Meddelelser om Grønland

The Coleoptera of Greenland

Jens Böcher

Bioscience

26 · 1988

Meddelelser om Grønland

The series *Meddelelser om Grønland* was started in 1879 and has since then published results from all fields of research in Greenland. In 1979 it was split into three separate series:

Bioscience
Geoscience
Man & Society

The series should be registered as *Meddelelser om Grønland, Bioscience (Geoscience, Man & Society)* followed by the number of the paper. Example: *Meddr Grønland, Biosci.* 1, 1979.

The new series are issued by Kommissionen for Videnskabelige Undersøgelser i Grønland (The Commission for Scientific Research in Greenland).

Correspondence
All correspondence and manuscripts should be sent to:

The Secretary
Kommissionen for Videnskabelige Undersøgelser i Grønland
Øster Voldgade 10
DK-1350 Copenhagen K.

Questions concerning subscription to all three series should be directed to the agent.

Agent
Nyt Nordisk Forlag – Arnold Busck A/S, Købmagergade 49, DK-1150 Copenhagen K. Tlf. +45.1.122453.

Meddelelser om Grønland, Bioscience

Meddelelser om Grønland, Bioscience invites papers that contribute significantly to studies of flora and fauna in Greenland and of ecological problems pertaining to all Greenland environments. Papers primarily concerned with other areas in the Arctic or Atlantic region may be accepted, if the work actually covers Greenland or is of direct importance to the continued research in Greenland. Papers dealing with environmental problems and other borderline studies may be referred to any of the series *Bioscience, Geoscience* or *Man & Society* according to emphasis and editorial policy.

Instructions to authors. – See page 3 of cover.

The Coleoptera of Greenland

Jens Böcher

MEDDELELSER OM GRØNLAND, BIOSCIENCE 26 · 1988

Contents

Accepted October 1987
ISSN 0106-1054
ISBN 87-17-05572-5
Printed in Denmark by AiO Print Ltd., Odense

The Coleoptera of Greenland

JENS BÖCHER

Böcher, J. 1988. The Coleoptera of Greenland. – Meddr Grønland, Biosci. 26, 100 pp. Copenhagen 1988-10-14.

Since the appearance of the latest published list of Greenlandic insects (Henriksen 1939), 27 species of Coleoptera have been added, including 7 indigenous, 15 introduced, and 5 exclusively known as subfossils. Totally 71 species are treated.

A special section presents information on each species: taxonomical position, variation and dynamics, general distribution, Greenlandic distribution, habitat, and life cycle (mainly indirectly deduced from the collections).

A general section treats and discusses the same subjects on a comparative basis: the taxonomical composition of the beetle fauna, the zoogeographical position of the fauna, the distribution types within Greenland, the disposition of the species in relation to biotopes, and the variation in life cycles. Major conclusions concerning the indigenous fauna include: 1) the zoogeographical situation is peculiar, with equal importance of circumpolar and palaearctic species, and only one purely nearctic species; 2) the fauna has a pronounced southern character, with only one species having a southern limit in Greenland and thus deserving the designation "arctic"; 3) the majority of species are associated with benign microclimates and fairly lush vegetation, but a number of widespread species are highly eurytopic; 4) most species appear to overwinter as adults, four species are undoubtedly biennial with both larval and adult hibernation, and four seem to possess indefinite, opportunistic life cycles with extended larval life. Exclusively larval hibernation is suspected in only one species.

A final chapter reviews and discusses the origin of the Greenlandic Coleoptera. It is concluded that 1) a survival from the Tertiary in Greenland of any beetle species is highly improbable; 2) at most a few, hardy species might have existed in refugia from the Eem Interglacial during the last glaciation; 3) only two species, one purely nearctic, one "western" holarctic, undoubtedly have come to Greenland from North America during the Holocene, and the same may be true for two more holarctic species, absent from Europe; 4) the remainder of the indigenous species most likely are Lateglacial invaders from Europe; 5) the Norsemen were responsible for a number of introductions, of which only very few, partly synanthropic species, have survived to the present day.

Jens Böcher, Zoologisk Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.

Introduction

Background, aim

As regards number of species, the beetles, order Coleoptera, is the most succesful of all animal groups, comprising more than quarter of a million described species. As a whole, however, beetles do not thrive in the far north, only very few species being truly arctic. This was already pointed out by Aurivillius (1883) and Lundbeck (1891–1892). The percentage made up by Coleoptera is steadily decreasing from world total (42%), through a temperate locality (Denmark: 21%), to arctic North America (12%), Greenland (6%), and high arctic North America (Queen Elizabeth Islands: 4%) (Table 1). Because of the paucity of species, the Coleoptera can be regarded a "key group" in a study of the hazards of being an insect in the Arctic.

This publication is a compilation and a survey of what is known about the coleopterous fauna of Greenland, including an up-to-date revision of the taxonomy and a discussion of the origin of the fauna. It is hoped that it will provide a basis for future work on the distribution and ecology of the Greenlandic beetles, studies which are badly needed.

Previous work

For a description of the history of exploration of the Greenlandic insect fauna, see Henriksen & Lundbeck (1917), Henriksen (1939), Wolff (1964), and Danks

Table 1. Numbers of insects in selected areas.

	World[1]	Denmark[2]	Arctic N. America[1]	Greenland[3]	Queen Elizabeth Islands[1]
Total insects (excl. Apterygota)	721 000	17 500	1547	580	359
Coleoptera	303 000	3650	185	33 (38)[4]	13
Percent	42	21	12	6	4

[1] Danks (1981a).
[2] Lomholdt et al. (1984).
[3] Henriksen (1939) incl. revisions.
[4] Introduced and synanthropic species in parenthesis.

(1981a: 111). It will suffice here to mention the basal entomological work by Lundbeck (1891, 1891–1892, 1895, 1896; Henriksen & Lundbeck 1917) and the extensive collections by Vibe and co-workers (e.g., Vibe 1950).

Collections were carried out by me (J.B.), partly during my term (1967–70) as scientific leader of the Arctic Station in Qeqertarsuaq/Godhavn, University of Copenhagen, partly as a member of the "Kap Farvel Expedition" (1970) and during later stays in western Greenland. More recently Peter Nielsen's extensive pitfall-collections from Qaqortoq/Julianehåb and Narsaq Districts have provided a large and highly valuable supplementary material, of which the Coleoptera are published here.

The last published list of the total insect fauna of Greenland, by Henriksen (1939), comprised 44 species of Coleoptera, of which at least 18 introduced by man. The present list totals 71 species recorded from Greenland, 38 of which are unquestionable introductions, and of these 5 are known only as subfossils. Native species added since Henriksen (1939) are: *Helophorus brevipalpis* Bedel, *Atheta hyperborea* Brundin, *Atheta vestita* (Gravenhorst), *Simplocaria elongata* Sahlberg, *Tylicus subcanus* Le Conte, *Caenoscelis ferruginea* (Sahlberg), and *Dorytomus imbecillus* Faust. Two species were formerly incorrectly identified, namely *Quedius fellmanni* (Zetterstedt) (Henriksen: *Q. boops* Grav.) and *Atheta groenlandica* Mahler (Henriksen: *Acrotona fungi* Grav.).

The first faunal list from Greenland, by O. Fabricius (1780), contained a number of dubious Coleoptera, the identities of which have been discussed by Lundbeck (1896) and Henriksen & Lundbeck (1917). The last-mentioned publication, and also Henriksen (1939), mention a number of other species, the Greenlandic records of which must be considered doubtful or erroneous. These are not included in the present account.

It should be noted that in the important work by Danks (1981a) it is not possible to get an overview of the Greenlandic arthropod fauna, since only species occurring in North America are included in the taxonomical surveys, and accordingly only eleven species of Coleoptera are mentioned from Greenland. These include two with a question mark: *Agabus congener* Paykull (Dytiscidae), already discarded by Henriksen & Lundbeck (1917) as erroneous, and *Hypolithus sanborni* Horn (Elateridae) which must be due to another mistake. For unknown reasons also *Arpedium beringense* Van Dyke (Staphylinidae) is included in the Greenland list, and both *Colymbetes dolabratus* Paykull and *C. groenlandicus* Aubé, which are synonyms (see p. 17). These mistakes reduce the Greenlandic beetles mentioned by Danks to seven. On the other hand, *Patrobus septentrionis* Dejean, *Trichocellus cognatus* (Gyllenhal), *Gyrinus opacus* Sahlberg, and *Micralymma marinum* (Ström) are not included, presumably because their ranges in North America do not, or only slightly, extend into the arctic zone.

Methods

The classification and order of species in the special section are in accordance with Silfverberg (1979). This also applies to the nomenclature, except in a few cases, where recent revisions by Danish specialists have been followed (Dytiscidae: M. Holmen; Hydrophilidae: M. Hansen; Staphylinidae: V. Mahler).

A number of species thus have changed name since Henriksen's list appeared. When this is the case, the name used by Henriksen is quoted next to the modern name heading the section dealing with the species.

The treatment of decidedly human introductions is brief. Photographs of these species are given in Figs. 51–55 (pp. 86–89), and a survey is presented in Table 13 (p. 78).

The term "indigenous" is used in a broad sense, so that all (modern) species which have been collected outdoor and apparently free-living in Greenland are included. Two species (*Quedius mesomelinus* (Marsham), *Latridius minutus* (L.)) are thus treated as native, but are principally synanthropic.

To identify indigenous Greenlandic Coleoptera, the figures illustrating each species should be consulted (scale always in millimetres), together with the short notes on the identification of the adults. A key is given only for the difficult genus *Atheta* (this has been worked out in collaboration with V. Mahler, Naturhistorisk Museum, Århus).

Introduced species are illustrated in Figs. 51–55. Keys to synanthropic species associated with stored products are found in Hinton (1945) and Manton (1945).

Most of the larvae (and pupae) depicted have not been properly identified, since descriptions and keys are lacking. However, because of the limited number of species in Greenland it is usually possible to refer larvae to species at a high level of confidence. In several species larvae and/or pupae have not yet been found in Greenland. In all cases except one (*Nebria rufescens* (Ström)) last-instar larvae are shown. (Note: some of the larvae depicted are somewhat swollen due to the preservation in alcohol).

In two cases Greenlandic specimens were not available for the figures. *Lathrobium fulvipenne* Gravenhorst was drawn from Icelandic material, and *Simplocaria elongata* Sahlberg from Canadian material (Churchill, Manitoba). The specimens of introduced beetles shown in Figs. 51–55 are not from Greenland.

Information about the general distribution of species is mainly adopted from the works by Poppius (1910), Henriksen & Lundbeck (1917), Lindroth (1931, 1945a, 1949, 1957, 1961b, 1963b, 1968b, 1985, 1986), Lindroth et al. (1973), Brundin (1934), Strand (1946), Larsson & Gigja (1959), Danks (1981a), Fjellberg (1983), Arnett (1983).

Greenland is traditionally included in the Nearctic Region, implying that the occurrence of a species in Greenland automatically renders it "nearctic". In order to avoid misunderstandings, in this work Greenland is considered a zoogeographical unit of its own, and accordingly palaearctic species occurring in Greenland, but not in North America, are not termed holarctic.

Material

The vast majority of Coleoptera collected in Greenland are kept in the Zoological Museum, University of Copenhagen (ZMUC), and this material is the primary foundation of the present work. Supplementary material, in particular concerning more difficult taxa, has been obtained from Naturhistorisk Museum, Århus; Naturhistoriska Riksmuseet, Stockholm; British Museum (Natural History), London; Hope Entomological Collections, Oxford; The University of Birmingham; University College of Wales, Aberystwyth.

Except for a few localities known only from the literature, the occurrences plotted on the distribution maps are mainly based on the material mentioned above. A list comprising the entire material consulted in this study is deposited in the ZMUC.

I am indebted to a number of colleagues who have contributed indispensably to the present work by revising and identifying difficult taxa. My sincere thanks are extended to the following:

P.J. Johnson, University of Idaho, Moscow, Idaho, U.S.A. (revision and identification of Byrrhidae: *Simplocaria*, *Tylicus*).

M. Hansen, Zoological Museum, University of Copenhagen, Denmark (identification of Hydrophilidae and Dermestidae: *Reesa vespulae* (Milliron)).

S. Lundberg, Luleå, Sweden (revision of Cryptophagidae, Latridiidae).

V. Mahler, Naturhistorisk Museum, Århus, Denmark (revision and identification of Staphylinidae: *Quedius*, *Atheta*).

T. Nyholm, Naturhistoriska Riksmuseet, Stockholm, Sweden (identification of a fragment of Dermestidae).

C.W. O'Brien, Florida Agricultural and Mechanical University, Tallahassee, Florida, U.S.A. (identification of Curculionidae: *Dorytomus*).

Annotated list of species

Carabidae

Nebria rufescens (Ström, 1768)

(Henriksen 1939: *Nebria gyllenhali* Schönh.)

Taxonomy and synonomy: see Henriksen & Lundbeck (1917), Lindroth (1931, 1955, 1961b, 1985); Erwin et al. (1977).

Identification

The largest of the Greenlandic Carabidae, length about 9–12 mm. Furrows (striae) of elytra deep. Pronotum much wider than long. Legs comparatively long and strong (Fig. 6,a-b).

Variation and dynamics

Nebria rufescens is highly polymorphic and a number of subspecies make up an intricate species complex (Lindroth 1955, 1961b; Holdhaus & Lindroth 1939). A red-legged variety, var. *balbi* Bonelli 1809, is found together with the palaearctic nominate form (with black legs), but appears to be more frequent towards higher latitudes and altitudes (Lindberg 1927). Poppius (1910) associated this variety especially with Atlantic beaches in spite of its widespread occurrence in Central European mountains. Larsson & Gigja (1959) proposed to name the populations of the species containing var. *balbi*: *N. gyllenhali munsteri* Larsson & Gigja.

In both the Faeroes (West 1937) and Iceland (Lindroth 1931, Lindroth et al. 1973, Larsson & Gigja 1959) the two forms are equally frequent, but Lindroth et al. (1973) demonstrated that the red-legged variety is com-

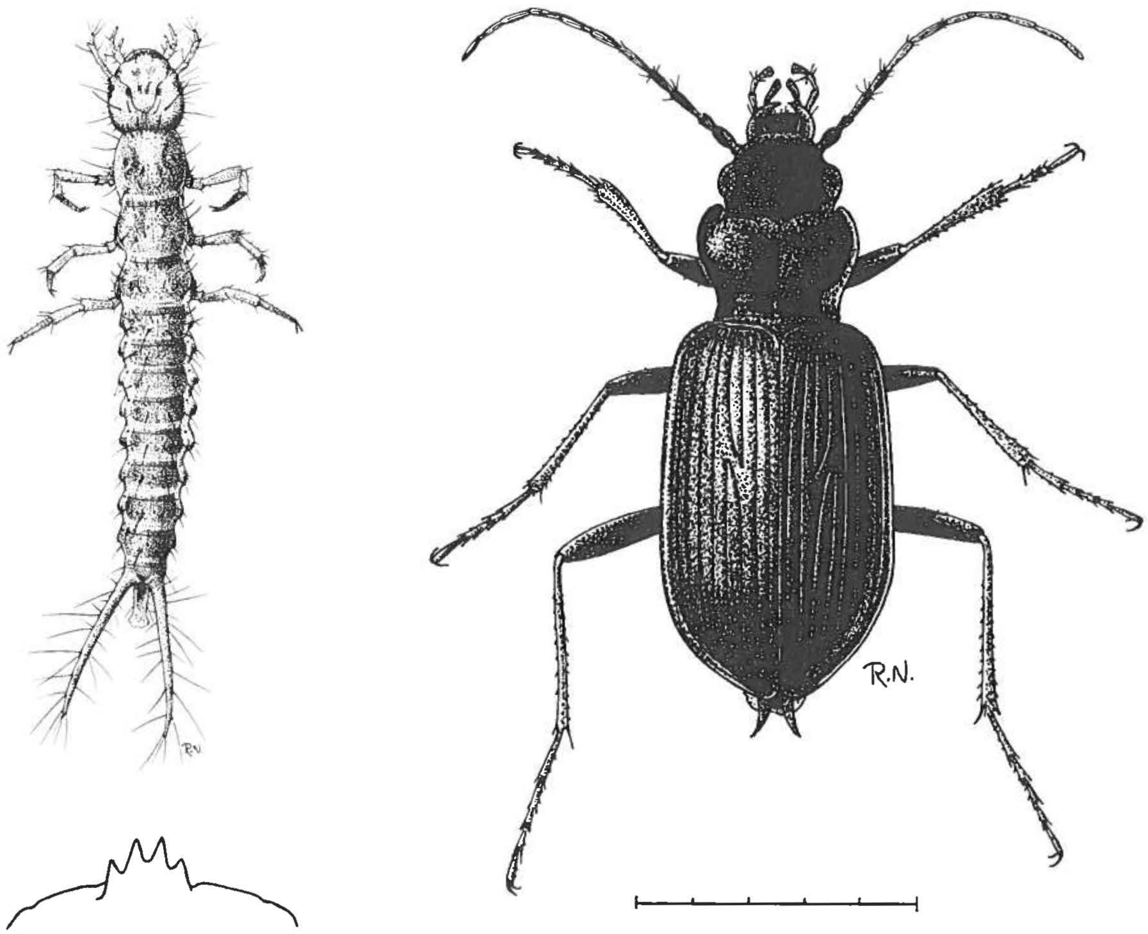


Fig. 1. *Nebria rufescens* (Ström). The larva is a second instar. The anterior margin of the larval nasale is shown at greater magnification. Scale: 5 mm.

paratively rare in central southernmost Iceland. Bengtson et al. (1983) found a highly varying ratio between the two forms among different localities in both Iceland and the Faeroes.

In Greenland var. *balbi* predominates. Of 198 specimens studied (ZMUC), 108 (67%) are red-legged, but this number includes about 25 intermediate, brown-legged individuals. Larsson & Gigja (1959) stated that in Iceland intermediate forms are absent, and this was confirmed by Bengtson et al. (1983) considering the species in both Iceland and the Faeroes.

Bengtson et al. (1983) established a strong negative correlation between the frequency of the red-legged form and both temperature and precipitation in Iceland

Table 2. A comparison of two collections of *Nebria rufescens* with regard to the occurrence of the red-legged var. *balbi*.

	N	var *balbi*	inter-mediate	forma *typica*	mean summer temperature (June-Aug.)	mean annual precipi-tation
Nuuk[1]	41	32	6	3	6.7°C[3]	515 mm[3]
		93%				
Narsarsuaq[2]	55	30	2	23	9.8°C[4]	696 mm[4]
		58%				

[1] 31 May 1944, C. Vibe leg. [2] June–August 1984, P. Nielsen leg.
[3] Fristrup (1981) [4] Feilberg (1984)

and possibly also the Faeroes. Regarding Greenland, the material of *N. rufescens* is too limited to allow a statistical treatment of the varying frequency of var. *balbi* among different localities. However, a comparison between fairly large samples from two places with a different climate agree with the findings of Bengtson et al. (Table 2). Narsarsuaq has a relatively warm, subarctic climate with a good deal of precipitation, whereas the climate of Nuuk/Godthåb is colder, low arctic, with less precipitation. At Nuuk the frequency of var. *balbi* is much higher and significantly different from the frequency at Narsarsuaq ($p<0.001$, if intermediates are counted red-legged, $p<0.02$ if counted black-legged).

In North America var. *balbi* appears to be entirely absent (Lindroth 1961b), another indication of the faunistic gap between Greenland and North America (see p. 82).

The hind wings are always fully developed, but the species has never been observed flying (Lindroth 1945a, Lindroth et al. 1973). In Scandinavian specimens the flight muscles may be reduced (Gislén & Brinck 1950). Larsson & Gigja (1959) mentioned a few Icelandic individuals with strikingly better developed wings than in most specimens.

General distribution

Circumpolar, subarctic to low arctic; in Europe boreoalpine (Holdhaus & Lindroth 1939): Scandinavia south to the large Swedish lakes, all the North Atlantic islands, British Isles, northern Russia, most Central European mountains. *N. rufescens* is absent from Denmark, but has been found in Lateglacial deposits on Sjælland (Henriksen 1933).

Distribution maps: Lindroth (1931: 469, Iceland; 1945b: 224, Fennoscandia), Holdhaus & Lindroth (1939: fig. 2, Europe), Kavanaugh (1980: fig. 7, North America).

Distribution in Greenland (map p. 11)

In Greenland *N. rufescens* is local and rare, quite common only in the subarctic, northwestern part of the Qaqortoq/Julianehåb Bugt area and in the western part of Godthåbsfjord, which appears to be the northern limit. The species has not been found south of Uunartoq (60°30'N) in spite of an intensive searching in the Kap Farvel area, where the climate of the interior fjord-system is favourable as well.

Habitat and notes on biology

In Greenland *N. rufescens* is mainly found under stones on sandy beaches and river banks (Lundbeck 1896, Henriksen & Lundbeck 1917). It may be fairly numerous along brooks surrounded by vigorous vegetation and in marshy areas with *Eriophorum*, and it also occurs in luxuriant grassy vegetation (see Tables 9, 11).

In Iceland the species is very common everywhere, up to 450 m alt.; it is absent only in very wet situations and on dry mountain heaths (Lindroth 1931, Larsson & Gigja 1959). It is also very frequent and widely distributed in the Faeroes, found even on the highest peak (882 m) (West 1937), but especially common in in-fields and on sandy beaches (Bengtson 1980, 1981).

In Scandinavia *N. rufescens* is almost ubiquitous in the lower alpine region on more or less humid ground, e.g., in snow-beds and along glacial streams, reaching altitudes of about 1400 m. In the lowland, however, it is fairly stenotopic on lake- and river banks, and on beaches at high latitudes. At lower altitudes the species is clearly dependent on the vicinity of cold water and almost confined to nearly barren, stony or gravelly shores of water courses and lakes (Lindberg 1927, Brundin 1934, Lindroth 1945a, Østbye 1969, Forsskål 1972). In Norway, however, it appears to be quite eurytopic even in the lowland (Andersen 1982). The species occurs as a relict on exposed shores of the great lakes Vänern and Vättern in southern Sweden (Brinck 1966).

In Central Europe *N. rufescens* is chiefly found in the subalpine and alpine zones, but it follows the cold mountain streams far into the zones below (Lindroth 1945a, Holdhaus & Lindroth 1939).

In North America it is a hygrophilous species, usually confined to the stony margins of running, cold waters. It seems to exceed the tree limit only on the coastal tundras of Labrador and northwestern Newfoundland (Lindroth 1955, 1961b). In the northern part of the distribution area the species is less stenotopic and, e.g., in Alaska is generally found in some distance from water, under *Alnus* bushes on silty, moderately moist ground – an ecological deviation which Lindroth (1961b) regarded as a sign of sub-speciation. This tendency to be less stenotopic towards the north is, however, paralleled in the northern, oceanic part of the European distribution (Iceland, Faeroes), but not in Greenland.

Nebria rufescens thus undoubtedly is highly hygrophilous and adapted to cool surroundings. Krogerus (in Lindroth 1949: 465; 1960: 136) demonstrated a preferred temperature of 5–8°C of individuals from Swedish Lapland and Finland. Ottesen (1985) showed that the species is strictly nocturnal in the South Scandinavian mountains.

Life cycle

In Greenland adult *N. rufescens* have been collected from 31 April to 1 September. A large sample from Nuuk/Godthåb, taken as early in the season as 31 May (1944, C. Vibe leg.), comprises 7 females and 23 males, indicating that adults hibernate, and also that males possibly appear earlier in the season than the females. Otherwise the sex ratio does not deviate from equality.

Few larvae have been collected in Greenland: first instar from 24 July and 12 August (Narsarsuaq) and second instar from 28 May, 8 July, and 12 August. Ten females caught in the middle of June had ripe or nearly ripe ovaries, and two females from 12 August had ripe-spent ovaries. Callow imagines have been collected on 24 July and 12 August.

The early find of a second-instar larva, in combination with the early appearance of adults and the presence of females with ripe ovaries in June, and of callow imagines in July-August, all point to a two-year reproductive cycle, just as in *Patrobus septentrionis* (p. 10).

According to Larsson (1939) and Lindroth (1945a, 1985), *N.rufescens* in Scandinavia apparently mates in the autumn and overwinters as larvae; but regularly it also hibernates as adults, so that the entire development in the northern area of distribution may take two years. Andersen (1970) reported larvae collected in September, October, and May in alpine Norway. From the Kilpisjärvi area (Finland), Forsskåhl (1972) described a biennial cycle very similar to that suggested for Greenland.

In Iceland, however, in spite of presence of imagines throughout the year, Larsson & Gigja (1959) concluded that the generation is annual with hibernation of larvae (mainly third instar), metamorphosis in spring and early summer, and egg-laying starting about mid-summer.

In Newfoundland most callow adults are found early in summer, and hibernation is normally larval, but occasionally adult, especially in the north (Lindroth 1955). A similar cycle appears to be found in Canada and Alaska (Lindroth 1961).

Patrobus septentrionis Dejean, 1821

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931, 1955, 1961b, 1985), Erwin et al. (1977).

Identification

Similar to *Nebria rufescens* in general shape and colour, but smaller, 8–10 mm long, legs comparatively shorter (Fig. 6,d), striae of elytra narrow and shallow, and pronotum about as wide as long. A key to the larvae of Danish *Patrobus* spp. is given by Larsson (1968).

Variation and dynamics

The elytra are often more or less rufous, probably a modification without taxonomic significance, especially frequent in alpine environments (Lindberg 1927: 13, 17; Lindroth et al. 1973). About one third of the Icelandic individuals are rufous (Lindroth 1931) and 16% in the Faeroes (West 1937). In Greenland the proportion of rufous specimens is much lower, but due to a continuous variation it is difficult to give an exact figure. Leg colouration also exhibits a continuous variation from dark brown to bright red.

The hind wings are always fully developed, and spontaneous flight has been observed in northern Norway (Lindroth 1945a).

General distribution

Perfectly circumpolar, boreal to low arctic. In Europe boreo-alpine, but Holdhaus & Lindroth (1939) did not include the species in their list of boreo-alpine species because an alleged subspecies of *P. septentrionis*, *P. s. australis* J. Sahlberg, 1875, is found in Denmark, southern Sweden, Finland and northern Germany, and accordingly between the northern and alpine areas of distribution. Silfverberg (1979), however, regarded *australis* a distinct species (see also Bangsholt 1983: 38, 170). In this case, *P. septentrionis* must be considered truly boreo-alpine.

The species has been found in several Lateglacial deposits in western Europe (Lindroth 1960, Lindroth & Coope 1971), including Denmark and southern Sweden (Henriksen 1933).

Distribution maps: Lindroth (1945b: 241, Fennoscandia; 1963: 94, Newfoundland).

Distribution in Greenland (map p. 11)

P. septentrionis is common and widespread in Southwest Greenland, probably with a northern limit around Fiskefjord (64°54'N).

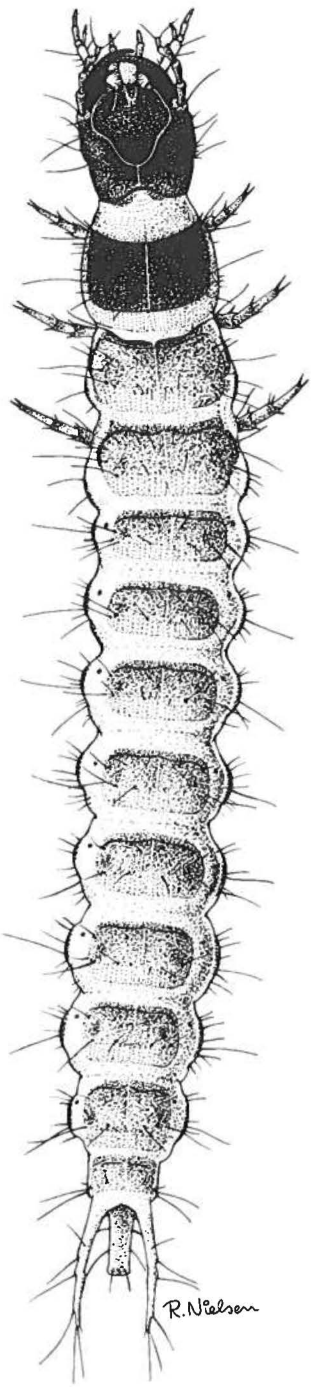
The species is frequent also in the Kap Farvel area (where *Nebria rufescens* is absent, p. 7) and found even on the southernmost stretch of the east coast. The exact position of the northernmost find on this coast is impossible to state, because R. Bøgvad (1932, label note) collected a specimen somewhere "between Lindenow Fjord and Graah Havn" (60°30'N and 63°25'N, respectively), without further details.

Habitat and notes on biology

Lundbeck (1896) and Henriksen & Lundbeck (1917) described the habitat in Greenland merely as "under moss and stones". Most characteristically, *P. septentrionis* is found in humid situations, but otherwise the nature of the biotopes is highly diverse (see Tables 9–11). It may be found in large numbers on lake shores and along water courses (in company with *Nebria rufescens*), as well as in lush shrubs, herbslopes, grasslands, and heaths, but always at low altitude. The species thus appears to be eurytopic, but hygrophilous.

In Iceland *P. septentrionis* occurs only in fairly moist localities, especially meadows, where it is one of the most characteristic insects. It is not found in heaths and not above 300 m altitude (Lindroth 1931, Larsson & Gigja 1959).

In the Faeroes the species is highly eurytopic and the dominant ground beetle in most plant communities, only absent from sand dunes. The habitat overlap with



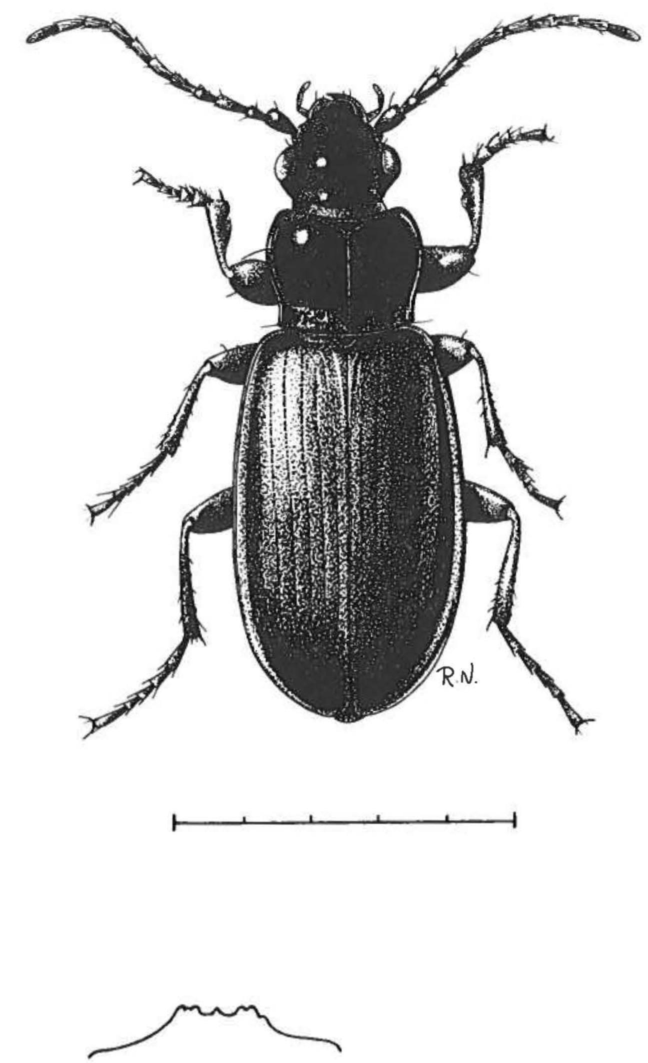


Fig. 2. *Patrobus septentrionis* Dejean. The anterior margin of the larval nasale is shown at greater magnification.
Scale: 5 mm.

Nebria rufescens is, however, only moderate (Bengtson 1980, 1981).

Lindroth (1945a) denoted the species as pronoucedly eurytopic in Scandinavia, occurring mainly in the alpine region and on the tundra, in meadows and heaths, often near snow patches on which it is frequently seen hunting for chilled insects. It is also found in swamps, only avoiding the driest and most barren localities. It is found up to at least 1300 m altitude (Östbye 1969). Lindberg (1927) mentioned finding *P. septentrionis* under *Salix* shrubs. Forsskåhl (1972) did not agree that the species should be considered eurytopic, since in the subalpine region he always found it in damp places near water, and in the alpine region in damp snow-beds and on shores.

According to Lindroth (1945a), in the alpine zone the species is usually found together with *Nebria rufescens* in humid biotopes, in drier places in company with

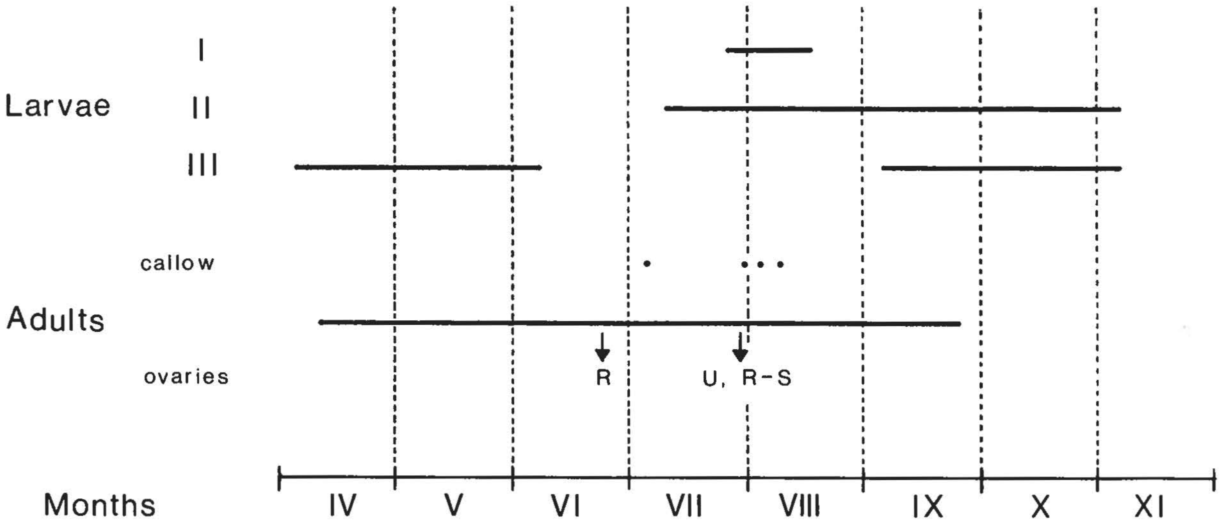


Fig. 3. Life cycle of *Patrobus septentrionis* in Greenland as inferred from the collections. I, II, III: first, second and third larval instar; R: ripe; U: undeveloped; S: spent.

Amara alpina (Paykull). In the upper coniferous region *P. septentrionis* is found in moist places with a rich vegetation of *Carex* spp. and associated plants at the margins of large rivers, often together with *Pelophila borealis* (Paykull) (Lindroth 1985).

In North America *P. septentrionis* is found at the border of lakes, ponds and slow streams on more or less clayish ground with a grass and *Carex* cover and little moss, on the foggy Aleutian Islands also on open ground far from water. It is remarkable that in North America the species appears to occur beyond the forest zone only on the coastal tundras of southern Labrador and on the Aleutian and Pribilof Islands, and not on the true tundra (Lindroth 1955, 1961b).

Ottesen (1985) showed that *P. septentrionis* is strictly nocturnal in the South Scandinavian mountains. He also observed the species crawling normally at a temperature of – 0.5°C during snowfall and strong wind in late autumn. Bakken (1985) found that the adults are susceptible to freezing and are killed at the supercooling temperature, which is – 14°C at a minimum.

Life cycle

Collections of this species are sufficient to show that the reproductive cycle in Greenland is biennial, with hibernation of both larvae and adults (Fig. 3).

First and second instar larvae have been found in July and August, second instar also in November, and third instar from September to November and from April to mid-June. Adults are present throughout the season (collected 10 April to 24 September), callow adults in July and the beginning of August. Only females with mature ovaries are present in June, whereas in July-August individuals with undeveloped ovaries are found together with individuals with ripe or spent ovaries.

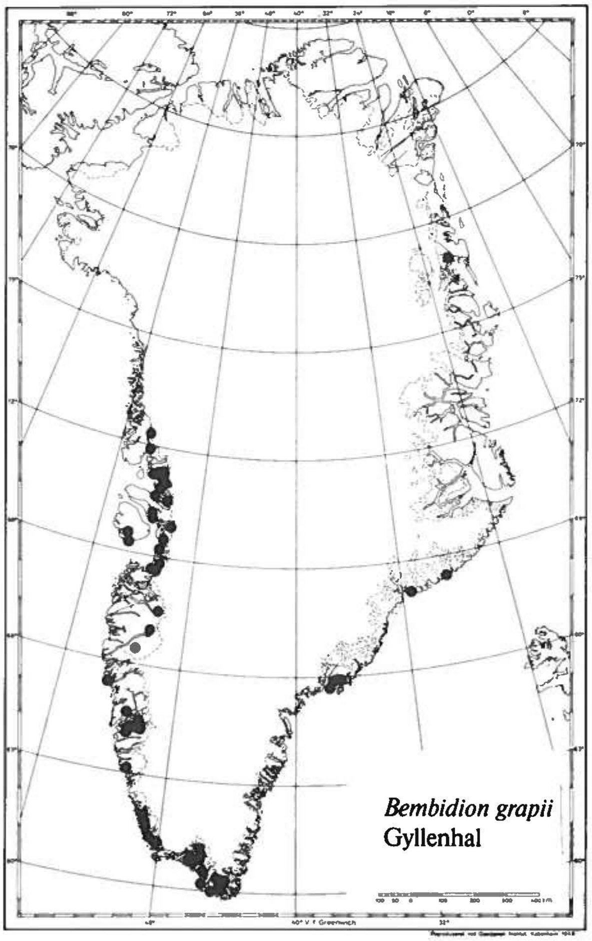
Accordingly, there is every reason to believe that the eggs are laid in early summer, the larvae hatching in mid-summer and passing the subsequent winter in instars II and III. Pupation probably takes place the following June, and the new adult generation emerges in mid-summer, passing the second winter as callow imagines. These mate next May-June, lay eggs, and die at the end of the season. – A pitfall-sample from the head of Tunulliarfik, 24 July 1983 (P. Nielsen leg.) showed a skew sex-ratio of 14 ♀ to 43 ♂, possibly showing a higher activity of the males.

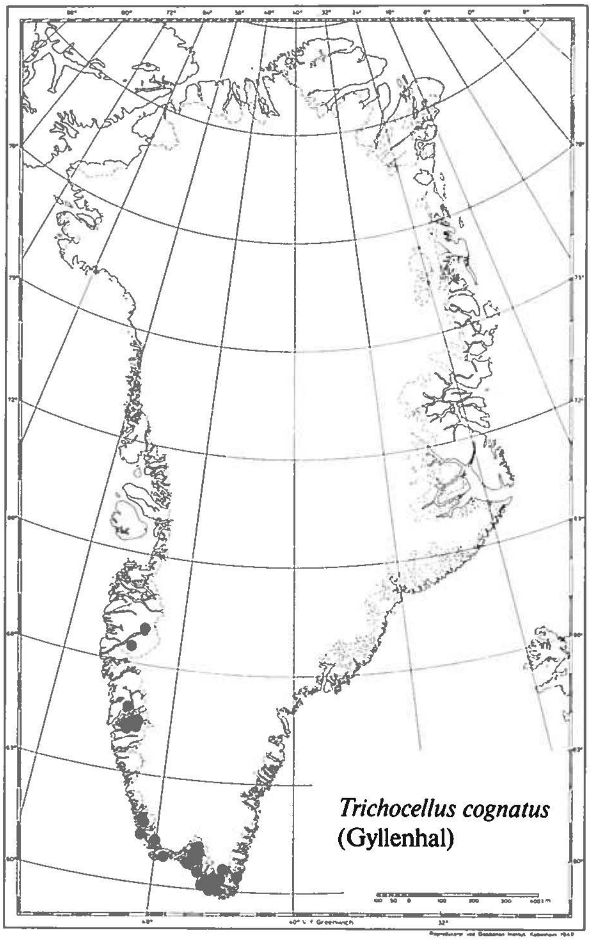
An important contribution to the knowledge of the life history was made by C. Vibe, who collected one second instar and five third instar larvae on the snow surface at Nuuk/Godthåb on 6 November 1942 – thereby showing not only that larvae do hibernate, but also that they may be active during milder spells of the winter.

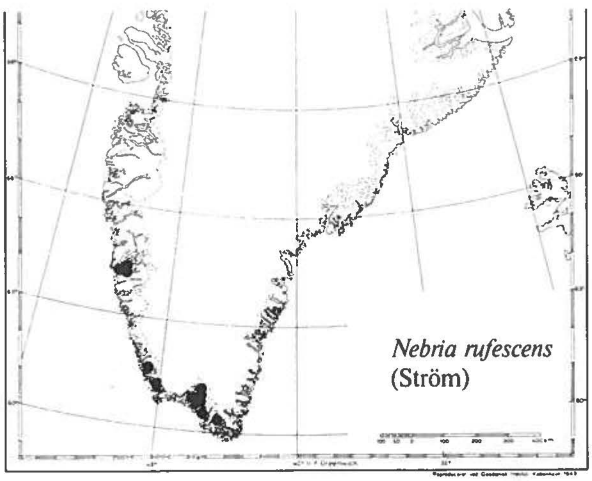
Larsson & Gigja (1959) stated that in Iceland *P. septentrionis* most probably has an annual life cycle. In Scandinavia, however, and also in North America, the life span is biennial with both imagines and larvae hibernating, just as in Greenland (Lindroth 1945a, 1955, 1961b; Forsskåhl 1972).

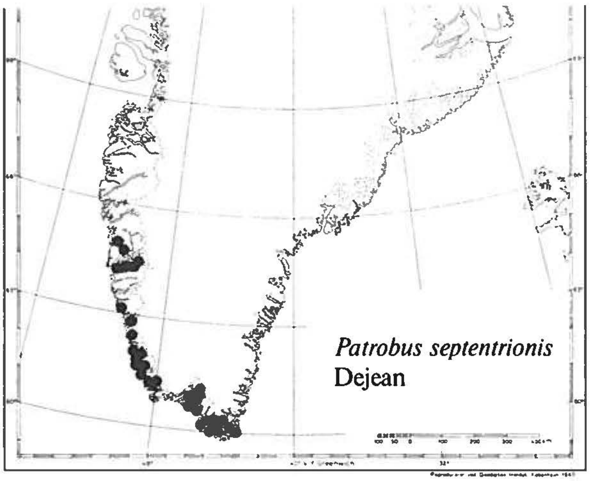
Note

Lundbeck (1896) stated that during winter *Patrobus septentrionis* frequently enters the Greenlanders' turf houses and thereby causes much fear, because it is believed to creep into and damage the ears of sleeping people. The Greenlandic name for the species is Siutisiortoq: "someone searching for the ears". This was originally mentioned by O. Fabricius (1780), who attributed this quality to *Tenebrio fossor* (non Linnaeus), thereby indicating that *Tenebrio fossor* O. Fabricius is identical with *P. septentrionis* (Lundbeck l.c.).


Bembidion grapii
Gyllenhal


Trichocellus cognatus
(Gyllenhal)


Nebria rufescens
(Ström)


Patrobus septentrionis
Dejean

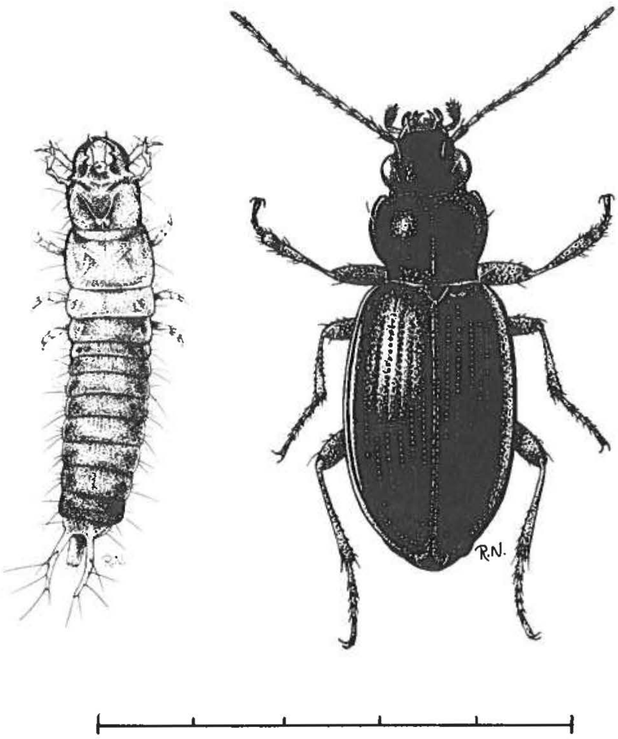


Fig. 4. *Bembidion grapii* Gyllenhal. Scale: 5 mm.

