All the alpine butterfly species found in Alberta have portions of their ranges in unglaciated areas south or north of the limits of the Wisconsinan Ice sheet.

If the character states of a population are intermediate between populations found in Alaska and Colorado, it would be reasonable to assume that this population is a relict of a former cline and may have moved to its present location from a nearby refugum. If character states of a geographically intermediate population are not intermediate between those of the geographically adjacent populations, but closely related to one of the populations it would then be more reasonable to assume that these populations share a common parental stock. Present distributions are the result of local extinctions, and migrations over time, creating the illusion of long distance dispersal. It would appear more parsimonious to propose that even for those taxa which show subspecific differentiation, and are not intermediates of a cline, that their parental stocks dispersed from refugia along the northern or southern margins of the ice sheet, and that their differentiation in Alberta is post-glacial in age. I believe this is true of *Erebia magdalena*, and the following scenario including the history of *Erebia mackinleyensis* is based on this belief.

At the zenith of the Wisconsinan Glacial stage the parent stock of *Erebia magdalena* is postulated to have occupied alpine-tundra habitat south of the ice in areas of Montana, Wyoming and Colorado (Figure 56). During melting of the ice mass, the butterflies followed newly developing habitat north along the Rocky Mountain foothills, probably in an ice free corridor (Prest 1969) (Figure 57). Dispersal rate would be affected by dispersal rate of host grasses. Continued climatic amelioration caused suitable lowland habitats to disappear, forcing populations up the east slopes of the Rockies. Isolation of butterfly populations occurred at this time (circa 10,000 years BP).

As the climate continued to ameloriate, alpine-tundra habitats were displaced higher up the mountains. Aridity in the alpine zone of southern Alberta and Montana may have led to shifts in floral composition resulting in local population extinctions of certain butterfly species possibly due to chinook conditions resulting in dry mild winters with very little protective snow cover. The vicariance of *Erebia magdalena* populations (Figure 58) is thus postulated. Three alpine butterfly species, *Oeneis polixenes brucei, Oeneis melissa beani.*and *Oeneis taygete edwardsii* have a similar vicariance with populations in the north (Alberta Rockies) and south (southern Montana, Wyoming and Colorado, Figure 53).

Isolation of relatively small populations of *Erebia magdalena* in the northern Rockies created conditions conducive for genetic drift, resulting in subspecfic differentiation.

CONCLUDING STATEMENT

Erebia magdalena is in the process of speciation, although isolation and speciation did not occur during, but after the Wisconsinan glacial and continues to the present. Other alpine-arctic butterflies in the Rockies of northern Alberta and British Columbia may be represented by unique populations as a result of recent isolation during the last 8,000 to 10,000 years. Additional study of the flora and fauna may reveal additional presently unrecognized subspecies with strong southern affiliations.

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COMMENTARY

[Commentary is a section of *Quaest. Ent.*that appears from time to time, and contains expressions of opinions about general items, controversial or otherwise, that ought to be of interest to many of our readers. These contributions are not refereed because they are intended to be free expressions of opinion. Changes by the Editor might be made to the form of presentation, but not to its substance. Remarks that are deliberately abusive or insulting will not be published. Rebuttals to previously expressed views will be considered, but the journal is under no obligation to publish them.

The Editor]

Linear, longitudinal markings on the outer elytral surface of beetles: interneurs or striae?

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Quaestiones Entomologicae
26: 695–699 1990

The reasons given for the substitution of the neologism "interneur" for "stria", when used as a collective noun in English, are examined. They are based on a *non sequitur*, a mistaken idea that use of "interneur" solves an important problem that "stria" does not, and on the oversight that "interneur" requires redefinition to make it fully synonymous with "stria". The physical basis, homologies, and non-homology of striae are outlined. It is recommended that "interneur" be abandoned; it is an unsuitable replacement for the old and universally familiar "stria".

Only Erwin (1974) appears to have responded to Spilman's (1971) examination of the word "stria" as used in discussions and descriptions of the elytra of beetles. Spilman recommends that the longitudinal, linearly-impressed markings, such as grooves, rows of puncta, and related sculptural forms collectively be called "*elytral striae*". As Erwin is aware, major taxonomists writing in English, including among others G. H. Horn, Andrewes, Casey, Jeannel, Lindroth, and Darlington have all, at some point, found it convenient to use "stria(e)" in the collective sense of "elytral stria(e)", as well as in the structural sense. None subsequently appears to have been misled by their and other's double usage of "stria". In what follows, "*stria(e)" will be used to designate and shorten repeated use of "elytral stria(e)" and its grammatical derivatives.

Spilman points out that an alternative to his suggestion would be coinage of a new collective term, but he does not advocate doing so. Nevertheless, Erwin has proposed the new generic term "interneur" to encompass the various forms taken by elytral striae. His grounds for advancing that neologism lack force; as will be pointed out, "interneur" has a disadvantage that *stria does not. Even so, "interneur" is now widely used among an important North American school of workers on Carabidae, of which Erwin is an influential member, as well as by a few describing other forms of Coleoptera. As "interneur" has strongly been urged upon others, as I have been told, this discussion may serve as a useful retardant to its acceptance and continued use.

The following questions awakened by Erwin's (1974; pp. 3-5) justifications of "interneur" will be discussed: 1) Is the argument sound that stria "... should have a name equivalent to 'interval'"? 2) Does "interneur" serve any special purpose that "*stria" does not? 3) Is "interneur" handicapped in any way that "*stria" is not? 4) What in fact do most *striae and interneurs represent?

1) Should *striae have a name equivalent to "interval"?

Erwin's argument that a new name is *needed* for *stria maintains that "If the intervals are the derived character state of the wing veins of the primitive beetle wing, and if the structures between the intervals are the derived character state of the wing 'cells' or membranes, then the latter [!] should have a name equivalent to 'interval'." Although "interneur" may provide a pleasing counterpart to "interval", the argument is a *non sequitur*. Assuredly no such nomenclatural necessity would arise even were those suppositions proven correct (see section 4), or were all intervals separated by phyletically equivalent structures (which they are not; see section 3). Furthermore, the "structures" in question are of course already named.

For nearly two centuries they have been called "striae" by coleopterists, a misfortune as Erwin sees it. He states that " ... coleopterists have used 'stria' for this structure since a 'stria' (in its proper definition) on a beetle elytron is common to most coleopterous families and thus to most coleopterists [*sic*!]. When the unnamed elytral structure described above [in the "syllogism"] is a serial row of unconnected punctures some coleopterists retain the term 'stria' as a structural name, rather than a descriptive name. Therein lies the problem."

That "problem", in the past and present, has caused little if any difficulty for most coleopterists. As with such nouns as "man", context readily indicates whether "stria" is in use as a collective or as a specific noun. In any case, *if* a change in nomenclature is to be made, Spilman's (1971) specific proposal that "*elytral stria*" be used as a collective noun is an alternative that avoids all assumptions and is senior to "interneur".

2) Does "interneur" serve any special purpose that "*stria" does not?

As the main reason for proposing "interneur", Erwin contends that "One cannot state 'stria 7 absent' without meaning the plesiomorphic elytral structure was indeed a stria ...", namely "an impressed line or furrow". Assuredly that is not so; "*stria 7 absent" (just as does "interneur 7 absent") implies *only* that in the presumed plesiomorphic state the external surface of the elytron displays a linear structural marking of some *unspecified* sort. When it is desired " ... to make ... descriptions comparative within a broad taxonomic framework" and " ... to take into account evolutionary changes within taxa ...", then of course the physical nature of the plesiomorphic elytral marking must be specifically stated for interneur and *stria alike. In this respect, each term is without specific meaning, and synonymous.

An analogy: shall a new term be coined to encompass the varied forms of pronotal hind angles, say, to avoid a fancied implication that the plesiomorphic state was in fact a true angle (and not rounded off at its apex) when it is stated, as Lindroth (1966; p. 158) does, "Prothorax without trace of hind angles"? To do so would be to give an illusory solution to an illusory problem.

3) Are the terms "*stria" and "interneur" equally applicable?