Bembidion grapii Gyllenhal, 1827

(Henriksen 1939: *Bembidion (Peryphus) grapei* Gyll.)

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931, 1955, 1963b, 1985), Erwin et al. (1977).

Identification

One of the two small Greenlandic Carabidae, about 4–4.5 mm long. Head, pronotum and elytra shining black, frequently metallic. Side margins of pronotum S-shaped, hind angles approximately rectangular. (Male front leg: Fig. 6,c).

Variation and dynamics

Bembidion grapii is polymorphic with respect to the hind wings, which may vary from fully developed to quite rudimentary, scale-like (Lindroth 1945a, 1949, 1957, 1958, 1963b, 1979; Lindroth et al. 1973). Four main types of wings ("a"-"d") can be distinguished (Lindroth 1957: 275), but at least in Greenland there are intermediates between the brachypterous forms ("c" and "d"). Lindroth (1957) counted the type "b" with nearly full hind wings as macropterous together with type "a" with folded wing apex. It is, however, uncertain whether wings of types "a" and "b" in fact are used in flight, because observations are lacking (apart from the indication offered by two macropterous specimens found in wind-drift material in Finland; Palmén 1944: 37).

The ratio between the wing types varies considerably among different localities, and Lindroth (1949, 1957, 1979, etc.) used the proportion between brachypterous and macropterous individuals as an indication of the "age" of a certain population. Predominance of short-winged individuals should be characteristic of old populations, and due to their better power of dispersal the long-winged individuals should predominate in the periphery of the distribution area.

Pearson (1964) pointed to the possibility that the wing polymorphism in *B. grapii* might be a temperature-controlled variation. A number of recent studies interprete wing polymorphism in Carabidae (and other taxa) in terms of ecological adaptations and consider it a stage in an evolutionary process (see p. 79).

Lindroth (1957: 178) examined 194 specimens from Greenland, mainly from the Nanortalik-Qaqortoq/Julianehåb area, and stated that in Greenland *Bembidion grapii* "occurs almost exclusively in the brachypterous form". This conclusion cannot be confirmed on the

Table 3. *Bembidion grapii*. Wing-polymorphism in selected Greenlandic localities.

Locality		Percentage					
		Macropterous		Brachypterous		N	♂:♀
	Wing type	'a'	'b'	'c'	'd'		
Inner Kap Farvel area		41	4	41	14	22	.75
Qaqortoq/Julianehåb		10	11	52	27	62	1.07
Narsarsuaq		14	18	36	32	22	.57
Neria		21	5	42	32	19	.19
Outer Godthåbsfjord		25	16	37	22	32	.94
Inner Godthåbsfjord		14	32	45	9	22	.69
Qeqertarsuaq/Godhavn		13	7	32	48	31	.76
Uumannaq District		82	–	18	–	17	1.43
Ammassalik		46	9	36	9	11	.43
Total		23.5	11.8	40.3	24.4	238	.78
		35.3		64.7			

basis of the material seen in the ZMUC collections. Of 238 specimens examined, 35% belong to types "a" and "b" (Lindroth: about 7%) and as a whole the proportions of wing types found in the collections are very close to those found in Iceland as a whole (Lindroth 1957: 278). The strongest wing reduction (type "d") appears to be less common in Greenland as compared to Iceland, whereas type "c" predominates. Table 3 gives the proportions found in those places in Greenland where collections are sufficient to allow a statistical treatment. Brachypterous individuals are prevalent in all places except in the Uummannaq District and, possibly, Ammassalik, but the material from these localities is small. There is a tendency that the lowest proportions of long-winged individuals are from places nearest the coast (Qaqortoq, Neria, Qeqertarsuaq; the outer stations in the Godthåbsfjord are not situated close to the sea). A larger material from the Uummannaq District is desirable, but not easily obtainable because of the rarity of the species here.

General distribution

Circumpolar, subarctic to low arctic, alpine except in the northernmost parts of the area. In Europe restricted to Fennoscandia (absent from Denmark and the Faeroes), Iceland and northern Russia.

Distribution maps: Lindroth (1945b: 91, Fennoscandia, also in 1949: 402, 1953, 1957:276, 1958; 1957:277, Iceland; 1957:279, Greenland; 1963a:99, Newfoundland; 1979, North America).

Distribution in Greenland (map p. 11)

Bembidion grapii is the only Greenlandic carabid extending far into the Low Arctic, reaching the High Arctic in Northeast Greenland, but it becomes rare approaching the northern limit. Along the east coast the finds are highly scattered, and there is an enormous gap from the Blosseville Kyst, considered the northern limit by Brændegaard et al. (1935) and Degerbøl (1937), to the remarkable find of a single specimen by Haarløv (1942) as far north as Mørkefjord (76°56′N). In all probability the species also occurs in between, e.g., in the Scoresby Sund region, where many places would offer ideal conditions.

On the west coast the northern limit is probably at the head of Ukkusissat Fjord (72°20′N). In West Greenland the species apparently disappears from the coastal areas as one goes north, its distribution hereby resembles that of many plant species preferring a more continental climate, with warm summers, approaching their northern limit (T.W. Böcher 1963b).

Habitat and notes on biology

In Greenland *B. grapii* is mainly found under stones, sometimes larvae and adults together, in fairly warm and dry situations: among low and sparse steppe-like vegetation on south-facing slopes, but most often close to more luxuriant vegetation, e.g., bordering small streams. It is never found on barren fell-fields or on really dry ground. De Lesse (1950a, 1950b) reported the species from snow-beds and stony banks of small brooks in moraines at Eqe, northeastern Disko Bugt. P. Nielsen collected it throughout the summer (1983) in pitfalls placed in a south-facing birch coppice at Narsarsuaq, Narsaq District (pers. commun.). Haarløv (1942: 12) described the locality where it was found in Mørkefjord, Northeast Greenland, as the coherent, dense (fertilized) vegetation of *Alopecurus alpinus* surrounding a bird-stone. Otherwise the vegetation was exceedingly sparse, with xerophilous gravel-soil species (*Poa abbreviata, P. glauca, Melandrium triflorum, Cerastium alpinum*).

The highest altitude of the species stated, 580 m, was from a heath rich in mosses and lichens at Narsarsuaq (P. Nielsen leg. 1985).

In Iceland the species is found in similar biotopes, but it is especially common in the surroundings of hot springs (Lindroth 1931, 1957; Larsson & Gigja 1959). In Scandinavia the species is confined to the high boreal coniferous and birch region. Lindroth (1945a, 1985) characterized the habitat as more or less loamy, sandy ground with a dry surface, where the vegetation is tiny mosses and often *Festuca ovina*, in general with some shade, e.g., at the edge of forests or on northern slopes. The species is almost always found together with *Trichocellus cognatus* (Gyllenhal) – the same combination so often encountered in Southwest Greenland.

In North America the habitat appears to be very similar to that in Scandinavia. Here the species is rarely found beyond the forest limit and never on true tundra (Lindroth 1955, 1963).

Experiments on the temperature- and humidity responses of *Bembidion grapii* were carried out by the author on individuals collected in Uunartorsuaq/Engelskmandens Havn at Qeqertarsuaq/Godhavn during late summer 1969. The species could maintain fairly normal activities down to –1°C. At the other extreme, normal activity was replaced by excessive activity at 35°C and at about 40°C attempts of flying were observed; heat stupor set in at 41°C. An initial preference for dry air was replaced by hygrophily following three hours' exposure to a gradient from 5% to 95% relative humidity.

Individuals kept in natural substrate in the laboratory were observed ingesting collembolans and oribatid mites.

Life cycle

In Greenland adult *B. grapii* have been collected from 2 April to 24 September, callow adults in August and September (five of eight adults from Narsarsuaq, 10 September 1970, were callow). Larvae have been found from 28 June to 12 August, the smallest stages in the beginning of the season. Thus nothing speaks against an assumption that the species hibernates as adult and passes through the larval stages during summer. A large sample of adults taken in the beginning of April (Qaqortoq/Julianehåb, G. Meldorf leg. 1900 & 1901) strongly supports this conclusion.

Outside Greenland, all individuals appear to hibernate as adults (Lindroth 1945a, 1955, 1963b). Larsson & Gigja (1959) stated that in Iceland adults as well as larvae in all stages have been collected throughout the summer, with several pupae and callow adults from July-August. According to these authors this indicates hibernation of the adults only, as is most frequent within the genus. A few finds deviate from this rule, "indicating that the period of reproduction is less strictly delimited than in *Bembidion* in Denmark" (Larsson & Gigja 1959: 23).

Note

According to Bell (1981), *Bembidion yukonum* Fall has been collected at Eqalummiut nunaat, West Greenland. It has not been possible to confirm this information (the specimen has disappeared), and most probably it is based on an incorrect identification of *B. grapii* (D. Stroud, University College of Wales, in litt.).

Trichocellus cognatus (Gyllenhal, 1827)

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931, 1955, 1968b, 1986).

Identification

Size and shape similar to *Bembidion grapii*, but readily distinguished from this species by the light brownish yellow margins of the pronotum and elytra. Hind angles of pronotum rounded, side margins convex. Length about 4–5 mm. (Male front leg: Fig. 6,e).

Variation and dynamics

According to Lindroth (1968b) the punctation and pubescence of the elytra are subject to much variation; setae may be found on the central parts of from two to all nine of the elytral intervals. In a sample from Fairbanks, Alaska, 62% of the individuals had setae on 7–9 intervals. In Greenland the pubescence is much more sparse. Of 64 specimens examined, 61% had setae on only two intervals, 19% on only one interval, and 20% on 3–4 intervals.

Hind wings are always well developed and at least in Europe flight is frequent (Lindroth 1945a, Den Boer et al. 1980)

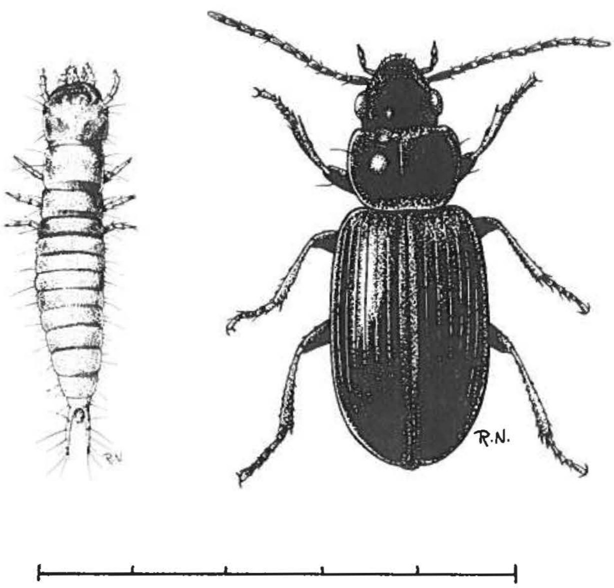


Fig. 5. *Trichocellus cognatus* (Gyllenhal). Scale: 5 mm.

General distribution

Perfectly circumpolar and very widespread, temperate to low arctic. In Europe south to northern Germany and Belgium; in Denmark found in several places, but fairly rare (V. Hansen 1968, Bangsholt 1983).

Distribution maps: Lindroth (1945b: 276, Fennoscandia), Bangsholt (1983: 204, Denmark, Europe).

Distribution in Greenland (map p. 11)

T. cognatus has a typical southwestern distribution, with the northern limit presumably at the head of Kangerlussuaq/Søndre Strømfjord and a southeastern limit in the Kap Farvel area. The species very often occurs together with *Bembidion grapii*, but is markedly less frequent and widespread.

Habitat

The habitat of *T. cognatus* in Greenland is not easily described, though it seems to be similar to that of *Bembidion grapii* (p. 13). The species is most often found under stones in both humid and dry, but fairly warm situations (see Tables 9, 10). Like *Bembidion*, it disappears from coastal areas going north in West Greenland.

In Iceland the species is found in nearly all heathlike localities, both dry and rather moist (Larsson & Gigja 1959), but preferring meagre soil and open ground covered with sparse vegetation (mosses) (Lindroth 1931, Lindroth et al. 1973).

In northern Scandinavia *T. cognatus* particularly occurs in glades and outskirts of coniferous forests, on

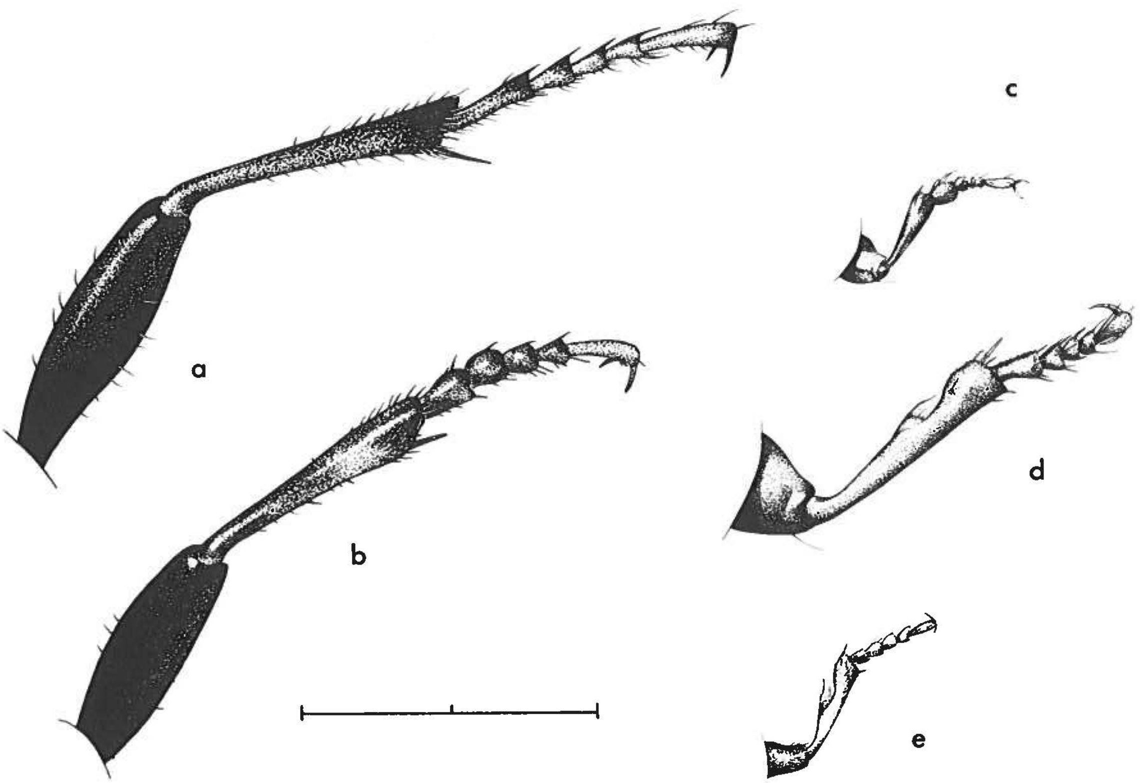


Fig. 6. Right front legs of the Greenlandic Carabidae, showing tarsal enlargement in the males. a-b: female and male of *Nebria rufescens*; c-e: males of *Bembidion grapii, Patrobus septentrionis, Trichocellus cognatus*. Scale: 2 mm.

more or less dry, sandy ground with sparse vegetation. At higher elevation it is found in the *Betula* region, rarely in the lower alpine region, but it also occurs in *Empetrum* heaths in the Petsamo area and on true tundra on the Kola peninsula (Poppius 1908, Lindberg 1933, Brundin 1934, Lindroth 1945a). In southern Scandinavia and in Central Europe the species is almost stenotopically confined to oligotrophic bogs, usually occurring on moist, heather-covered peaty soil (Lindroth 1945a, 1986; V. Hansen 1968; Den Boer et al. 1980).

In North America the habitat corresponds well with the findings from northern Scandinavia. The species does not occur in true tundra but is found in the coastal treeless zones of, e.g., Newfoundland and Labrador (Lindroth 1955, 1968b).

Life cycle

Adults have been collected from 23 March to 1 October, and callow adults from 30 July through August; third instar larvae have been taken from 18 June to 3 August and second instar larvae on 19–20 July.

Probably *T. cognatus* in Greenland overwinters both as adult and as larva, as the finds of third instar larvae already in June suggest a biennial life cycle.

This conclusion only partly agrees with the findings in Iceland, where the youngest larvae are supposed to be the chief hibernating stage, "but that in addition a number of imagines hibernate, to complete the egg-laying in the early spring" (Larsson & Gigja 1959: 46).

In Europe the species is assumed to have an annual cycle, spending the winter as adult and breeding in the spring (Larsson 1939, Lindroth 1945a), and the same appears to be the case in North America (Lindroth 1968b). According to Den Boer et al. (1980) in Central Europe *T. cognatus* is a "winter breeder", reproducing from November through April.

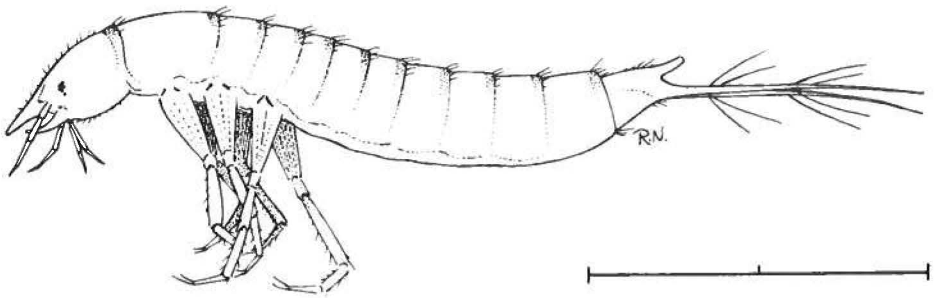
Dytiscidae

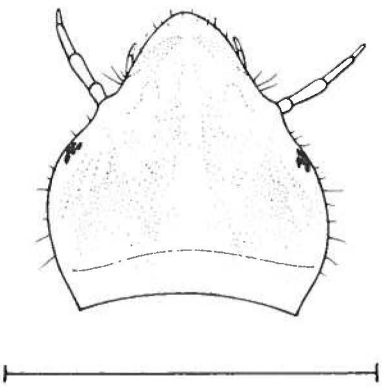
Hydroporus morio Aubé, 1838

(Henriksen 1939: *Hydroporus melanocephalus* Marsh.)

Taxonomy and synonymy

The nomenclature of this species is still confusing and discussed. Here the synonymy adopted from Balfour-Browne (1934, 1936, 1938) and approved by the Danish specialist M. Holmen (1985, pers.commun.) is followed: *Hydroporus morio* Aubé, 1838 (Dejean, 1821) (*melanocephalus* Gyllenhal, 1808: not Marsham, 1802). – See also Henriksen & Lundbeck (1917), Blair (1930).





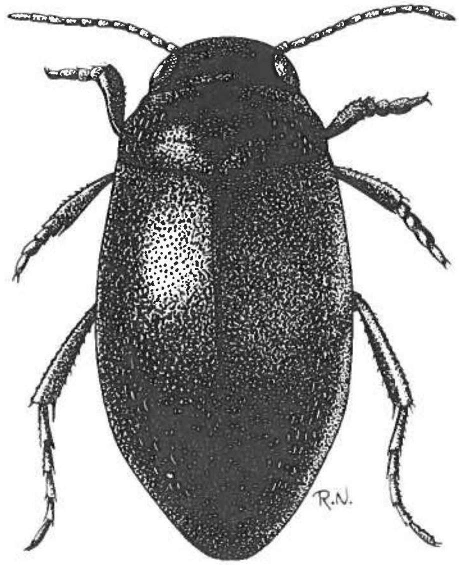


Fig. 7. *Hydroporus morio* Aubé. Larval head seen from above at greater magnification. Scales: 2 mm and 1 mm.

Identification

Unmistakable among Greenlandic beetles due to the rounded, somewhat flattened shape, the small size (about 3–3.5 mm in length), and the habitat. – Henriksen (1973 (1930)) gives a key to the larvae of the Danish species of *Hydroporus*, including *H. morio*, and Jeppesen (1986) describes and gives keys to the larval instars.

Variation and dynamics

According to Balfour-Browne (1940), *H. morio* is one of a complex of related forms, some of which are regarded as good species, others as varieties or synonyms, and he gives a list of the associated names.

The species is always fully winged and able to fly.

General distribution

Circumpolar, boreal to arctic. In Europe boreo-alpine, but absent from Iceland and the Faeroes (found once in Denmark). Recorded from Fennoscandia, British Isles, Central European mountains southwards to northern Italy, northern Russia; northern Siberia; Alaska, Canada, northern U.S.A. The general distribution is uncertain due to frequent nomenclatorial problems (see above).

Distribution map: Balfour-Browne (1940: British Isles).

Distribution in Greenland (map p. 20; see also Jeppesen 1986).

H. morio is very common in West Greenland northwards to about 76°N (Dundas, Thule District). According to Fredskild et al. (1975) it has been found in southern Peary Land. This find (1965, at Midsommersøerne) has recently been confirmed by A. Downes (1987, pers. commun.), but the fate of the specimens collected is obscure (D. Oliver 1986, in litt.; D. Larson 1988, in litt.). On the east coast the northernmost finds are from Ammassalik; thus the species has not here been recorded as far north as *Colymbetes dolabratus*.

Remains of *Hydroporus morio* (erroneously identified as *H. polaris* (Fall.)) have been found in Holocene lake sediments from two places in South Greenland: Tupaasat at the head of Kangikitsoq fjord, Kap Farvel area, and Qassiarsuk at the head of Tunulliarfik fjord, Narsaq District (Fredskild et al. 1975). The deposits containing *H. morio* from Tupaasat are approximately 2200–2400 years, whereas in Qassiarsuk the species occurs almost throughout the entire series of sediments, i.e, the last 8600 years.

Habitat and notes on biology

H. morio inhabits any kind of small ponds and pools, frequently temporary pools and also marshes; when found in lakes the biotope proper is in a sheltered cove or in a small secluded portion (Madsen 1959). There is no indication of a migration to deep lakes in autumn (as in *Colymbetes dolabratus*), so that *H. morio* must be able to tolerate freezing, possibly in the bottom sediment, during winter.

Madsen (1959) observed adult *H. morio* attacking and eating chironomid larvae, frequently a number of beetles devouring the same larva. Røen (1981) and Jeppesen (1986) mentioned small crustaceans, e.g., *Daphnia* spp., as food for the adults, and Jeppesen (1986) suggested small crustaceans and rotifers as probable diet for the larvae.

In Scandinavia *H. morio* is recorded from many different kinds of stagnant water bodies in the alpine and subalpine region, including *Sphagnum* bogs and *Eriophorum* marshes, but also lakes (Lindberg 1927, Brundin 1934, Strand 1946).

Life cycle

In Greenland adults have been collected from 4 May throughout the summer until 22 September and even in October (Madsen 1959). Imaginal hibernation is thus unquestionable. According to Jeppesen (1986), first-instar larvae have been collected on 5 and 16 July, second-instar from 25 June to 12 August, and third-instar from 25 June to 16 August. These findings suggest that some larvae hibernate (Jeppesen 1986). Females collected on 4 May in Grønnedal produced eggs which were attached to the walls of an aquarium; the eggs hatched on 23 May (Madsen 1959).

The pupa has newer been found in Greenland (or anywhere else). Newly hatched imagines date from late July and August.

Colymbetes dolabratus (Paykull, 1798)

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931), Henriksen (1937), Brinck (1940), Lindroth et al. (1973), Arnett (1983).

Identification

The largest beetle in Greenland, about 12.5–15 mm long, and quite unmistakable due to the rounded, flat shape, the flattened, hairy middle and hind legs (adapted for swimming) – and the habitat. The larval stages and the pupa have been described and figured by Galewski (1967, 1968). Nilsson (1982) gives a key to the larvae of the Fennoscandian species of *Colymbetes*.

Variation and dynamics

According to Brinck (1940), the Greenlandic *C. dolabratus* belongs to a distinct subspecies, *C. d. groenlandicus* Aubé, which is also found in arctic North America. Another subspecies, *C. d. thomsoni* Sharp, closely related to the former, is found in Iceland. The subspecies *C. d. groenlandicus* differs from *C. dolabratus* (from northern Scandinavia) in being smaller and more narrow, in the reticulation of the pronotum, in the striation of the elytra, etc. Lindroth et al. (1973) considered it doubtful whether the Icelandic form should be regarded as subspecifically distinct from ssp. *groenlandicus*, and Henriksen (1937) mentioned two males collected together in northern Canada (Keewatin, N.W.T.), of which one appears to be ssp. *groenlandicus*, the other ssp. *dolabratus*.

The hind wings are constantly full and functional, and the species has frequently been observed flying.

General distribution

Circumpolar, boreal to arctic. In Europe, Iceland, northern Scandinavia, northern Russia; through northern Siberia eastward to Kamchatka; Alaska, Canada through Northwest Territories to Labrador. Apart from Iceland, *C. d. dolabratus* is found throughout the Palaearctic Region.

Distribution in Greenland (map p. 20; see also Røen 1981, Jeppesen 1986).

C. dolabratus is one of the most common, widest distributed, and best known of the Greenlandic beetles. It is found in both coastal and inland situations, from Kap Farvel in the south to Upernavik on the west coast and Clavering Ø on the east coast.

C. dolabratus was also present in the Holocene lake sediments mentioned above. Approximate ages of the sediments containing fragments of the species were 1100–2900 years (Tupaasat) and 3900 years (Qassiarsuk) (Fredskild et al. 1975).

Habitat and notes on biology

In Greenland *C. dolabratus* typically lives in ponds with a rich vegetation, but it is highly eurytopic and may be

2

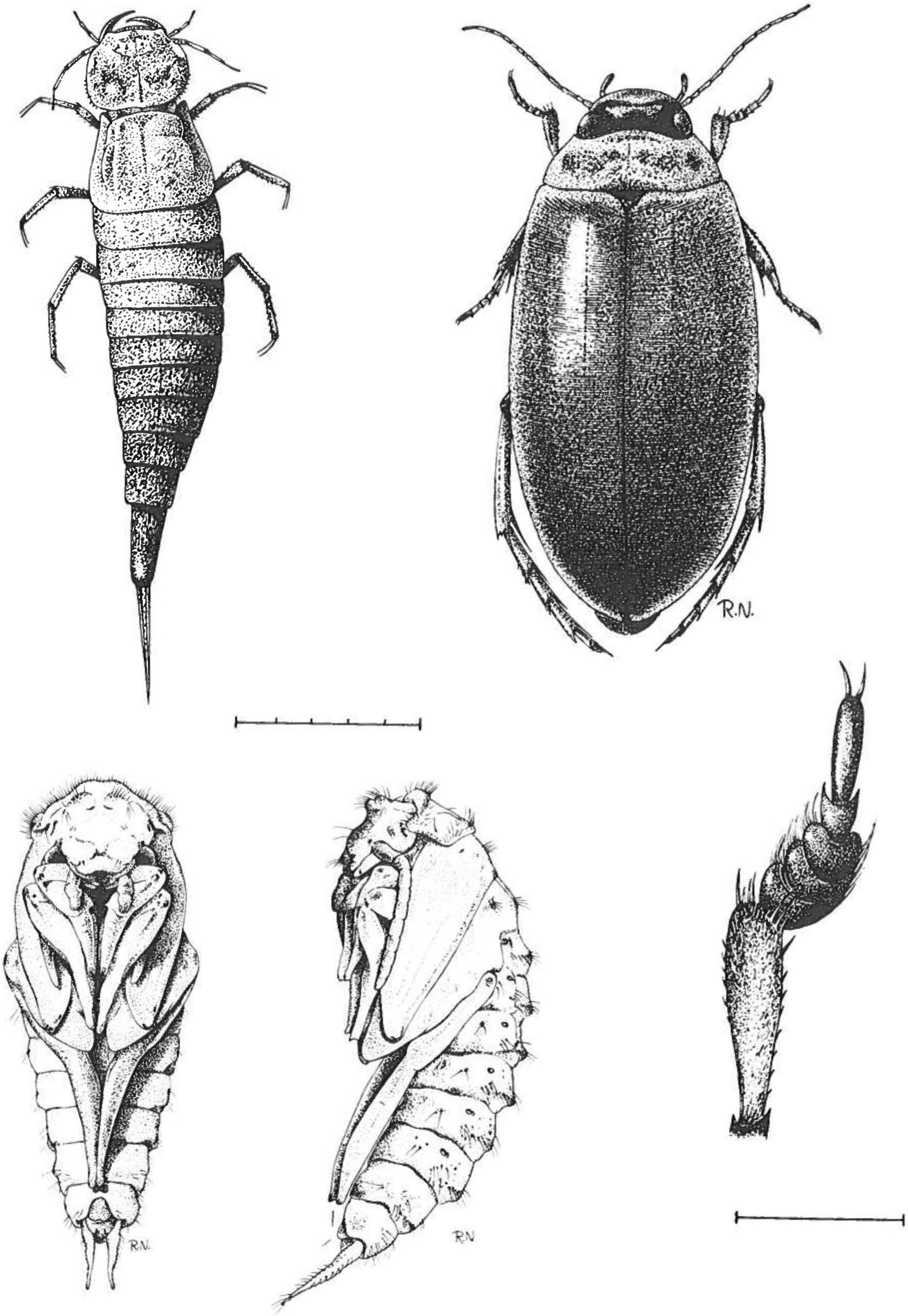


Fig. 8. *Colymbetes dolabratus* (Paykull). Adult female; right front leg of male; pupa seen from left and ventral side.

found in almost any kind of stagnant water, except possibly temporary pools (Madsen 1959). In summer adults and larvae are found together, but in late summer and autumn the imagines migrate to hibernate in lakes which do not freeze to the bottom, i.e., deeper than about 3 m (Røen 1963, 1981). Deichmann (1895) reported the species "flying merrily about" (my translation) in October (1891, at Hekla Havn, Scoresby Sund). Røen (op.cit.) related the northern limit of distribution of the species in Greenland (around 74°N) to the adult hibernation below the ice in lakes. During winter the beetles are dependent on the diffusion of oxygen into the respiratory air bubble under the elytra, but this decreases in size when not replenished, so that ten months is the ultimate length of time it can function. At about 74°N the lakes are covered by ice for approximately ten months, thus limiting the existence of *C. dolabratus* further north. – The species has been found up to 500 m alt.

The wide ecological span, but with a preference for ponds rich in vegetation, appears to be the case everywhere in the distribution area of the species. However, only in Greenland does the species appear to migrate to deep lakes in the autumn.

In Iceland *C. dolabratus* is encountered even in clayey pools close to the glacier front (Larsson & Gigja 1959). In Scandinavia it is alpine and subalpine and may be found in marshes, *Sphagnum* bogs, and ponds devoid of vegetation (Lindberg 1927, Brundin 1934, Strand 1946, Fjellberg 1972). On Hardangervidda, Norway, the species is almost confined to ponds above 1000 m alt. without vegetation but with *Carex* spp., grasses and mosses along the shores (Fjellberg 1972).

Henriksen (1937) stated that in Northwest Territories, Canada, the main occurrence of *C. dolabratus* is in tundra pools, but that it also extends southwards into the boreal zone.

The feeding biology apparently has not been studied, but in Greenland probably crustaceans (*Brachinecta*, Cladocera) play a significant role in the diet.

Life cycle

In Greenland, adult *C. dolabratus* have been collected all year round. In winter holes cut into the ice of lakes attract imagines, undoubtedly in order to replenish their air stores (Røen 1963, 1981). Madsen (1959) reported the appearance of adult beetles in a hole cut through one-meter-thick ice on 10 March. The water temperature was 0°C and the movements of the beetles were very slow. The water had an odor of H_2S, indicating oxygen deficit.

According to Røen (1981) the eggs are laid immediately following the thawing of the lake ice and the migration back to the ponds. Porsild (1924, label note) caught an individual in flight at Qeqertarsuaq/Godhavn on 24 May.

Dissections of eight females from June (Godhavn) showed three with quite undeveloped ovaries, two with developing ovaries, and three with ripe eggs. Three females from 16 September had undeveloped ovaries and were newly hatched.

Fig. 9. Pupa and cast larval skin of *Colymbetes dolabratus* in a hollow in moss on a lake shore, near the head of Kangerlussuaq/Søndre Strømfjord.
J.B. phot., August 1977.

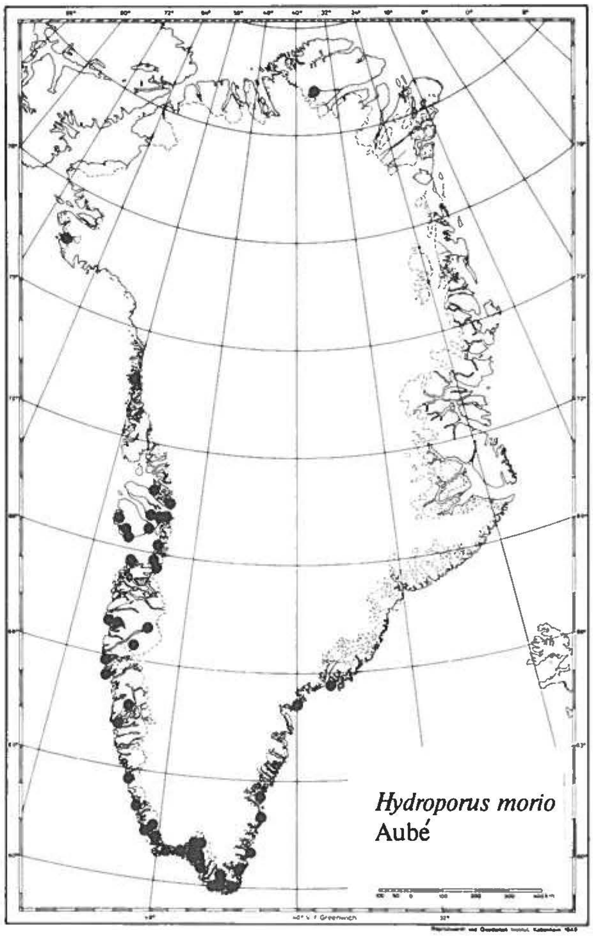
Small larvae (instars I and II) are found predominantly in June, with some in July; large larvae (instar III) in July and the beginning of August. South of about 67°N the larval and pupal stages are passed during summer, so that only adults hibernate. Further north fully grown larvae have been caught in spring, completely overgrown with microorganisms. These must represent individuals which take two years to complete their life cycle (Røen 1963, 1981). Occasionally the same may happen in South Greenland, as a second-stage larva was collected at Grønnedal on 10 September.

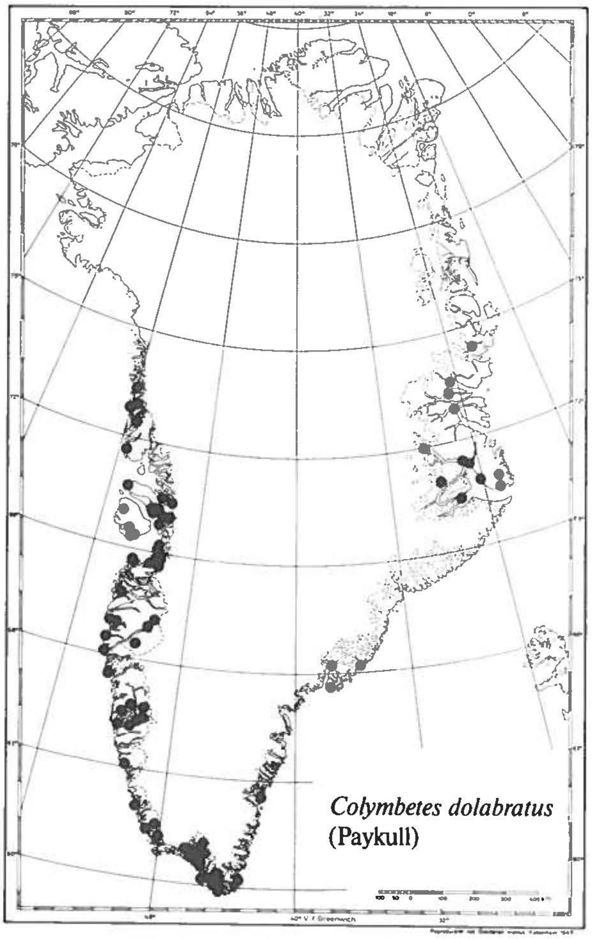
The pupa is terrestrial and found in small hollows under moss close to the shore of ponds (Fig. 9). The only dated pupae collected in Greenland were found by B. Fredskild (at Kapisillit, 29 August 1973), and by the author on August 16 (1977, northeast of the head of Kangerlussuaq/Søndre Strømfjord).

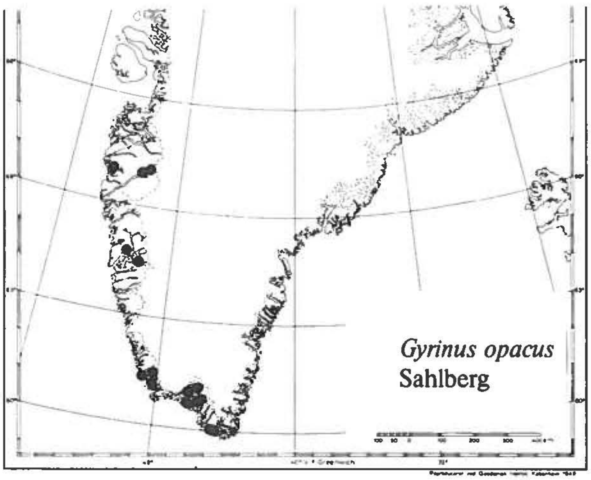
In Iceland Larsson & Gigja (1959: 54) assumed that the species predominantly hibernates as larvae which metamorphose in early summer, but that a great many individuals also hibernate as adults which lay eggs in the spring, "possibly as a continuation of a reproduction commenced already in the autumn".

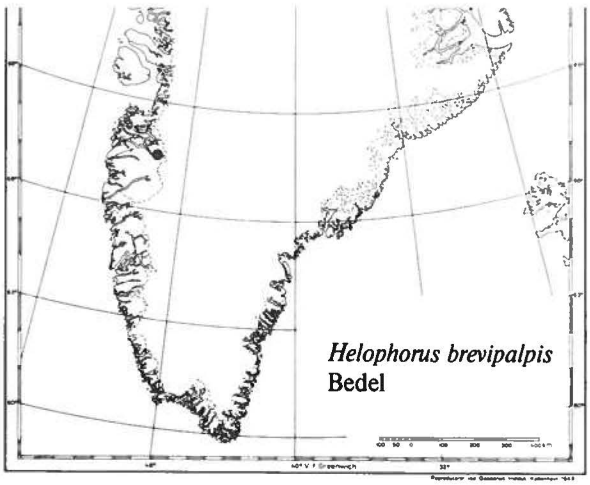
Note

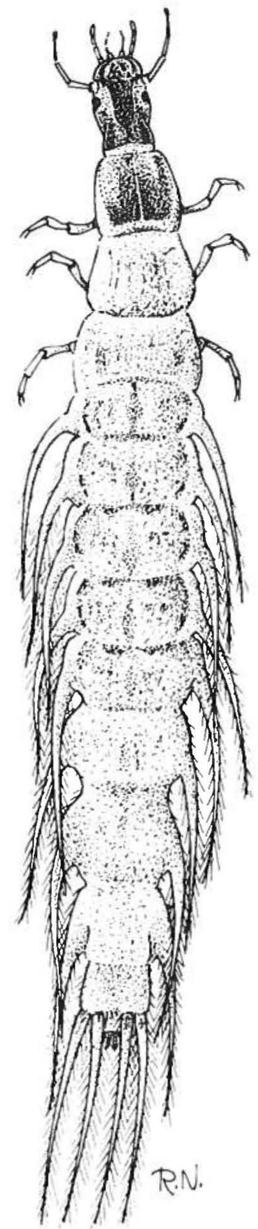
According to Schiødte (1857) and Lundbeck (1891, 1896), both referring to Fabricius (1780), the Greenlanders were very afraid of the adult *C. dolabratus* (Greenlandic: Minngoq, the larva: Pamiortooq). They feared

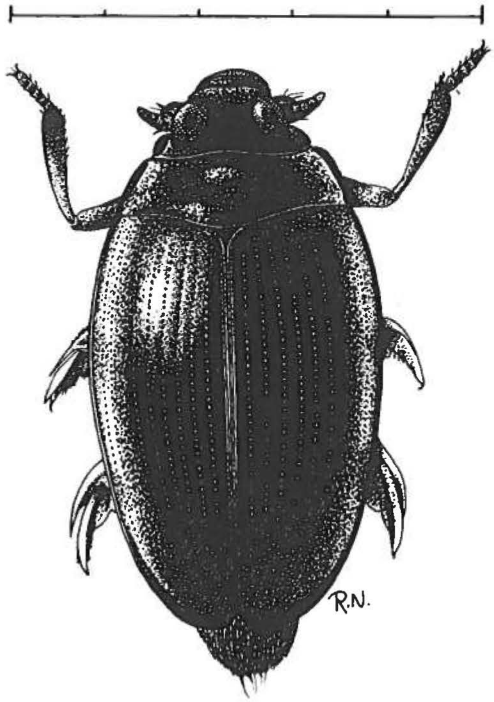

Hydroporus morio
Aubé


Colymbetes dolabratus
(Paykull)


Gyrinus opacus
Sahlberg


Helophorus brevipalpis
Bedel





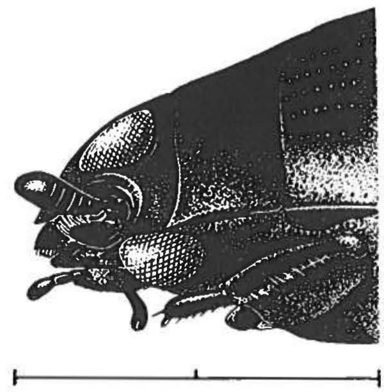


Fig. 10. *Gyrinus opacus* Sahlberg. Anterior third of adult seen from left side, showing the divided compound eye. Scales: 5 mm and 1 mm.

to swallow the beetles by drinking water, whereupon these should be able to attack and destroy the bowels of the victim. In order to purify the water the Greenlanders would introduce amphipods (*Gammarus locusta*) into the "infested" water bodies. A war was then believed to break out between the beetles and the amphipods, leading to the extintion of both species.

Gyrinidae

Gyrinus opacus Sahlberg, 1819

Taxonomy and synonymy: see Balfour-Browne (1950); also Henriksen & Lundbeck (1917), Blair (1930), Lindroth (1931), Henriksen (1939), Brinck (1940), Arnett (1983).

Identification

Unmistakable due to the short, paddle-like middle- and hind legs, the very short antennae, and the specialized compound eyes, which are divided into an upper and a lower part (adapted for vision in air and water, respectively). Length about 5.5–6 mm.

Variation and dynamics

According to Omer-Cooper (1930, 1931) a variety, *G. opacus* var. *blairi* Cooper, 1931, is found in North America and Greenland. It differs from the type form "in being much more polished, with the reticulation of the thorax and elytra almost entirely defaced. The front tarsi are deeply infuscated and the proximal region of the tibia is almost black" (Omer-Cooper 1930: 68). A defacement of the reticulation is not apparent in a number of Greenlandic specimens in the collections of the ZMUC; that the legs are darker as compared to the main form is, however, valid. Balfour-Browne (1950) showed that the variety with smooth elytra, "*blairi*", is not a geographical race, but a variation occurring in various places along with the type form.

The hind wings are always fully developed and functional.

General distribution

Circumpolar, boreal to low arctic. In Europe reported from Fennoscandia (absent from Denmark, the Faeroes and Iceland), Scotland, northern Russia; Siberia (Yenissei Valley), Mongolia; in North America apparently restricted to Labrador.

Distribution map: Balfour-Browne (1950: 361, British Isles).

Distribution in Greenland (map p. 20)

G. opacus is found from Pamialluk island, Kap Farvel area, in the south, to Sisimiut/Holsteinsborg District in the north. Fairly common only in the Julianehåb Bugt area. Northwards scattered occurrences and only inland.

Habitat and notes on biology

The species inhabits the surface of different stagnant waters, most often ponds with a rich vegetation, but also lakes (Madsen 1959). In Scandinavia it is found especially in peatholes and marshes (Holmen 1987), but also (in Enontekis Lappmark, Finland) in slowly running rivers (Lindberg 1927). It has been collected up to 1000 m alt. in Swedish Lappland (Brundin 1934, Brinck & Wingstrand 1951).

Like other members of the family, *G. opacus* is a gregarious predator, sometimes seen in large number skating on the surface of the water, hunting for fallen insects. Presumably it also feeds on small limnic invertebrates, diving into the water and thereby using the lower parts of the divided compound eyes.

Life cycle

In Greenland imagines have been collected from 28 May to September, presumably indicating adult hibernation. The larva has only been found once (Sermiliarsuk, 4 August 1889; Lundbeck leg.). In Denmark the larvae of *G. marinus* Gyll. overwinter in the water to pupate the following early summer (Henriksen 1973 (1930)).

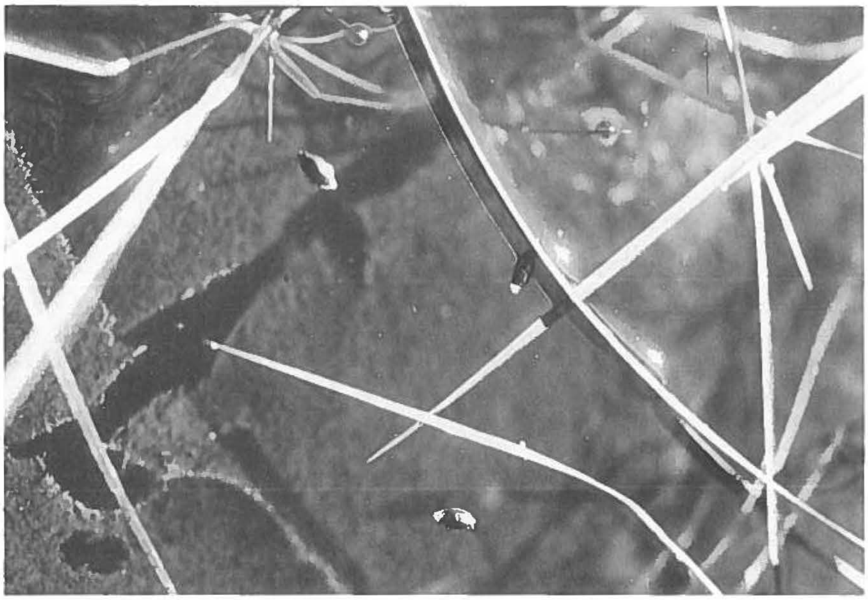


Fig. 11. *Gyrinus opacus* on the surface of a pond rich in vegetation, near the head of Kangerlussuaq/Søndre Strømfjord.
J.B. phot., August 1977.

Hydrophilidae

Helophorus brevipalpis Bedel, 1881

Taxonomy and synonymy: see Balfour-Browne (1958), Angus (1973), M. Hansen (1983, 1986).

Identification

Easily distinguished from the other Greenlandic water beetles by its elongate shape, the bronze-metallic glow of head and pronotum, both rugged and with furrows, and the brownish yellow elytra with marked striae. Antennae short and club-shaped, of the same length as the maxillary palps.

Variation and dynamics

M. brevipalpis is a variable species as regards body size and colour, shape and size of the terminal segment of maxillary palpi, and granulation of the head and pronotum (M. Hansen 1986).

The hind wings are always fully developed, and the species is an active flyer (Balfour-Browne 1958), frequently found in wind drift material on seashores in Denmark (M. Hansen 1986).

General distribution

Palaearctic, temperate to boreal. Whole of Europe (except northernmost Fennoscandia and Iceland), eastward to the Urals; Asia Minor, Caucasus; introduced to North America (Utah). In Denmark and England the most common species in the genus (M. Hansen 1983).

Distribution map: Angus (1973: 318, total).

Distribution in Greenland (map p. 20)

This species represents one of the latest additions to the fauna of Greenland. Only one specimen is known, caught in a pitfall trap at the head of Kuup akua (Nordre Strømfjord), Eqalummiut nunaat, by a British expoedition in 1984 ("Greenland White-Fronted Goose Study", University College of Wales).

Habitat

The habitat is unknown in Greenland. The pitfall was placed in a *Vaccinium uliginosum*-heath on a dry, south-facing slope (J. Stroud, in litt.).

In Europe the species is fairly eyrytopic in stagnant fresh water, preferring shallow, more or less open, often temporary pools with a grassy bottom, but also found in slower reaches of running waters (M. Hansen 1983, 1986).

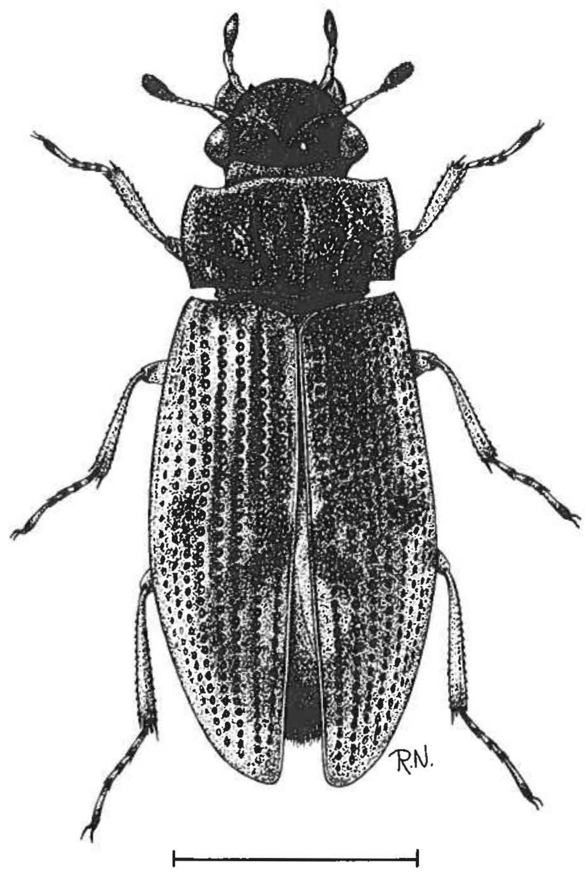


Fig. 12. *Helophorus brevipalpis* Bedel. Scale: 1 mm.

Life cycle

The single Greenlandic specimen was caught on 13 June.

In Europe the eggs are normally laid in spring (sometimes in late autumn). The egg cocoons are placed in mud at the waterline. The larvae emerge during spring and are fully grown in two or three weeks. Pupation is terrestrial, in the soil, and the new generation of adults returns to the water in late summer to hibernate there (M. Hansen 1986).

Cercyon obsoletus (Gyllenhal, 1808) (*lugubris* Olivier, 1790))

(Fig. 55,a)

One specimen collected in July 1984 at Kilaarsarfik (Sandnæs) in Ameralla fjord east of (Nuuk/Godthåb) by P.C.Buckland (in litt.). Considering the general distribution and habitat of the species, the occurrence in Greenland is provisionally regarded as an accidental introduction.

Distribution: Palaearctic. Widespread in Europe, though less frequent towards the north (only southern part of Scandinavia, absent from the Faeroes and Iceland). Also in northern Africa (Algeria) and the Caucasus (M. Hansen 1986).

Habitat and biology: Particularly in droppings of various mammals (cow, deer), but also in other kinds of decaying organic matter (compost, old mushrooms, carrion, etc.), both on open ground and in woodlands (V. Hansen 1973, M. Hansen 1986).

Staphylinidae

Philonthus politus (Linnaeus, 1758)

(Fig. 55,d)

Only known as subfossils from a Norse farm at Nipaatsoq in Ameralla fjord east of Nuuk /Godthåb (Buckland et al. 1983). Most probably introduced by the Norsemen and later extinct.

Macropterous and often flying (Lindroth et al. 1973). The larva has been described by Paulian (1941).

Distribution: Circumpolar and introduced to Southern Hemisphere.

Habitat and biology: According to Larsson & Gigja (1959) a pronounced dung-beetle, both as larva and adult preying on other dung insects. Lindroth et al. (1973) also mentioned the species from carrion and rotten vegetables.

Philonthus cf. *cephalotes* (Gravenhorst, 1802)

(Fig. 55,c)

Only known as subfossils from a Norse farm at Kilaarsarfik (Sandnæs) in Ameralla fjord east of Nuuk/Godthåb (Buckland 1986, in litt.). Most probably introduced by the Norsemen and later extinct.

Macropterous. – The larva has been described by Paulian (1941).

Distribution: Widespread on the Northern Hemisphere (including Iceland and the Faeroes).

Habitat and biology: A synanthropic predator in dung, carrion and decaying plant material (Larsson & Gigja 1959, Lindroth et al. 1973).

Quedius mesomelinus (Marsham, 1802)

Taxonomy and synonymy: see Smetana (1965b, 1971); also Henriksen & Lundbeck (1917), Blackwelder (1974).

Identification

The largest of the Greenlandic Staphylinidae, about 6.5–11 mm in length. Easily distinguished from *Q. fellmanni* by the size and the relatively much smaller compound eyes (length about one-third of head length).

Variation and dynamics

The species varies considerably in size and shows sex-related differences in general shape. There is also a considerable variation in the male genitalia, especially in the shape of the paramere (Smetana 1971).

The hind wings are slightly reduced and according to Lindroth et al. (1973) possibly nonfunctional.

General distribution

Almost cosmopolitan, in most places synanthropic and probably introduced by man. In Scandinavia found to the northernmost parts.

Distribution maps: Smetana (1965b: fig. 74, North America; 1971: map 12, North America).

Distribution in Greenland (map p. 27)

According to Henriksen & Lundbeck (1917), *Q. mesomelinus* is common in the settlements along the entire west coast of Greenland, but in fact the occurrences are concentrated in a southern area (Julianehåb Bugt) and a northern area (southern Disko Bugt) with Nuuk/Godthåb and Sisimiut/Holsteinsborg in between. The species nowadays appears to have become rare (see below).

Habitat and notes on biology

According to Henriksen & Lundbeck (1917), *Q. mesomelinus* is found principally in the Greenlanders' turf huts, mainly in the walls, but also under stones close to the huts. Apparently free-living individuals have been taken only a few times in the southernmost part of the country (Narsaq District).

It is interesting that practically all the Greenlandic collections of *Q. mesomelinus* (176) date from the period 1876–1902 and earlier. Since then the species has been found only three times (Aappilattoq 1932, Nuuk/Godthåb 1942 and 1944). This suggests that the frequency of the species has decreased drastically, and that it may now be extinct in Greenland. The decline has taken place during the period when the original turf huts have been replaced by wooden houses; because the walls of the turf huts seemingly represented the most

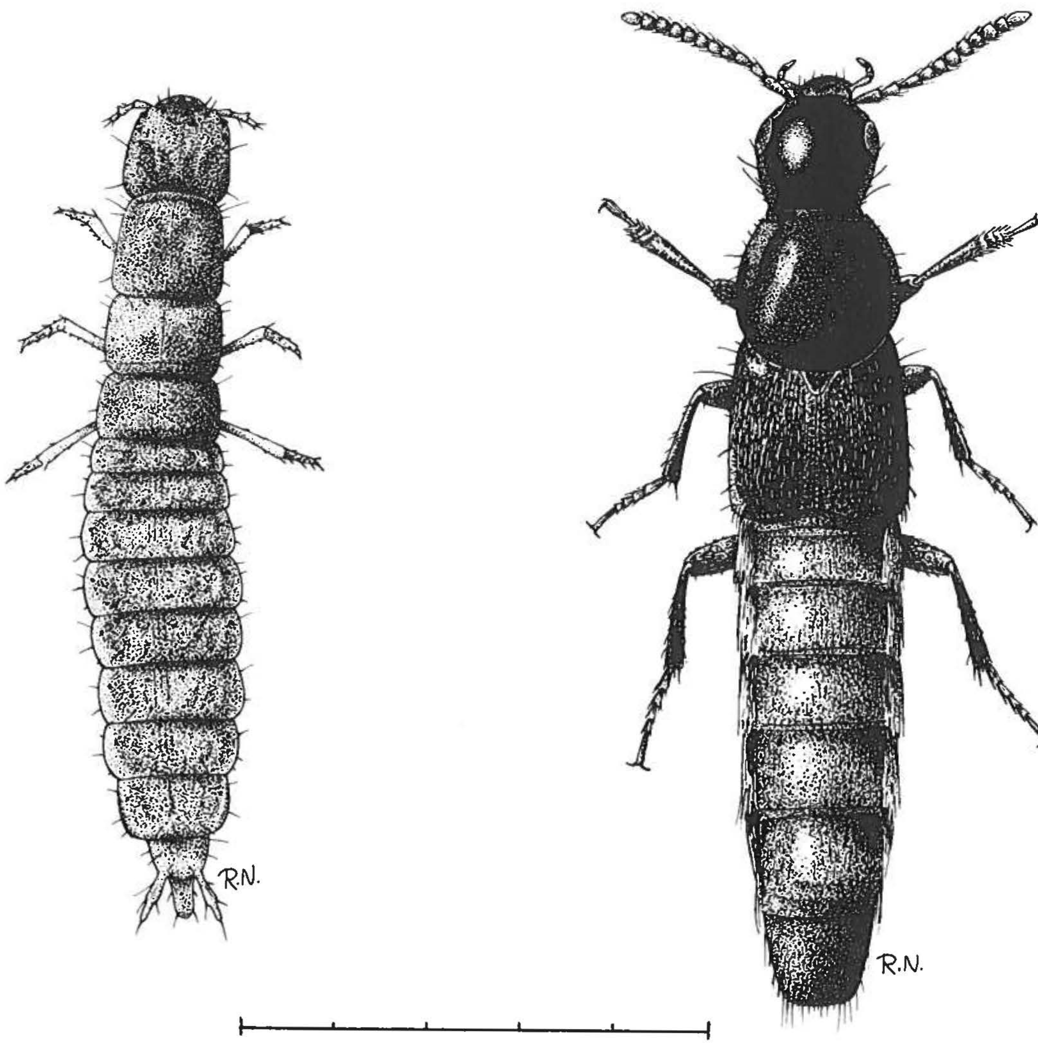


Fig. 13. *Quedius mesomelinus* (Marsham). Scale: 5 mm.

important biotope of the species, this is probably the main cause of its disappearance.

In Iceland the species is pronouncedly synanthropic, living in decaying vegetable matter of various kinds (compost, sod, old hay, etc.), but it has also been found in cow manure and in birch coppices (Larsson & Gigja 1959, Lindroth et al. 1973). In the Faeroes the species is almost exclusively found in in-field localities (Bengtson 1981).

In northern Norway, *Q. mesomelinus* does not appear to be markedly synanthropic; it has been collected in washed-up material on river banks and under stones in grass fields (Strand 1946). In Scandinavia it has never been found above the tree limit.

In more southern areas of Europe the species often occurs in burrows of various mammals, caves, treeholes, old mushrooms, etc., besides being synanthropic in cellars, outhouses, bakeries and the like; it is thus a typical obscuricol (West 1942, Smetana 1971).

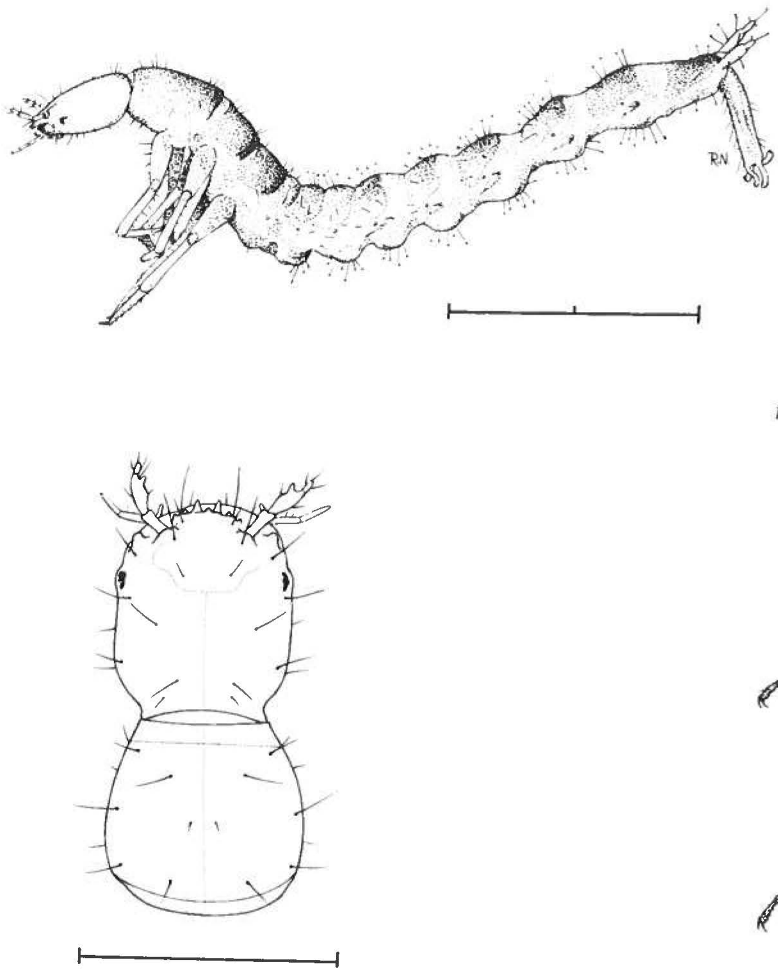
Life cycle

Adults have been collected all the year round; there are finds even from December and January. Larvae, nearly all fully grown, have only been found in August and September. Possibly the larval and pupal development is completed during one summer, so that only adults hibernate (see Larsson & Gigja 1959).

Quedius fellmanni (Zetterstedt, 1838)

(Henriksen 1939: *Quedius boops* Grav.)

Taxonomy and synonymy: see Smetana (1965b, 1971). In Henriksen & Lundbeck (1917) and Henriksen (1939) the species was wrongly identified as *Q. boops* (Gravenhorst).



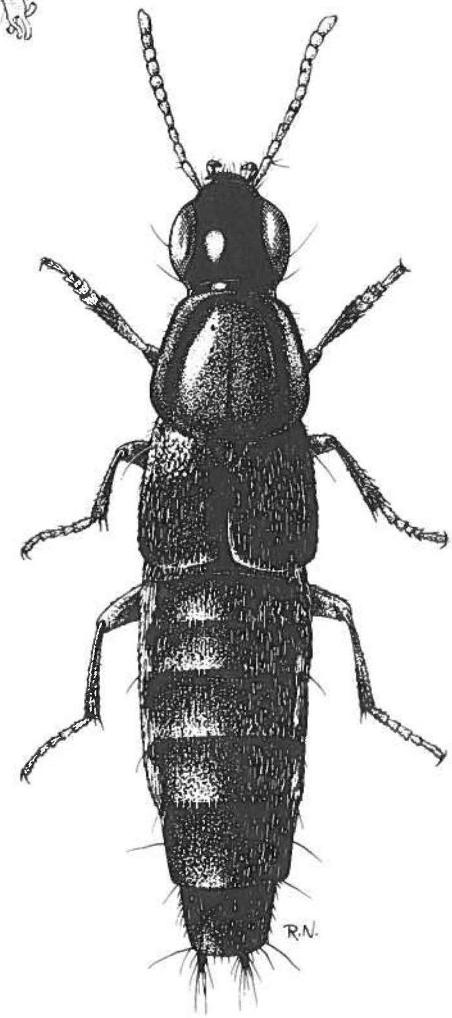


Fig. 14. *Quedius fellmanni* (Zetterstedt). Larval head and pronotum seen from above at greater magnification. Scales: 2 mm and 1 mm.

Identification

Similar to *Q. mesomelinus*, but smaller (length about 5–6 mm) and with very large compound eyes (length more than two-thirds of head length).

Variation and dynamics

The hind wings are reduced and not fit for flight (Smetana 1964).

General distribution

Circumpolar, boreal to low arctic: northern Scandinavia and Russia; Yenissei Valley, Mongolia, Kamchatka; in North America transcontinental from Alaska to Labrador and Newfoundland.

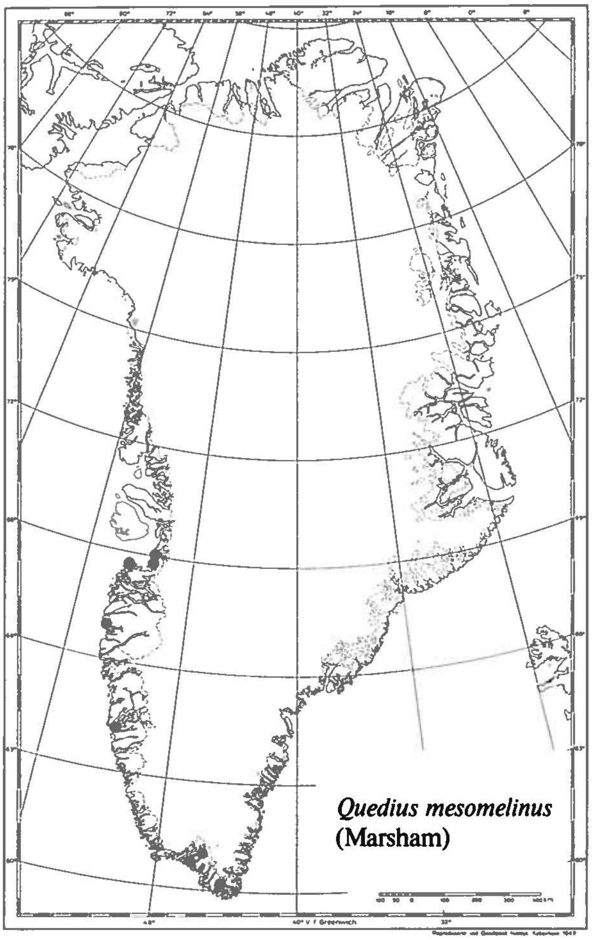
Distribution maps: Smetana (1965b: 56, total; 1971: 233, North America), Campbell (1980: 1171, North America).

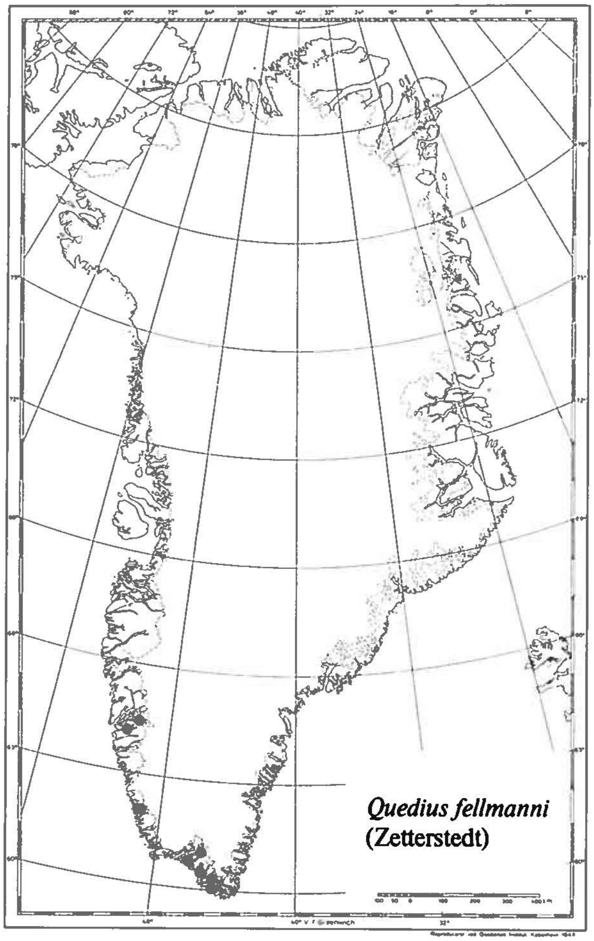
Distribution in Greenland (map p. 27)

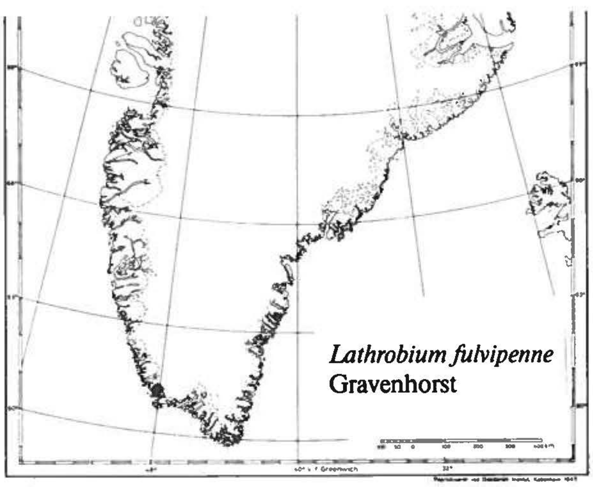
Typical southwestern distribution, from Frederiksdal in the south to Godthåbsfjord in the north.

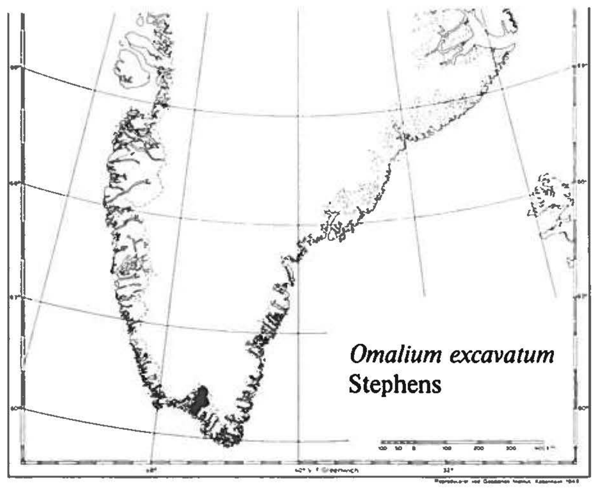
Habitat

At Kapisillit, inner Godthåbsfjord, I collected *Q. fellmanni* under stones and in pitfalls both in fairly dry, south-facing plant communities (with *Thymus praecox*, *Draba lanceolata*, *Cerastium alpinum*, *Poa glauca*, *Ca-*


Quedius mesomelinus
(Marsham)


Quedius fellmanni
(Zetterstedt)


Lathrobium fulvipenne
Gravenhorst


Omalium excavatum
Stephens

rex rupestris, Agrostis borealis, etc.); on a very rich south-facing slope dominated by *Kobresia myosuroides* and *Luzula multiflora*; and also in a heath of *Salix glauca, Betula nana* and *Ledum groenlandicum with Vaccinium uliginosum* ssp. *microphyllum* and *Empetrum hermaphroditum*. In South Greenland P. Nielsen caught the species in a dry heath, a grassland slope, a low coppice of *Salix glauca*, a *Sphagnum*-bog, an *Eriophorum* marsh, and on a lake shore (in the Qinngua valley) (see Table 9).

In the subalpine region of the Scandinavian mountains, Strand (1946) mentioned *Q. fellmanni* from washed-up material on lake shores and river banks and under plant debris in *Salix* shrubs, but he also collected the species above the tree limit.

Smetana (1964, 1965b, 1971) described the habitat in North America as more or less wet biotopes (meadows, marshes and bogs) in moss and various debris and fallen leaves under the vegetation. However, the species is not strictly hygrophilous and may also be found on open, dry ground, sometimes in localities with agricultural influence.

The habitat of *Q. fellmanni* thus appears to be extremely wide, both in Greenland and elsehwere.

Life cycle

Adults have been collected from 3 April to 6 September (more than one-third of the total material was collected in April and May at Qaqortoq/Julianehåb by G. Meldorf, 1900–1901). Thus, at least some adults hibernate. Only one larva has been found in Greenland (Narsarsuaq, *Sphagnum*-bog, 6 August 1985; P. Nielsen leg.).

Othius angustus Stephens, 1833

(*O. melanocephalus* Gravenhorst, 1806 nec Fourcroy, 1785)
(Fig. 55,b)

Only known as subfossils from a Norse farm at Kilaarsarfik (Sandnæs) in Ameralla fjord east of Nuuk/Godthåb (Buckland 1986, in litt.). The species could be indigenous in Greenland, but has most probably been introduced by the Norsemen and later become extinct. Brachypterous (Lindroth 1931: fig. 40).

Distribution: Northern and Middle Europe, including the Faeroes and Iceland.

Habitat and biology: Meadows and commons, open woods and coppices, in Scandinavia also above the tree limit. Often on cultivated ground and close to human habitations, but not really synanthropic (Lindroth 1931, Lindroth et al. 1973, Larsson & Gigja 1959).

Lathrobium fulvipenne Gravenhorst, 1806

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931).

Identification

The species resembles a small *Quedius mesomelinus*, but is much more elongate, with the head constricted behind, forming a "neck", and the prothorax constricted behind forming a "waist". The forelegs have extensions on the inner side of the femora and tibiae.

The larva is undescribed, but should be easy to recognize on the basis of Paulian's (1941) descriptions of larvae of other species of *Lathrobium*.

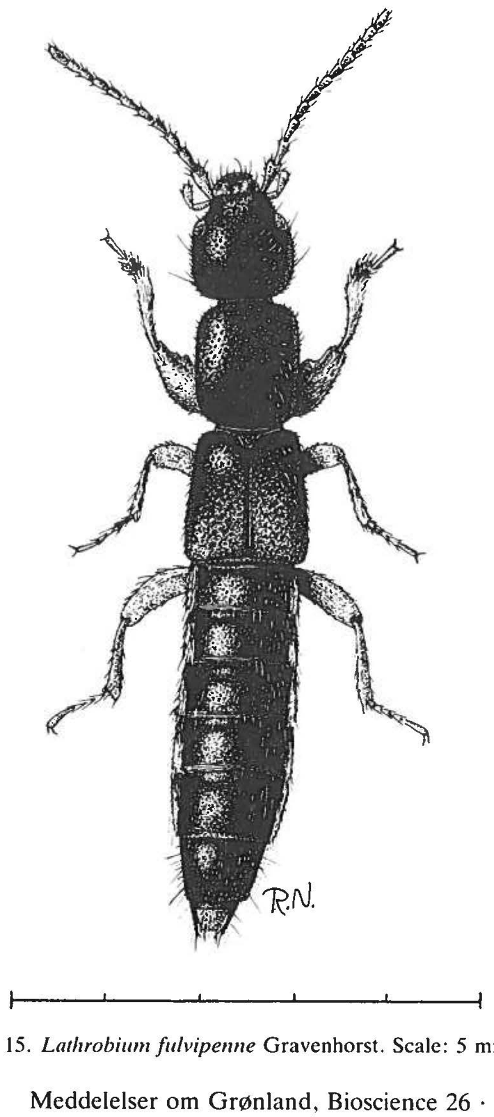


Fig. 15. *Lathrobium fulvipenne* Gravenhorst. Scale: 5 mm.

Variation and dynamics

In Iceland (and Greenland) the hind wings are rudimentary, but a macropterous form is known from the European Continent (Lindroth et al. 1973).

General distribution

Palaearctic, temperate to subarctic: central and northern Europe, to northernmost Scandinavia, including the Faeroes and Iceland; Siberia, Caucasus, Turkmenistan.

Distribution in Greenland (map p. 27)

L. fulvipenne is one of the rarest Greenlandic beetles, as it has only been found once, at Ivittuut (by Nordenskjöld's expedition in 1883). It might thus be assumed that the species was introduced to Greenland. However, species of *Lathrobium* are never synanthropic and not easily transported by man, and taking into account the general distribution of *L. fulvipenne*, it might well be indigenous in Greenland (Lundbeck 1896; Henriksen & Lundbeck 1917; Lindroth 1931, 1957).

Habitat

Nothing is known about the circumstances pertaining to the single find in Greenland.

In Iceland *L. fulvipenne* is most often encountered singly under stones in fairly dry grassfields (Lindroth 1931, Larsson & Gigja 1959). In the Faeroes it is reported from rich grassland near the shore (Bengtson 1981)

In the rest of Europe it lives in more humid biotopes, e.g., on fertile ground under fallen leaves in coppices or small woods. In Scandinavia it reaches the alpine zone (Lindroth 1931, Lindroth et al. 1973, Larsson & Gigja 1959, Brundin 1934, Strand 1946). In Hardangervidda, Norway, the species is mostly found in foerna in *Alnus incana* woods and in meadows (Fjellberg 1972).

Life cycle

The Greenlandic specimen was caught on 20–21 August. According to Larsson & Gigja (1959), in Iceland *L. fulvipenne* hibernates as adult, passing through the larval stages during summer.

Eusphalerum sorbi (Gyllenhal, 1810)

(Henriksen 1939: *Anthobium sorbi* Gyll.)
(Fig. 53,a)

One specimen without locality, collected by Holbøll (Schiödte 1857). Most probably an accidental introduction. The species has also been found as subfossils in a Norse farm at Kilaarsarfik (Sandnæs) at Ameralla fjord east of Nuuk/Godthåb (Buckland 1986, in litt.). Thus the species was apparently also introduced by the Norsemen.

Distribution: Most of Europe, but absent from northern Scandinavia, the Faeroes and Iceland. North America (?).

Habitat: Mostly found in flowers of, e.g., *Crataegus, Spiraea, Viburnum*.

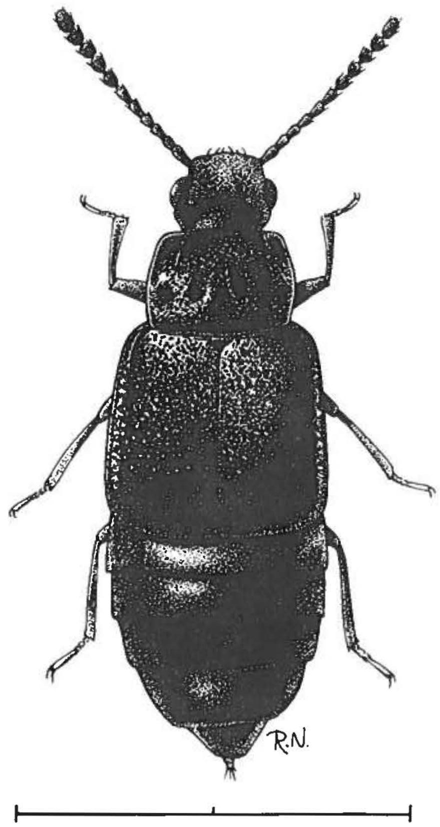


Fig. 16. *Omalium excavatum* Stephens. Scale: 2 mm.

Omalium excavatum Stephens, 1834

Taxonomy and synonymy: see Henriksen & Lundbeck (1917).

Identification

Easily distinguished among the Greenlandic Staphylinidae by the broad and relatively long, black elytra, which are at least as long as the visible, dorsal portion of the abdomen. Pronotum with two hollows in the middle. Length about 3–4 mm. The larva has not yet been found in Greenland (the similar larva of *O. rivulare* Paykull is described and figured by Paulian (1941) and Steel (1970)).

Variation and dynamics

The hind wings are fully developed and no doubt functional (Lindroth et al. 1973).

General distribution

Palaearctic, temperate to subarctic: Europe to northernmost Scandinavia, including the Faeroes and Iceland; western Siberia; northern Africa.

Distribution in Greenland (map p. 27)

Only found sparsely in Qaqortoq/Julianehåb and Narsaq Districts, and here apparently confined to a few localities along Tunulliarfik and Igaliku Fjords.

Habitat

Until very recently only one specimen was known from Greenland, collected by W. Lundbeck 1889 under the old Norse ruin stones at Igaliku (Gardar) (Henriksen & Lundbeck 1917). In 1983–84, however, P. Nielsen caught a total of seven specimens, always singly, in pitfall traps: four from cultivated grass-fields at Qassiarsuk, one from Rosenvinges Plantage at the head of Tunulliarfik (vigorous vegetation with coppice of *Salix glauca* and *Betula pubescens*), and two from rich, grassy vegetation bordering a stream at Upernaviarsuk (close to the entrance of Igaliku Fjord). The four localities are all within or close to old cultivated land in the centre of the Norse settlement (Østerbygden), which is now the main sheep-rearing district, and *O. excavatum* is one of the few likely candidates for having been introduced by the Norsemen (see p. 89).

In Iceland *O. excavatum* is distinctly synanthropic, found in decaying plant material and sometimes in manure (Lindroth 1931, Larsson & Gigja 1959). In the Faeroes it is fairly common, but only encountered in in-fields and mainly close to settlements (Bengtson 1981).

In Scandinavia the species is only partly synanthropic, occurring under stones, in moss, under different plant remains in humid places, in washed-up material along freshwater shores and under seaweed on seashores. It is also found in compost, manure, carcasses and fungi (West 1942, V. Hansen 1951, Strand 1946).

Life cycle

The Greenlandic specimens were caught between 22 July and 31 August. No larvae have been found.

In Iceland and Scandinavia the imagines hibernate and larval development normally takes place during the summer (Larsson & Gigja 1959).

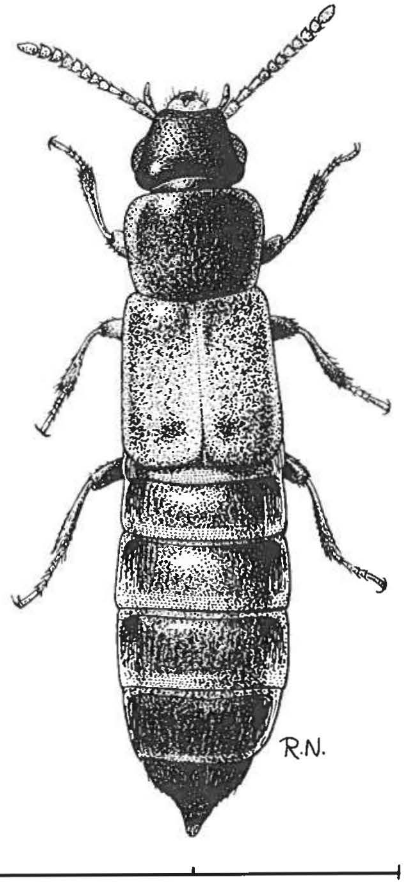


Fig. 17. *Xylodromus concinnus* (Marsham). Scale: 2 mm.

Xylodromus concinnus (Marsham, 1802)

Taxonomy and synonomy: see Henriksen & Lundbeck (1917), Lindroth (1931), Blackwelder (1973).

Identification

Elytra light brown and relatively long, but shorter than the uncovered portion of the abdomen. Macropterous. The larva is described by Larsson & Gigja (1959) and Steel (1970).

General distribution

Probably cosmopolitan. Europe northwards to northern Norway, including the Faeroes and Iceland.

Distribution in Greenland

The species has been collected in some towns in West Greenland: Ilua (Aappilattoq?) 1890 (?), Qaqortoq/Julianehåb 1898, 1899; Nuuk/Godthåb 1945; Sisimiut/Holsteinsborg 1890; Aasiaat/Egedesminde 1876; Qasiannguit/Christianshåb 1876. It is now possibly extinct (see below). Large numbers of subfossil specimens have been found in an excavated Norse farm at Nipaatsoq in Ameralla fjord east of Nuuk/Godthåb (Buckland et al. 1983).

Habitat and notes on biology

In Greenland the species is exclusively synanthropic, occurring in the Greenlanders' turf huts and never found outdoors (Henriksen & Lundbeck 1917). Like *Quedius mesomelinus*, it was collected almost exclusively during 1876-1899 (54 specimens), with only one find since then (Nuuk/Godhåb 1945, in wheat flour). The explanation must be the same as for *Q. mesomelinus* (p. 24): the transition from turf huts to wooden buildings destroyed the biotope of the species, so that it is now presumably extinct in Greenland. If Henriksen & Lundbeck (1917) are right in identifying *Staphylinus lignorum* of O. Fabricius (1780) with *X. concinnus*, the species has had a long history in Greenland. This statement is now further supported and elaborated by the subfossil finds. Possibly the species was originally introduced by the Norsemen and has survived in Greenland almost to the present day.

According to Larsson & Gigja (1959), *X. concinnus* is indigenous in temperate Europe, and already in Denmark it is rarely met with outdoors (in hollow trees, and fungi on trees) but far more frequently synanthropically (in stables, cellars, bakeries, etc.). In Iceland it is exclusively synanthropic, but may in summer be found in old hay in fields close to the farms.

The species is probably predacious (Hinton 1945).

Micralymma marinum (Ström, 1783)

Taxonomy and synonymy: see Schiödte (1845), Poppius (1908), Lindroth (1931), Steel (1958, 1962); also Henriksen & Lundbeck (1917).

Identification

According to Steel (1958), the genus *Micralymma* Westwood differs from all other Omaliinae genera in the combination of very short elytra, palpal segments of about equal breadth, and posterior coxae which are not expanded above (dorsal to) the femora. The species are broad and rather flat, the widest place being just posterior to the middle of the abdomen. The elytra are distinctly widened behind, barely extending beyond apex of the metasternum; the hind wings are entirely reduced. Schiödte (1844–1845) stressed the specialized mandibles with a basal, filelike molar portion.

M. marinum is distinguished from *M. brevilingue* (p. 34) by the larger compound eyes and the large facets,

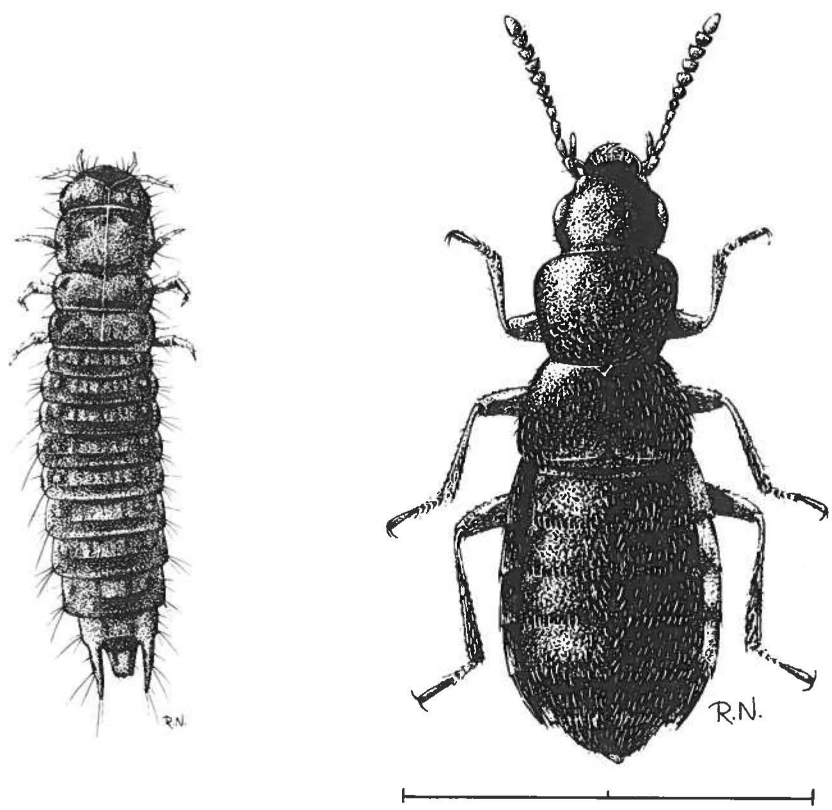


Fig. 18. *Micralymma marinum* (Ström). Scale: 2 mm.

Fig. 19. Typical biotope of *Micralymma marinum*: the stones in the tidal zone of a fjord-beach, here at Anorliuitsoq, Pamialluk island, in the Kap Farvel area. The seaweed is *Ascophyllum nodosum*. J.B. phot., July 1970.

which are separated by less than their diameter, and by the short mesosternal process, which does not meet that of the metasternum (Steel 1958: fig.9). The colour is dull black (shining in *M. brevilingue*), the body is generally broader than in *M. brevilingue*, and the antennal segments are more elongate (none of them distinctly wider than long). Length about 3 mm. The larva is described and figured by Paulian (1941) and Steel (1970).

Steel (1962) presented a key to the three known species of *Micralymma*. In King et al. (1979) are found scanning electron micrographs of the external morphology of the species.

Variation and dynamics: The hind wings are always entirely reduced.

General distribution

Holarctic (amphiatlantic), temperate to subarctic. *M. marinum* is a marine insect, distributed along practically all the Atlantic coasts of northern Europe, from the Channel to the White Sea, and on all the North Atlantic islands: the Shetlands, the Faeroes, Iceland, Bear Island, Svalbard. In North America the species is found on the coasts of Newfoundland and Maine (originally under the name of *M. stimpsoni* Le Conte; Lindroth 1931, Thayer 1985).

Distribution maps: Lindroth (1931: fig.41, 1957: fig. 32), Campbell (1980: map 9), Thayer (1985, North America).

Lindroth (1931, 1957) pointed to the striking accordance between the distribution of *M. marinum* and the Atlantic area influenced by the Gulf Stream (the North Atlantic Drift), and he assumed that this current is directly responsible for the spread of the species from an origin in eastern North America to Europe (and Greenland). This hypothesis has been criticized by, e.g., Larsson & Gigja (1959) and Larsson (1959: 41), who considered the complicated relationship between ocean currents and surface drifting, and also argued that the voyage would take too long in relation to the normal life history of the species.