*Striae are certain longitudinal modifications of elytral structure, and the term "*stria" is defined and may be used without a stated or implied evolutionary overtone. "Interneur", on the contrary, properly refers to a structure that is presumed to be "the derived character state of wing 'cells' or membranes", that lay between veins of the primitive beetle wing. Here then *is* a problem: the actual number of *striae may significantly exceed the possible number of interneurs marking the elytra of a fair number of not-primitive, living carabids.

Nine or ten *striae (possible interneurs) on an elytron is the probable modal number for beetles today, including carabids. How then are the five (some *Omophron* with 15 striae) to eight (some *Scaphinotus* with 18) extra sculptured elytral lineations[1] to be referred to under Erwin's proposal? It can be done only by altering the evolutionary definition and meaning of "interneur" to complete synonymy with *stria.

It has been shown by Kolbe (1886, 1893), Bonsdorff (1890), Ganglbauer (1909), Jeannel (e.g., 1925, 1940), and others that the extra impressed lineations are supernumerary formations that subdivide particular not-tracheated intervals, hence are not primitive. No problem arises by denoting these extras as "secondary", "tertiary", *etc.* *striae, as is done. However, "interneur" does not accept such modification without loss of consistency and meaning, for interneurs are characterized as sharing a primary homology (owing to their supposed origins). So far as the interneur concept is concerned, supernumerary *striae must represent one or more classes of unnamed structures.

4) What in fact do *striae and interneurs represent?[2]

Surface expressions of aligned trabeculae (= columnae, columellae) is the answer. Apart from the margins where the upper and lower lamellae of the elytron meet, the elytron is strengthened within and, unlike a flight wing, its two lamellae are held apart by more or less vertical skeletal pillars - the trabeculae. The haemocoel of the elytron is continuous through the interspaces between trabeculae, and is therefore much larger in volume than is that of the hind wing which remains confined to sinuses enclosed within certain veins (see Arnold, 1964).

When *striae are counted and their lengths measured, the *minimal* number and *least* lengths of the underlying longitudinal rows of trabeculae of an elytron have been estimated. This can be confirmed by examination of the inner surface of an elytron where the bases of the trabeculae ("endoreticulum" of Smrz, 1982) are ordinarily visible through the relatively thin surface of the lower lamella[1,3], a fact known since at least the observations of Heer (1847) and Erichson (1848). As trabeculae are not structures unique either to elytra or to Coleoptera (Weber, 1933), and may occupy sites scattered about an elytron (see below), they are very likely *not* homologous with structures of a flight wing above the level of specialized hypodermal cell products and not specifically with the sclerotized outer walls of wing veins.

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[1] Or the 21 or 22 *striae on an elytron of the fossil *Calosoma heeri* Scudder, referred to by Ganglbauer (1909) in his analysis of supernumerary striae. Jeannel (1940) holds the elytron to be that of a carabid on the testimony of Lapouge who examined the specimen, but not a species of *Calosoma*. Supernumerary striae are not limited to Adephaga. I count 14 striae (thus 15 intervals) on the elytra of several species of *Eleodes* (Tenebrionidae). That count would have proved extremely difficult without examination of the aligned bases of the trabeculae on the elytral undersurface.

[2] The general statements of this and section 4 hold for the great majority of beetles, but not necessarily all.

[3] The presence or absence of lines of trabeculae visible on the undersurface of an elytron, so easily examined, in certain cases should make determination of the abbreviation or absence of lineations on the upper surface as plesio- or apomorphies a simple matter. If, for brevity's sake, a single word be desired for aligned trabeculae, *substria(e)* should do satisfactorily.

Where *striae (interneurs) are shortened, faint, or even absent externally in certain members of a group in which many species have *striated elytra, a complete complement of serially aligned trabeculae of full length may nevertheless be present in all, whether with *striated elytra or not. Rows of trabeculae therefore provide the morphological basis of externally visible *striae (and interneurs). Unaligned trabeculae provide a basis for scattered puncta that dot the surface of an otherwise smooth elytron. Puncta of intervals lying between *striae frequently (but not always[4]) have a different basis; in such cases, they are unrelated to trabeculae as Kolbe (1893) comments. Though evidently necessary for the production of *striae and most puncta, the presence of trabeculae is obviously not a sufficient cause for puncta.