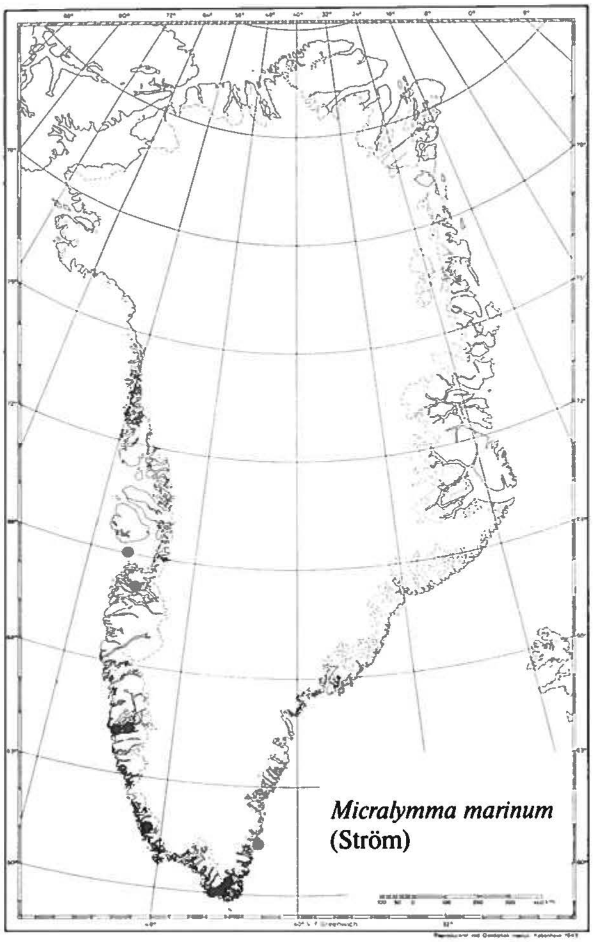
The last objection does not seem convincing. One could well envisage small colonies of the species, which is completely adapted to marine life, drifting on islands of seaweed and completing a number of reproductive cycles there.

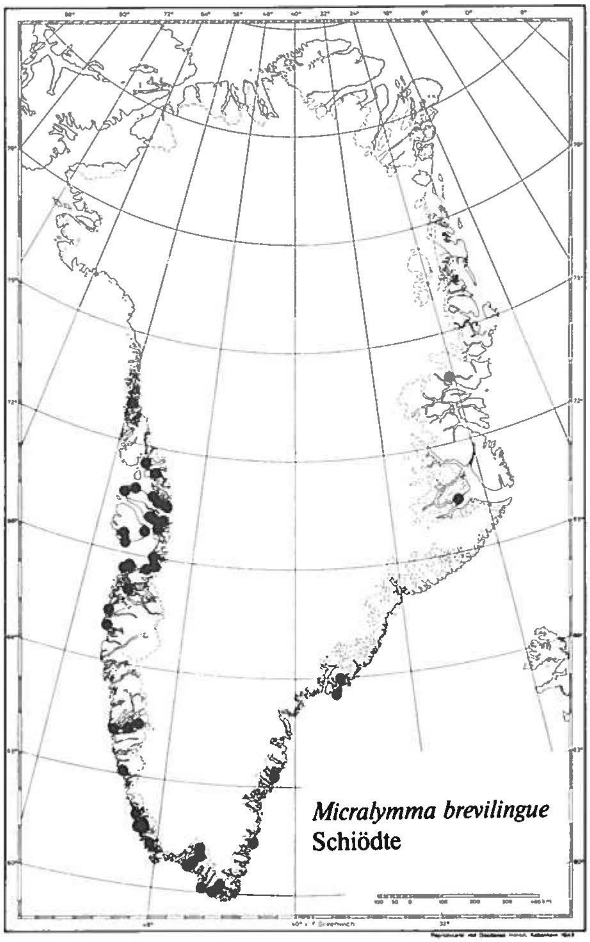
Larsson & Gigja (1959: 68) concluded that the populations of *Micralymma marinum* in northern and western Europe must be regarded as original, and that the occurrence in North America "is in full agreement with the description given by Lindroth (1957 chapter II) in his classical treatment of the importance of the ballast for the spreading of European species to North America". Campbell (1980) expressed a similar view.

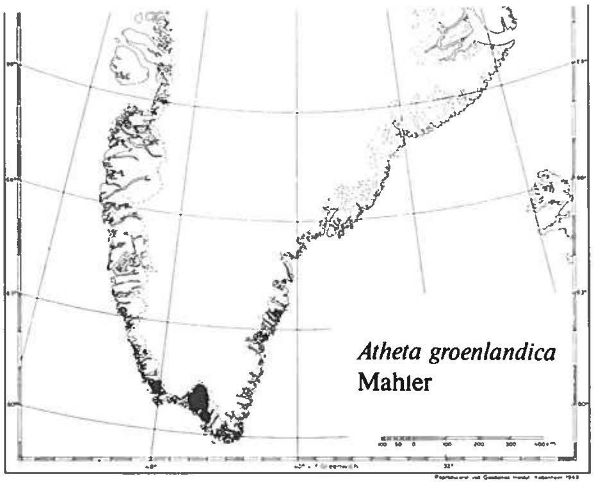
On the other hand, the species could have had an amphiatlantic distribution since the Tertiary, shifting southwards and northwards along the coast according to the climatic vicissitudes.

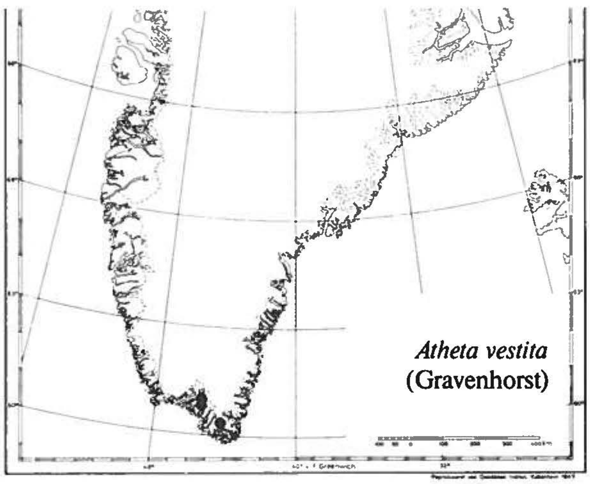
Distribution in Greenland (map p. 33)

Disjunct finds from Kap Tordenskjold on the east coast (61°25'N) to Disko Bugt on the west coast (Kronprinsens Ejland; R.M. Kristensen, pers.commun.).


Micralymma marinum
(Ström)


Micralymma brevilingue
Schiödte


Atheta groenlandica
Mahler


Atheta vestita
(Gravenhorst)

Habitat and notes on biology

M. marinum is a true marine insect, presumably spending its entire life cycle in the tidal zone, where it is regularly submerged during high tide. Adults and larvae are generally found together, on vertical parts or the underside of stones and rocks, and according to Lindroth (1931), Strand (1946), and Larsson & Gigja (1959), also "under seaweed". In Iceland the species was once taken on bare rock near the top of a small island (Geirfuglasker) together with *Atheta vestita* (Lindroth et al. 1973). In the Faeroes Bengtson (1981) found it among plants on sand near the shore. In Greenland *M. marinum* sometimes is occurring rather abundantly, e.g., at Anorliuitsoq, Pamialluk island, in the Kap Farvel area (Fig. 19), and at Tarajornitsoq, Arfersiorfik fjord (J.B.).

Lindroth (1931) assumed that the species is carnivorous, possibly feeding on mites, and West (1937) considered Thysanura to be a likely prey. Steel (1958, 1970) stated, without direct evidence, that both larva and adult are predacious and that the main food appears to be the collembolan *Anurida maritima* (Guerin). The peculiar shape of the larval mala of the maxillae, which is triangular and much broader across the middle than at the base (Paulian 1941, Larsson & Gigja 1959) might suggest that at least the larva is phytophagous, possibly feeding on algae.

However, Thayer (1985) was able to keep the species in culture on a purely carnivorous diet. She concluded that *M. marinum* clearly is a predator, but that the usual natural food is uncertain, possibly mainly collembolans and mites.

Life cycle

Imagines have been collected from 22 May to 21 August. Larvae have only been found on two occasions (Tarajornitsoq, Arfersiorfik, 14 June 1967, and Anorliuitsoq, Pamialluk island, Kap Farvel area, 21 August 1970; J.B.), in both cases fully grown larvae.

In Greenland nothing is known about overwintering stages and biotopes of egg-laying, pupation and hibernation. The present data suggest overwintering of both larvae and adults (the early appearance of fully grown larvae).

Larsson & Gigja (1959) assumed hibernation "almost exclusively in the larval stage". Steel (1970) on the basis of collecting in Scotland and southern England suggested that the adults overwinter to lay eggs in early summer. King et al. (1979) from collections in southern Wales, Great Britain, suggested overwintering of eggs or adults, hidden deep in rock crevices.

Thayer (1985) presented evidence that in Maine at least some beetles overwinter as larvae, possibly indicating that the life cycle may be longer than one year.

Micralymma brevilingue Schiödte, 1845

Taxonomy and synonymy: see Schiödte (1845), Poppius (1908), Lindroth (1957), Steel (1958, 1962).

M. brevilingue was long considered a Greenlandic endemic (Henriksen & Lundbeck 1917, Jensen 1928, Lindroth 1931). However, E. Strand (1905) reported the species from Cocked Hat Island off the eastern coast of Ellesmere Island (78°48'N), a find overlooked by Henriksen & Lundbeck. Brown (1937) found the species at Lake Harbour, Baffin Island, and Weber (1950) reported it from Point Barrow, Alaska. Lindroth (1957) compared Brown's specimens and Greenlandic material with *Micralymma dicksoni* Mäklin (1881) from arctic Siberia and concluded that all belonged to the same species. He found that the differences between *M. brevilingue* and *M. dicksoni* mentioned by Mäklin (1881) are by no means constant, and that the male genitalia are almost identical. *M. dicksoni* has also been reported from the Pribilof Islands off Alaska (Leng 1927, Arnett 1983), and Lindroth (1957) thus concluded that only one, although variable, circumpolar, arctic species of *Micralymma* exists: *M. brevilingue* Schiödte. This was confirmed by Steel (1958), who distinguished two subspecies: *M. brevilingue brevilingue* Schiödte and *M. brevilingue dicksoni* Mäklin. *M. brevilingue* has been found in Pleistocene deposits in Alaska (Cape Deceit) and Canada, Yukon Territory (Matthews 1974, 1975; Morgan & Morgan 1980).

Identification

Body dark brown to black, somewhat shining; antennae, legs and palpi yellowish brown to dark brown. Antennal segments 8–10 decidedly transverse. Eyes smaller than in *M. marinum*, the facets often separated by spaces as large as their diameter or even larger; mesosternal process meeting that of metasternum (Steel 1958: fig.11). Length about 3 mm.

Steel (1962) presented a key to the three known species of *Micralymma*.

Variation and dynamics: see above. Hind wings always entirely reduced.

General distribution: Circumpolar, arctic (see above under "Taxonomy and synonymy").

Distribution in Greenland (map p. 33)

M. brevilingue is one of the most widespread beetles in Greenland, common along the west coast from Kap Farvel to north of Upernavik. Apart from a number of places in the Ammassalik District, the species is only found in two more East Greenlandic localities (Hekla Havn, Danmark Ø, and Nordfjord, Strindberg Land). Most likely the species is present fairly continually along

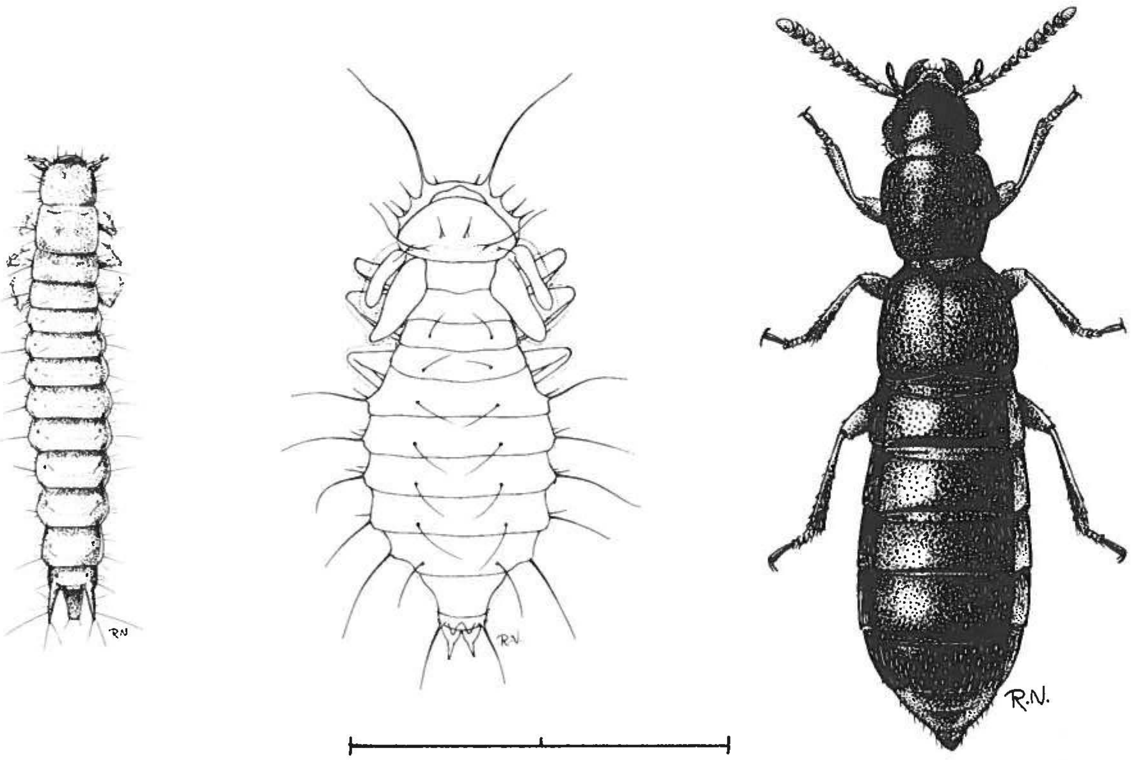


Fig. 20. *Micralymma brevilingue* Schiödte.

the east coast as well, the small number of finds being due to lack of collecting effort, since this inconspicuous beetle is easily overlooked.

Habitat and notes on biology

According to Henriksen & Lundbeck (1917), *M. brevilingue* is common under stones on beaches, sometimes on the foreshore (in company with *Gammarus locusta*), where it is submerged during high tide. H. Madsen (1936) mentioned the species (two larvae) from a lagoon in Nordfjord, Strindberg Land. In Kangersuneq fjord, southern Disko Bugt, I found the species numerously under stones close to the high water mark on a sandy beach; in Disko Fjord and Uummannaq Fjord it was similarly located on stony beaches.

However, *M. brevilingue* also occurs at some distance from the beach, e.g., under the moss-cover on rocks and below rosettes of *Cochlearia groenlandica* (Henriksen & Lundbeck 1917).

I frequently found *M. brevilingue* on a herbslope (Østerlien, at Qeqertarsuaq/Godhavn; Fig. 21), although not far from the beach, but also under stones in fairly dry snow-beds in the Uummannaq District, several hundred metres from the seashore. In southern Disko Bugt (Qeqertasussuk island) I found the species in shaded gorges with a luxuriant vegetation.

P. Nielsen caught the species in a snow-bed, 350 m alt., at Qassiarsuk, Narsaq District (Table 11). Haarløv (1985, label note) collected it in a nest of *Larus marinus* together with *Atheta islandica* (at Eqaluit, Qaqortoq/Julianehåb District). In only one case *M. brevilingue* has been found together with *M. marinum* (at Qoornoq, Godthåbsfjord; C. Vibe leg.).

At Lake Harbour, Baffin Island, Brown (1937) found the species to be abundant beneath stones that were flooded regularly by the sea during spring tides and storms.

The habitat thus appears to include both the upper part of the tidal zone (to some extent overlapping the habitat of *M. marinum*) and damp situations in different plant communities further inland, close to the sea or fjord, but a number of finds are from areas with a continental climate. The habitat of *M. brevilingue* is accordingly decidedly not confined to the marine littoral.

Steel (1962) pointed to the interesting gradation in habitat of the three known species of *Micralymma*. The third, *M. caucasicum* (Melichar), is an inland species.

The feeding biology of *M. brevilingue* is unknown.

Life cycle

Imagines have been collected as early in the season as 16 March (Qeqertarsuaq/Godhavn, M.P. Porsild leg. 1923) and 6–10 April (Qaqortoq/Julianehåb, G. Meldorf leg. 1901). C. Vibe found adults 16 May 1943 at Nuuk/Godthåb "under stones at sudden thaw" (label

Fig. 21. Herbslope vegetation and *Salix glauca* coppice on a south-facing slope, Østerlien, at Qeqertarsuaq/Godhavn. *Micralymma brevilingue* was collected here fairly frequently.
J.B. phot., August 1968.

note; my translation). Imagines have been collected throughout the summer and autumn (e.g., Østerlien, Qeqertarsuak/Godhavn, 22 September 1967, J.B. leg.; Kap Dan, Ammasalik, 1 October 1933, R.Bøgvad leg.). Larvae have been collected from 26 May to 7 August. A pupa (Fig. 20) dates from 11 July (1949).

The data indicate imaginal and probably also larval hibernation.

Ocalea cf. *picata* (Stephens, 1832)

(Fig. 55,e)

Only known as subfossils from a Norse farm at Kilaarsarfik (Sandnæs) in Ameralla fjord east of Nuuk/Godthåb (Buckland 1986, in litt.). Most probably introduced by the Norsemen and later extinct.

Distribution: Europe, northern Africa, Caucasus. In Scandinavia a southern species, but also present in the Faeroes and Iceland.

Habitat and biology: In Scandinavia mainly found on moist ground in withered vegetation and moss in forests, but also under washed-up seaweeds on the beach. In Iceland mostly synanthropic on soil rich in humus, in the Faeroes exclusively in infields (Lindroth 1931, Larsson & Gigja 1959, Lindroth et al.1973, Bengtson 1981).

Gnypeta cavicollis Sahlberg, 1880

Taxonomy and synonymy: see Sahlberg (1880), Henriksen & Lundbeck (1917).

G. Lohse, Hamburg, (1987, pers. commun.) assumes that the Greenlandic *Gnypeta* is an undescribed species distinct from *G. cavicollis*. Even the Greenlandic material of *Gnypeta* is varied, especially regarding the shape of pronotum, and undoubtedly a revision of the arctic species of *Gnypeta* is needed.

Identification

Fairly alike an *Atheta* (p. 37), but the head distinctly constricted behind, forming a "neck", and the antennae relatively shorter than in any of the Greenlandic *Atheta* spp. (antennal length approximately equal to the length of head + prothorax). The first tarsal segment of the

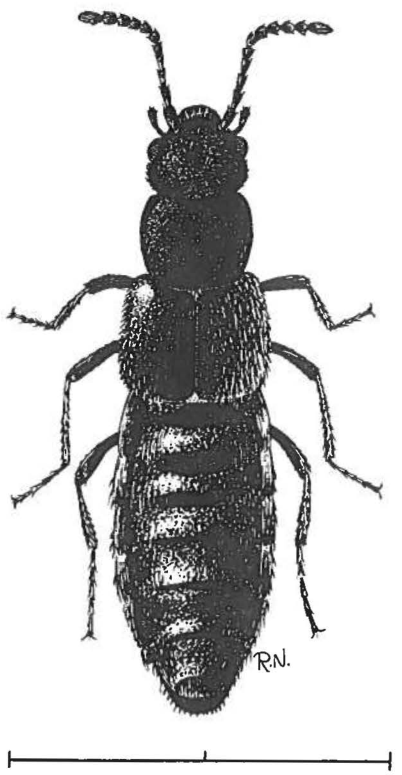


Fig. 22. *Gnypeta cavicollis* Sahlberg. Scale: 2 mm.

hind feet longer than the second (shorter or equal to the second in the Greenlandic *Atheta* spp.). Black, dull on head and pronotum, shining on abdomen. Head with a conspicuous hollow in the middle, pronotum with a shallow depression along the midline. Length about 3–3.5 mm. The larva is undescribed.

Variation and dynamics: The hind wings are fully developed.

General distribution

Outside Greenland *G. cavicollis* is only known from two localities in the northern, arctic part of the Yenissei valley, Siberia (Sahlberg 1880, 1901) and from Novaja Semlja (Munster 1925).

Distribution in Greenland (map p. 38)

The species has been found in four localities in the high arctic Northeast- and North Greenland: Noret, at Mesters Vig, Scoresby Land (Cotton 1979: *Calodera* (?) sp.); Hurry Inlet, Jameson Land (Lack 1934); Lille Pendullum Ø off Wollaston Forland (Aurivillius 1900, Sahlberg 1901); and Heilprin Land at Midsommersøerne in central Peary Land (B. Fristrup leg. 1949, "Canadian Pearyland Expedition 1966" leg.). (An attempt to trace the specimen from Hurry Inlet proved unsuccesful, but almost certainly the identification is correct).

The finds are thus well separated geographically, possibly indicating a wide distribution of the species in Northeast Greenland. C. Vibe (pers. commun.) in 1952 saw a glimpse of a small staphylinid, most probably *G. cavicollis*, among gravel at Thule (Dundas; 76°35′N).

Habitat

The specimen from Hurry Inlet, Jameson Land, was caught under a stone (Lack 1934). In the central, continental Peary Land (Heilprin Land) the species was found under a stone at the north-facing margin of a meadow, c. 200 m alt. (B. Fristrup leg., 1949). In the same area a number of specimens were caught in pitfalls at the lake Nordre Midsommersø (A. Downes 1987, pers. commun.). At Mesters Vig Cotton (1979) found *G. cavicollis* to be abundant on wet, slightly south-facing sand flats adjacent to a dune area. The vegetation consisted of *Salix arctica, Saxifraga oppositifolia, Silene acaulis* and *Stereocaulon alpinum*. The species was never found in the main body of the dunes or in the dune tundra. Larvae, probably of this species, were also found in a somewhat drier dune hummock-area with *Salix arctica* and *Dryas octopetala*. *G. cavicollis* was the only species of terrestrial Coleoptera found in the area.

In Siberia the species was collected in a tundra environment (Sahlberg 1901). In Novaja Semlja it was found "by sifting earth, refuse and old nests of mice" and under stones and planks (Munster 1925).

Life cycle

Cotton (1979) stated that the species was common "in the early season" and that larvae, presumably of this species, were found in late July. The other finds are from 6 July (Lille Pendullum Ø) and "August" (Hurry Inlet). Most probably the adults hibernate.

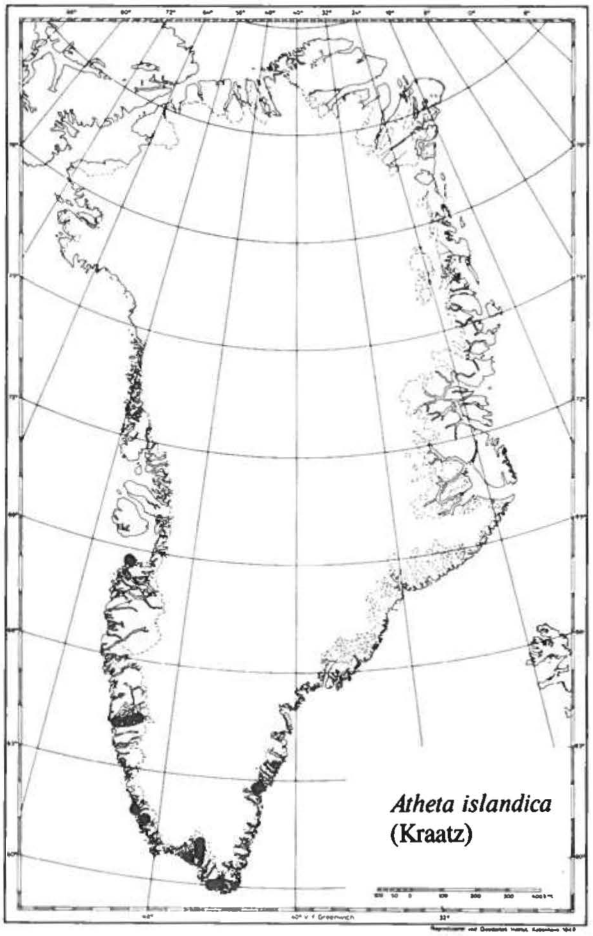
Atheta Thomson, 1858

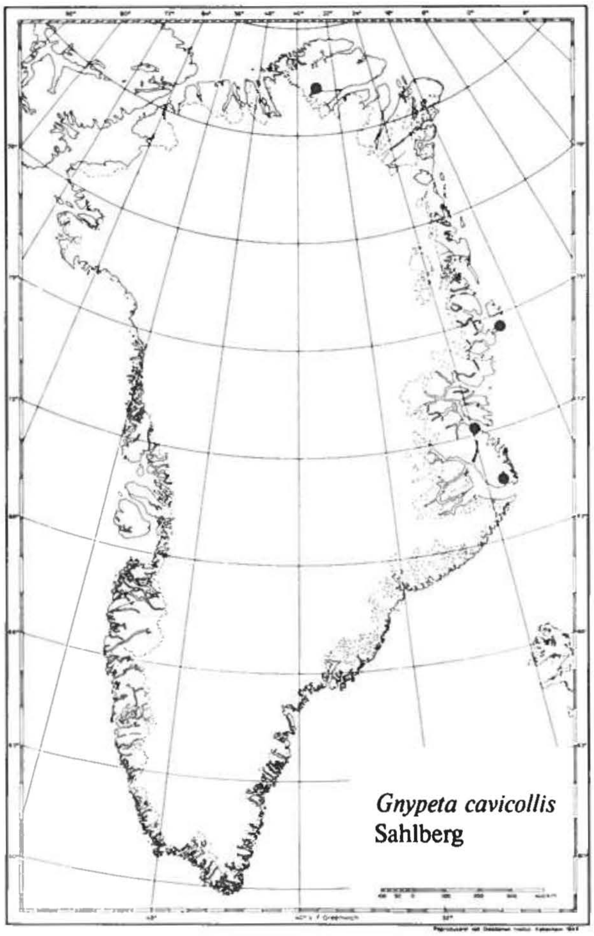
Small, dark, elongate staphylinids with head and pronotum of about equal width, and the head not or only slightly constricted behind.

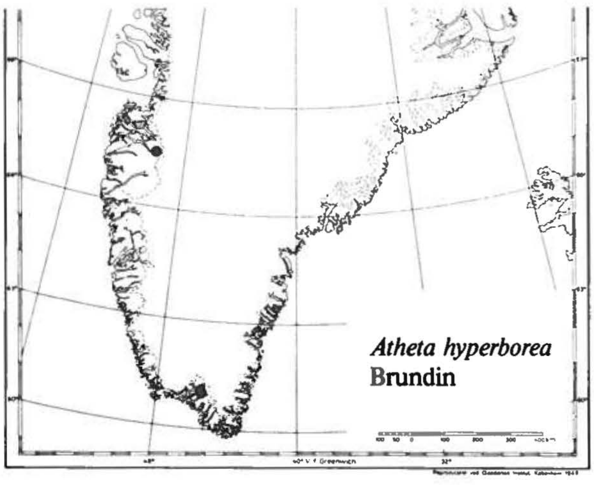
Key to the species of *Atheta* occurring in Greenland:

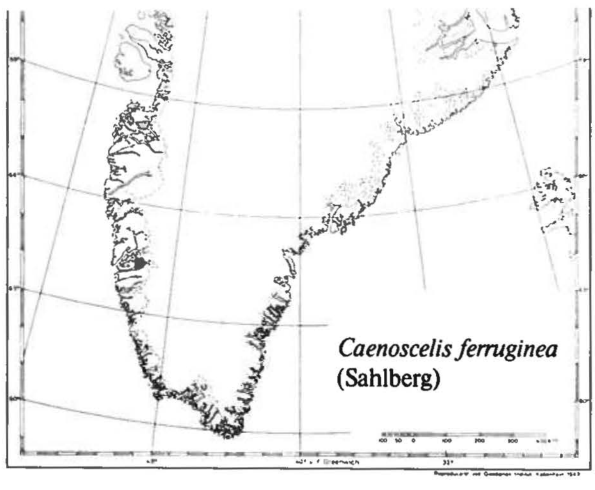
1. Head with scattered, large but shallow punctures. Pronotum about same width as head at level of the eyes, side margins backwards slightly concave. Length about 3–4 mm. *A. (Thinobaena) vestita* (p. 41)

1*. Head with fine punctures. Pronotum distinctly wider than head at level of the eyes, side margins not concave. 2


Atheta islandica
(Kraatz)


Gnypeta cavicollis
Sahlberg


Atheta hyperborea
Brundin


Caenoscelis ferruginea
(Sahlberg)

2. Midline hairs of pronotum directed backwards; in lateral view with inwards-bent lateral parts of pronotum barely visible from the side and side margins slightly and evenly curved. Length about 2–2.5 mm. *A. (Mocyta) groenlandica* (p. 39)

2*. Midline hairs of pronotum directed forwards; in lateral view with inwards-bent lateral parts of pronotum visible and front part of side margins curved down towards front-angles. 3

3. Pronotum with a shallow, wide depression in middle of posterior half. Inner margins of elytra longer than pronotum. ♀: Hind margin of 6th abdominal sternite distinctly concave in the middle and with a fringe of long hairs. Length about 3.5–4 mm. *A. (Boreophilia) hyperborea* (p. 41)

3*. Pronotum without, or with only a slight, narrow depression along midline. Inner margins of elytra shorter than pronotum. ♀: Hind margin of 6th abdominal sternite evenly curved and with a fringe of short hairs. Length about 3–3.5 mm. *A. (Boreophilia) islandica* (p. 40)

No *Atheta* larvae have hitherto been collected in Greenland. Larvae of *Atheta* spp. sensu latu are described and pictured by Paulian (1941) and Topp (1975a).

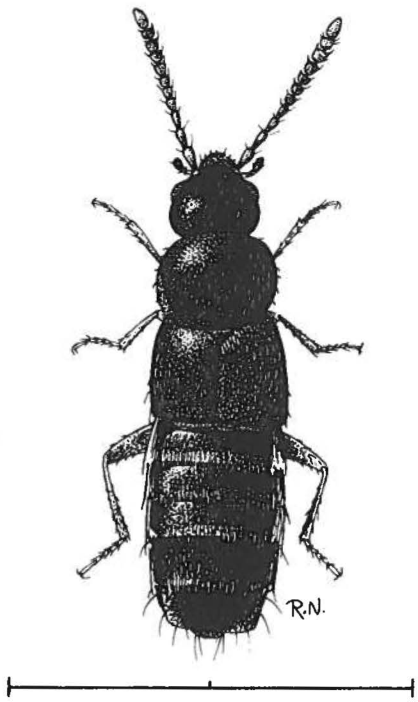


Fig. 23. *Atheta groenlandica* Mahler. Scale: 2 mm.

Atheta (Mocyta) groenlandica Mahler, 1988

(Henriksen 1939: *Acrotona fungi* Grav.)

Taxonomy and synonymy

In a revision of the entire material of *Atheta* from Greenland, Mahler (1988) found that what had formerly been identified as *A. fungi* (Gravenhorst) deviated so considerably from this species that it was necessary to refer the individuals from Greenland to a new species, *A. groenlandica*, although closely related to *A. fungi* and similarly a highly variable species.

Identification: see the key (p. 37).

The larva is unknown, but presumably very much like that of *A. fungi* (described by Topp 1975a).

Variation and dynamics

According to Mahler (1988), only females have been found so far, and the fairly large material examined (149 specimens) makes it probable that *A. groenlandica* is parthenogenetic, at least in its known geographic range. *A. fungi* is known to be parthenogenetic in southern Scandinavia, and in Iceland males are frequent, so that a hypothetical occurrence of *A. fungi* in Greenland would most likely be in the bisexual form. This also indicates that *A. groenlandica* is a species distinct from *A. fungi*.

The hind wings are always fully developed and no doubt functional.

General distribution

A. groenlandica is so far only known from Greenland.

Distribution in Greenland (map p. 33).

A. groenlandica has a subarctic distribution and appears to be common in the eastern part of the Julianehåb Bugt area.

Habitat

According to Henriksen & Lundbeck (1917) *A. groenlandica* ("*A. fungi*") is found under stones and leaf litter in glades and outskirts of willow coppices. This is confirmed by P. Nielsen's pitfall collections (see Tables 9, 11), but the species was taken most abundantly in grassland communities, and moreover on a lake shore and in a *Sphagnum* marsh. In the last-mentioned biotope it was caught together with *A. islandica*, the only occasion when these two species have been taken together. *A. groenlandica* thus appears to be fairly hygrophilous.

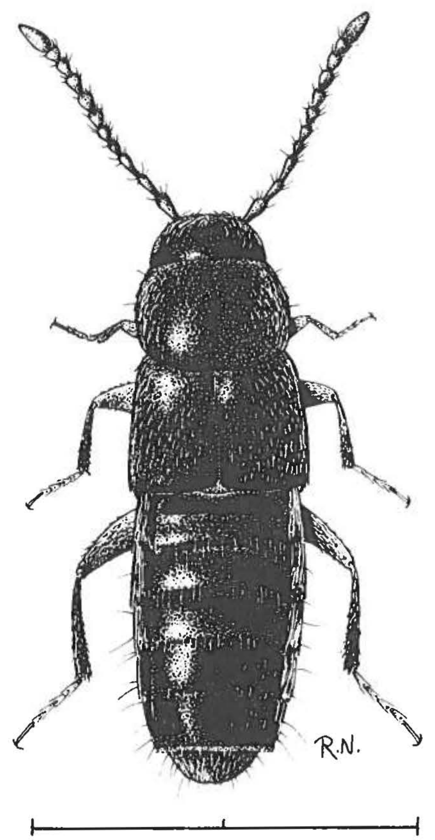


Fig. 24. *Atheta islandica* (Kraatz). Scale: 2 mm.

Life cycle

Adults have been collected throughout the summer, from 20 May to 5 September, newly hatched specimens in May and June. Most probably the adults hibernate, which, according to Topp (1975b), is the case in *A. fungi*.

Atheta (Boreophilia) islandica (Kraatz, 1856)

Taxonomy and synonymy: see Poppius (1910), Brundin (1943, 1953).

This species was formerly considered boreo-alpine (e.g., by Henriksen & Lundbeck 1917, Holdhaus & Lindroth 1939). Brundin (1943) showed that *A. islandica* (Kraatz) comprises two closely related species: the arctic-subarctic *A. islandica* (Kraatz) Brundin which in southern Europe is replaced by *A. hercynica* (Renkonen) Brundin. The two species can only be separated by means of male genital characters. This presents a problem in identifying the species in areas such as Greenland where only females have been found, and where the species consequently reproduces parthenogenetically. Here one must rely on probability, and it is unlikely that *A. hercynica* would occur in Greenland (see Brundin 1943: 18).

Identification: see the key (p. 37)

The larva is undescribed.

Variation and dynamics

Normal sex-distribution in Scandinavia and Iceland, but exclusively females found in Greenland.

The hind wings are full and functional (Lindroth et al. 1973).

General distribution

Palaearctic, subarctic to arctic; in Scandinavia mainly alpine: Northern Fennoscandia (southwards to Dovre in Norway), northern Russia, the Faeroes, Iceland. The distribution is insufficiently known; Brundin (1943) assumed that the species occurs in the British Isles.

Distribution in Greenland (map p. 38)

The species is probably widely distributed in southern Greenland, because in addition to a number of finds in the Qaqortoq/Julianehåb and Narsaq Districts there are single finds from Aasiaat/Egedesminde and from Timmiarmiut Fjord on the southern east coast.

Habitat

Lundbeck found *A. islandica* under stones at some distance from the beach, e.g., under the Norse ruin stones at Igaliku (Henriksen & Lundbeck 1917). At Anorliuitsoq, Pamialluk island, in the Kap Farvel area, the species was caught in pitfalls in an old settlement and at a water course (Table 10), and P. Nielsen caught it in a *Sphagnum* bog and a *Sphagnum* marsh at Narsarsuaq (Table 9). Thus a certain preference for humid biotopes appears to be the case in Greenland. The species has also been collected in a nest of *Larus marinus* (together with *Micralymma brevilingue*; Eqaluit, Haarløv leg. 1985).

In Iceland *A. islandica* is regarded a typical meadow-species (Lindroth 1931), found in both humid and quite dry grass-areas, up to 600 m alt. In the Faeroes it occurs in a variety of localities, ranging from fell-fields to infields (Bengtson 1981).

In Scandinavia the species is found on shores and beaches, in heathland, moist meadows, grassland, under plant debris in *Salix* shrubs, and also in more dry places under mosses, up to 1000 m alt. at Abisko and 1320 alt. in Hardangervidda (Lindberg 1927, 1936; Brundin 1934; Strand 1946; Fjellberg 1972).

Life cycle

Adults have been collected from 2 April to 31 August (a large sample of 23 specimens was taken 2–10 April 1901

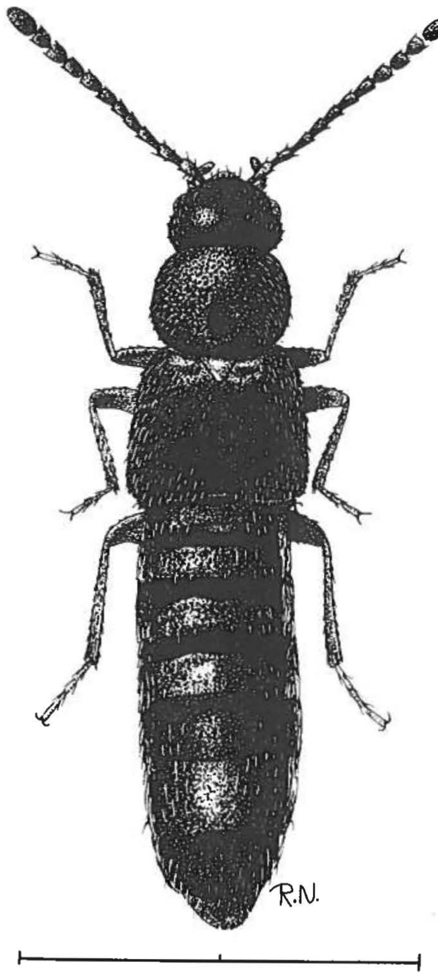


Fig. 25. *Atheta hyperborea* Brundin. Scale: 2 mm.

at Qaqortoq/Julianehåb, G. Meldorf leg.). This indicates adult hibernation. Larvae have not been found in Greenland.

Atheta (Boreophilia) hyperborea Brundin, 1940

Taxonomy and synonymy: see Brundin (1940, 1953).

Identification: see the key (p. 37).
The larva is undescribed.

Variation and dynamics

Only females have been collected in Greenland. The hind wings are fully developed.

General distribution

Palaearctic, boreal to low arctic. Hitherto only known from northern Norway and Finland and middle Sweden (apart from Greenland), but probably the distribution is insufficiently known.

Distribution in Greenland (map p. 38)

A. hyperborea is undoubtedly a rare species in Greenland. Only three specimens have been collected, from two different areas separated by about 800 km: Igaliku and Qassiarsuk in subarctic Southwest Greenland; and Equalummiut nunaat at the head of Nordre Strømfjord, in a fairly dry, continental low arctic area.

Habitat

The only information available is that the specimen from Qassiarsuk was caught in a pitfall in a typical snow-bed vegetation dominated by *Salix herbacea* (P. Nielsen, pers. commun.).

Life cycle

The Greenlandic specimens were collected on 9 June, 21 July (South Greenland), and 1 July (Eqalummiut nunaat).

Atheta (Thinobaena) vestita (Gravenhorst, 1806)

Taxonomy and synonymy: see Lindroth (1931).

Identification: see the key (p. 37)
The larva is undescribed.

Variation and dynamics

The hind wings are fully developed and probably functional (Lindroth et al. 1973).

General distribution

Palaearctic, temperate-subarctic: the North and central European Atlantic area to northernmost Norway, including the British Isles, the Faeroes and Iceland; in the Baltic area northwards to Gotland.

Distribution in Greenland (map p. 33)

Only found in three localities in the southernmost, subarctic part: Igaliku and Qanisartuut (one specimen in each place) and Tupaasat in Kangikitsoq fjord, Kap Farvel area (five specimens).

Habitat

In Tupaasat I found *A. vestita* under stones on a sandy beach close to the high-water mark.

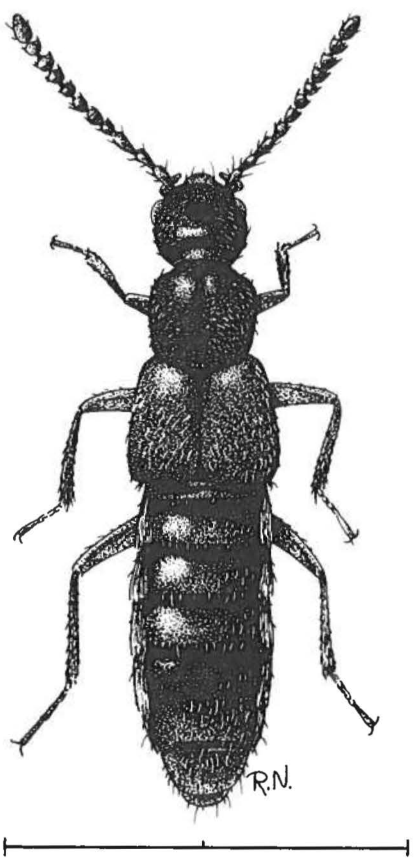


Fig. 26. *Atheta vestita* (Gravenhorst). Scale: 2 mm.

In Europe the species is found almost exclusively on sandy or gravelly seashores, chiefly under washed-up seaweeds (Lindroth 1931, West 1942, Strand 1946, Larsson & Gigja 1959). However, in Iceland Bengtson (1981) reported it from grassland and wasteland vegetation close to the shore.

Life cycle

The Greenlandic finds date from 9 June, 18 June and 27 July. According to Larsson & Gigja (1959), in Iceland the species probably hibernates chiefly in the larval stage.

Buprestidae

Melanophila acuminata (Degeer, 1774)

(Fig. 51,b)

Qaqortoq/Julianehåb, 1898. Probably introduced with timber.

Distribution: Circumpolar, boreal.

Habitat and biology: The larva lives in and feeds on conifer wood, mostly pine.

Byrrhidae

Simplocaria metallica (Sturm, 1807)

Taxonomy and synonymy

There has been some uncertainty regarding the identity of the common species of *Simplocaria* found in Greenland. Henriksen & Lundbeck (1917) identified it as *S. metallica* Sturm, whereas Lindroth (1957) referred it to the North American *S. tesellata* Le Conte, based on differences from *S. metallica* in pilosity of the elytra and in the shape of the median lobe of the penis. However, Székessy (1936) declared the genitalia of Greenlandic and European males to be identical. Arnett (1983) considered *tesellata* a synonym of *metallica*, and this view is supported in a recent study by P.J.Johnson, University of Idaho (1985, in litt.).

Identification

Dorsal surface black, shining, with light hairs. Tibiae flattened on outer side (to receive feet during withdrawal). Length 2.5–3 mm. (Distinction from *S. elongata*, see p. 44). The larva is undescribed.

Variation and dynamics

For differences between Greenlandic and European specimens, see Lindroth (1957: 262). The hind wings are always fully developed.

General distribution

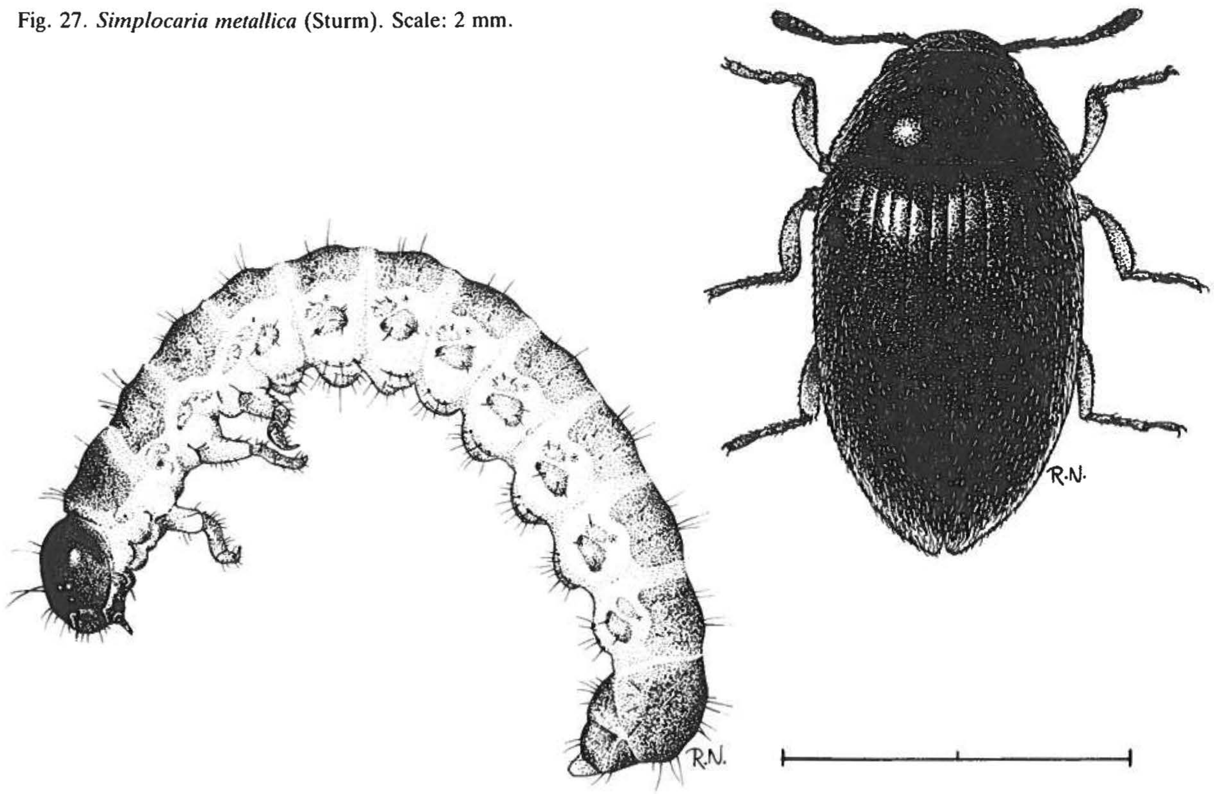
Holarctic, boreal to low arctic, in Europe boreo-alpine: Scandinavian mountains, southern Finland, and very scattered occurrences in the Riesengebirge, the Carpathians, and the Alps (Holdhaus & Lindroth 1939). In America found in parts of southern Canada and northern U.S.A. including Alaska. In northeastern U.S.A. the species is alpine and found in the White Mountains of New Hampshire and Maine (P.J.Johnson, in litt.).

Distributions maps: Holdhaus & Lindroth (1939: fig. 5, Scandinavia, and plate 13, Europe), Lindroth (1949: 739, Scandinavia; 1953, 1958: Scandinavia).

Distribution in Greenland (map p. 45)

S. metallica has been found in scattered localities along the southern stretch of the west coast, northwards to Disko. It is quite common in the subarctic, northeastern

Fig. 27. *Simplocaria metallica* (Sturm). Scale: 2 mm.



part of the Qaqortoq/ Julianehåb Bugt area and in the Godhåbsfjord area. The species has been found as subfossils in Norse farms at Ameralla fjord east of Nuuk/ Godthåb (Buckland et al. 1983).

Habitat and notes on biology

In Greenland *S. metallica* is most often found under stones and in moss, but otherwise it is not easy to characterize the habitat, which is as diverse as that of *Byrrhus fasciatus* (p. 47). *S. metallica* appears, however, to be more dependent upon the presence of water, at least it has been found most abundantly on fjord beaches, river banks, and along brooks (see Table 9), but also in different xeric inland plant communities. In Eqalummiut nunaat at the head of Nordre Strømfjord (Kuup akua), the species was frequently caught by pitfall-trapping in a south-facing *Salix glauca* coppice and in *Betula nana-Vaccinium uliginosum* heath with a dominant underlayer of *Polytrichum commune*; also in mixed vegetation of *Salix glauca, Betula nana* and herbs with moss cover of *Aulacomnium, Polytrichum* and *Peltigera* (J. Stroud 1985, in litt.).

On Disko the species has been found exclusively in two highly different localities: at the hot spring in Uunartorsuaq/Engelskmandens Havn near Qeqertarsuaq/ Godhavn (Fig. 50), and at a melt-water brook on a barren moraine in the interior of the island (Daugaard Jensen Dal). Presumably the presence of the right species of mosses, on which it like other byrrhids is assumed to feed, is the most important prerequisite for the existence of the species. However, six specimens were taken on *Cerastium alpinum* (at Kapisillit; C. Vibe leg. 3. July 1950).

In Europe *S. metallica* is found in the lower part of the alpine region, among mosses in sandy places, most often in the vicinity of water courses and lakes. It also occurs in the subalpine region and, rarely, in coniferous forests (Jansson 1926, Brundin 1934, Holdhaus & Lindroth 1939, Strand 1946, Brinck 1966).

In northeastern U.S.A. the species was found on mosses (?*Bryum* sp.) about 2000 m alt. The mosses were always growing on sandy gravel soil in niches in boulder fields and northerly aspects of other protected sites. The larva is a burrower in moss mats (P.J.Johnson 1985, in litt.).

Life cycle

Adults have been collected from 7 June to 28 August, newly hatched imagines in the middle of June and on 31 July. Four fully grown larvae date from 30 June, 8 July, 17 July, and 4 August. These data suggest that both larvae and adults hibernate, and possibly also that the reproductive cycle is not determined.

In northeastern U.S.A. the first and second stage

Fig. 28. *Simplocaria elongata* Sahlberg. Scale: 2 mm.

larvae are active and growing during winter, with third stage larvae present from May through July. Pupation lasts approximately ten days, and adult activity until the first hard frosts in autumn (P.J. Johnson, in litt.)

Simplocaria elongata Sahlberg, 1903

Taxonomy and synonymy

According to P.J. Johnson, University of Idaho (1986, in litt.), *Simplocaria remota* Brown is a synonym of *S. elongata*, and another synonym is *S. frigida* Krogerus.

Identification

Very much like *S. metallica*, but larger (length about 3.5 mm) and more elongate. Pronotum 4/7 as long as wide (in *S. metallica* pronotum is twice as wide as long). The elytral striae are more strongly impressed than in *S. metallica* (Brown 1932).

Dynamics: The hind wings are fully developed.

General distribution

Circumpolar, subarctic to arctic. Europe: Kanin peninsula; Siberia: Yenissei Valley; North America: widely distributed in northern Canada (Yukon, Mackenzie, Keewatin, Manitoba; P.J. Johnson, in litt.).

Distribution in Greenland (map p. 45).

Only one specimen has hitherto been collected, from Kilaarsarfik (Sandnæs) at Ameralla fjord east of Nuuk/Godthåb (by P.C. Buckland, 1984; in litt.)

Habitat and notes on biology

Poppius (1910) mentioned the species under moss in humid places. P.C. Johnson (in litt.) suggested that *Bryum* spp. may be likely hosts.

Life cycle

The Greenlandic specimen was caught in July. In Canada adults have been collected from 30 May to 19 August.

Tylicus subcanus Le Conte, 1878

Taxonomy and synonymy: see Le Conte (1878: 609). The Greenlandic material has been identified by P.J.Johnson, University of Idaho, U.S.A.

Identification

Looks like a small *Byrrhus* (p. 46). Dorsal surface very dark and rather dull with faint, black longitudinal markings and light hairs; elytra smooth. Only front tibiae somewhat flattened on outer side. Length about 4 mm.

Dynamics

At least in Greenland the hind wings are so short that flight is impossible.

General distribution

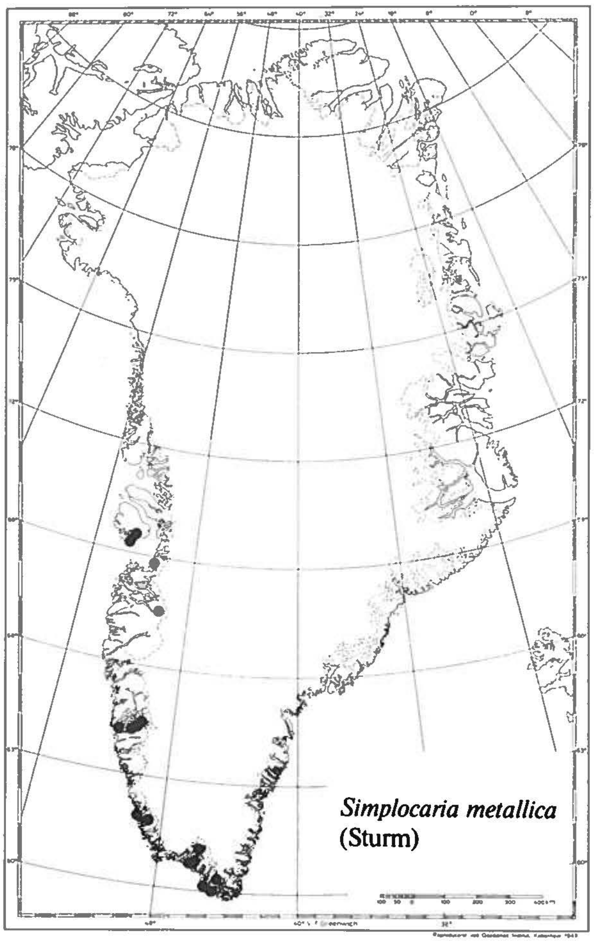
Nearctic, boreal to subarctic. Outside Greenland *T. subcanus* is only known from northwestern U.S.A. and southwestern Canada (Rocky Mountains, Great Lakes region northwards to White Mountains and Quebec; P.J.Johnson, in litt.).

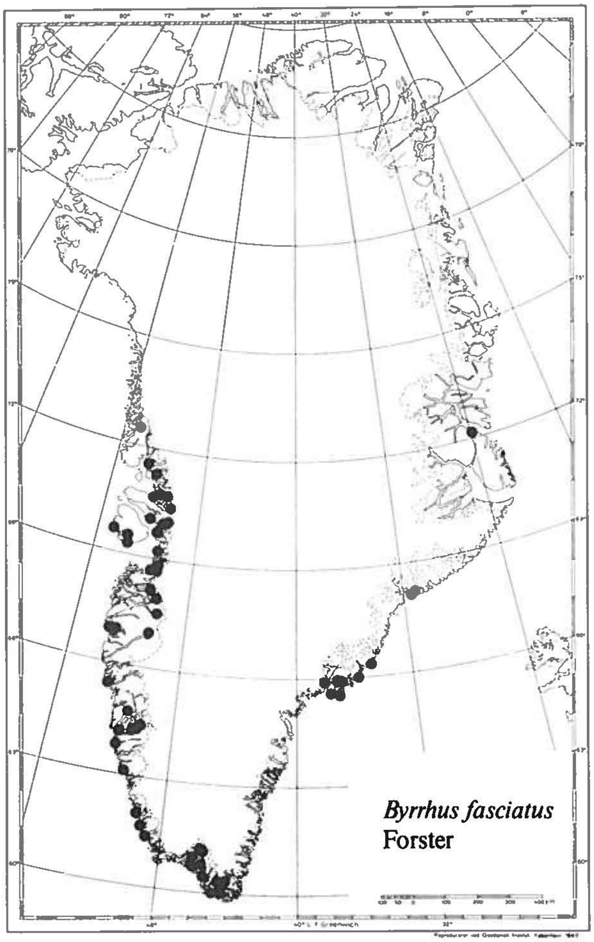
Distribution in Greenland (map p. 45)

T. subcanus is a recent addition to the known beetle fauna of Greenland. In 1984 P. Nielsen caught the species in pitfall traps in two localities in the subarctic Southwest Greenland: Narsarsuaq and Qinngua valley (seven and four specimens, respectively). The sites are separated by about 100 km.

Habitat and notes on biology

In Narsarsuaq *T. subcanus* was caught in a dry heath rich in lichens and mosses, in Qinngua on the shore of


Simplocaria metallica
(Sturm)


Byrrhus fasciatus
Forster


Simplocaria elongata
Sahlberg

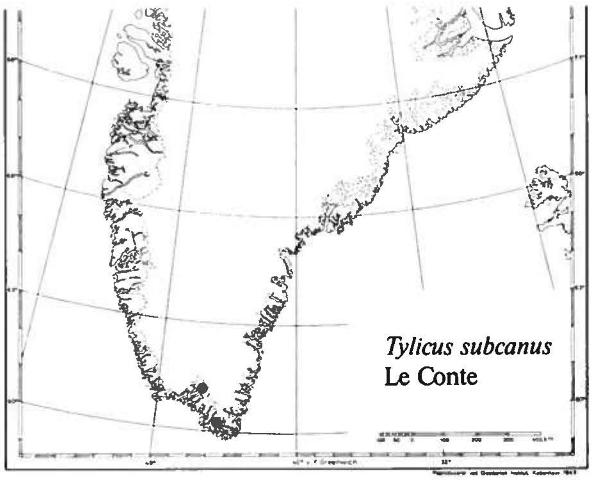
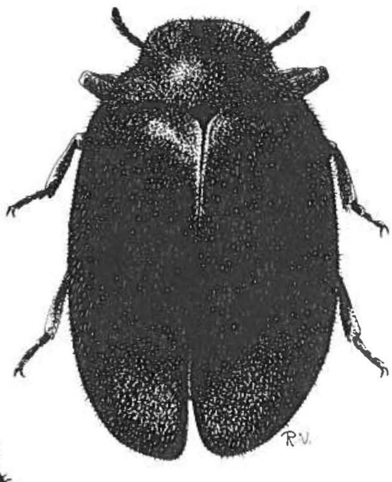
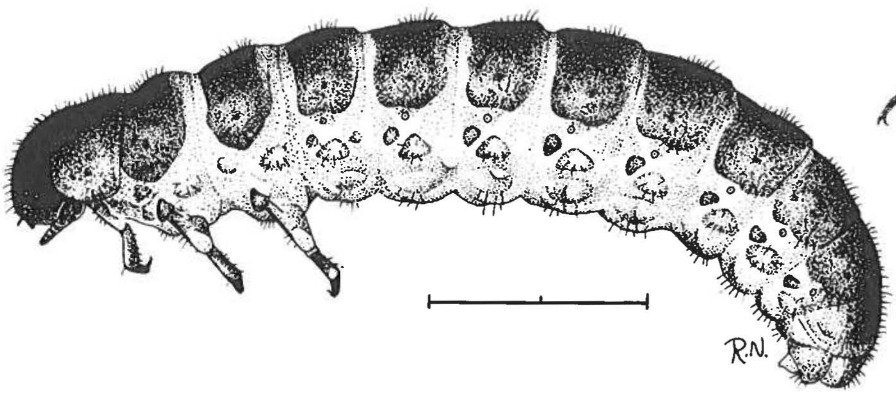

Tylicus subcanus
Le Conte

Fig. 29. *Tylicus subcanus* Le Conte. Scale: 2 mm.





the great lake Tasersuaq (P. Nielsen, pers. commun.; see Table 9).

P.J.Johnson (1985, in litt.) studied the species near Spokane, Washington. Here both adults and larvae feed on a moss species (unidentified) in association with *Polytrichum* sp. in seasonally xeric places. The microsite is on fine sandy-loam on or adjacent to exposed rock. Occasional specimens have been collected by other workers at high elevation in Montana in similar situations. The larva is surface-active and does not burrow except to pupate.

Life cycle

The Greenlandic finds date from 23 June to 31 July. A larva undoubtedly belonging to this species (Fig. 29), was taken together with the adults at Narsarsuaq on 16 July.

In North America (Washington, vicinity of Spokane) the first instar larvae are active from late autumn through mid-winter. Snow cover and cold inhibit activity, but do not provoke a distinct dormancy-period. Second and third instars are found in spring and early summer, with adults becoming evident by late June (P.J.Johnson 1985, in litt.). The species is thus here univoltine with larval overwintering; but the cycle may be different in Greenland, where larval activity and growth during winter probably is excluded.

Byrrhus fasciatus Forster, 1771

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931), Arnett (1983).

Identification

Dorsal surface dull and very hairy, dark brown with a variable pattern of longitudinal, black stripes and spots and light transverse bands. Tibiae highly flattened and with grooves to receive the feet during withdrawal (like other members of the family, legs and antennae can be withdrawn into grooves on the underside of the body, the insects feigning death in this manner). Length about 6–8 mm.

Variation and dynamics

A highly variable species, both as regards colour and general shape and size (Lindroth 1931, V. Hansen 1973). In Greenland the variation is less pronounced, the general colour being dark brown with more or less distinct black, brown and grey markings caused by differently coloured hairs. The variation in size is of the same magnitude as in Denmark (V. Hansen 1973).

The hind wings are fully developed, and the species regularly flies in sunny weather (Lindroth 1931, Lindroth et al. 1973).

General distribution

Perfectly circumpolar, temperate to high arctic. The whole of Europe to northernmost Scandinavia, including the Faeroes and Iceland.

Distribution in Greenland (map p. 45)

B. fasciatus has been collected from Upernavik in the northwest to Mesters Vig in the northeast, but is apparently especially common along the southern part of the

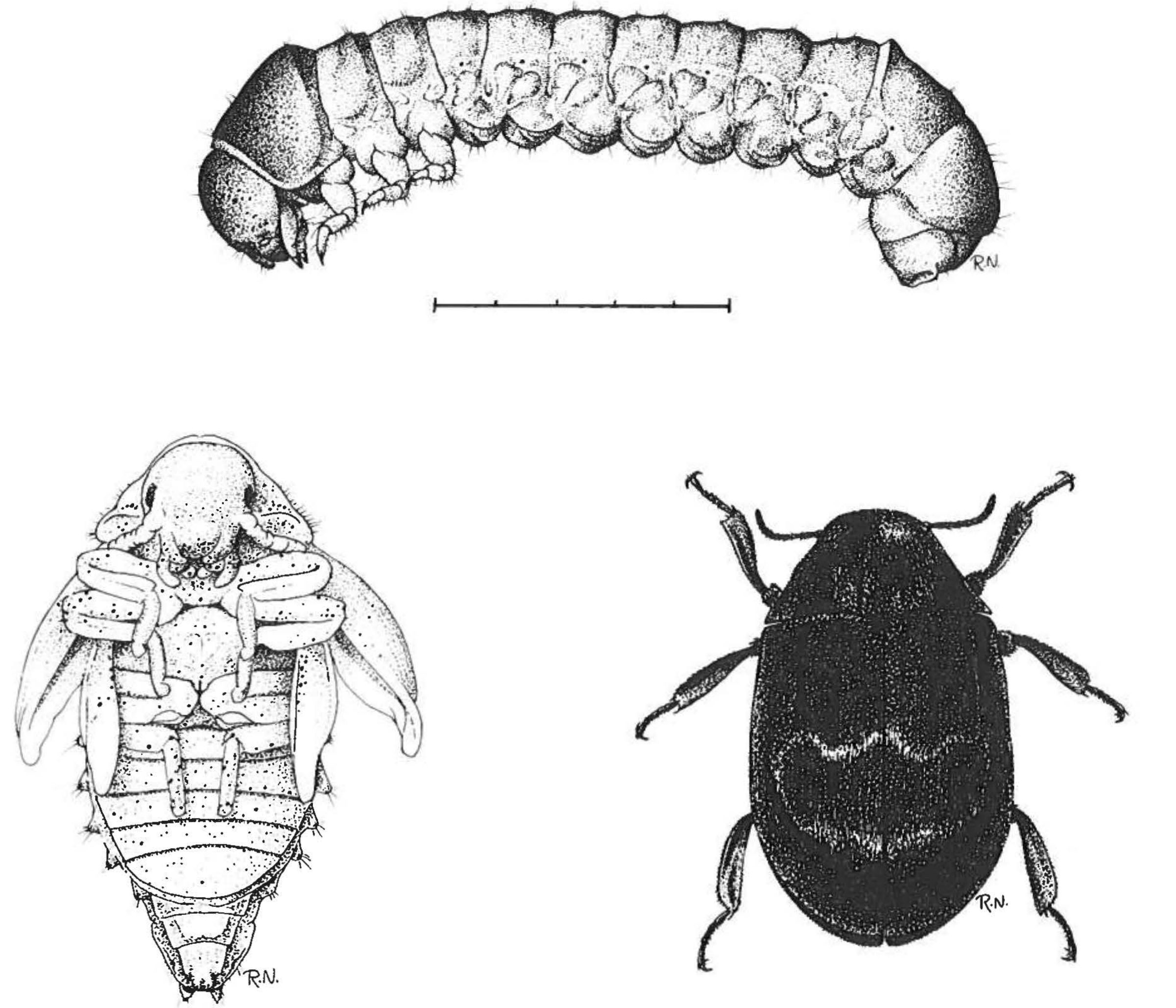


Fig. 30. *Byrrhus fasciatus* Forster. Scale: 5 mm.

west coast. Along the east coast there are large gaps, presumably due to lack of collecting effort. The species has been found as subfossils in excavated Norse farms in the Nuuk/Godthåb area (Buckland et al. 1983, Buckland 1986, in litt.).

Habitat and notes on biology

The species is commonly found under stones, under vegetation and in moss, but otherwise in highly different, both humid and dry situations: along water courses, in snow-beds, coppices, herbslopes, grassland areas, humid and dry heaths (Tables 9–10). In Eqalummiut nunaat, head of Nordre Strømfjord (Kuup akua), *B. fasiatus* was caught by pitfall trapping both in a number of xeric plant communities and also in some humid, including a *Calamagrostis lapponica* marsh with *Aulacomnium* ground layer (J. Stroud 1985, in litt.).

At Qeqertarsuaq/Godhavn the species occurs to at least 400 m alt.

Both adults and larvae feed on mosses and are often found together. Lindroth (1931) observed the species eating *Philonotis tomentella*.

In Iceland and the rest of Europe, *B. fasciatus* is associated with meagre, dry and sandy ground, in most cases covered with different kinds of heath vegetation rich in mosses. In Iceland it ascends to 1300 m alt., and in the Torneträsk area (northern Sweden) to 1150 m alt. (Lindroth 1931, Lindberg 1933, Brundin 1934, Brinck & Wingstrand 1951, Larsson & Gigja 1959).

Life cycle

Imagines have been collected from 3 May to 29 August, larvae in all three instars from late May to late August, third instar also in the beginning of September and even on 1 October, and pupae during the interval 26 June-7 August. On 1 August 1973 at Kapisillit, Godthåbsfjord, I took a sample containing two imagines and six larvae in the instars I:3, II:2, III:1.

These data seem to show that both adults and larvae (in all stages) hibernate, and that pupation takes place during the middle of the summer. The life cycle thus appears to be fairly indefinite, and more than one hibernation in each generation cannot be excluded.

In spite of very similar phenological data from Iceland, Larsson & Gigja (1959: 158) concluded: "There is no doubt that the generation is normally annual, and that hibernation takes place in the imago stage, probably in the pupal cell".

Dermestidae

Dermestes lardarius Linnaeus, 1758

(Fig. 51,c)

Narsalik 1885, Qaqortoq/Julianehåb 1900, Ivittuut 1931, 1938, Qeqertarsuaq/Godhavn 1936, Ammassalik 1936. Undoubtedly introduced.

Distribution: Cosmopolitan.

Habitat and biology: Synanthropic pest in stores of animal matter. Henriksen & Lundbeck (1917) pointed to the strange fact that Dermestidae have never been recorded from skin-stores in Greenland.

Attagenus pellio (Linnaeus, 1758)

(Fig. 52,a)

One specimen without locality. Undoubtedly introduced.

Distribution: Cosmopolitan.

Habitat and biology: The larva feeds on dry animal matter (synanthropic pest); the adult is found outdoors in flowers of, e.g., *Crataegus*.

Reesa vespulae (Milliron, 1939)

(Fig. 52,b)

Upernaviarsuk 1985. Undoubtedly introduced. Parthenogenetic.

Distribution: North America, introduced to Scandinavia.

Habitat and biology: Synanthropic pest in dry plant and animal matter.

Anthrenus museorum (Linnaeus, 1761)

(Fig. 52,c)

Ilua (Aappilattoq?) 1890. Undoubtedly introduced.

Distribution: Palaearctic Region.

Habitat and biology: The larva is a synanthropic pest in dry animal matter; the adult is found outdoors in flowers of, e.g., *Crataegus, Filipendula,* Umbelliferae.

Lyctidae

Lyctus brunneus (Stephens, 1830)

(Fig. 52,l)

Ella Ø, Kong Oscar Fjord, 1934. Introduced with expedition goods.

Distribution: Cosmopolitan, originating from Central America.

Habitat and biology: The larva lives in exotic timber.

Anobiidae

Ernobius mollis (Linnaeus, 1758)

(Fig. 52,d)

Qaqortoq/Julianehåb 1899, Aasiaat/Egedesminde ?, Ammassalik 1933. Introduced.

Distribution: Palaearctic Region, also introduced to North America.

Habitat and biology: Living in and feeding on the bark of conifers. Synanthropic in the northern area of distribution.

Anobium punctatum (Degeer, 1774)

(Fig. 52,e)

Nuuk/Godhåb 1942. Introduced.

Distribution: Palaearctic Region, introduced to North and South America.

Habitat and biology: Living in and feeding on dry wood of both deciduous trees and conifers, a pest indoors in furniture and other wooden objects. In temperate Europe also found outdoors.

Ptinidae

Ptinus fur (Linnaeus, 1758)

(Fig. 52,g-h)

Ilua (Aappilattoq?) 1890, Ammassalik 1936. Undoubtedly introduced.

Distribution: Almost cosmopolitan.

Habitat and biology: Partly synanthropic. Feeding on a variety of dry plant and animal matter.

Ptinus tectus Boieldieu, 1856

(Fig. 52,k)

Paamiut/Frederikshåb 1940, Nuuk/Godthåb 1942, 1949, Saqqaq 1947, Qaqortoq/Julianehåb 1948, Ivittuut 1950. Undoubtedly introduced.

Distribution: Origin in Australia, now cosmopolitan.

Habitat and biology: Synanthropic, living in and feeding on a variety of dry plant and animal substances. In Greenland found in skin clothing, shops and stables.

Ptinus raptor Sturm, 1837

(Fig. 52,i-j)

Nuuk/Godthåb 1944. Undoubtedly introduced.

Distribution: North and Central Europe.

Habitat and biology: Synanthropic, in plant debris. In temperate Europe partly outdoors.

Trogositidae

Tenebroides mauritanicus (Linnaeus, 1758)

(Fig. 51,d)

Nuuk/Godthåb 1944. Introduced.

Distribution: Cosmopolitan.

Habitat and biology: Synanthropic in stored products, carnivorous on other grain and flour pests.

Malachiidae

Malachius aeneus (Linnaeus, 1758)

(Fig. 51,a)

Nuuk/Godthåb 1944. Accidental introduction.

Distribution: Circumpolar, boreal.

Habitat and biology: Carnivorous, in flowers.

Cucujidae

Oryzaephilus surinamensis (Linnaeus, 1758)

(Fig. 53,b)

Nuuk/Godthåb 1944, Nanortalik 1981. Undoubtedly introduced.

Distribution: Cosmopolitan.

Habitat and biology: Synanthropic. The larva lives in and from stored vegetable products. Adults also feed on animal substances.

Cryptophagidae

Cryptophagus acutangulus Gyllenhal, 1827

(Fig. 53,c)

According to Henriksen & Lundbeck (1917) and Munster (1924), found in Hekla Havn (70°27'N) and Foulke

Fjord (78°18′N) on the west coast. Presumably introduced with expedition goods.

Distribution: Circumpolar.

Habitat and biology: Of sporadic occurrence outdoors in northern Scandinavia, exclusively synanthropic in Iceland (Larsson & Gigja 1959). Both larva and imago are found on mouldy objects and feed on fungal hyphae and spores.

Cryptophagus lapponicus Gyllenhal, 1827

(Henriksen 1939: *Cryptophagus validus* Kraatz)
(Fig. 53,d)

Ilua (Aappilattoq?) ?1890, Qaqortoq/Julianehåb 1901, 1902. Introduced.

Distribution: Northern Palaearctic Region.

Habitat and biology: In Greenland found in dried fruits, otherwise reported from nests of birds and mammals. Presumably feeding on moulds.

Caenoscelis ferruginea (Sahlberg, 1820)

Taxonomy and synonymy: see Arnett 1983.

Lindroth (1957: 263) identified Greenlandic specimens as *C.? cryptophaga* Reitter, which he assumed synonymous with *C. macilenta* Casey. S. Lundberg, Umeå, Sweden, has recently revised the Greenlandic material.

Identification

Elongate oval, yellow-red, hairy, fairly shining. Antennae very strong, clubbed. A fine groove along the side margins of pronotum separates a narrow rim. Length about 2 mm.

Dynamics: The species is fully winged.

General distribution

Circumpolar, temperate to low arctic. Central and northern Europe to northernmost Scandinavia, but absent from the Faeroes and Iceland. In North America found in Alaska and the eastern U.S.A.

Distribution in Greenland (map p. 54).

C. ferruginea has only been found in one locality: Kapisillit in Godhåbsfjord (18 July 1950, C. Vibe leg.; seven specimens).

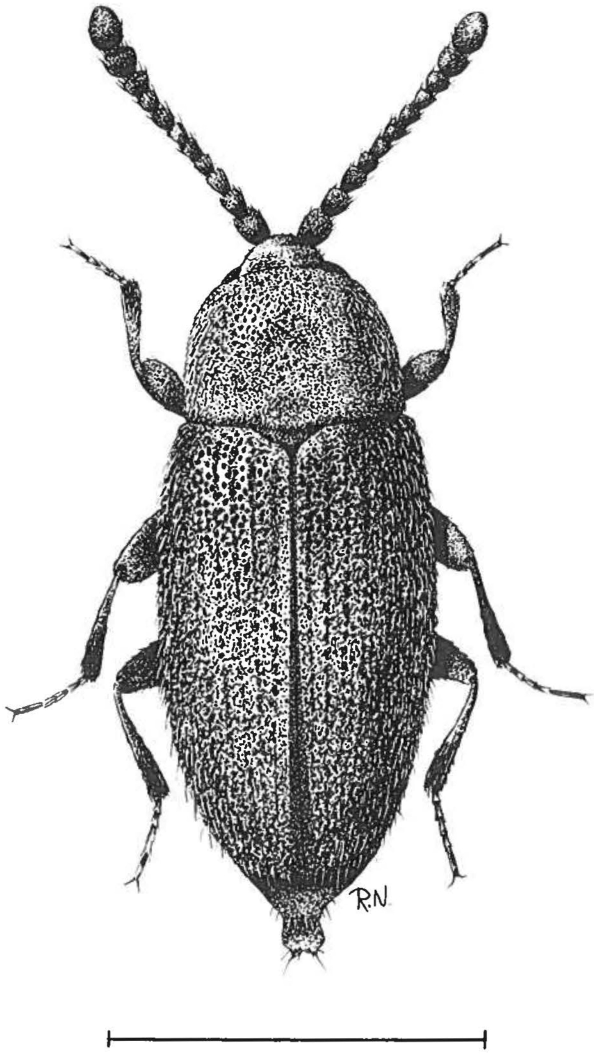


Fig. 31. *Caenoscelis ferruginea* (Sahlberg). Scale: 1 mm.

Habitat and notes on biology

The Greenlandic specimens were collected by sweeping a dry, grassy, south-facing slope (Vibe 1981).

In Scandinavia the species is mostly connected with trees, found, e.g., under bark and in decaying stumps (Strand 1946, V. Hansen 1951), but has also been collected in hay in a barn and by sweeping a meadow (Jansson & Palm 1936). It presumably feeds on moulds.

Atomaria sp.

According to Buckland (1986, in litt.), one subfossil specimen belonging to this genus was collected in a Norse farm at Kilaarsarfik (Sandnæs) at Ameralla fjord east of Nuuk/Godthåb. The species was undoubtedly introduced by the Norsemen and later became extinct.

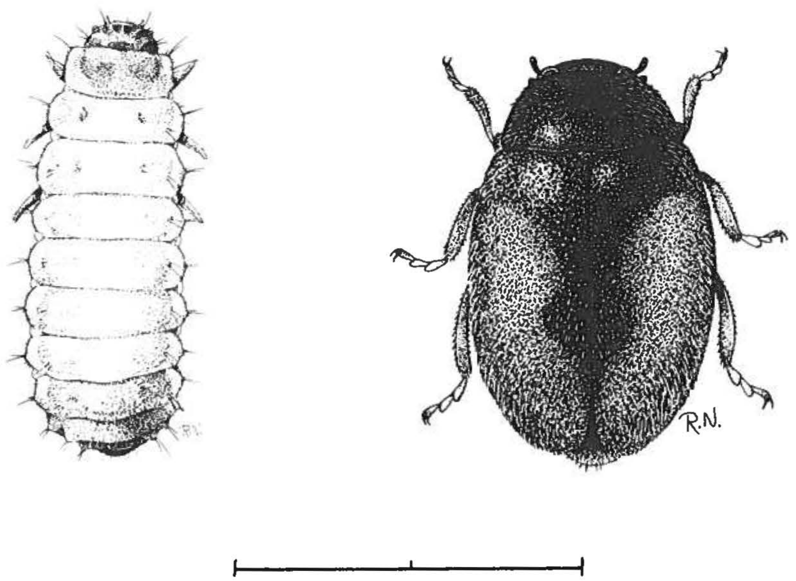


Fig. 32. *Nephus redtenbacheri* (Mulsant). Scale: 2 mm.

Coccinellidae

Nephus redtenbacheri (Mulsant, 1846) var. *limonii* (Donisthorpe, 1903)

(Henriksen 1939: *Scymmus (Nephus) limonii* Donis.)

Taxonomy and synonymy: see Henriksen & Lundbeck (1917).

Lindroth (1929) revised the Greenlandic material of *Nephus (Scymmus)* and stated that it belonged to *S. limonii* Donisthorpe. Later on (1931) he concluded that *S. limonii* is merely a melanic variety of *S. redtenbacheri* Mulsant. This view was followed by Larsson & Gigja (1959), whereas Lindroth et al. (1973) once again used *S. limonii* for Icelandic specimens, regarding it "undecided whether *limonii* is a distinct species or a form (probably sbsp.) of *redtenbacheri* Muls.". Lindroth's argumentation from 1931, however, still appears convincing and valid, so that *limonii* is here given the rank of a variety.

Identification

A small, hairy ladybird. Antennae very short (length less than half width of head). A characteristic black and orange-brownish pattern of elytra. Length about 2 mm.

Variation and dynamics

The melanic *N. r. limonii*, with dark legs, antennae and palps, has only been found in England, Iceland and Greenland.

The hind wings are always fully developed and functional.

General distribution

Palaearctic, temperate to subarctic.

N. redtenbacheri has a wide distribution in northern and Central Europe and mountaneous areas of southern Europe and northern Africa. Northwards it reaches 70°N in Norway. The species is absent from the Faeroes.

Distribution in Greenland (map p. 54)

N. redtenbacheri seems to have a very limited Greenlandic distribution, confined to the subarctic, eastern part of Qaqortoq/Julianehåb and Narsaq Districts. Most finds are from the inner parts of Tunulliarfik and Igaliku Fjords, and in addition the species has been found in the Qinngua valley at Tasermiut fjord and at Anorliuitsoq, Pamialluk island, in the Kap Farvel area.

N. redtenbacheri might have been introduced by the Norsemen (see p. 89).

Habitat and notes on biology

N. redtenbacheri was considered very rare by Henriksen & Lundbeck (1917). Pitfall collecting has recently shown (P. Nielsen; see Table 9) that the species occurs fairly abundantly in a number of different plant communities, including birch coppices, hygrophilous vegetation along water courses, grasslands, and dry heaths. A remarkably high number was encountered at 350 m alt. on a south-facing, mainly grass-covered slope at Qassiarsuk, where ten pitfalls during 25 days collected 49 specimens (Tables 9, 11). In the Kap Farvel area, larvae were taken in a dry *Empetrum* heath and in the grass-dominated vegetation of an old settlement (Table 10).

In Iceland the species lives on rather dry ground, most often grassfields, but it has also been collected in

Dryas heaths and on sandy river banks. It is often found under stones, and is regularly associated with Coccoidea (*Pseudococcus thulensis* Green, *Rhizococcus granulatus* Green), on which it undoubtedly feeds (Lindroth 1931, Lindroth et al. 1973, Larsson & Gigja 1959). – In Greenland *N. redtenbacheri* has often been found together with *Orthecia cataphracta* Olafsen, and probably it feeds mainly on this species.

On the European continent *N. redtenbacheri* is found in more humid situations: heaths rich in mosses, bogs, meadows, along edges of woods and in open, light woods with a rich ground vegetation (Brundin 1934, Larsson & Gigja 1959).

Life cycle

Imagines have been collected rather evenly during the interval 23 June to 5 September, but with four specimens found as early as 19 and 22 May (Narsarsuaq). The few finds of larvae are from the middle of July (Table 10). Thus a life cycle similar to that of *Coccinella transversoguttata* is suggested: Hibernation as adult and larval development during summer. This is in accordance with the conclusion arrived at by Larsson & Gigja (1959) regarding the species in Iceland.

Coccinella transversoguttata Falderman, 1835

Taxonomy and synonymy: see Brown (1962), Belicek (1976), Arnett (1983); also Henriksen & Lundbeck (1917).

Identification

The Greenlandic ladybird is unmistakable. Length about 4–6 mm.

Variation and dynamics

The colour pattern of the species is relatively constant in Greenland. According to Brown (1962) the Greenlandic form should be given subspecies rank, *C. t. ephippiata* Zetterstedt, 1838, differing from the North American form in generally smaller size, high incidence of sublateral spot on the elytra (90%), more rounded median and apical spots, and slight differences in the shape of the median lobe of the male genitalia.

However, only 52 of 163 Greenlandic specimens investigated had a sublateral spot (between the scutellar transverse band and the median, discal, spot). The size of this spot is highly variable, from minute to about half the size of the median spot, sometimes coherent with the scutellar transverse band. Rarely the median and subapical spots are confluent (Fig. 33), or the scutellar band is incomplete. Sometimes the general reddish orange colour is very dark, brownish. No geographical pattern in the variation described is evident from the present material.

The hind wings are always fully developed, and the species is quite often seen flying short distances, especially when disturbed.

General distribution

Holarctic, temperate to low arctic. Widely ranging in North America and Siberia, but absent from Europe. Transcontinental in temperate and subarctic North America, but not found beyond tree limit (Brown 1962). Henriksen & Lundbeck (1917) erroneously mentioned the species from Lapland as var. *quinquenotata* Kirby. Distribution map: Belicek (1976: fig. 139, North America).

Distribution in Greenland (map p. 54)

C. transversoguttata has the widest distribution of the terrestrial Greenlandic beetles, ranging from Upernavik in the northwest to Kejser Franz Joseph Fjord in the northeast. It is most common in inland areas with dry, warm summers. The species has been found as subfossils in Norse farms in the Nuuk/Godthåb area (Buckland et al. 1983; Buckland 1986, in litt.).

Habitat and notes on biology

In Greenland *C. transversoguttata* appears to be rather eurytopic, found in almost any kind of vegetation, and up to 600 m alt. It is most abundant in dry heaths with *Betula nana* and *Salix glauca*, where adults and larvae hunt for psyllids and aphids (Vanhöffen 1897, Koponen 1978; see Tables 9, 10). In Andrée Land, Northeast Greenland, P. Henrichsen (pers. commun.) found *C. transversoguttata* very frequently hiding in the shed wool of muskoxen (August, 1978).

In North America the species is found in mixed parkland and coniferous forests, foraging on different Aphidoidea on a variety of plant species (*Pinus, Populus, Circium, Trifolium, Epilobium*), and on psyllids on *Alnus* (Belicek 1976).

Life cycle

Imagines have been collected throughout the summer (16 May-9 October), but one find was as early as 6 April (Qaqortoq/Julianehåb, 1901). The larval stages appear to be confined to a relatively short period (10 July-20 August), but de Lesse (1950) captured a larva as early as 27 June (Eqe, Disko Bugt). Pupae have been collected on 23 and 29 July. A sample of 67 specimens from Anorliuitsoq, Pamialluk island, Kap Farvel area from 19–20 July 1970 showed the following composition: Larvae I: 7%, larvae II: 13%, larvae III: 24%, larvae IV:

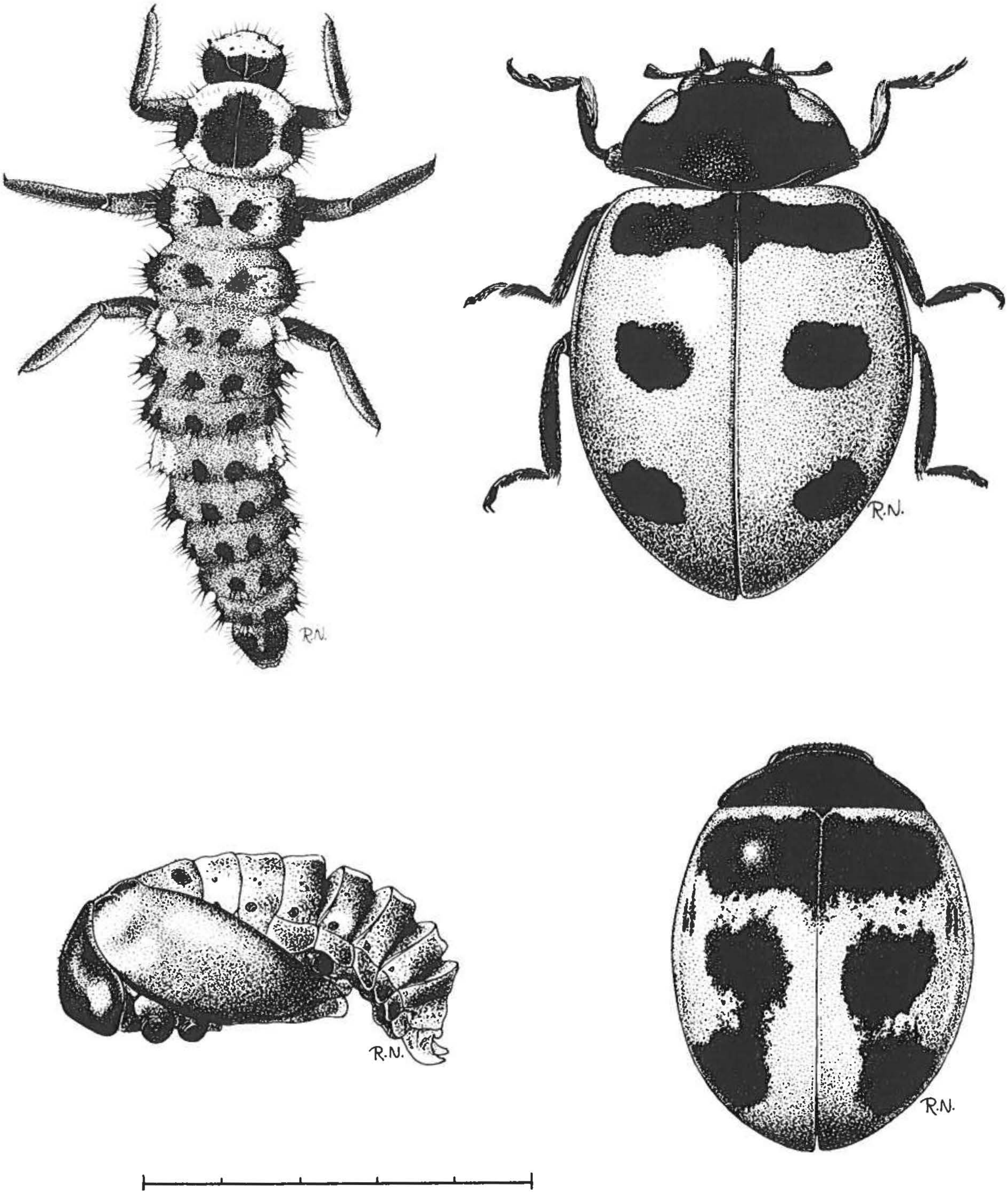
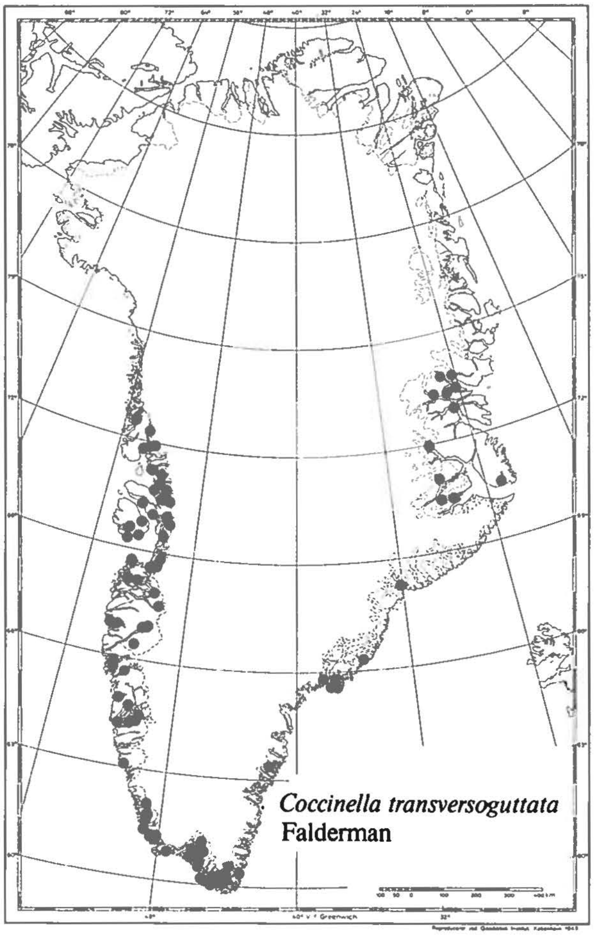
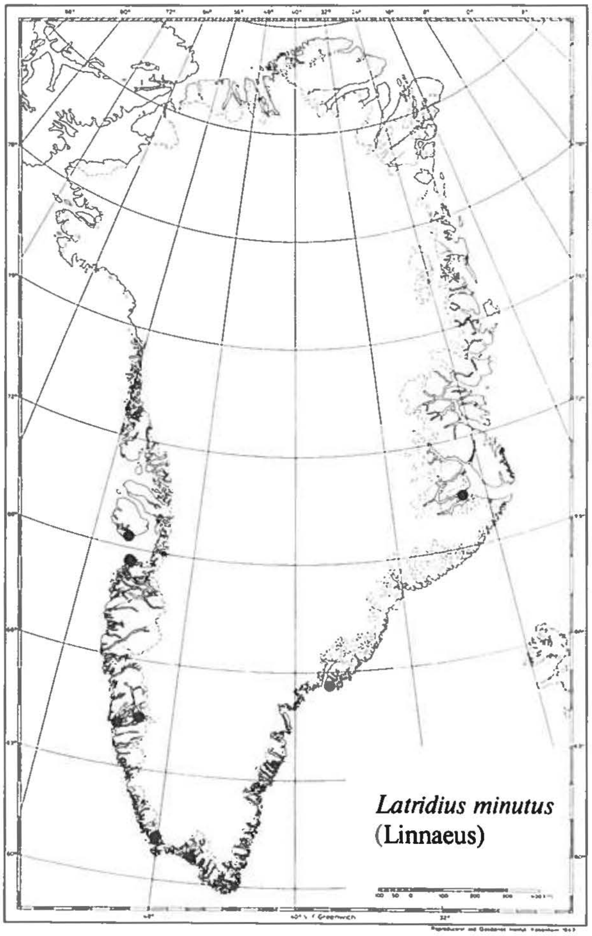
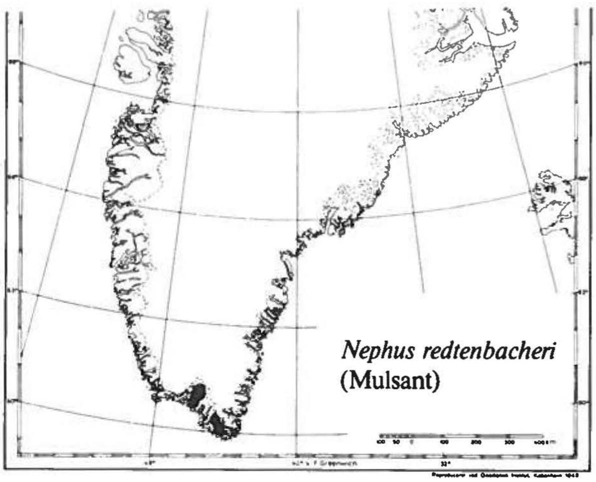
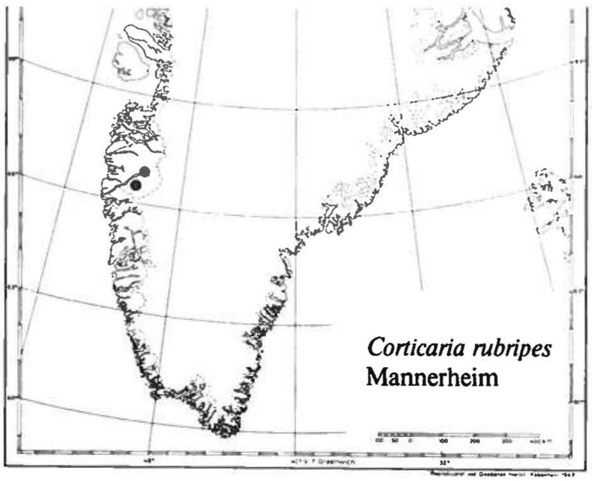


Fig. 33. *Coccinella transversoguttata* Falderman. One variety of the adult colour pattern is shown (with sublateral spots and confluent median and subapical spots). Scale: 5 mm.