However manifested on an elytral outer surface, *striae ("interneurs") therefore share structural homology, as do their underlying components with those of unaligned puncta (but not with seta-bearing or sensory pits).

CONCLUDING COMMENTS

Finally a minor point, perhaps, for today few scientists endeavor to compound new technical terms with attention to their construction: "interneur" is a compound of Latin and clipped Greek; it should be in plural form, for nothing can be between one thing.

It is a strange invention, arising from unsound premises, solving only an imaginary problem, and not literally applicable to all elytral striae. It merits suppression[5]. "Stria" has a long history of useful application, and its uses are readily understandable by all. In his excellent fieldguide, White defines "stria" in its generic sense: "A groove or impressed line or a row of punctures ... " (1983; see pp. 46, 342). And so new generations of budding coleopterists are welcomed with "stria", not "interneur"; may that tradition continue[6].

ACKNOWLEDGMENTS

Two reviewers, Dr. T. J. Spilman of the Systematic Entomology Laboratory, U.S.D.A., and Prof. John D. Pinto of the University of California at Riverside, provided meticulous critical reviews of the penultimate draft of this commentary. Prof. S. L. Straneo of Milano, Italy, and Dr. John F. Lawrence of the C.S.I.R.O. of Australia, were kind enough to comment on "interneur", and to read and express approval of the manuscript. To each I express warm gratitude for their observations. However, it must be noted that the analysis presented is mine alone.

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[4] Puncta on intervals in many carabids are not underlain by trabeculae; in some beetles they are produced by trabeculae, for example in the meloid *Pleuropompha carinata* (Le Conte).

[5] Bequaert (1929) has commented pointedly on new names for old familiar structures.

[6] Prof. S.L. Straneo has informed me that in his forthcoming paper about the South American species of *Loxandrus*, he too is offering objection to the use of "interneur" (1990 Annals of the Carnegie Museum, in press).

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NOTE

NEW NEARCTIC REGION RECORDS OF PALEARCTIC *MEGASELIA* SPECIES(DIPTERA: PHORIDAE)

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Quaestiones Entomologicae
26: 701–702

In the summer of 1990 we conducted an informal survey of insects of the boreal region of Alberta (Brown *et al.* 1990), to document more fully the distribution of taxa of interest to us. Among the material collected in this survey, and in other Alberta collections, were specimens of five species of the paraphyletic genus *Megaselia* Rondani, all of which are new records for the Nearctic Region. These species are *M. coccyx* Schmitz, *M. eccoptomera* Schmitz, *M. gartensis* Disney, *M. humeralis* (Zetterstedt) and *M. sordescens* Schmitz. All except *M. humeralis* are similar to the Holarctic Region species *M. sordida* (Zetterstedt), but the differences between them are discussed by Disney (1985). Specimens of *M. sordida,* a species which is widely distributed in Alberta, were also collected in our survey.

All of the five newly recorded taxa are distinctive species, and are recognized easily using Disney's Handbook of the British *Megaselia* (Disney 1989; Brown 1989), a publication which is extremely useful even in Alberta, far outside of its intended area of coverage. I suggest that anyone attempting to identify North American specimens of *Megaselia* should spend some time becoming familiar with the illustrations of male terminalia found in Disney's book. This will help to supplement identifications based on the hopelessly out of date keys of Borgmeier (1964, 1966).

Most of the material is deposited in my collection, but some voucher specimens also will be placed in the collection of the Provincial Museum of Alberta and the Strickland Museum, University of Alberta. Some records for the above mentioned taxa are as follows:

M. coccyx Schmitz, 2♂ CANADA: Alberta, 8km W Edmonton, Wagner Natural Area, 27.vi.-5.vii.1990, B.V.Brown, Malaise trap, poplar/ spruce.