Coccinella transversoguttata
Falderman


Latridius minutus
(Linnaeus)


Nephus redtenbacheri
(Mulsant)


Corticaria rubripes
Mannerheim

49%, adults: 7% (see Table 10). Copulation has been observed on 28 June (Hale Carpenter & Holm 1939).

Evidently *C. transversoguttata* in Greenland hibernates as adult and reproduces in early summer of the following year. The new generation reaches the adult stage well before winter, spending the warmest part of the summer as larvae.

Latridiidae

Latridius minutus (Linnaeus, 1767)

(Henriksen (1939): *Enicmus minutus L.)*

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931), Hinton (1945), Arnett (1983: *Microgramme minutus* L.).

Identification

The small size (length about 1.5–2.5 mm) and the shape of pronotum renders this species unmistakable among Greenlandic beetles. The larva is described by Hinton (1945).

Variation and dynamics

A highly variable species. The hind wings are fully developed and functional.

General distribution

Almost cosmopolitan. In Europe to northernmost Norway, the Faeroes, Iceland.

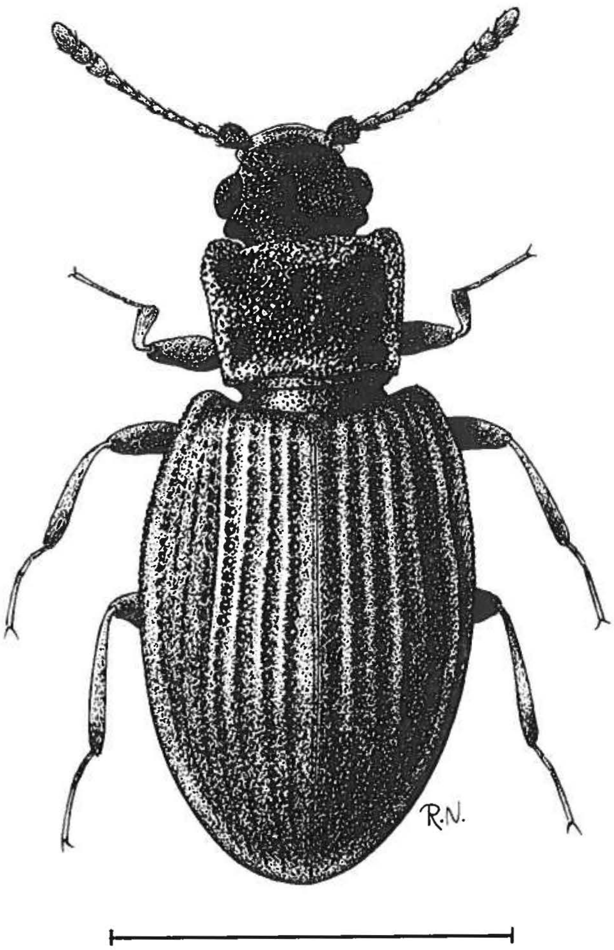


Fig. 34. *Latridius minutus* (Linnaeus). Scale: 1 mm.

Distribution in Greenland (map p. 54)

Scattered occurrences in the southern part of the country, northwards to Qeqertarsuaq/Godhavn on the west coast and to Hekla Havn, Danmark Ø, on the east coast.

L. minutus appears to have had a long history in Greenland. Lundbeck (1896) and Henriksen & Lundbeck (1917) rendered probable that "*Silpha pedicularis*" of O. Fabricius (1780) is identical with *L. minutus,* and the species has been found in abundance as subfossils in excavated Norse farms in the Nuuk/Godthåb District (Buckland et al. 1983; Buckland 1986, in litt). Nielsen (1907) assumed that *L. minutus* might be original in Greenland.

Habitat and notes on biology

L. minutus is generally considered highly synanthropic (Lindroth 1931, Larsson & Gigja 1959). In Greenland most specimens have been collected inside buildings (e.g., in a stable at Ivittuut and among victuals in a shop in Nuuk/Godthåb), but the species has also been caught far from human habitations (for instance in pitfalls at Saqqaq about 2 km from Kapisillit, Godthåbsfjord, and at Tasiusaq, Ammassalik, in moss, 200 m alt.). There is, however, always the possibility that *L. minutus* has been transported in expedition goods by the collector (most likely for the find at Hekla Havn by Deichmann, 1892). Larsson & Gigja (1959) stated that since the species commonly flies, it may occasionally be taken far from inhabited places, and that the immense distribution of the species depends to a great extent on its inclination to fly in combination with dispersal by wind. However, in Iceland overwintering can only take place under synanthropic conditions.

In Scandinavia the species has frequently been collected in the wild. Brundin (1934) found it to be quite numerous in subarctic Lapland (Torneträsk), especially on *Polyporus* spp. and among plant debris in birch forests. Fjellberg (1972) collected the species in Hardangervidda in an alder wood (170 m alt.), on a slope with dense vegetation (490 m alt.), and in a dry, alpine meadow (1275 m alt.). The majority of the individuals collected in the Faeroes by Bengtson (1981) were from a meadow rich in *Rumex*.

L. minutus is associated with rotting and mouldy vegetable matter and feeds exclusively on moulds, hyphae as well as spores (Hinton 1945, Larsson & Gigja 1959).

Life cycle

In Greenland the species has been collected in buildings from 4 March to 25 August. Here it presumably reproduces almost continuously like other synanthropes. The remarkable find at Ammassalik was as early as 24 May, the other outdoor collections date from July. Larvae and pupae are not known from Greenland.

Dienerella filum (Aubé, 1850)

(Fig. 53,f)

Thule (Dundas) 1940, Upernaviarsuk 1985. Undoubtedly introduced.

Distribution: Cosmopolitan.

Habitat and biology: Synanthropic. In mouldy plant and animal material, feeding on moulds.

Thes bergrothi (Reitter, 1880)

(Henriksen 1939: *Lathridius (Thea) bergrothi* Reitt.)
(Fig. 53,e)

Qaqortoq/Julianehåb 1898; Washington Land, Vardefjeld, 1941.

Undoubtedly introduced.

Distribution: North and Central Europe.

Habitat and biology: Synanthropic, in mouldy places; in temperate areas also outdoors in plant debris. Feeding on moulds.

Corticaria serrata (Paykull, 1798)

(Fig. 53,g)

Kuummiut, Ammassalik District, 1933; Nuuk/Godthåb 1959 (incomplete specimen, found in the tidal zone). Probably introduced.

Distribution: Cosmopolitan.

Habitat and biology: In mouldy plant debris both indoors (stables etc.) and outdoors, feeding on moulds.

Corticaria rubripes Mannerheim, 1844

(Henriksen 1939: *Corticaria linearis* Payk.)

Taxonomy and synonymy: see Silfverberg (1979), Arnett (1983).

Identification

Of similar size as *Latridius minutus* (length about 2–2.5 mm), but readily distinguished by the rounded pronotum and the more elongate shape. From *C. serrata* it is separated by the small, blunt spines along the side margins of pronotum (the spines are very prominent and pointed in *C. serrata*). The larva is undescribed, but larva and pupa of *C. fulva* (Comolli) are described and figured by Hinton (1945).

Dynamics: The hind wings are always fully developed.

General distribution

Palaearctic, temperate to low arctic: Northern and Central Europe (absent from the Faeroes and Iceland), southwards mainly in mountain coniferous forests; Siberia, eastwards to Lena Valley and Transbaikal.

Distribution in Greenland (map p. 54)

The Oxford University Greenland Expedition 1936 collected one specimen at Camp Lloyd (Strømfjordshavn) at the head of Kangerlussuaq/Søndre Strømfjord (Carpenter 1938). In 1984 I caught 9 specimens in pitfall traps about 5o km south of this locality, in Arnangarnup Qoorua. The species has furthermore been found as subfossils in an excavated Norse farm at Nipaatsoq, Ameralla fjord east of Nuuk/Godthåb (Buckland et al. 1983).

Habitat and notes on biology

At Camp Lloyd *C. rubripes* was found in moss in grassland on a silt moraine (Carpenter 1938). In Arnangarnup Qoorua the pitfalls were placed along a stream bordered by relatively luxuriant, varied vegetation, including *Salix glauca* coppice.

In Scandinavia the species has been collected by sifting foerna in forests, in spruce debris on the ground, under bark of both conifers and deciduous trees, and on *Polyporus* sp. It also occurs synanthropically, e.g., in old hay in barns and in cow and horse manure (Lind-

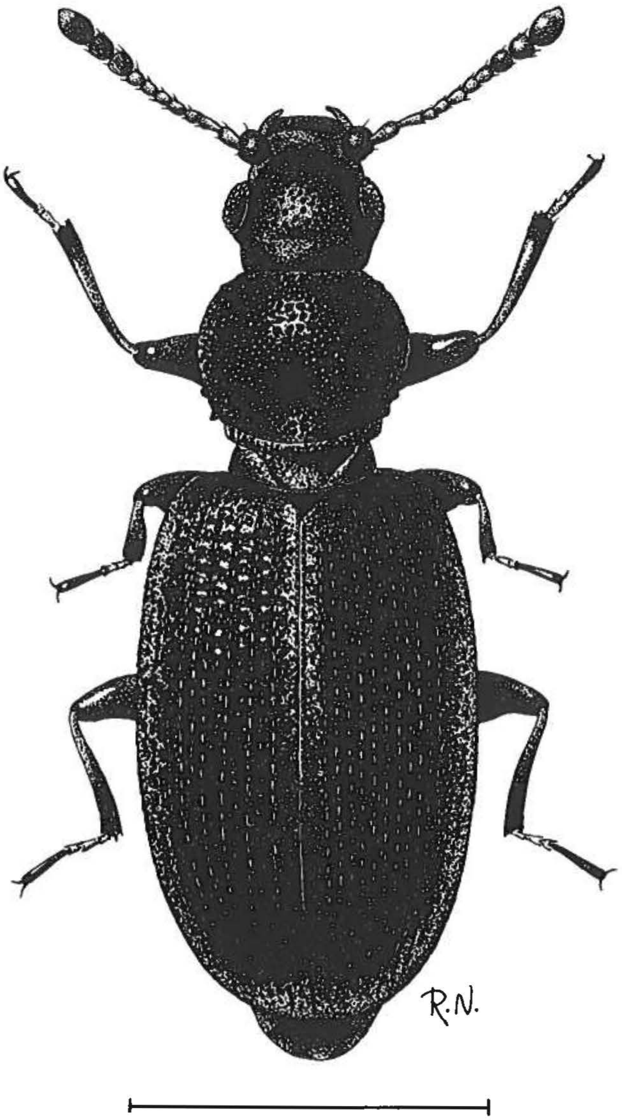


Fig. 35. *Corticaria rubripes* Mannerheim. Scale: 1 mm.

berg 1927, Brundin 1934, Jansson & Palm 1936, Strand 1946, V. Hansen 1951).

The species feeds on moulds.

Life cycle

The two Greenlandic finds date from 13 July (Arnangarnup Qoorua) and 9 August (Camp Lloyd). Most Latridiidae pass the winter as adults.

Tenebrionidae

Tribolium destructor Uyttenboogart, 1934

(Fig. 52,f)

Nuuk/Godthåb 1963. Introduced.

Distribution: Probably cosmopolitan.

Habitat and biology: Synanthropic in stores of flour and other crushed vegetable products; both larvae and imagines living from the substratum.

Tenebrio obscurus Fabricius, 1792

(Fig. 54,a)

Nuuk/Godthåb 1944. Introduced.

Distribution: Cosmopolitan.

Habitat and biology: Synanthropic; both larvae and adults living in and feeding on stored grain and flour.

Cerambycidae

Tetropium castaneum (Linnaeus, 1758)

(Fig. 54,b)

West Greenland, without locality. Introduced with timber.

Distribution: Palaearctic Region.

Habitat and biology: Larva in conifers, mostly dying spruce.

Gracilia minuta (Fabricius, 1781)

(Fig. 51,e)

Qaqortoq/Julianehåb 1951. Introduced with timber.

Distribution: Europe; introduced to U.S.A.

Habitat and biology: Larva in wood of different deciduous trees, e.g., *Salix, Betula, Quercus*.

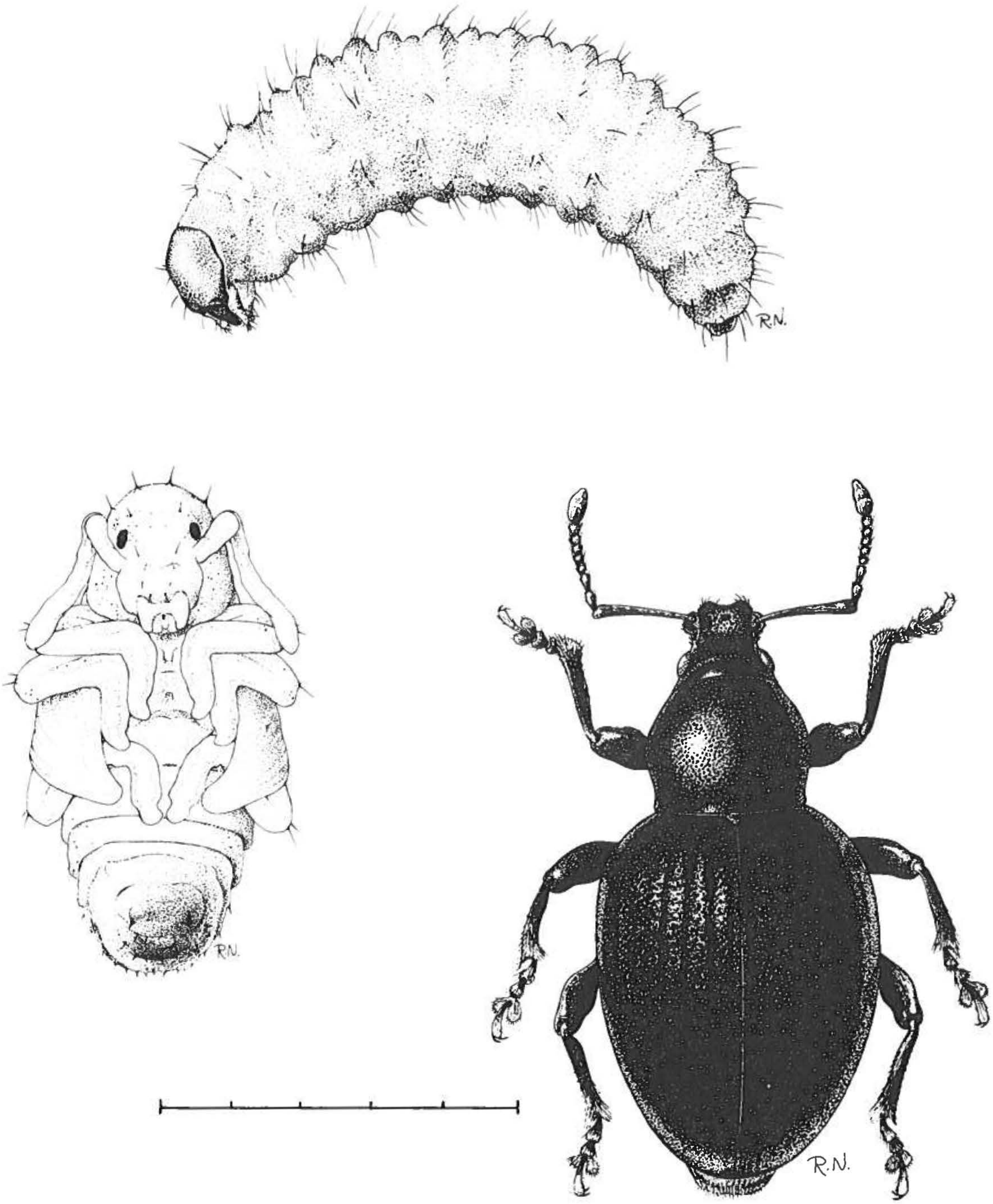


Fig. 36. *Otiorhynchus arcticus* (O. Fabricius). Scale: 5 mm.

Molorchus minor (Linnaeus, 1758)

(Fig. 54,f)

Qeqertarsuaq/Godhavn 1924. Introduced with timber.

Distribution: Palaearctic Region.

Habitat and biology: Larva in conifers, especially dead spruce. Adults in flowers of, e.g., *Crataegus* and Umbelliferae.

Callidium violaceum (Linnaeus, 1758)

(Fig. 54,c)

Ivittuut 1888, Qeqertarsuaq/Godhavn 1924, 1933. Introduced with timber.

Distribution: Palaearctic Region; introduced to North America.

Habitat and biology: In northern Europe synanthropic, a pest in house-timber with bark.

Phymatodes testaceus (Linnaeus, 1758)

(Henriksen 1939: *Callidium variabile* L.)
(Fig. 54,d)

Qaqortoq/Julianehåb 1902. Introduced with timber.

Distribution: Circumpolar, subtropical-temperate.

Habitat and biology: Larva in dead wood, mostly from deciduous trees. Both outdoors and indoors (pest) in Europe.

Xylotrechus colonus (Fabricius, 1775)

(Fig. 54,e)

Nuuk/Godthåb 1942. Probably introduced with timber from U.S.A.

Distribution: North America.

Pogonocherus fasciculatus (Degeer, 1775)

(Fig. 51,f)

Ilua (Aappilattoq?) 1893. Introduced with timber.

Distribution: Palaearctic Region.

Habitat and biology: Larva in dead branches of spruce and pine.

Curculionidae

Otiorhynchus arcticus (O. Fabricius, 1780)

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931), Székessy (1936), Holdhaus & Lindroth (1939), O'Brien & Wibmer (1982).

Identification

Shining black, glabrous. Pronotum with fine, dense punctures. Length about 5.5–8.5 mm. For comments on the larva, see below under "Variation and dynamics".

Variation and dynamics

In Greenland *O. arcticus* exhibits a considerable variation in size (in length from about 5.5 to 8.5 mm). The elytral striae vary from being almost invisible to fairly marked grooves (see Holdhaus & Lindroth 1939).

In contrast to most members of the genus, the species is always bisexual (Suomalainen 1962). A series of pitfall collections from a dry heath at Narsarsuaq, South Greenland (P. Nielsen leg., 1984), showed the sex-distribution seen in Table 4. A significant surplus of males was caught early in the season, but the situation was reversed after the middle of July.

The hind wings are always rudimentary.

The identification of larvae of *Otiorhynchus* presents great difficulties. The larvae of the two Greenlandic species are undescribed, and Lindroth (1931) was not able to separate them.

Table 4. Sex-distribution of *Otiorhynchus arcticus* in pitfall samples from a dry heath at Narsarsuaq, South Greenland (1984, P. Nielsen leg.)

Date	23 June	5 July	16 July	24 July	12 August
Percentage of ♀	61	62	40	39	37
Percentage of ♂	39	38	60	61	63
N	109	24	78	33	43

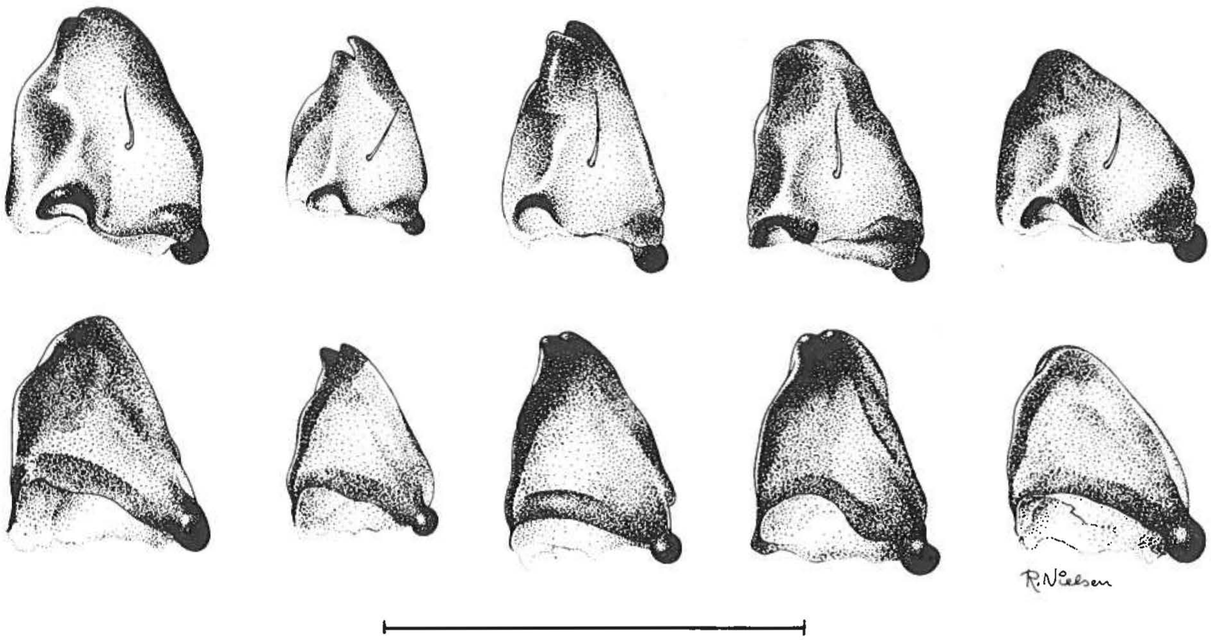


Fig. 37. Mandibles of fourth instar larvae of *Otiorhynchus* (?) *arcticus*. Upper row: right mandibles seen from above; lower row: left mandibles seen from below. Upper and lower mandibles of each pair are from same individual. Scale: 1 mm.

An examination of the material of *Otiorhynchus*-larvae from Greenland in the ZMUC-collections (68 specimens), revealed a great variation in size and shape of the mandibles (Fig. 37). The variation is continuous and approximately normally distributed.

Because *O. nodosus* (p. 63) is absent from nearly the whole southeastern coast of Greenland, larvae found on the northern stretch of this coast must belong to *O. arcticus*. Only one larva has been collected here (Ravn Fjord, Blosseville Kyst, M. Degerbøl leg. 3 July 1932). This is, as regards the mandibles, in all respects placed in the middle of the variation (Fig 38). Thus mandibular characters are of no use in distinguishing between the two species.

However, one larva was found in which the shape of the antennal sockets clearly deviates from that in the remainder of the larvae in being approximately circular, in contrast to the normal compressed, lentil-shape (Fig 39). It has not yet been possible to find other features separating this form from the remainder, but for the present, until further material is obtained, it is assumed that this individual is the only known larva of *O. nodosus*. Of the 137 *Otiorhynchus*-larvae from Iceland in the ZMUC-collections, none have circular antennal basis. The same variation in the mandibles as found in Greenland was established.

General distribution

Palaearctic, boreal to low arctic, boreo-alpine: northern and northwestern coastal Europe, including the British Isles, the Faeroes and Iceland, Scandinavia (absent in Denmark); in U.S.S.R. only coastal tundras of Kola and Kanin. In Central Europe the Pyrenees, Auvergne, the Sudetes and the Carpathians, but not found in the Alps.

Distribution maps: Holdhaus & Lindroth (1939: 253, Scandinavia; plate 17, Europe), Steinböck (1943: Europe), Lindroth (1957: 267, total).

Distribution in Greenland (map p. 64)

In southern Greenland *O. arcticus* is the most frequent and widespread of all beetles (see Tables 9–11). On the west coast it is not found north of Maniitsoq/Sukkertoppen, i.e., not as far north as *O. nodosus* (p. 63). Henriksen (1939) mentioned a collection labelled "Agpat Fjord at Umánaq 70°50', 28.7.32, R. Bøgvad (Z.M.)". This is erroneous. Bøgvad's label refers to a locality called Arnat Fjord in Sehested Fjord (= Ũmánaq kangertiva) at 63°05'N on the east coast. This mistake led a number of authors to comment on a surprisingly northerly occurrence of *O. arcticus* in West Greenland – which is in fact 600 km north of the real known northern limit (Brændegaard 1946, Larsson & Gigja 1959, Lindroth 1957: fig. 41).

On the east coast, however, where *O.nodosus* is present only on the southernmost stretch, *O. arcticus* reaches Miki Fjord and Ravn Fjord on the Blosseville Kyst.

The species has been found as subfossils in excavated Norse farms in the Nuuk/Godthåb area (Buckland et al. 1983; Buckland 1986, in litt.).

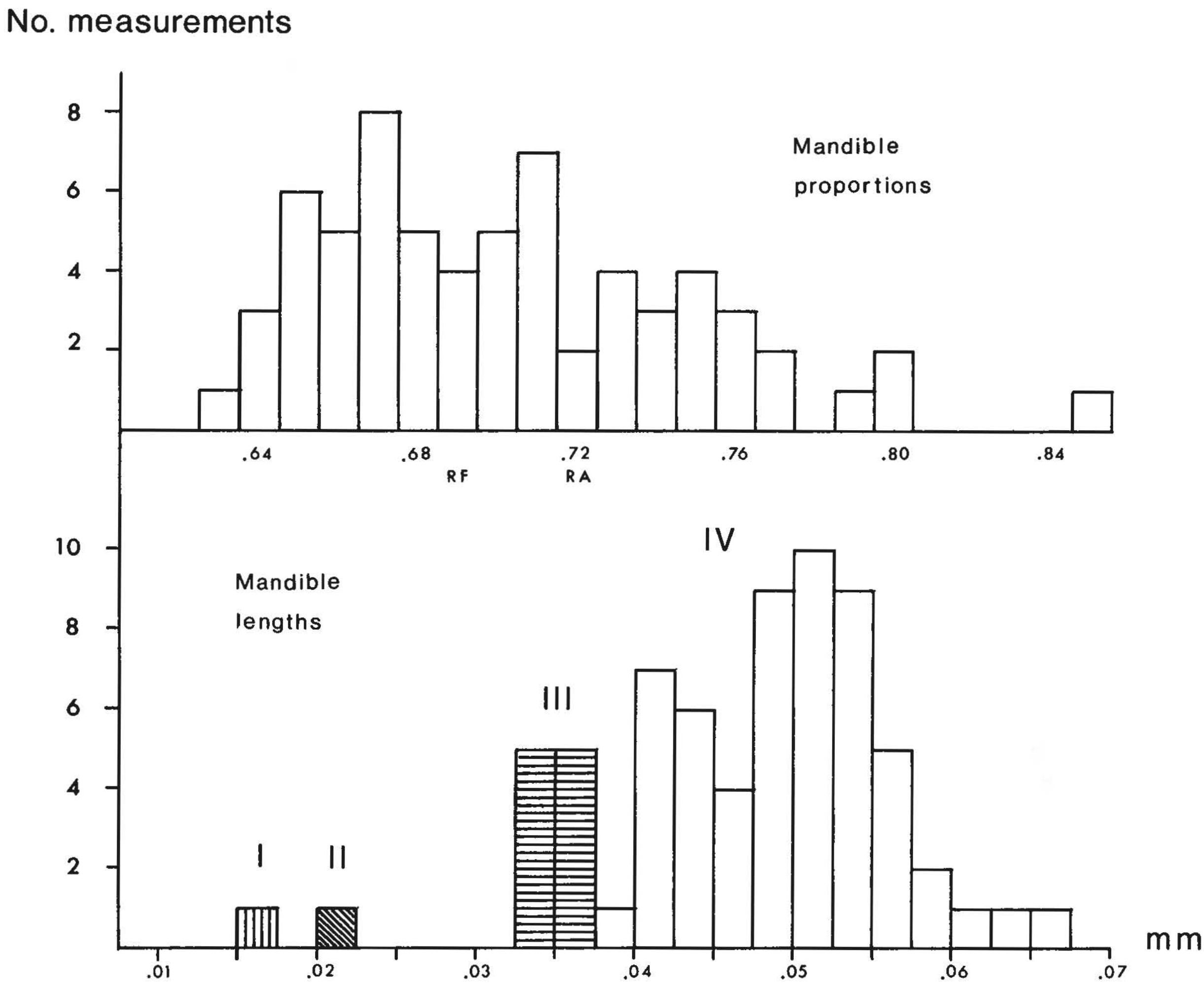


Fig. 38. Variation in shape and length of mandibles in *Otiorhynchus* larvae (total ZMUC material from Greenland). "Mandible proportions" means the ratio between the distance from the ventral condyle to the dorsal fossa, and the distance from ventral condyle to apex, of right mandibles. RF: placing of specimen from Ravn Fjord, East Greenland. RA: placing of specimen with round antennal sockets. I, II, III, IV: first – fourth instar larvae.

Habitat and notes on biology

O. arcticus is highly eurytopic in Greenland, occurring in almost any plant community. Probably the most typical biotope is fairly dry, mixed heaths with *Empetrum hermaphroditum* and *Vaccinium uliginosum* ssp. *microphyllum* (Lundbeck 1891: 121). The species is frequently found at elevations up to about 600 m. Astonishingly, the find from highest altitude is from Lake Fjord, East Greenland, i.e., close to the (known) northern limit of the species.

In most situations *O. arcticus* is found together with *O. nodusus* and by far outnumbering this species (see Tables 9–11), but in some humid biotopes *O. arcticus* may be less frequent or absent. On the other hand, moving towards more dry, exposed localities with sparse vegetation, *O. nodosus* disappears before *O. arcticus* (Tables 9, 11).

In most cases the species has been collected under stones, where it hides during day, and where huge assemblages of "shells" (exoskeletons) may accumulate.

In Iceland Lindroth (1931) characterized *O. arcticus* as the most frequent and widespread of the Icelandic Coleoptera, preferring the dry commons and grass-fields, especially on gravelly and sandy ground, but also occurring in more humid meadows. On shifting sand it may be the only beetle species (but often together with *Amara quenseli* Schönherr), and it is able to tolerate being completely buried in sand (Fristrup 1943). More frequently than any other insect it is found in high-alpine heaths and fell-fields, up to 900 m alt. (Fristrup 1943, Larsson & Gigja 1959).

On the Faeroes *O. arcticus* is widespread and found in most kinds of habitats (West 1937, Bengtson 1981). In Scandinavia the species appears to be closely associated with seashores, where it is found predominantly in the

Fig. 39. SEM micrographs of heads of two *Otiorhynchus* larvae, showing (top) one with the normal lentil-shaped antennal sockets, probably *O. arcticus*, and (bottom) one with approximately circular antennal sockets, which may be *O. nodosus*.

epi-littoral zone. In addition, however, it occurs scattered in alpine heaths (700–800 m alt.), more rarely along water courses in the subalpine zone. Also on the British Isles the species is found both along the coast and inland in the mountains. In Central Europe it is found exclusively above tree-limit. (Lindberg 1933, Brundin 1934, Holdhaus & Lindroth 1939, Steinböck 1943).

C. arcticus is nocturnal. During night and in dark weather the imago climbs different herbaceous plants on which it feeds. Lindroth (1931) observed the species gnawing the leaves of *Polygonum viviparum, Rumex acetosa, Silene acaulis, Plantago maritima, Galium verum, Gentiana campestris, Thymus serpyllum, Taraxacum* sp. and the stem of *Equisetum arvense*. Fristrup (1943) mentioned it feeding on *Honckenya peploides* on the beach in northwestern Iceland.

The larva lives in the soil as a root-feeder and is presumably highly polyphagous (Lindroth 1931). Besides under stones, larvae have been collected in moss and under dead leaves in a birch coppice.

Life cycle

In Greenland adults have been collected from 10 May to 3 October, and T. Bøgvad even collected one specimen on 4 January (1932, Graah Havn, Nuugaarfik). Three pupae were taken on 5 August and newly hatched imagines on 31 July. Larvae have been collected 12 May to 24 September. Nearly all the larvae in the collections of the ZMUC are fully grown, but on 7 August (1950, Kapisillit, C. Vibe leg.) a series of all four instars was collected together (I: 1, II: 1, III: 3, IV: 5). Of ten females collected each of the dates 23 June, 16 July, and 12 August (1984, Narsarsuaq, P. Nielsen leg.), nine, eight, and five, respectively, had ripe eggs in the ovaries, the remainder undeveloped or developing ovaries.

A tentative conclusion based on these confusing phenological data is that both adults and larvae in different stages hibernate. The larvae may hibernate more than once. There is probably no determined reproductive cycle.

According to Larsson & Gigja (1959: 189) in Iceland the species passes the winter both as larvae and adults ("the majority of the imagines very likely die before the onset of winter, though a great many hibernate"). These authors further stated that the possibility that the larvae take, or may take, more than one year to grow up is very great.

Otiorhynchus nodosus (Müller, 1764)

(Henriksen 1939: *Otiorrhynchus dubius* Strøm)

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Lindroth (1931), Holdhaus & Lindroth (1939), O'Brien & Wibmer (1982).

Identification

Black, fairly dull and unevenly hairy. Pronotum coarsely warty-punturate and elytra with marked, wrinkled striae. Length about 7–9 mm. – For comments on the larva, see *O. arcticus* (p. 59).

Variation and dynamics

In Europe *O. nodosus* is highly variable, and some of the varieties were formerly given species rank (Holdhaus & Lindroth 1939). In Greenland there is some variation in size, but not as pronounced as in *O. arcticus*.

O. nodosus is parthenogenetic throughout its northern European area and in Greenland, where only females have been found. In Finland the species has a tetraploid chromosome set; in parts of Central Europe it is triploid, while it has a normal diploid constitution in its bisexual Central European population (Suomalainen 1962, Suomalainen et al. 1976, Lindroth 1954). The ploidy level in Greenland has not been studied.

The hind wings are always rudimentary.

General distribution

Palaearctic (Europe), boreal to low arctic, boreo-alpine: Iceland, the Faeroes, the British Isles, Scandinavia (in Denmark very rare, found only before 1840), northern Russia and part of the Baltic U.S.S.R.; in Central Europe the Alps, the Carpathians, etc.

Distribution maps: Henriksen (1933: 294, Europe), Holdhaus & Lindroth (1939: plate 17, Europe).

Distribution in Greenland (map p. 64)

O. nodosus is very common and almost ubiquitous in the southernmost part of the country, reaching Lindenow Fjord on the southeast coast. On the west coast northwards to Sisimiut/Holsteinsborg, but hitherto it has been found in only three localities north of Nuuk/Godthåb.

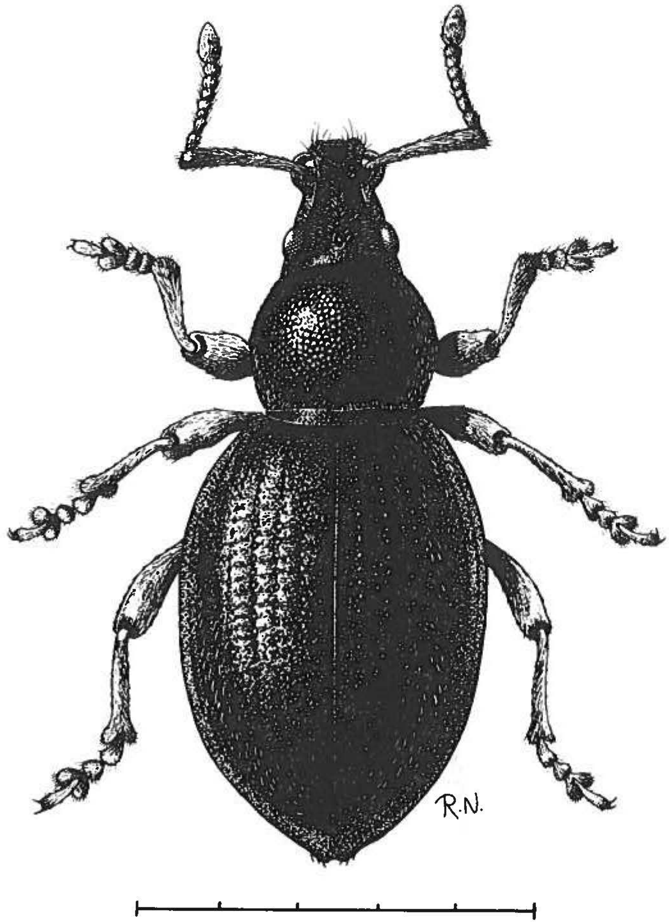


Fig. 40. *Otiorhynchus nodosus* (Müller). Scale: 5 mm.

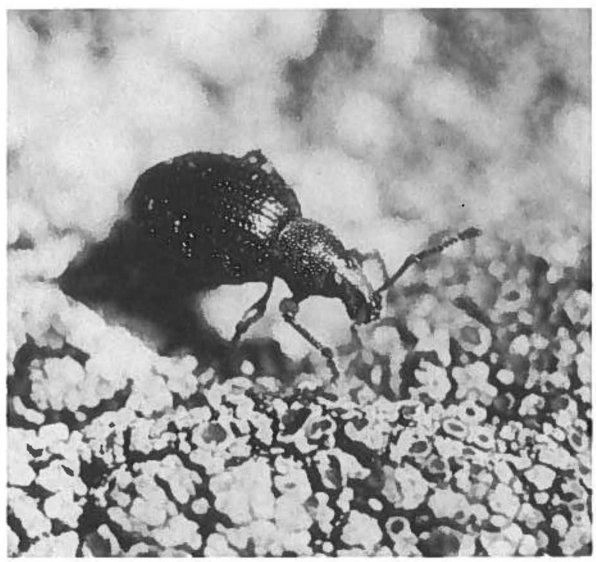
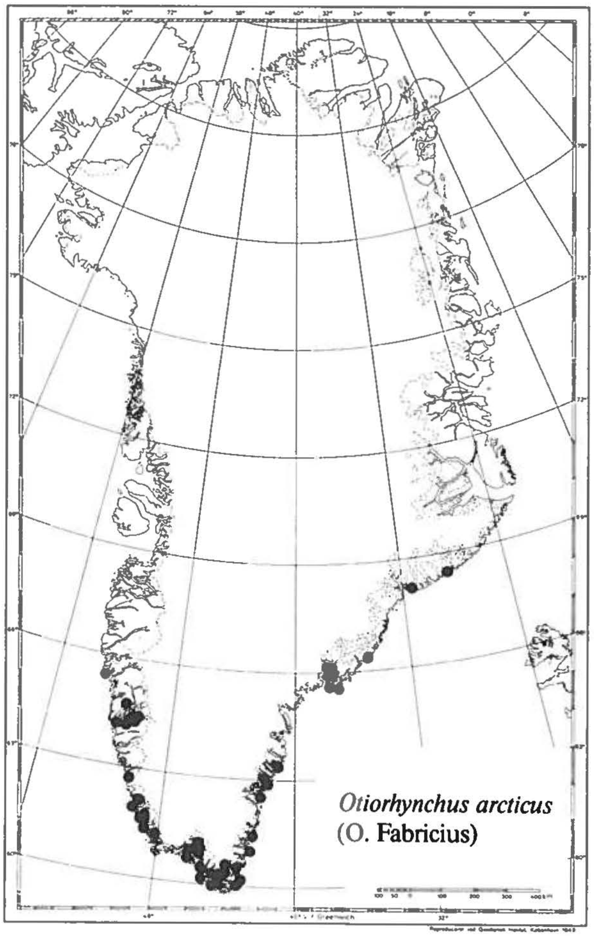
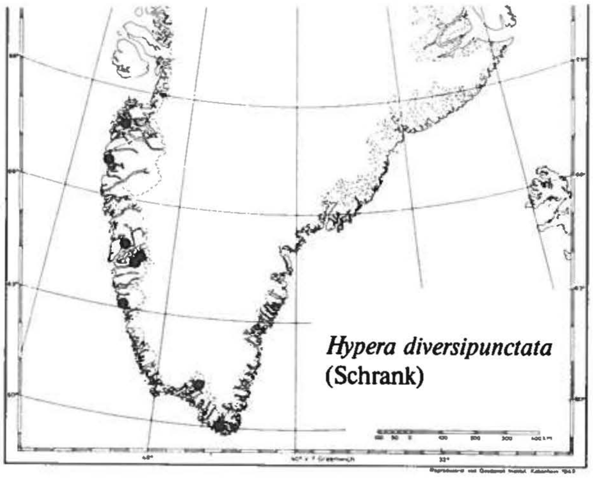


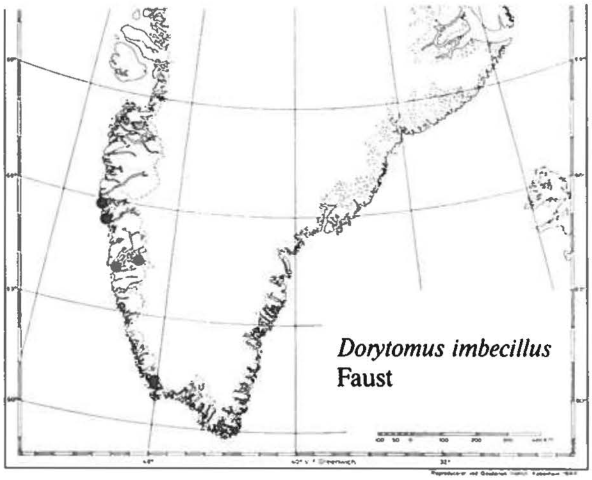
Fig. 41. *Otiorhynchus nodosus* in activity during day. Anorliuitsoq, Pamialluk island, Kap Farvel area.
J.B. phot., July 1970.



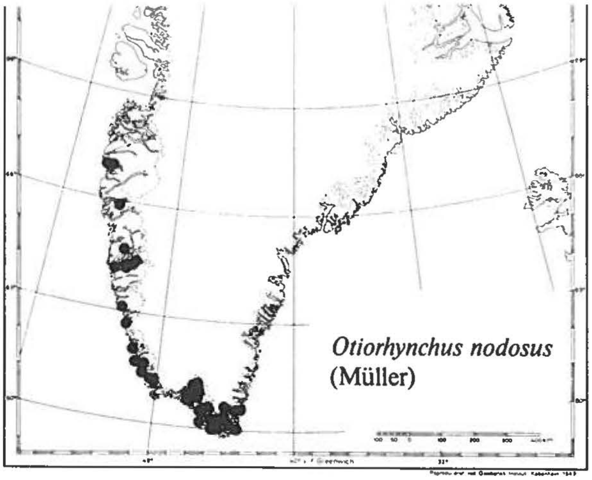
Otiorhynchus arcticus
(O. Fabricius)



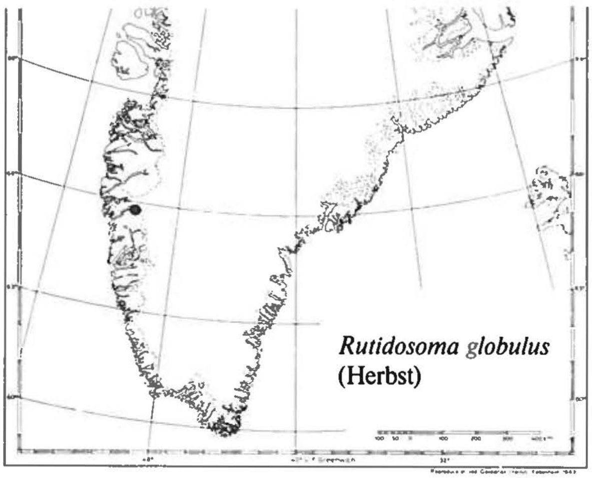
Hypera diversipunctata
(Schrank)



Dorytomus imbecillus
Faust



Otiorhynchus nodosus
(Müller)



Rutidosoma globulus
(Herbst)

Habitat and notes on biology

In Greenland *O. nodosus* is highly eurytopic. Most typically it is found "under stones and in heather in the lowlands and a little up the slopes" (Henriksen & Lundbeck 1917); moreover, under stones in heathlands regular deposits of the resistant exoskeleton are common, together with the "shells" of *O. arcticus*. The species has been collected in almost all kinds of vegetation (see Tables 9–11) and up to 580 m alt. As a rule it is found together with *O. arcticus*, but there is a clear tendency that *O. nodosus* prefers more humid biotopes than *O. arcticus*, and the species is absent or scarce in some fairly dry localities, where *O. articus* is abundant (Table 9).

The single larva at present ascribed to *O. nodosus* (with circular antennal socket; see p. 60 and Fig. 39) was caught in a pitfall at Tupaasat in Kangikitsoq Fjord, Kap Farvel area (J.B. leg. 1970). The vegetation was a rich herbslope-like meadow surrounded by coppices of *Salix glauca* (Fig. 47).

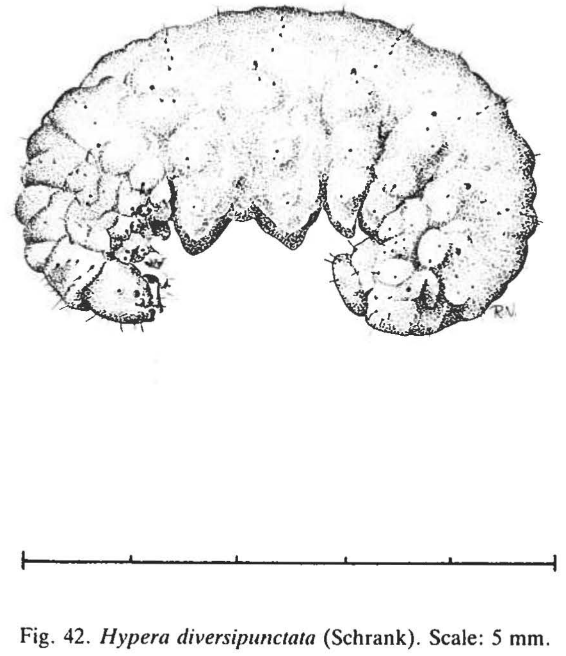
If the assumption that only one larva of this species has been collected is correct, in contrast to 67 of *O. arcticus*, this disproportion needs an explanation, which might be in terms of an ecological difference between the larvae of the two species.

In Iceland *O. nodosus* is very common everywhere, but is primarily found in grass areas (together with *O. arcticus*) in drier situations than those in which it lives on the European continent, but never on very dry, sandy ground devoid of vegetation (Lindroth 1931, Larsson & Gigja 1959). On the Faeroes the species is widespread and found in all biotopes except wetlands and sand dunes (Bengtson 1981).

In Scandinavia and the British Isles the species is mainly alpine and subalpine (ascending to at least 1200 m alt.), but it is also common on the tundras of Kola and Kanin (U.S.S.R.). In the mountains it has been found in a great variety of biotopes: heaths (*Empetrum, Dryas*), grassfields, meadows, coppices, subalpine birch forest, and even on spruce (Jansson 1926, Lindberg 1933, Brundin 1934, Holdhaus & Lindroth 1939, Brinck & Wingstrand 1951). Brinck & Wingstrand (1951: 96) found the species at 950 m alt. in the Virihaure area (Swedish Lapland) on vast snow fields where many specimens crept slowly on the snow, sometimes 20–30 m from the bare ground.

In Europe *O. nodosus* is nocturnal, hiding under stones or in moss during day. In Greenland I once observed a specimen in activity during bright sunshine (Fig. 41). In Iceland the imago climbs the vegetation to feed during the night or in dark weather. It has been observed foraging on leaves of *Rumex acetosa, R. domesticus, Dryas octopetala, Saxifraga hirculus*, and on flowers of *Trifolium repens* (Lindroth 1931).

The larva is presumably a polyphagous root-feeder, living permanently in the soil.



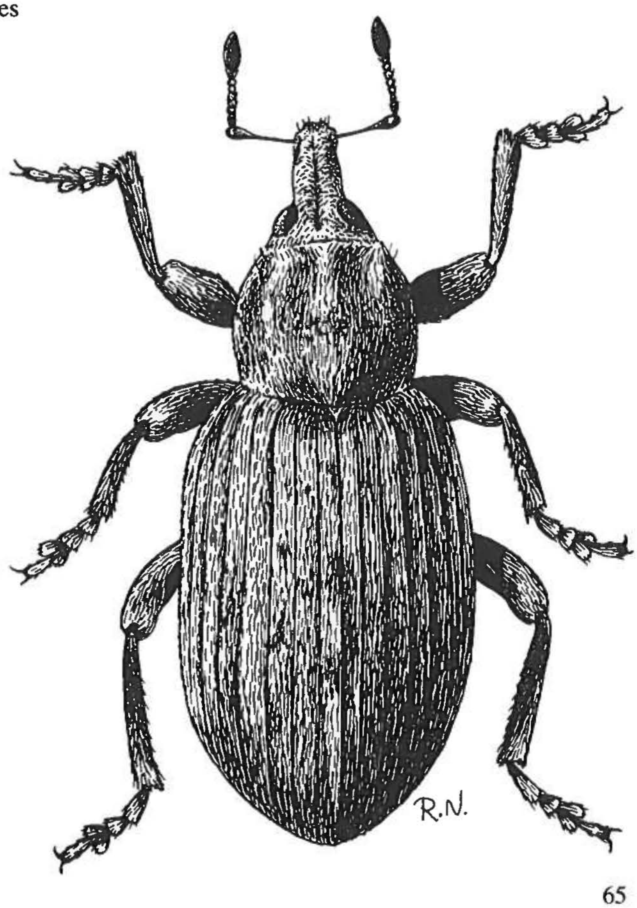


Fig. 42. *Hypera diversipunctata* (Schrank). Scale: 5 mm.

Life cycle

Adults have been collected from 5 April to 13 September. Newly hatched imagines are most frequent in the last part of May through June, but have also been collected on 5 July, 16 July and 12 August. Two pupae date from 9 July and 23 July. The single larva at present ascribed to this species (a fourth instar, Fig. 39) is from 25 July.

Of ten females collected on 2 July, one had undeveloped ovaries and nine had mature ovaries; the same proportion was found in a sample of ten females from 12 August (1984, Upernaviarsuk and Narsarsuaq, respectively; P. Nielsen leg.). These confusing phenological data seem to indicate both larval and imaginal hibernation and probably the absence of a determined reproductive cycle.

Hypera diversipunctata (Schrank, 1798)

(Henriksen 1939: *Phytonomus elongatus* Payk.)

Taxonomy and synonymy: see Henriksen & Lundbeck (1917), Silfverberg (1979).

Identification

Covered by hairs and bifurcate scales in colours grading from pale grey to reddish brown. Length about 5.5–6.5 mm. The larva is undescribed.

Variation and dynamics: In Greenland the hind wings are highly reduced.

General distribution

Circumpolar, boreal to low arctic: northern Europe (except Iceland and the Faeroes), Siberia (Yenissei Valley), Canada (Quebec: Fort Chimo; Elias 1984).

Distribution in Greenland (map p. 64)

H. diversipunctata is rare and found remarkably scattered and singly in Southwest Greenland, from the Kap Farvel area northwards to Ataneq, in both coastal and inland localities.

Habitat and notes on biology

In the Kap Farvel area the species was caught in pitfalls in a dry *Empetrum* heath and in the vigorous grass-vegetation of an old settlement, in the last locality imagines and larvae together (Table 10). At Qorloqtoq, Qassiarsuk, larvae and adults were caught in pitfalls on a luxuriant, south-facing slope, 350 m alt., with *Anthoxanthum odoratum* and *Salix glauca* as dominant plants (P. Nielsen 1984, pers. commun.; Table 11:16).

Poppius (1910) mentioned the species on small plants and under stones in grassy places. Strand (1946) found it under leaves and stones in grassy fields in Norway. In Canada the species has been reported at small *Sphagnum*-choked pools (Elias 1984).

According to West (1942) the larva has been found on *Stellaria crassifolia, S. uliginosa, Cerastium* spp., *Plantago major* and *P. media*. V. Hansen (1965) mentioned the adult feeding on Papilionaceae (*Vicia cracca, Lotus* spp., *Lathyrus* spp.).

Life cycle

Adults have been found from 19 June to 29 August, larvae on 21 and 30 July. The material is too small to permit suggestions about the life cycle in Greenland.

Dorytomus imbecillus Faust, 1882

Taxonomy and synonymy

W.O. Brien, Florida, U.S.A., identified the Greenlandic material of *Dorytomus imbecillus* using Korotyaev's

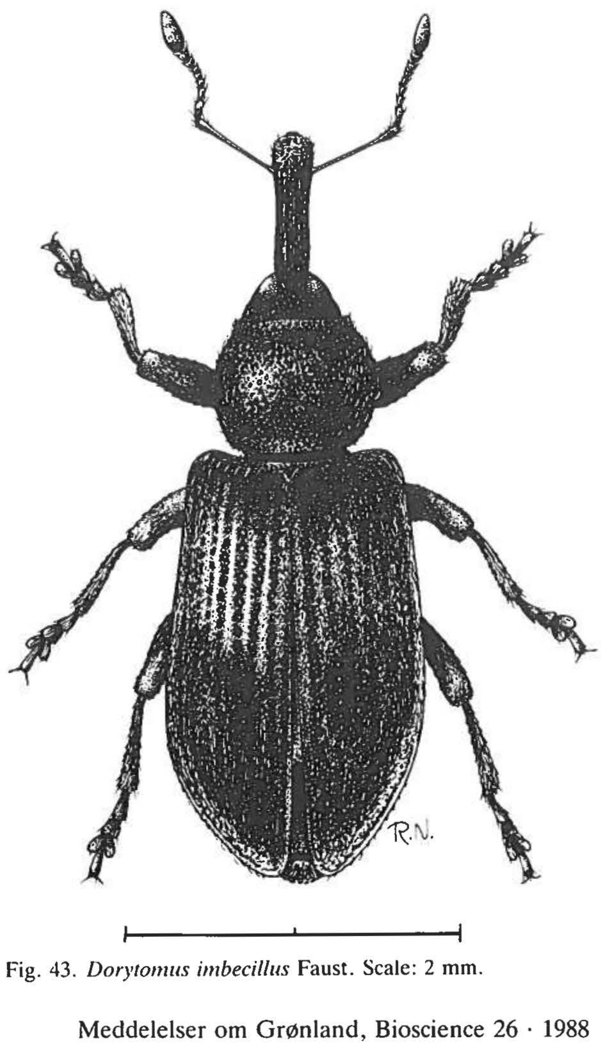
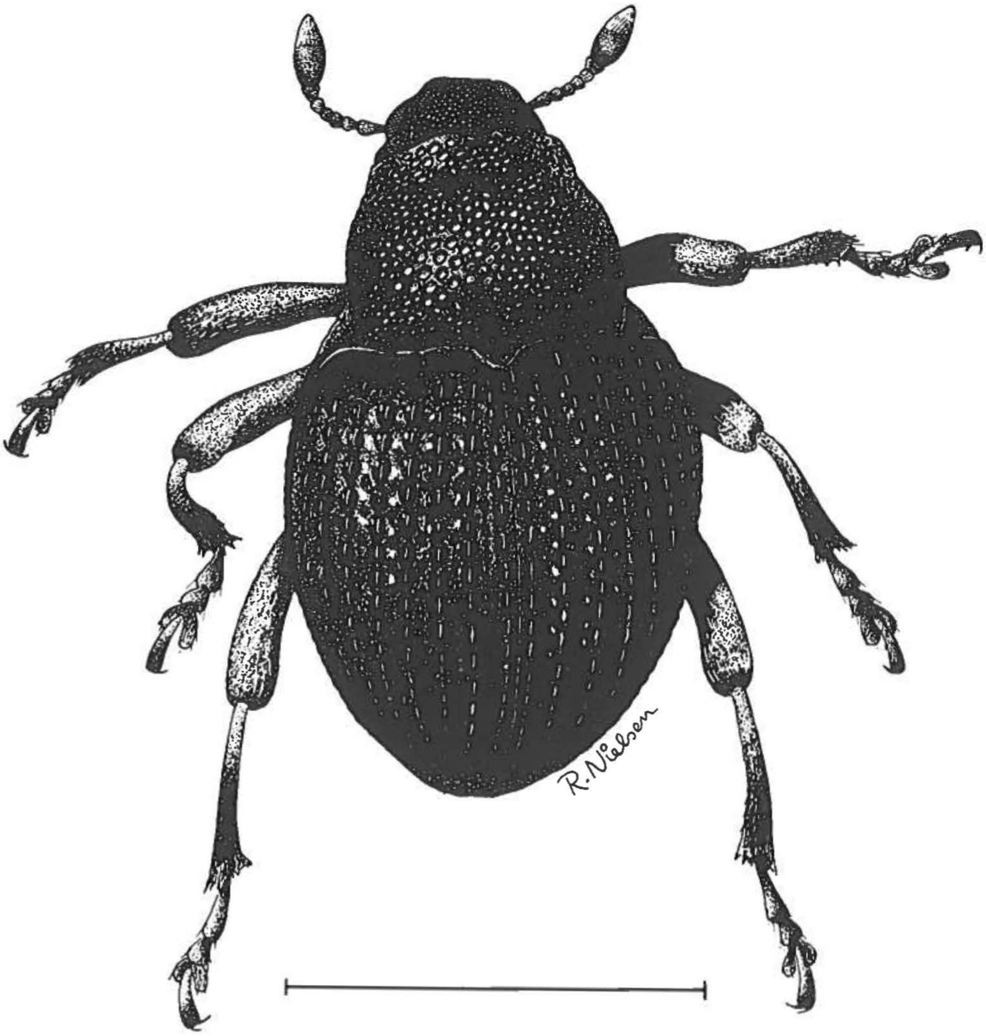


Fig. 43. *Dorytomus imbecillus* Faust. Scale: 2 mm.

Fig. 44. *Rutidosoma globulus* (Herbst). Scale: 1 mm.



revision (1976). Korotyaev synonymized two of the North American species, *alaskanus* Casey and *subsimilis* Blatchley with the Siberian *imbecillus* Faust.

Identification

Head and pronotum almost black, densely puncturate. Elytra reddish brown with darker markings, somewhat shining, with marked puncturate striae. Length about 3.5–4 mm.

General distribution

Holarctic, boreal to low arctic: northern U.S.S.R. from Vorkuta to Kamchatka, Mongolia; northern U.S.A. including Alaska, eastern Canada.

Distribution in Greenland (map. p. 64)

Very rare, but collected in five localities in Southwest Greenland between Nunarsuit and Kangerlussuaq/Søndre Strømfjord.

Habitat and notes on biology

C. Vibe, the only collector of the species in Greenland, caught it by sweeping vigorous vegetation, including coppices of *Salix glauca* (pers.commun.). In Siberia the species is found on *Salix* spp. (Korotyaev 1976).

In most European species of *Dorytomus*, the adults gnaw on leaves of *Salix* and *Populus*, the larvae living in and feeding on the inflorescences.

Life cycle

Adults have been caught from 3 June to 6 September; a newly hatched adult was taken on 6 September, possibly pointing to imaginal hibernation. The larva has not been found in Greenland.

In European species pupation takes place in the soil and the winter is passed as adult (V. Hansen 1965).

Rutidosoma globulus (Herbst, 1795)

(Henriksen 1939: *Rhytidosomus globulus* Hbst.)

Taxonomy and synonymy: see Lundbeck (1896), Henriksen & Lundbeck (1917).

Identification

Unmistakable among Greenlandic beetles due to the small size and the almost spherical abdomen. Length about 2 mm.

Dynamics: The hind wings are rudimentary.

General distribution

Northern and Central Europe (absent from Iceland and the Faeroes).

Distribution in Greenland (map p. 64)

R. globulus has only been collected twice: one old find without locality, and one from Søndre Isortoq south of Maniitsoq/ Sukkertoppen, 5 July 1885 (S. Hansen leg.).

Habitat and notes on biology

In Denmark the species has been found on *Populus tremulus* (V. Hansen 1965). In Greenland the food plant accordingly might be *Salix glauca* or another willow species.

Table 5. Taxonomical survey of Greenlandic Coleoptera*)

Number of species in families:	Indigenous	Introduced
Carabidae	4	–
Dytiscidae	2	–
Gyrinidae	1	–
Hydrophilidae	1	1
Staphylinidae	10 (11)	3 (4)
Buprestidae	–	1
Byrrhidae	4	–
Dermestidae	–	4
Lyctidae	–	1
Anobiidae	–	2
Ptinidae	–	3
Trogositidae	–	1
Malachiidae	–	1
Cucujidae	–	1
Cryptophagidae	1	2
Coccinellidae	2	–
Latridiidae	1 (2)	3 (4)
Tenebrionidae	–	2
Cerambycidae	–	7
Curculionidae	5	–
Scolytidae	–	1
Total	31 (33)**)	33 (35)**)

*) Five species only found as subfossils not included.
**) Including *Quedius mesomelinus* and *Latridius minutus*.

Scolytidae

Pityogenes chalcographus (Linnaeus, 1761)

(Fig. 53,h)

Different places in West Greenland (Henriksen & Lundbeck 1917). Introduced with timber.

Distribution: Palaearctic Region.

Habitat and biology: Living in and feeding on bark of conifers, especially spruce.

General part

Taxonomy

Table 6 lists all the indigenous Coleoptera of Greenland (including *Quedius mesomelinus* and *Latridius minutus*, which may be introduced). A survey of the introduced species is found in Table 13 (p. 78).

Table 5 shows the families of beetles recorded from Greenland. The indigenous species belong to 10 families, whereas the introduced species belong to 14 families. Only four families (Hydrophilidae, Staphylinidae, Cryptophagidae, Latridiidae) include both native and imported species.

Zoogeography

General distributions

Surveys of the general distribution and the zoogeographical grouping of the indigenous Greenlandic beetles are presented in Tables 6–7. Of the 33 species, the majority are palaearctic (12: 36 %) or circumpolar (11: 33%). A "western holarctic" element (i.e. lacking in Europe) accounts for 4 species (12%), and only 1 species (3%) is purely nearctic. (Regarding the use of the terms "palaearctic" and "nearctic", see p. 4).

The only real nearctic species, *Tylicus subcanus*, was detected very recently and is probably rare in Greenland.

For a discussion of the zoogeographical problems pertaining to the Greenlandic beetle fauna, see: Origin and immigration of the Greenlandic Coleoptera (p. 81).

It is interesting to note that a number of holarctic and circumpolar species that reach well into the low arctic zone in Greenland are in North America almost con-

Table 6. Indigenous Greenlandic Coleoptera. Distribution in selected circumpolar areas and distribution in Greenland.

	North America	Ellesmere Island + Baffin Island	Iceland	Faeroes	Svalbard	Scandinavia	Siberia	S	sSW	nSW	SE	NW	NE	N
Nebria rufescens (Ström)	×		×	×		×	×	×	×					
Patrobus septentrionis Dejean	×		×	×		×	×	×	×					
Bembidion grapii Gyllenhal	×		×			×	×	×	×	×	×		×	
Trichocellus cognatus (Gyllenhal)	×		×	×		×	×	×	×	×				
Hydroporus morio Aubé	×	×				×	×	×	×	×	×	×		×
Colymbetes dolabratus (Paykull)	×	×	×			×	×	×	×	×	×	×	×	
Gyrinus opacus Sahlberg	×					×	×	×	×	×				
Helophorus brevipalpis Bedel				×		×				×				
Quedius mesomelinus (Marsham)	×	×	×	×		×	×	×	×	×				
Quedius fellmanni (Zetterstedt)	×					×	×	×	×					
Lathrobium fulvipenne Gravenhorst			×	×		×	×		×					
Omalium excavatum Stephens			×	×		×	×	×						
Micralymma marinum (Ström)	×		×	×	×	×		×	×	×	×			
Micralymma brevilingue Schiödte	×	×					×	×	×	×	×	×	×	
Gnypeta cavicollis Sahlberg							×						×	×
Atheta groenlandica Mahler								×						
Atheta islandica (Kraatz)			×	×		×		×	×	×	×			
Atheta hyperborea Brundin						×		×	×	×				
Atheta vestita (Gravenhorst)			×	×		×		×						
Simplocaria metallica (Sturm)	×	×				×		×	×	×				
Simplocaria elongata Sahlberg	×						×		×					
Tylicus subcanus LeConte	×							×						
Byrrhus fasciatus Forster	×		×	×		×	×	×	×	×	×	×	×	
Caenoscelis ferruginea (Sahlberg)	×					×	×		×					
Nephus redtenbacheri (Mulsant)			×			×		×						
Coccinella transversoguttata Falderman	×						×	×	×	×	×	×	×	
Latridius minutus (Linnaeus)	×	×	×	×	×	×	×	×	×	×	(×)			
Corticaria rubripes Mannerheim						×	×			×				
Otiorhynchus arcticus (O. Fabricius)			×	×		×		×	×	×	×			
Otiorhynchus nodosus (Müller)			×	×		×		×	×	×				
Hypera diversipunctata (Schrank)	×					×	×	×	×	×				
Dorytomus imbecillus Faust	×						×		×	×				
Rutidosoma globulus (Herbst)						×	×			×				
Total	20	6	16	14	2	26	22	25	24	21	9	5	5	2

fined to the boreal zone; they are only exceptionally found in southern parts of the real tundra, but in some cases occur on coastal tundras of, e.g., Newfoundland and Labrador. This applies to *Nebria rufescens, Patrobus septentrionis, Bembidion grapii, Trichocellus cognatus, Gyrinus opacus, Quedius fellmanni, Caenoscelis ferruginea, Hypera diversipunctata, Dorytomus imbecillus* (Lindroth 1961b, 1963b, 1968b; Smetana 1965, 1971; Danks 1981a).

This remarkable ecological difference may be considered in connection with the limited extension of tundra biotopes in North America during the last (Wisconsinan) glaciation (Matthews 1980: 72), which suggests that the ecological amplitude of these species here became more narrow, largely restricted to forest environments. By contrast, the palaearctic populations of the same species, with access to huge areas of varied arctic biotopes, became more eurytopic. This consid-

Table 7. Indigenous Greenlandic Coleoptera distributed into zoogeographical groups.

Cosmopolitan:	*Quedius mesomelinus* *Latridius minutus*
Circumpolar:	*Nebria rufescens* *Patrobus septentrionis* *Bembidion grapii* *Trichocellus cognatus* *Hydroporus morio* *Colymbetes dolabratus* *Gyrinus opacus* *Quedius fellmanni* *Byrrhus fasciatus* *Caenoscelis ferruginea* *Hypera diversipunctata*
Holarctic:	*Micralymma brevilingue* (÷ Europe) *Simplocaria metallica* (÷ Siberia) *Simplocaria elongata* (÷ Europe) *Coccinella transversoguttata* (÷ Europe) *Dorytomus imbecillus* (÷ Europe)
Amphiatlantic:	*Micralymma marinum*
Palaearctic:	*Helophorus brevipalpis* *Lathrobium fulvipenne* *Omalium excavatum* *Gnypeta cavicollis* (÷ Europe) *Atheta islandica* *Atheta hyperborea* *Atheta vestita* *Nephus redtenbacheri* *Corticaria rubripes* *Otiorhynchus arcticus* *Otiorhynchus nodosus* *Rutidosoma globulus*
Nearctic:	*Tylicus subcanus*
Endemic:	*Atheta groenlandica*

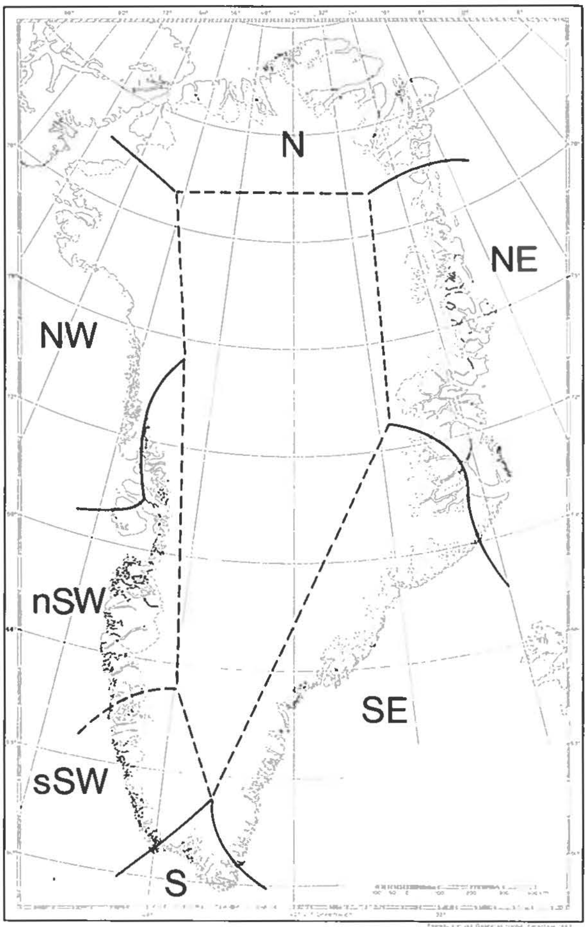


Fig. 45. Faunal districts of Greenland.

eration also constitutes another argument in favour of a European, Lateglacial origin of most Greenlandic Coleoptera (see p. 86).

Distributions in Greenland

Table 6 summarizes the distribution in Greenland of the indigenous beetle species (including the partly synanthropic *Quedius mesomelinus* and *Latridius minutus*) in relation to faunal districts (Fig. 45). These districts are based upon distributional types found among beetles and other insects, in agreement with Salomonsen (1981) and partly with the floristic provinces and districts (T.W. Böcher et al. 1959, 1968).

The districts may be characterized as follows: *S* comprises the climatically most favourable, subarctic part of Greenland, where *Betula pubescens, Sorbus groenlandica* and *Salix glauca* form small woodlands in inland areas. *SW* is the low arctic West Greenland with a relatively mild, oceanic climate along the coast and a continental climate with fairly warm, dry summers in the interior. *SE* is the low arctic East Greenland with a cool, oceanic climate. *NW* and *NE* are relatively dry, high arctic areas, and *N* is the extreme high arctic, also with a dry climate. The northern boundary of districts *SW* and *SE* coincides approximately with the northern limits of real willow coppices and herbslope communities (cf. T.W. Böcher 1979, 1981; Salomonsen 1972, 1979).

In all the districts there are marked differences between the outer coast, with an oceanic, humid, foggy and cool climate, and the continental climates in the interior, with little precipitation and warmer summers due to a high incidence of sunshine. In southernmost Greenland summer temperatures are lowered so much by floating ice, carried along with the East Greenland Current, that the coastal areas give a high arctic impression – in striking contrast to the luxuriant, subarctic communities at the head of the fjords (Fig. 48).. Almost arid areas are found where the icefree land is broadest, most often in combination with rain-shadow effect from

Fig. 46. The subarctic Greenland. A south-facing slope covered by coppices of *Betula pubescens* and *Salix glauca* at Narsarsuaq, Narsaq District.
J.B. phot., September 1970.

tall mountains along the coast (e.g., the Kangerlussuaq/Søndre Strømfjord area in West Greenland, several areas in the high arctic districts *N* and *NE*).

A remarkable drop in the number of beetles species, from 25 to 9, takes place from *S* to *SE*. The decrease apparently is accomplished within a few kilometres, from the interior of the Kap Farvel area in a northeasterly direction. The cool and humid climate of the southern east coast is undoubtedly unfavourable to insect life, and the icefree land areas are too narrow to effectively diminish the influence of the ocean. On the other hand, the southern portion of East Greenland is very poorly investigated entomologically, and an effort here might change the picture of abrupt change from *S* to *SE*. However, the flora of vascular plants in South Greenland is very well investigated (Feilberg 1984) and shows a quite parallel situation.

Along the west coast the decrease in number of species northwards is more even, although with a pronounced change into the high arctic from *SW* to *NW*. The subdivision of district *SW* in a southern and northern part (*sSW* and *nSW*) is justified by the sudden disappearance of a number of species north of the Godthåbsfjord (*Nebria rufescens, Patrobus septentrionis, Quedius fellmanni*). Some rare species have hitherto only been found in *nSW* (*Helophorus brevipalpis, Corticaria rubripes, Rutidosoma globulus*).

In both *NW* and *NE* are found five species, but they are only partly the same. *Colymbetes dolabratus, Micralymma brevilingue* and *Coccinella transversoguttata* are present in both districts, whereas *Hydroporus morio* and *Byrrhus fasciatus* occur only in *NW*, *Bembidion grapii* and *Gnypeta cavicollis* only in *NE*.

In *N* only two species have been found: *Hydroporus morio* and *Gnypeta cavicollis*, and exclusively in a restricted area in the southern, interior Peary Land (at the lakes Midsommersøerne). Here the high arctic climate is dry and sunny (Holmen 1957).

Of the 33 Greenlandic beetles (Table 6) thus 5 (15%) are entirely subarctic, 3 (11%) subarctic-southern low arctic, 11 (33%) subarctic-low arctic, 7 (21%) low arctic, 6 (18%) subarctic-low arctic-high arctic, and 1 (3%) exclusively high arctic.

As one goes north in Greenland beetles become increasingly scarce. Not only does the number of species decrease, but the populations become still more sparse, so that individuals are rarely found. For instance, the Danmarks Ekspedition to Northeast Greenland (lat. 76°46′) did not collect any beetles at all (Johansen & Nielsen 1910, Johansen 1911).

Only one species, *Gnypeta cavicollis*, must be considered truly arctic, apparently with a southern limit at the transition from low to high arctic East Greenland.

It would not be fair to conclude this chapter without stressing that we are still in the initial phase of exploring the Greenlandic insect fauna. The size of the country is huge in comparison with the collecting effort hitherto performed, and vast areas have never been visited by entomologists. This even applies to the relatively densely populated West Greenland, where, e.g., the stretch from Paamiut/Frederikshåb to Nuuk/Godthåb, and also the Maniitsoq/Sukkertoppen District, are practically unknown entomologically.

Because of the insufficient collections, conclusions about distributions in Greenland must necessarily be tentative and preliminary.

Ecology and adaptations

Habitats

Detailed knowledge of the habitats of Greenlandic beetles is scanty, and in several cases almost nothing is known.

In his excellent account on the insect fauna of Neria Fjord, Paamiut/Frederikshåb District, Lundbeck (1891:

Fig. 47. The subarctic Greenland, here encountered innermost in the northern part of the Ilua fjord (Tupaasat, Kangikitsoq fjord) in the Kap Farvel area. The bottom of the valley is mainly covered with coppices dominated by *Salix glauca*, intermingled with patches of meadow and grassland. In the photo a rich meadow with *Taraxacum croceum, Angelica archangelica, Ranunculus acer, Thalictrum alpinum, Alchemilla glomerulans, Potentilla crantzii, Polygonum viviparum, Phleum commutatum, Carex* spp. *Patrobus septentrionis* was abundant here, together with *Bembidion grapii, Trichocellus cognatus, Coccinella transversoguttata, Otiorhynchus arcticus, and O. nodosus.*
J.B. phot., August 1970.

109–123) described the associations of insects in relation to plant communities, aspect, etc. Close to the beach, in a herbslope community along a river (with *Angelica archangelica*, *Alchemilla vulgaris*, *A. alpina*) he found under stones a rich fauna of beetles, including *Patrobus septentrionis*, *Bembidion grapii*, *Trichocellus cognatus*, *Quedius fellmanni*, *Micralymma brevilingue* (a multitude), two species of *Atheta*, *Simplocaria metallica*, *Byrrhus fasciatus*, *Otiorhynchus arcticus*, *O. nodosus*. Sweeping a near-by *Salix glauca*-coppice yielded *Coccinella transversoguttata*. In a heath (*Empetrum* with scattered *Vaccinium uliginosum*) at higher altitude (about 100 m) he collected, under stones, *Bembidion grapii*, *Byrrhus fasciatus* (some individuals crawling in moss), *Otiorhynchus arcticus* (a multitude), and *O. nodosus* (less common).

Table 8. Survey of preferred biotopes of indigenous Greenlandic Coleoptera.

A. Lakes and ponds:	*Colymbetes dolabratus* *Gyrinus opacus*
B. Ponds and pools:	*Hydroporus morio*
C. Sea-shores (partly also freshwater shores and other humid-cool localities):	*Nebria rufescens* *Micralymma marinum* *Micralymma brevilingue* *Gnypeta cavicollis* *Atheta vestita*
D. Various damp localities:	*Patrobus septentrionis* *Atheta islandica*
E. Moderately damp, fairly warm localities, including coppices:	*Bembidion grapii* *Trichocellus cognatus* *Omalium excavatum* *Corticaria rubripes* *Dorytomus imbecillus*
F. Fairly dry and warm, grassy localities:	*Atheta groenlandica* *Caenoscelis ferruginea* *Nephus redtenbacheri* *Hypera diversipunctata*
G. Dry and warm localities:	*Tylicus subcanus*
H. Higly varied localities:	*Quedius fellmanni* *Simplocaria metallica* *Byrrhus fasciatus* *Coccinella transversoguttata* *Otiorhynchus arcticus* *Otiorhynchus nodosus*
I. Partly synanthropic localities:	*Quedius mesomelinus* *Latridius minutus*

Not included: *Helophorus brevipalpis, Lathrobium fulvipenne, Atheta hyperborea, Simplocaria elongata, Rutidosoma globulus.*

Table 8 is a preliminary attempt to group the species ecologically and under preferred biotopes. Reference is made to Tables 9–11 and details are found in the list of species. Only a few comments to the table will be given here.

In *C* are included the species more or less associated with beaches. They range from *Micralymma marinum*, which must be termed really marine – living stenotopically in the littoral zone – and *Atheta vestita*, found around the high water mark, to the more eurytopic *Micralymma brevilingue*, which may be found together with *M. marinum* but otherwise lives in cool, truly terrestrial surroundings (e.g., snow-beds). *Nebria rufescens* is frequently found on fjord beaches, but also along lake shores, water courses, etc. *Gnypeta cavicollis* has been found in different humid surroundings, e.g., on wet sand flats close to the beach at Mesters Vig.

That *Tylicus subcanus* is classed with true xeric biotopes is partly based on information about the habitat of the species in North America (P.J. Johnson, in litt.). One of the localities of the species in Greenland is a stony lake shore inland in South Greenland (Qinngua valley) which may easily fulfill the requirements of a xerophilous species.

Category *H* comprises most of the common, widely distributed Greenlandic species. However, there are differences as to their humidity preferences. *Otiorhynchus arcticus* is markedly less hygrophilous than *O. nodosus*, and *Simplocaria metallica* is more hygrophilous than *Byrrhus fasciatus*. *Patrobus septentrionis* is also eurytopic, but with a pronounced preference for damp localities and thus classed with category *D*.

Dominance and constancy

The pitfall samples presented in Tables 9–11 not only provide information about the occurrence of the species in different localities, but also, with caution, may be used as a basis for a treatment of the species' dominance and constancy. It must, however, be borne in mind that pitfall trapping does not give a reliable picture of the quantitative relations among different taxa, because some are readily caught whereas others tend to avoid the traps (for a review of the problems involved in the quantitative use of pitfalls, see Southwood 1978). This means that most emphasis should be laid on the faunistic information from the tables. The numerical data, nonetheless, may be regarded as an approximation of the quantitative relationships, and at present no better material exists.

Table 9 illustrates, and may be fairly representative of, the coleopterous fauna of the central Julianehåb Bugt area. Table 10 shows the somewhat more meager fauna of quite favourable sites in the central Kap Farvel area, southeast of the former (Fig. 48).

The dominance of a species is defined as the relative frequency of the species. Table 12, presenting the totals from Table 9, shows three species: *Otiorhynchus arcticus, Patrobus septentrionis* and *O. nodosus* to be highly dominant, together making up nearly 3/4 of the total individuals caught. A second group: *Atheta groenlandica, Byrrhus fasciatus, Simplocaria metallica, Nephus redtenbacheri, Nebria rufescens, Coccinella transversoguttata* makes up from 2.5 to 5.1% of the total. The remaining 11 species each contribute less than 1% of the total. (In his ornithological work, Palmgren (1930) used the limits >5%, 2–5%, <2% to define "dominant", "influent", and "recedent" species, respectively, a classification suiting the present material perfectly.)

The beetles from three chosen pitfall-samples are presented in Table 11 (cf. Table 9).

No. 7, from a brook shore overshaded by *Salix glauca-Betula pubescens* coppice at Narsarsuaq, is characterized by the equal dominance of *Nebria rufescens* and *Otiorhynchus nodosus*, a lower frequency of *Patrobus septentionis*, and *O. arcticus* playing a minor role than usual. This "beetle community" is thus dominated

Table 9. Survey of the Coleoptera in 25 pitfall samples from Southwest Greenland (P. Nielsen leg. 1983–85). The biotopes sampled are arranged according to decreasing humidity, from top to bottom: 1–3: marshes and bogs; 4–7: shores of lakes and water courses; 8–9: snow-beds; 10–14: coppices; 15–18: grassland slopes; 19–25: different fairly xeric vegetation types. N: Narsarsuaq; Q: Qassiarsuk; Qinngua: Qinngua valley, Nanortalik District; R: Rosenvinges Plantage, head of Tunulliarfik fjord; U: Upernaviarsuk.

		Nebria rufescens	*Patrobus septentrionis*	*Bembidion grapii*	*Trichocellus cognatus*	*Hydroporus morio*	*Colymbetes dolabratus*	*Quedius fellmanni*	*Omalium excavatum*	*Micralymma brevilingue*	*Atheta groenlandica*	*Atheta islandica*	*Atheta hyperborea*	*Simplocaria metallica*	*Tylicus subcanus*	*Byrrhus fasciatus*	*Nephus redtenbacheri*	*Coccinella transversoguttata*	*Otiorhynchus arcticus*	*Otiorhynchus nodosus*	*Hypera diversipunctata*	No. species	No. individuals	No. traps	No. days
1.	*Eriophorum* marsh (U)		●			×	×	×								×				×		6	49	10	81
2.	*Sphagnum* marsh (N)	×	■					●			×	×						×		×		6	369	10	93
3.	*Sphagnum* bog (N)	×	●									×										3	33	10	71
4.	Stony lake shore (Qinngua)							●						■	■							3	12	10	4
5.	Lake shore with sparse vegetation (N)	×	●								●			●		×		×		×		7	85	10	63
6.	Brook shore in vigorous grassland (U)	●	●				×		×					■		×	×	×		●		5	163	10	54
7.	Brook shore in *Betula pubescens-Salix glauca* coppice (N)	■	●	●								×				●		×	●	■		8	209	10	63
8.	Snow-bed, 480 m alt. (N)		×													×		×	×	×		5	38	20	93
9.	Snow-bed, 400 m alt. (Q)									×			×	●		●	●		■	●		7	109	10	25
10.	Tall *Betula pubescens-Salix glauca* coppice (Qinngua)		■																●	●		3	12	10	4
11.	*Betula pubescens* coppice, south-facing (N)		●	●							×					●			●	●		6	188	10	90
12.	Low coppice and coniferous plantation (R)		■						×		●					×	×		×	●		7	106	10	58
13.	Low coppice, south-facing, 100 m alt. (U)		●					×								×	●	●	●	■		7	152	10	54
14.	Low coppice, 180 m alt. (Q)				×						●					×		×	●			5	68	10	64
15.	Grassy area in low coppice, south-facing, 100 m alt. (U)		×					×								×	●	×	●	×		7	53	10	81
16.	Vigorous *Salix glauca*-grassland slope, south-facing, 350 m alt. (Q)	×	●			×					■					×	■	×	■	●	●	10	227	10	25
17.	Manured grassland ("Timothé") (Q: Nunataq)	×	●		×				×		■			×		×		●		×		9	103	15	64
18.	Manured natural grassland (Q)		×		●						×			×		×		×	■	●		8	86	5	64
19.	Dry herbslope in coppice (U)		●					×								×		×	●	●		6	63	10	54
20.	*Salix glauca-Betula glandulosa* heath, 400 m alt. (Q)													●		●	●	×	■			5	62	10	25
21.	Dry SW-facing slope (Qinngua)															●	●	●	■			4	14	7	4
22.	Dry hill top, 150 m alt. (Q)	×												×			×	×	×	×		6	15	10	64
23.	Lichen-heath surrounded by coppice (N)			×											●	●	×	●	■	●		7	404	10	63
24.	Dry heath in low coppice on hill-side, south-facing (N)		×		×												×	×	●	×		6	17	10	71
25.	Heath rich in lichens and mosses, 580 m alt. (N)			×												×		×	×	×		5	12	8	93
	Present in number of samples:	8	17	4	4	2	2	6	3	1	8	2	1	8	2	19	11	18	18	20	1				

×: < .1 individuals/10 traps/day
●: .1–.9 individuals/10 traps/day
■: ≥ 1 individual/10 traps/day

Table 10. Coleoptera caught in pitfall traps at Anorliuitsoq, Pamialluk island, Kap Farvel area, July–August 1970. L: larvae.

	Empetrum heath	Old settlement	River bank	Herb-slope	Total	%
Patrobus septentrionis	1+1L	21	46	4	73	15.5
Bembidion grapii	1	–	1L	–	2	.4
Trichocellus cognatus	1+2L	5	2+4L	1+3L	18	3.8
Micralymma brevilingue	–	3	–	–	3	.6
Atheta islandica	–	3	–	–	3	.6
Byrrhus fasciatus	4	2+1L	14+2L	8	31	6.6
Nephus redtenbacheri	1L	4L	–	–	5	1.1
Coccinella transversoguttata	7+48L	2+22L	3+40L	1+17L	140	29.8
Otiorhynchus arcticus	9	54	97	18	178	37.9
Otiorhynchus nodosus	1	3	6	3	13	2.8
Hypera diversipunctata	1	1+2L	–	–	4	.9
Number of pitfalls	24	24	25	20	93	
Number of days	16	16	16	13	–	

by hygrophilous species (including *Atheta islandica* and *Bembidion grapii*) and eurytopic species.

No. 16 is from a vigorous, south-facing slope dominated by grasses (*Anthoxanthus odotatum*) and low *Salix glauca*, 350 m above sea level, at Qorloqtoq, Qassiarsuk. Here *O. arcticus* is strongly dominant, but it is remarkable that next in frequency come *Nephus redtenbacheri* and *Atheta groenlandica*, and the rare *Hypera diversipunctata* is common – altogether a rich and unusual beetle association.

Fig. 48. Anorliuitsoq, Pamialluk island, in the Kap Farvel area, about halfway into the Ilua fjord. The vegetation is here dominated by different kinds of heaths (with *Empetrum hermaphroditum, Betula glandulosa, Salix glauca, Nardus stricta, Deschampsia flexuosa, Festuca rubra*). The pitfall samples presented in Table 10 were taken at this locality. The main camp of the "Kap Farvel Expedition 1970" is seen to the right in the middle distance.
J.B. phot., July 1970.

Table 11. Numbers of Coleoptera from three selected pitfall samples (P. Nielsen leg.). The sample numbers refer to Table 9.