M. eccoptomera Schmitz, CANADA: Alberta, 1♂, 12km N Boyle, 19.v.-10.vi.1990, B.V.Brown, FIT 1a, *Populus*/ *Picea*; 3♂, 91km S Fort McMurray, 19.v.-10.vi.1990, B.V.Brown, FIT 1d, *Picea*; 1♂, 58km S Fort McMurray, 19.v.-10.vi.1990, B.V.Brown, FIT 1e, *Pinus*/ *Picea*; 1♂, 750km NW Edmonton, Bistcho Lake, 20-22.vi.1987, Malaise trap, leg. A.T. Finnamore; 1♂, Hondo, 29.v.-9.vii.1990, E.R.Fuller, FIT 2a, *Pinus*/ *Picea*/ *Populus*; 12♂, 10km N Slave Lake, Muskeg Lake, 29.v.-9.vii.1990, E.R.Fuller, FIT 2b, *Pinus*/ *Picea*/ *Populus*; 3♂, 30km N Slave Lake, Marten Mountain, 29.v.-9.vii.1990, E.R.Fuller, FIT 2c, *Picea*/ *Populus*; 2♂, 61km N Slave Lake, 29.v.-9.vii.1990, E.R.Fuller, FIT 2e, *Populus*/ *Picea*; 1♂, 13km N Hinton, 9-30.vi.1990, T.G.Spanton, FIT 3a, *Picea*/ *Populus*; 3♂, 48km N Hinton, 9-30.vi.1990, T.G.Spanton, FIT 3b, *Picea*/ *Pinus*; 5♂, 84km N Hinton, 9-30.vi.1990, T.G.Spanton, FIT 3c, *Picea*/ *Pinus*; 1♂, 8km W Edmonton, Wagner Natural Area, 4-13.vi.1990, B.V.Brown, Malaise trap, poplar/ spruce; 20km S Nordegg, 4♂, 27.v-24.vi., 7♂, 24.vi-23.vii.1990, D.A.Pollock, FIT 4e, *Picea*/ *Pinus*/ *Populus*; 21♂, 38km S Robb, 27.v.-24.vi.1990, D.A.Pollock, FIT 4c; 1♂, 10km S Nordegg, 24.vi-23.vii.1990, D.A.Pollock, FIT 4d.

M. gartensis Disney, 1♂, CANADA: Alberta, 190km S Fort McMurray, 10.vi.-22.vii.1990, B.V.Brown, FIT 1b.

M. humeralis (Zetterstedt), 2♂, 2♀, CANADA: Alberta, 61km N Slave Lake, 29.v.-9.vii.1990, E.R.Fuller, FIT 2e.

M. sordescens Schmitz, CANADA: Alberta, 2♂, 38km S Robb, 27.v-24.vi.1990, D.A.Pollock, FIT 4c; 4♂, 20km S Nordegg, 24.vi-23.vii.1990, D.A.Pollock, FIT 4e, *Picea*/ *Pinus*/ *Populus*; 2♂, 30km N Slave Lake, Marten Mountain, 29.v.-9.vii.1990, E.R.Fuller, FIT 2c, *Picea*/ *Populus*.

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EDITOR'S ACKNOWLEDGEMENTS AND FAREWELL

As noted previously, *Quaestiones Entomologicae* ceases publication with this volume. That note produced expressions of sympathy and condolence from subscribers, friends and associates. I appreciate the thoughtfulness of those who took the time to write. I appreciate also the efforts of the reviewers (names and abbreviated addresses listed below), whose comments and suggestions contributed significantly to the general quality of the publications in Volume 26.

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I acknowledge especially the cooperation of R. B. Aiken and R. E. Roughley, organizers of the Hydradephaga Symposium that was held in 1988 as part of the program of the XVIII International Congress of Entomology, in Vancouver. It was a pleasure to work with them, in producing The Proceedings of their symposium, which were published in the Spring and Summer issues of *Quaest. Ent.*

The prompt, cheerful and efficient service provided by our printers, Hallis Graphics Ltd., has added to the pleasure of publication. I will miss the association with the President of Hallis, Mr. J. Haukedal. I take this opportunity to wish him well in these trying times for the smaller businesses.

Mrs. Suseela Subbarao has served for 10 years as the Publications Manager of *Quaest. Ent.* In that capacity, she kept us up to date as publishing operations became more complex and sophisticated. She developed and maintained good working relations with the various individuals and groups involved in production of our journal. She endeavored to satisfy the requirements of authors, even those who seemed to be unreasonably demanding. From time to time, she complained— with justification— but she did what was needed, taking satisfaction from the excellent issues that she produced. It is difficult for me to accept that our working relationship is at an end. She will be leaving the Department of Entomology, taking with her my gratitude and appreciation for a job well done.

For 26 years, *Quaest. Ent.* has been an integral part of the operations of our Department. During that period, the Editors (Brian Hocking first, and then me) have called upon our colleagues from time to time for assistance in one form or another. Our requests were met and our expectations fulfilled. For this cooperation, willingly given, I am very grateful.

The Cameron Library of the University of Alberta has been one of our staunch supporters. Subscriptions to *Quaest. Ent.* were offered in exchange for a wide variety of other journals. Thus, we were able to contribute toward development of what was hoped to be a great library in Western Canada. I appreciated the opportunity to be involved in this form of contribution to the general improvement of the University. I regret that this contribution must cease, and especially at this time, when the Library budget is being reduced.

One year ago in the "Editor's Acknowledgements", I noted that *Quaest. Ent.* had reached its 25th year of publishing, but that a celebration would be held off until 2014, the year of the 50th anniversary of the journal. I would have made more of it, had I known that Volume 25 was to be the penultimate, rather than the half-way mark to the Golden Anniversary. What happened? This year, the Department's budget was cut as part of a general reduction in University funding. Loss of our journal was deemed to be the most endurable of the many possible losses that were required in the face of the reduced budget.

I believe that I am at fault for not having foreseen the possibility of the loss of University funding through the departmental budget for *Quaest. Ent.* The handwriting was, so to speak, on the wall, but, like Belshazzar, the last ruler of the kingdom of Babylon, some 2500 years ago, I failed to understand the urgency of the message, a failure best described as complacency. After all, the journal had been in existence for more than 20 years. Surely, its continued existence was assured? Nothing in this world is assured, and an individual should be able to learn this before the near midpoint of his sixth decade of existence.

In the world of free enterprise, or perhaps I should say economic freebooting and buccaneering that has been foisted on us by the likes of Thatcher, Reagan, and lesser national leaders of similar right-wing persuasion, endeavors that do not pay directly for their operations must perish— in spite of other aspects of merit that might justify expenditures from the public purse. Because *Quaest. Ent.* had not become self-sustaining, it became a victim to financial exigency. However, its passing is symptomatic of the stifling of funding for the public institutions, such as universities, libraries, and museums, that contribute to the cultural life of the world.

It is claimed loudly by right-wing politicians (including some nearly brain-dead provincial ministers of education) and their wealthy supporters that there is not enough money to fund properly these institutions. Yet, some years ago, there was funding more adequate than at present. Where has it gone? It's there alright, available for corporate take-overs that contribute to destruction of the system through the looting of pension funds and other necessary reserves; available to purveyors of junk bonds and other unscrupulous manipulators of a nation's wealth; available to a host of lawyers intent on turning the legal system, developed originally as an instrument of justice, into a route to excessive personal financial gain; and available to large corporations as tax rebates made by grateful politicians who cannot distinguish their own private interests from the public interest.

This dislocation of funds has had a profound effect on citizens, generally. It has led to loss of jobs, and loss of opportunity for even modest gain, the reward for doing a job well. The effect of this period of unneeded financial upheaval on the unemployed and under-employed citizenry is encapsulated in a phrase I heard the other day: "their dreams are dying". As I write these words, the Canadian Broadcasting System is carrying Margaret Thatcher's last address as leader of the British Conservative Party. As one of the symbols of destruction of the dreams of the economically unprivileged, her political demise might be taken as a sign of hope that things are changing, but I doubt it. I expect her replacement to be of an ilk similar to that of the "Iron Lady".

In brief, I believe that the world is in the grip of a system based on excessive financial competition that encourages and rewards greed, and that is without respect for the institutions that enrich the process of living, and that is without regard for the environment in which living takes place. To paraphrase one of Sir Winston Churchill's wartime statements, the lights are going out, not only in Europe, but all over the world. When they come on again— whenever that kinder, gentler time may be— perhaps along with the reawakening of other dreams, someone will breathe life back into the remains of the entomological journal *Quaestiones Entomologicae*. Until then, *requiescat in pace*.

George E. Ball
Editor