7. Brook shore in *Betula pubescens-Salix glauca* coppice, Narsarsuaq. 10 traps for 63 days.		
Nebria rufescens	68	32.5 %
Otiorhynchus nodosus	64	30.6 –
Patrobus septentrionis	31	14.8 –
Byrrhus fasciatus	19	9.1 –
Otiorhynchus arcticus	14	6.7 –
Bembidion grapii	9	4.3 –
Coccinella transversoguttata	3	1.4 –
Atheta islandica	1	.5 –
16. Vigorous *Salix glauca*-grassland slope, south-facing, 350 m alt., Qassiarsuk. 10 traps for 25 days.		
Otiorhynchus arcticus	122	53.7 %
Nephus redtenbacheri	49	21.6 –
Atheta groenlandica	34	15.0 –
Patrobus septentrionis	7	3.1 –
Hypera diversipunctata	6	2.6 –
Otiorhynchus nodosus	3	1.3 –
Nebria rufescens	2	.9 –
Byrrhus fasciatus	2	.9 –
Hydroporus morio	1	.4 –
Coccinella transversoguttata	1	.4 –
23. Lichen-heath surrounded by coppice, Narsarsuaq. 10 traps for 63 days.		
Otiorhynchus arcticus	289	71.5 %
Otiorhynchus nodosus	61	15.1 –
Byrrhus fasciatus	21	5.2 –
Coccinella transversoguttata	21	5.2 –
Tylicus subcanus	8	2.0 –
Nephus redtenbacheri	3	.7 –
Bembidion grapii	1	.2 –

No. 23 is from a dry lichen-heath surrounded by vigorous shrub at Narsarsuaq. Dominant are, as usual, the two species of *Otiorhynchus, Byrrhus fasciatus* and *Coccinella transversoguttata*, but here in company with the rare, xerophilous *Tylicus subcanus*.

Table 10 also shows the relative frequency of the species. The division into dominance-classes is similar to that of Table 12, but there are differences, such as the high frequency of *Coccinella transversoguttata* and *Trichocellus cognatus*, and the minor part played by *Otiorhynchus nodosus*.

If the 25 series of pitfalls in Table 9 are regarded as 25 samples (but they are not really comparable), the table may yield information about the *constancy* of the species (the percentage of the total samples in which a species occurs). The degree of constancy may be divided into three classes (originally suggested by Brockmann-Jerosch 1907): *Constant* species occurring in more than 50% of the samples, *accessory* species in 25 – 50% of the samples, and *accidental* species in less than 25% of the samples. According to this classification (in decreasing order), five species are constant: *Otiorhynchus nodosus, Byrrhus fasciatus, Coccinella transversoguttata, O. arcticus, Patrobus septentrionis*; five are accessory: *Nephus redtenbacheri, Nebria rufescens, Atheta groenlandica, Simplocaria metallica* and the remaining (10 species) are accidental.

Not surprisingly, the most eurytopic species are the most constant.

Table 12. Total Coleoptera caught by pitfall trapping in Southwest Greenland, 1983–85, by P. Nielsen. Cf. Table 9.

	N	%
Otiorhynchus arcticus	851	32.1
Patrobus septentrionis	739	27.9
Otiorhynchus nodosus	336	12.7
Atheta groenlandica	136	5.1
Byrrhus fasciatus	126	4.8
Simplocaria metallica	112	4.2
Nephus redtenbacheri	98	3.7
Nebria rufescens	97	3.7
Coccinella transversoguttata	67	2.5
Bembidion grapii	20	.8
Quedius fellmanni	19	.7
Trichocellus cognatus	13	.5
Tylicus subcanus	12	.5
Omalium excavatum	7	.3
Hypera diversipunctata	6	.2
Colymbetes dolabratus	3	.1
Atheta islandica	3	.1
Hydroporus morio	2	.1
Micralymma brevilingue	1	.04
Atheta hyperborea	1	.04
Total	2649	100

Altitude

Information about the occurrence of beetles in relation to altitude in Greenland is limited. Fig. 49 summarizes what is known and is mainly based on P. Nielsen's pitfall collections from southernmost West Greenland. It is a general rule that the closer one gets to the poles, the lower the altitude at which the species are found; still, some species may be found at fairly high elevations, e.g., in protected situations on south-facing slopes. I found *Byrrhus fasciatus* 400 m above sea level on Lyngmarksfjeldet, Disko, and the northernmost find of *Simplocaria metallica* is from 300 m alt. (Daugaard-Jensen Dal, Disko). It is surprising that the highest altitude recorded for *Otiorhynchus arcticus* (600 m) is from Tuttilik (Lake Fjord) at 66°20′ on the east coast; and close to its northern limit on the west coast (Ulua, Prøven Fjord, 72°25′), *Colymbetes dolabratus* was collected in a shallow lake 500 m above sea level.

Species not included in Fig. 49 have only been found below 100 m alt.

The most widely distributed, eurytopic species thus also occur at the highest elevations.

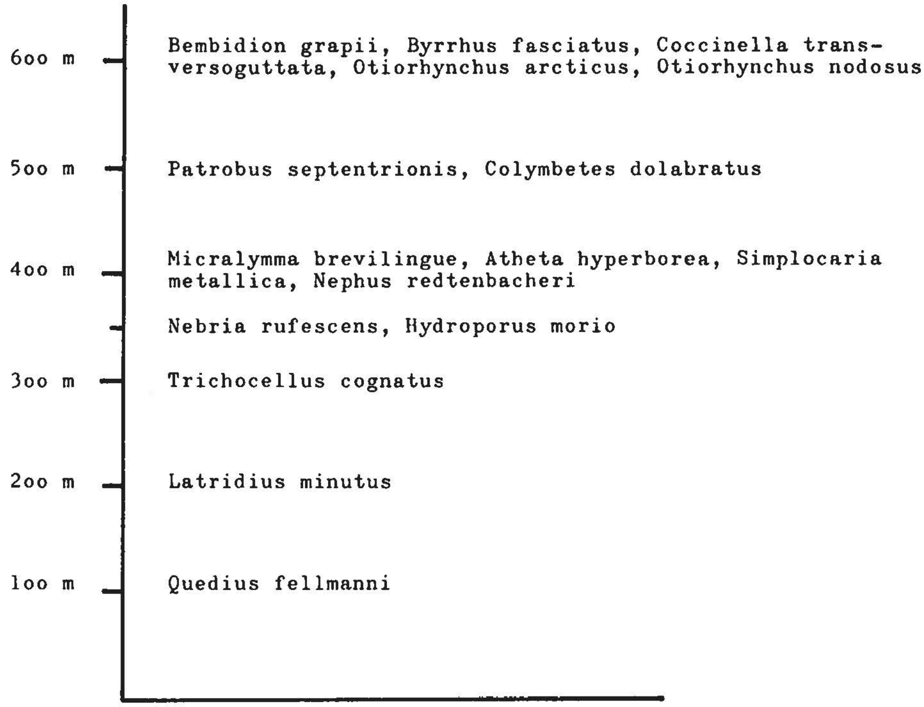


Fig. 49. The highest altitude at which some Coleoptera have been recorded in Greenland. Species not included have exclusively been found below 100 m alt.

Food

The habitat, of course, is related to the food source of a species. No studies – apart from a few observations – have been undertaken on the feeding habits of Greenlandic beetles. By inference, however, it is feasible to state that carnivores dominate, comprising up to 64% of the native species (assuming all Staphylinidae included). Decidedly herbivorous species account for 27% (Byrrhidae, Curculionidae) and the remaining 9% are fungivorous (Cryptophagidae, Latridiidae). The high proportion of carnivorous species in relation to herbivores is characteristic of island coleopterous faunas as compared to faunas of neighbouring mainlands (see Becker 1975, Bengtson 1981).

Life cycles

Table 14 gives a survey of life cycles of Greenlandic Coleoptera in those cases where the phenological events appear reasonably well documented on the basis of collections. It must thus be stressed that we are merely dealing with estimates. Apart from Røen's studies on *Colymbetes dolabratus* (p. 19), no investigations have been carried out on life cycles of Greenlandic beetles.

It appears that the majority of species (9 of 16: 56%) are *univoltine with adult hibernation* (14 of 23: 61%, if species probably belonging to this group are included). Four species (17 %) are *biennial with both larval and adult hibernation*. Four species presumably have *indefinite life cycles*. Only one, *Tylicus subcanus*, may be univoltine with larval hibernation, because this is the case in North America (P.J. Johnson, in litt.).

The hibernation of Greenlandic Coleoptera thus is not in agreement with the statements of Johansen (1921), MacLean (1975), and Danks (1978, 1981a: 280 ff.) that at high latitudes most insect species overwinter as larvae. This is, however, undoubtedly true considering the arctic insect fauna as a whole, because it is so strongly dominated by Diptera with larval or pupal hibernation.

Larsson (1939: 528 ff.), also quoted by, e.g., Thiele (1977: 249), stated that regarding Carabidae the proportion of spring breeders to autumn breeders in the North Atlantic islands including Greenland is 1:1. However, the evidence offered by the collections points to spring breeding in all of the four Greenlandic species. This also seems to contradict Andersen (1984), who demonstrated a positive correlation between the proportion of imaginal hibernators and the summer temperature.

A development lasting two years can be interpreted as an adaptation to the extreme climatic conditions in arctic and alpine environments (Forsskåhl 1972, Thiele 1977, Refseth 1980, Andersen 1984).

Three of the most widespread and eurytopic species in Greenland, *Byrrhus fasciatus, Otiorhynchus arcticus*, and *O. nodosus*, appear to have "opportunistic", extended life cycles, and these species may be able to spend several years as larvae. This is a typical trend among arctic insects, especially found in Lepidoptera and Diptera (Downes 1964, 1965; Oliver 1968; MacLean 1975; Danks 1981a). Kaufmann (1969, 1971) showed that the subarctic species *Upis ceramboides* (L.)

Table 13. Survey of synanthropic and introduced Greenlandic Coleoptera. (+): exclusively known as subfossils; probably introduced by the Norsemen in the Middle Ages and later extinct.

1) More or less synanthropic species associated with cultivated ground, dung and carrion:
   - *Cercyon obsoletus* (Gyllenhal)
   - *Philonthus politus* (Linnaeus) (+)
   - *Philonthus* cf. *cephalotes* (Gravenhorst) (+)
   - *Quedius mesomelinus* (Marsham)
   - *Othius angustus* Stephens (+)
   - *Omalium excavatum* Stephens
   - *Ocalea* cf. *picata* (Stephens) (+)

2) Synanthropic species in human habitations, barns, stables etc. associated with fungi:
   - *Xylodromus concinnus* (Marsham)
   - *Cryptophagus acutangulus* Gyllenhal
   - *Cryptophagus lapponicus* Gyllenhal
   - *Atomaria* sp. (+)
   - *Latridius minutus* (Linnaeus)
   - *Dienerella filum* (Aubé)
   - *Thes bergrothi* (Reitter)
   - *Corticaria serrata* (Paykull)

3) Synanthropic species associated with dry organic, chiefly animal matter:
   - *Dermestes lardarius* Linnaeus
   - *Attagenus pellio* (Linnaeus)
   - *Reesa vespulae* (Milliron)
   - *Anthrenus museorum* (Linnaeus)
   - *Ptinus fur* (Linnaeus)
   - *Ptinus tectus* Boieldieu
   - *Ptinus raptor* Sturm

4) Synanthropic species associated with dry vegetable matter, mainly grain and flour:
   - *Tenebroides mauritanicus* (Linnaeus)
   - *Oryzaephilus surinamensis* (Linnaeus)
   - *Tribolium destructor* Uyttenboogart
   - *Tenebrio obscurus* Fabricius

5) Introductions with timber:
   - *Melanophila acuminata* (Degeer)
   - *Lyctus brunneus* (Stephens)
   - *Ernobius mollis* (Linnaeus)
   - *Anobium punctatum* (Degeer)
   - *Tetropium castaneum* (Linnaeus)
   - *Gracilia minuta* (Fabricius)
   - *Molorchus minor* (Linnaeus)
   - *Phymatodes testaceus* (Linnaeus)
   - *Xylotrechus colonus* (Fabricius)
   - *Pogonocherus fasciculatus* (Degeer)
   - *Pityogenes chalcographus* (Linnaeus)

6) Casual introductions:
   - *Eusphalerum sorbi* (Gyllenhal)
   - *Malachius aeneus* (Linnaeus)

Table 14. Life cycle of Greenlandic Coleoptera. (?): species most probably belonging to the category in question, but material too limited to allow proper conclusions.

1) Univoltine, adult hibernation:	*Bembidion grapii* *Hydroporus morio* *Colymbetes dolabratus* *Gyrinus opacus* (?) *Quedius mesomelinus* *Quedius fellmanni* (?) *Atheta groenlandica* (?) *Atheta islandica* (?) *Nephus redtenbacheri* *Coccinella transversoguttata*
2) Univoltine, larval hibernation:	*Tylicus subcanus* (?)
3) Biennial, both larval and adult hibernation:	*Nebria rufescens* *Patrobus septentrionis* *Trichocellus cognatus* *Micralymma brevilingue*
4) Indefinite life cycle:	*Simplocaria metallica* (?) *Byrrhus fasciatus* *Otiorhynchus arcticus* *Otiorhynchus nodosus*
5) Continual reproduction:	Most synanthropic species
(Life cycle unknown in Greenland:	14 species)

(Tenebrionidae) and *Pterostichus brevicornis* Kirby (Carabidae) can hibernate in any developmental stage beyond the egg. The individuals of *P. brevicornis* require from 14 to 36 months to complete their life cycle, depending on the time of oviposition. In this species the adult life is prolonged and may include two hibernations. Also the subarctic *Pytho americanus* Kirby (Pythidae) has an extended life cycle of 2–3 years (Ring & Tesar 1981).

Overwintering

The general low temperature and the short growing season constitute the master factors delimiting life in the Arctic (Downes 1964, 1965; Corbet 1972; Danks 1981a: chapters 1,2 & 11,2).

In Greenland there is a gradient of climates from south to north, from mild subarctic to extreme high arctic, and along this gradient the number of species of Coleoptera decreases to zero, fairly evenly along the west coast, abruptly along the east coast (p. 71). A similar decrease is indeed found in most groups of organisms, but is much more pronounced in the beetles than in, e.g., vascular plants, Diptera and Lepidoptera, because in these taxa a significant number of well-adapted high arctic species are found (Downes 1966, Danks 1980a). In the Coleoptera, however, only one Greenlandic species (*Gnypeta cavicollis*) can be denoted truly arctic.

Seven species of beetles occur in high arctic Greenland, and only ten have been found in high arctic North America (Danks 1981a). Considering the number of species further south, the Coleoptera is not a successful taxon in the Arctic (p. 3 and Table 1).

The cause of this is open to discussion, but may be understood in an evolutionary context. Practically all recent species of Coleoptera already existed by late Tertiary, so adaptations to the much colder and fluctuating climate during the Pleistocene might have been difficult (Coope 1970; Matthews 1977, 1979).

Most arctic insects overwinter as larvae (MacLean 1975, Danks 1978, 1981a: 284), and as late as in 1966, Asahina stated that "all of the frost resistant insects so far known are in the larval or pupal stage" (p. 468). Miller (1982), however, listed six species of Coleoptera and a few other insects hibernating as cold-hardy adults in interior, subarctic Alaska. MacLean (1975: 285) suggested that "the tendency to overwinter as adults limits the success of Coleoptera under arctic conditions". Thus, if it is more difficult for adult insects than for the juvenile stages to become frost resistant, we have got another explanation of the few arctic Coleoptera.

One effect of permafrost in the arctic soils is that during winter all terrestrial biotopes are exposed to temperatures below freezing (Corbet 1972, Danks 1981a: 278). However, in formerly volcanic areas (Qeqertarsuaq/Disko, Nuussuaq, Blosseville Kyst) many hot springs create positive winter temperatures in their immediate surroundings. This situation pushes the northern limit of several species north of the limit determined by the general climate. Among plants this is well documented (e.g., T. W. Böcher 1963, Fredskild 1981, Lægaard 1981, Feilberg 1985) and probably the same is the case for many insects (e.g., the occurrence of *Otiorhynchus arcticus* on the Blosseville Kyst; Degerbøl 1937). See also Fig. 50.

Leaving out synanthropic biotopes, mammals and birds as hosts for parasites, and hot springs, there is only one place in the Arctic where subzero temperatures can be entirely escaped: deep lakes that do not freeze to the bottom. This possibility appears to be utilized by only one Greenlandic beetle: *Colymbetes dolabratus* (p. 19). All other species must be able to tolerate temperatures below freezing, either by remaining unfrozen even at temperatures below their freezing point (supercooling), or by surviving freezing of the body fluids (freezing tolerance) (see, e.g., the reviews in Danks 1978 and 1980a: 279).

However, although frost during winter reigns in all other biotopes, the intensity varies greatly depending on the physical factors of the site, the most important undoubtedly being the amount of snow cover. Deep snow insulates against low air temperatures and modifies the violent thermal oscillations found on the surface of the snow (e.g., Corbet 1972). Insects with a less effective cryo-protective device (such as possibly many adult beetles), may accordingly survive in winter-habitats where protection against the extreme low temperatures is provided by the snow.

Apart from *Colymbetes dolabratus*, nothing is known about overwintering sites of the Greenlandic Coleoptera. But it is evident that most species are found in areas where fairly high summer temperatures are combined with fairly large amounts of winter snow (i.e., the subarctic and southern low arctic areas along the west coast). Most species are here confined to lush vegetation – herbslopes, coppices along water courses, snowbeds – where the snow generally is especially thick. Accordingly, the restricted occurrence of most beetles northwards and inland in Greenland could partly be due to the decreasing and still more unstable protection by snow.

Evidently, studies on the ecology of arctic beetles are badly needed. In particular, investigations of hibernating stages, cold-hardiness and overwintering sites in relation to snow cover should be highly rewarding.

Reduction of flying wings

According to Lindroth (1957: 296), the proportion of circumpolar Coleoptera with hind wings more or less reduced or lacking entirely increases from low to high latitudes. Of the 33 species considered indigenous in Greenland, 10 are constantly brachypterous or apterous (*Quedius mesomelinus, Q. fellmanni, Lathrobium fulvipenne, Micralymma marinum, M. brevilingue, Tylicus subcanus, Otiorhynchus arcticus, O. nodosus, Hypera diversipunctata, Rutidosoma globulus*) and one is polymorphic (*Bembidion grapii*).

Flightlessness is a typical trait among arctic insects (Downes 1964, 1965) and may be regarded adaptive and one of the means of diminishing energy expenses. Moreover, flightless beetles may be less subject to population losses caused by passive wind-transport into unfavourable environments.

Den Boer et al. (1980) convincingly demonstrated that wing polymorphism must be considered the first stage in a common evolutionary trend among Carabidae, leading from the original macropterous state via dimorphism to, eventually, complete brachyptery. Populations living in stable habitats tend to become brachypterous, and populations inhabiting both stable and unstable habitats tend to become dimorphic as regards length of the flying wings. Accordingly, the more stable the biotope (the older the successional stage in a community sere), the lower the number of macropterous individuals of poly(di)morphic species to be expected. This expectancy is fulfilled by Icelandic populations of the wing-polymorphic *Amara quenseli* (Schönherr) (Bengtson & Erikstad 1984).

The present arctic ecosystems may all be regarded as immature (Downes 1965) and, geologically speaking, very young (Matthews 1979a, Funder et al. 1984). The high incidence of brachypterous Coleoptera in Greenland might thus seem to contradict Den Boer et al.'s statement. On the other hand, most of the flightless species belong to genera which are as a rule brachypterous or apterous – a condition that may be of adaptive value in the Arctic (see above).

Fig. 50. Herbslope community along a hot spring in Uunartorsuaq/ Engelskmandens Havn at Qeqertarsuaq/Godhavn. The benign conditions, especially during winter, enable a number of species to exist here north of their "real" northern limit. The dominant plants are *Alchemilla glomerulans, Bartsia alpina, Platanthera hyperborea, Carex rariflora, Equisetum arvense*. *Bembidion grapii* and *Simplocaria metallica* have been taken here. In Iceland *B. grapii* is especially common around hot springs (Lindroth 1931), and Engelskmandens Havn is one of the northernmost known localities of *S. metallica*.
J.B. phot., July 1968.

Parthenogenesis

Four species of beetles occur in Greenland in a parthenogenetic form, indicated by the absence of males. These are *Atheta groenlandica, A. islandica, A. hyperborea* and *Otiorhynchus nodosus*. Apart from the recently described *A. groenlandica* (Mahler 1988) all species are known in bisexual forms at lower latitudes. In the genus *Otiorhynchus*, the parthenogenetic populations as a rule are found in areas that were glaciated during the latest ice age (Weischselian), whereas the bisexual populations occur at the southern margin of the formerly glaciated area. The relative proportion of parthenogenetic *Otiorhynchus* species (which are at the same time polyploid) is considerably higher in northern Europe (Fennoscandia) than in Central Europe (Austria, Switzerland) (Suomalainen 1962).

The tendency towards higher incidence of parthenogenetic species is pronounced among arctic insects and may be considered one of the means of adaptation to the severe conditions here (Downes 1962, 1965; see also J. Böcher 1971, Böcher & Enghoff 1984). It should be pointed out that, in comparison with bisexual populations, parthenogenetic populations have a greater potential for dispersal. A single individual, in any stage of development, is sufficient to colonize a new area – a significant point considering formerly glaciated areas, such as in the Arctic.

The genotype of a parthenogenetic (apomictic) population is described as highly generalized ("general-purpose genotype"; Lynch 1984), with a high degree of heterozygosity in combination with heterosis in polyploid forms (Suomalainen et al. 1976). Such a genotype is well adapted to a wide range of physical conditions, but is fairly inflexible and does not enable the population to compete successfully with sexual populations in rich and complicated biotic communities. Therefore, parthenogenesis seems most advantageous in low-competitive biotopes, e.g., early successional communities, disturbed sites, xeric areas, and at high altitude and latitude (see the discussion by, e.g., Cuellar 1977, Glesener & Tilman 1978, Vepsäläinen & Järvinen 1979, Lynch 1984). A rigid, generalized genotype is probably of special value in the unpredictably changing oceanic low arctic areas (see, e.g., J. Böcher 1975).

Origin and immigration of the Greenlandic Coleoptera

Review of opinions

The origin of the Greenlandic Coleoptera is, of course, only part of the comprehensive problem concerning the origin of the Greenlandic biota, and of the North Atlantic biota as a whole. This question has been extensively and, at times, vigorously discussed during the last century. A full review will not be attempted here, only the broad outline with particular emphasis on arguments dealing with the Coleoptera. Jensen (1928) summarized the controversy from its very outset.

One major aspect of the discussion has been the biogeographical assignment of Greenland, i.e., whether the biota are primarily nearctic or palaearctic. The position of the country, so close to and traditionally included in the North American Continent, would naturally suggest a strong nearctic influence in the biota.

This is also the case in the easily dispersed groups – plants, Diptera, Lepidoptera, Araneae, birds and mammals. In the flora of vascular plants the western element predominates over the eastern element (T.W. Böcher et al. 1959), and the same is the case with the Araneae (Brændegaard 1938, 1946; Holm 1967). Downes (1966) showed that the Greenlandic Lepidoptera fauna mainly consists of two elements: l) a high arctic element which is identical with the fauna of arctic Canada, and undoubtedly has immigrated from there, and 2) a southerly fauna of adventitious and mixed origin, immigrated through casual dispersal from overseas (Labrador, Iceland, etc.). A low arctic element is almost missing, and Downes concluded that Greenland, with respect to its fauna of southern type, is an oceanic island of postglacial age, very much like Iceland. The conclusions are extended to cover several other groups of (mobile) insects (Diptera, Hymenoptera: Bombidae) and also mammals, including man. Thus Downes, and also Danks (1981a), leave little doubt as to the principally nearctic nature of the Greenlandic biota. It may be added here that also the Greenlandic Trichoptera, recently revised by Stoltze (1981), show marked American affinities. Of a total of eight species, six are nearctic and two are holarctic.

On the other hand, Lundbeck (1891) and Henriksen & Lundbeck (1917) stated without comments that by far the majority of the Greenlandic terrestrial arthropods are European or holarctic. Henriksen (1924) commented on the entomological results of the Canadian Arctic Expedition 1913–18 (Johansen 1921) and concluded that "all things considered, the Canadian expedition has emphasized that the Greenlandic fauna essentially is of European origin – with an element of circumpolar species" (translated from Danish). These statements were criticized by Jensen (1928), who pointed out the insufficient knowledge of the North American fauna, demonstrated the evident American origin of the Greenlandic butterflies, and critically examined the Coleoptera. Of the 41 species of beetles then known from Greenland (Henriksen & Lundbeck 1917) Jensen found 13 common to both America and Europe, 10 common to Greenland and Europe, 1 (*Gnypeta cavicollis*) exclusively found in East Greenland and Siberia, 1 endemic, and 16 undoubtedly introduced, synanthropic species. Jensen pointed out that the European species are all restricted to Southwest Greenland, primarily found in the districts colonized by the Norsemen in the Middle Ages, and that the same species occur in Iceland, from where the vikings started off for Greenland. He suggested that seven species might have been introduced by the Norsemen with hay, bedding, etc. for the domestic animals brought with them onboard their ships. In this assumption Jensen was inspired by Ostenfeld (1926), who was convinced that a significant fraction of the flora of southern Greenland was introduced by the Norsemen. This view has later been abandoned by the botanists (e.g., Porsild 1932; Fredskild 1969, 1973).

Lindroth (1931: 567 ff.) strongly opposed Jensen's conclusions and pointed out that there is practically no evidence of introductions of insects to Iceland and the Faeroes except in the decidedly synanthropic groups, in spite of the fact that these islands had many more commercial connections with Europe.

In 1932 Degerbøl (1937) collected *Bembidion grapii, Byrrhus fasciatus* and *Otiorhynchus arcticus* in central East Greenland, thereby displacing the known northern limit of these beetles far northwards, and far away from Norse habitations. Degerbøl accordingly claimed that "the new finds made on the Blosseville Coast decidedly give the impression that the species cannot have been imported there by man", and like Lindroth (l.c.), he pointed to an interglacial land connection to Europe, and argued that part of the fauna and flora could have survived the last glaciation in icefree refugia on the east coast of Greenland. This view thus supported the conclusions of the botanists Gelting (1934, 1941) and T.W. Böcher (1938), who considered a large portion of the Greenlandic flora to have survived the last glaciation in Greenland. Lindroth (1931) claimed that practically all the indigenous insects of Iceland were glacial survivors.

As to the terricolous fauna, from a study of Greenlandic oribatids and collemboles Hammer (1944: 154) concluded: "This investigation of the microfauna (Orib. and Coll.) of Greenland, which is of European and, according to all appearances, of pre-glacial origin, has shown that the soil fauna of Greenland as a whole must likewise be of pre-glacial origin, segregated from some European area of distribution. In the post-glacial period the fauna was augmented with flying and other mobile forms, probably mostly from American regions". This statement was criticized by Brændegaard (1946), who demonstrated the strong nearctic influence in the fauna of Araneae of Greenland, and also maintained that Hammer and others underestimated the degree to which the North American fauna was poorly known in comparison with that of Europe (1946: 104 ff.). Later Hammer (1955) modified her view and stressed the similarity of the arctic nearctic and palaearctic faunas of collemboles and oribatid mites, pointing to an old age (preglacial) of the entire fauna of these taxa in the circumpolar area. This conviction was further supported by Omodeo (1957), and Nurminen (1970, 1973), studying earthworms and enchytraeids, respectively.

One group of botanists (Seidenfaden & Sørensen 1937, Iversen 1952–1953) thought that only a minor part of the biota, the most hardy species, could have survived the glaciation; Iversen's conclusions were based on pollen analyses of the Holocene succession of vegetation. The geologists (Wegmann 1941), moreover, pointed out that traces of glaciation had been found everywhere in Greenland, precluding the possibility that any species could survive throughout the Pleistocene.

Nevertheless, some biologists maintained the conviction that a number of organisms, including most beetles, must have existed throughout the glacial epoch in Greenland, at least during the last glaciation (Spärck 1943; Vibe 1953a, 1953b), and possible refugial areas were suggested (T.W. Böcher 1956, 1963a). Ives (1974) presented a review of the "nunatak hypothesis".

Brændegaard (1946: 111–116) compared the Greenlandic distribution of spiders with that of other animal groups, including the Coleoptera. He attempted to fit the beetles into his zoogeographical groupings of Araneae. Brændegaard refused to accept the absence of the palaearctic beetles from North America, and as regards *Otiorhynchus arcticus* he maintained that "it is almost unthinkable that it should not be found in these areas which are situated so close to Greenland ... It is most probable that in nearctic areas it lives as far south as New Foundland".

Lindroth (1957: 255 ff) gave a detailed account of the Greenlandic coleopterous fauna. He pointed out that after Brown's (1937) preliminary survey of the beetles of Baffin Island we are able to discuss the peculiar zoogeographical character of Greenland, and that the beetles "contain many flightless, not easily dispersed forms which may, in their present distribution, reflect faunal history with unusual clarity" (p. 257). Lindroth concluded that "the purely Palaearctic element is not only quantitatively dominant [11 species], but ... it furthermore contains the following *flightless* species with consequently reduced powers of disperal: [six species]" (p. 257).

Lindroth (1957) included 6 beetle species in the nearctic element, now reduced to 4 (see pp. 68, 85). He pointed out that only 3 of the 16 beetles known from Baffin Island occur in Greenland, so that "within the Arctic of the entire northern circumpolar area, the comparatively narrow strait between Baffin Island and Greenland has constituted the most effective barrier to dispersal of soil-bound animals" (1957: 264, 1961a, 1968a). This point was illustrated by contrasting the distribution of *Amara alpina* (Paykull) with that of *Otiorhynchus arcticus* (1957: 264, maps: 266–267). The first mentioned is circumpolar and widely distributed in the North American Arctic, including the east coast of Baffin Island and Devon Island (Lindroth 1963b: 60), but absent from Greenland and the North Atlantic islands. The other species is European and has its western limit just on the eastern side of Davis Strait, northwards to 65°30′N in West Greenland (see the map p. 64).

Lindroth further stressed the great similarity among the indigenous beetle faunas of Greenland, Iceland, and the Faeroes (1957:264 ff.). He pointed out that passive dispersal would favour an eastward transport across the North Atlantic because of the predominating western winds and the direction of the Gulf Stream; and it is well established that several Lepidoptera and "ballooning" spiders have reached Greenland from North America, but not a single example of aerial transport from Greenland to Baffin Island has been suspected (see also Danks 1981a: 246).

Lindroth admitted that a small number of beetle species, not at all associated with human culture, might have been brought to Greenland (and the North Atlantic islands) by pure chance. But he was "completely unable to accept the idea that, for instance, the culture-avoiding, wingless, sluggish, and, contrary to the majority of species within the genus, obligatorily *bisexual* Weevil *Otiorhynchus arcticus* O. Fbr. should have been introduced into Greenland or Iceland" (1957: 268).

Considering the undoubtedly imported, synanthropic species of Coleoptera, Lindroth (1957: 268–269) demonstrated the accidental nature of introduction reflected in the dissimilarity of the faunas of introduced species in Greenland, Iceland and the Faeroes. Therefore, one weighty argument against the opinion that the European element was imported by man is the large number of indigenous species in common in these islands (Table 6).

Lindroth finally concluded (1957: 270 ff.) that the palaearctic fauna element of the Faeroes, Iceland and Greenland must have colonized these islands by means of a Pleistocene landbridge, probably during the next to the last interglacial period. – The existence of Pleistocene land bridges in the North Atlantic area, however, now is regarded as totally excluded by geological evidence (Matthews 1980, Eldholm & Thiede 1980, Coope 1986).

Larsson (1959) discussed the origin of the Icelandic Coleoptera and also included considerations about the Greenlandic beetles. He largely agreed with and supported Lindroth's (1931) conclusions. He considered the coleopterous fauna of Iceland and Greenland to be very old and, apart from the obvious human introductions, as composed of species surviving from the Tertiary in a number of icefree refugia.

In his impressive survey of arctic arthropods, Danks (1981a: 238–247, 354–355) briefly summarized the discussion about the origin of Greenlandic biota. He dismissed the special zoogeographical problems presented by the Coleoptera by saying that "the palaearctic elements" in Greenland comprise only 11 species. Most of these belong to the two families Staphylinidae and Curculionidae, both of which are inadequately known taxonomically and in other parts of the world contain many introduced species" (1981a: 240–241).

Coope (1969a, 1970, 1979, 1986, etc.) introduced into the discussion precise knowledge of the faunal history, based on comprehensive studies of subfossil, Pleistocene insects, mainly Coleoptera, and chiefly from Britain. He stated (1969) that many species that occur in the Lateglacial fauna of Britain and the modern fauna of Scandinavia are among those that were thought to have survived the full glacial phase in refugial areas on the west coast of Norway (see Lindroth 1949, 1953, 1958, 1969, 1970, 1979, etc.). Coope suggested that these species, possibly in Lateglacial time, reached the newly deglaciated areas on the Norwegian coast by drifting across the intervening sea on ice or frozen flood refuse washed to sea during the presumably violent spring thaws of that time. The British fauna of the climatically favourable Allerød interstadial could have provided Scandinavia with the relatively thermophilous species that have always been a puzzling element in the fauna that was thought to have survived the Glacial time, or part of it, in Norwegian refugia.

Coope (1970) expanded the argument to cover even the North Altantic islands and Greenland. He wrote (p. 116) that "this passive transport might also explain the existence in the North Atlantic of a puzzling consistent biota which has so strong affinities with that of the Palaearctic, even as far as Greenland. The common occurrence, in these areas, of plants with low dispersal capabilities and flightless, soil-bound insects, has led biogeographers to postulate land bridges connecting these islands at various periods ranging from the Pleistocene to the Tertiary; suggestions that have not on the whole met with geological approval".

Brinck (1966) expressed a similar view and stressed the importance of the existence of the huge Lateglacial North Sea Land ("Dogger Land") traversed by numerous rivers, and "courses of fresh water tend to act as aids rather than obstacles to dispersal" (p. 258). Fjellberg (1972) also accepted the significance of the North Sea Land for the recolonization by Coleoptera of southern Norway after the glaciations.

Coope (1986) further elaborated his theory concerning the colonization of the North Atlantic islands. He gives an account of the immense increase in our knowledge of Quaternary geology during the two last decades, pointing not only to the existence of many more glacial-interglacial cycles than hitherto known, but also showing that the conditions during the glacial phases were much more severe than envisaged, e.g., when Lindroth and others proposed refugia in Scandinavia, Iceland and Greenland. Coope suggested that the North Atlantic islands lost almost all their biota at the height of the ice ages and that they were invaded and colonized almost entirely from northwestern Europe during two short phases in Lateglacial, when masses of fresh melt water floating on the salt water, and ocean surface currents different from those of today would have acted as aids to the dispersal in the North Atlantic. The decreasing faunal diversity, e.g., in the Coleoptera, from the Shetlands over the Faeroes and Iceland to Greenland might reflect the progressive loss of soil-bound insects as they were transported for increasing distances across the ocean.

Discussion

In general the Greenlandic biota are dominated by circumpolar and holarctic species, and in addition most higher taxa contain both a nearctic and a palaearctic element. The share of nearctic and palaearctic species highly differs among the systematic groups, but on the

Table 15. Greenlandic Coleoptera found as subfossils in North America and/or Europe.*) (Modern distributions: P, palaearctic; N, nearctic; WH, western holarctic; the remainder are circumpolar).

	North America	Europe
Nebria rufescens	×	×
Patrobus septentrionis	×	×
Bembidion grapii	×	
Trichocellus cognatus	×	×
Hydroporus morio	×	×
Colymbetes dolabratus	×	×
Gyrinus opacus		×
Helophorus brevipalpis		× (P)
Quedius fellmanni	×	
Omalium excavatum		× (P)
Micralymma brevilingue	× (WH)	
Simplocaria metallica	×	×
Simplocaria elongata	×	×
Tylicus subcanus	× (N)	
Byrrhus fasciatus		×
Nephus redtenbacheri		×
Otiorhynchus arcticus		× (P)
Otiorhynchus nodosus		× (P)
Hypera diversipunctata	×	×

*) According to Morgan & Morgan (1980), and J. V. Matthews, Ottawa; S. A. Elias, Boulder; G. R. Coope, Birmingham, (in litt.).

whole the flora and fauna of Greenland represent a transition from the Nearctic to the Palaearctic Region. This is not surprising. However, considering the geographical position of Greenland, it is astonishing and biogeographically very important that purely palaearctic elements are so well represented in most taxa.

The Coleoptera have played a significant role in the discussion of the origin of the biota of Greenland – and elsewhere in the North Atlantic area. This is largely because of their generally limited capacity for dispersal: One-third of the native Greenlandic species are brachypterous or apterous, and most of the winged species use their wings only exceptionally. Being compact and relatively heavy, the beetles are not commonly fit for passive aerial transport. Accordingly, the beetles should be regarded as indicators of dispersal: where they can be transported, most other components of the flora and fauna can also go (Coope 1986).

In the Greenlandic Coleoptera the palaearctic influence is exceptionally high. There is, of course, still the possibility that some of the species considered palaearctic do occur in North America (e.g., *Atheta* spp.), but the efforts in recent years in arctic Canada and Alaska have not yet revealed any of them. On the other hand, one purely nearctic species (*Tylicus subcanus*) has recently been discovered in Greenland.

The rapidly increasing knowledge of subfossil Quaternary insect faunas from western Europe and North America (e.g., Coope 1970, 1979b; Morgan & Morgan 1980) have shown still more convincingly, that great caution is needed when faunal history is deduced from present distributions. It could be, for instance, that the palaearctic weevils found in Greenland might some day be revealed as fossils in North America, thereby indicating a former circumpolar distribution. But so far only Greenlandic species with a circumpolar modern distribution (and one nearctic: *Tylicus subcanus*) have been found in Pleistocene and late Tertiary deposits from North America (e.g., Matthews 1974, 1975, 1977; Matthews et al. 1986; Morgan & Morgan 1980; Hughes et al. 1981). See Table 15.

On the other hand, in addition to some of the circumpolar species, a number of the palaearctic Greenlandic species have been found in European Pleistocene and Lateglacial sediments (Table 15), namely *Helophorus brevipalpis, Omalium excavatum, Nephus redtenbacheri, Otiorhynchus arcticus*, and *O. nodosus*. Especially the *Otiorhynchus*-species are very common European fossils (Henriksen 1935; Coope 1969b, 1977; Morgan 1969).

There is accordingly not yet any fossil evidence that the palaearctic element in the coleopterous fauna of Greenland originated in America. How and when did these species then manage to colonize Greenland?

Tertiary fauna

The easiest explanation (see Haarløv 1942, Hammer 1944, Brændegaard 1946, Omodeo 1957, Larsson 1959, Nurminen 1973) would be to consider the soil-bound fauna, including the Coleoptera, of Greenland and the other North Atlantic islands, so remarkably uniform and like that of northwestern Europe, to be the remains of the fauna common to these areas when they were united by a number of land bridges during the late Tertiary (Matthews 1980, Eldholm & Thiede 1980).

The Kap København Formation in northeastern Peary Land, at first assumed interglacial (Fredskild & Røen 1982), has now been dated as late Pliocene (Funder & Hjort 1979; Funder et al. 1984, 1985a, 1985b).

These deposits contain numerous insect fragments, mainly of Coleoptera, which when identified will yield invaluable evidence of the insect fauna inhabiting the subarctic forest-tundra, which existed in northernmost Greenland just before the commencement of Pleistocene glaciations (Bennike 1984; Böcher, in press; Bennike & Böcher, in press).

From preliminary samples, Fredskild & Røen (1982) identified a number of animal remains, including the beetles *Bembidion grapii, Gyrinus opacus, Hydroporus* sp., and cf. *Phyllodecta* sp. Not least the last-mentioned is remarkable, as it is the first record of a chrysomelid from Greenland.

Pleistocene fauna

Concerning survival of biota from the Tertiary, the Quaternary glaciations present the great problem. Nowadays most geologists and biologists studying the conditions of life during the Pleistocene agree that several times, at the height of the numerous glaciations, a "tabula rasa" prevailed in the glaciated areas (Coope 1979, 1986). Still, however, it seems possible that a small fraction of the most hardy species could survive the hostile conditions of icefree refugia. The existence of icefree areas at least in some places along the east coast of Greenland (Jameson Land, Hold with Hope, Wollaston Forland), from the last (Eemian) interglacial during the Weichselian (Wisconsinan) glaciation, now appears well established (Funder 1979, 1982). Fredskild (1973: 216) stated: "The Wisconsin glaciation was not one uninterrupted glaciation covering the whole area with a heavy ice blanket. Interstadials, changing centers of glaciation etc. altered the conditions through space and time, and with the effective dispersal of many arctic plants these were able to settle as soon as an ice-free ground was exposed".

Even given the possibility of icefree areas in shifting positions in Greenland during the entire Pleistocene epoch, this would not solve our problem. With one exception, the Greenlandic beetles are not truly arctic species, most of them being confined to or most frequent in the southwestern, subarctic part of the country (p. 70 and Table 6). Lindroth (1931, 1957, 1965: 70 ff.) and Larsson (1959) admited that the beetle faunas of both Iceland and Greenland are principally low arctic to subarctic, with a number of species preferring forest biotopes in Scandinavia! It is accordingly not realistic to associate these forms (e.g., *Trichocellus cognatus, Quedius fellmanni, Lathrobium fulvipenne, Nephus redtenbacheri)* with the harsh conditions in a glacial refugium envisaged by, e.g., Fredskild (1973), Funder (1979), and Coope (1979, 1986). Some of the more eurytopic, northerly occurring species (*Hydroporus morio, Colymbetes dolabratus, Micralymma brevilingue, Byrrhus fasciatus)* could possibly have lived in refugia. The only high arctic Greenlandic beetle, *Gnypeta cavicollis*, might of course be a glacial survivor.

Unfortunately, Pleistocene terrestrial and limnic fossils have not yet been found in Greenland, apart from some dubious calcareous concretions containing pollen (Bryan 1954). It would be especially interesting to find fossiliferous deposits from the East Greenland areas which have probably been icefree since the Eemian Interglacial (Funder 1979, 1982).

Holocene immigration

The geographical position of Greenland – a large, arctic island totally isolated from other land masses in a southerly direction – imposes special problems as regards the recolonization following glaciations. In other areas – North America, Europe, Siberia – the biota could simply follow the retreating ice northwards. This possibility did not exist in Greenland, where the only immigration route for the less mobile forms was through the high arctic Canadian islands and across the narrow straits separating Ellesmere Island and northern Greenland. This route, however, can only have served the immigration of high arctic species able to get across not only the straits between Ellesmere Island and Greenland but also a number of straits, sounds and channels separating the Queen Elizabeth Islands from the Canadian mainland. During summer the spread could be achieved by means of active flight in combination with wind, or by passive wind-dispersal of light animals, possibly dispersal by rafting on floating blocks of ice carrying soil and plant debris; in winter, wind-dispersal of cold-hardy hibernating stages across the frozen straits is another possibility (see the discussion by McAlpine 1964, 1965).

However, this immigration route is unsuitable and very unlikely for most Greenlandic Coleoptera, whereas it is undoubtedly of importance for a number of other taxa (notably higher plants, freshwater Entomostraca, Lepidoptera, Diptera, Araneae, and mammals, including man; see Jensen 1928, T.W.Böcher et al. 1959, Røen 1962, Downes 1966, Holm 1967, Danks 1981a).

The restrictions on the immigration imposed by the position of Greenland undoubtedly have caused many taxa to be much more deficient in species than what might be expected by comparison with climatically similar areas (Jensen 1928: 18). Coope (1986) showed that Greenland has got only 17% of the expected number of Coleoptera, and Lindroth (1985: 17) estimated the number of Carabidae of the northernmost, arctic Fennoscandia as at least 50 species – contrasting with the 4 carabids in Greenland.

Jensen (1928) pointed out that during the Postglacial Hypsithermal (warm period), when distributions presumably extended farther northwards than at present, a number of species with a southern distribution in Greenland (and North America) might have used the northwestern immigration route.

Still, this gateway can only be considered as likely for the nearctic or circumpolar (holarctic) species, some of which might have survived part of the Pleistocene in Greenland. We know that the dytiscids, *Hydroporus morio* and *Colymbetes dolabratus*, were present in southern Greenland already 8600 and 3900 years ago, respectively (Fredskild et al. 1975).

Some winged, circumpolar species with a subarctic to low arctic distribution (*Gyrinus opacus, Simplocaria metallica, Caenoscelis ferruginea*) might have used the northwestern route, or could have blown over the Davis Strait, during the Hypsithermal, since none of them occur today in arctic parts of North America.

Coccinella transversoguttata undoubtedly has immigrated from North America. It is "western holarctic", not found in Europe, not even as subfossil, and it frequently flies.

Micralymma brevilingue and *Dorytomus imbecillus* are also western holarctic, but these are flightless (apterous and brachypterous, respectively). Interestingly enough, the only purely nearctic species, *Tylicus sub-*

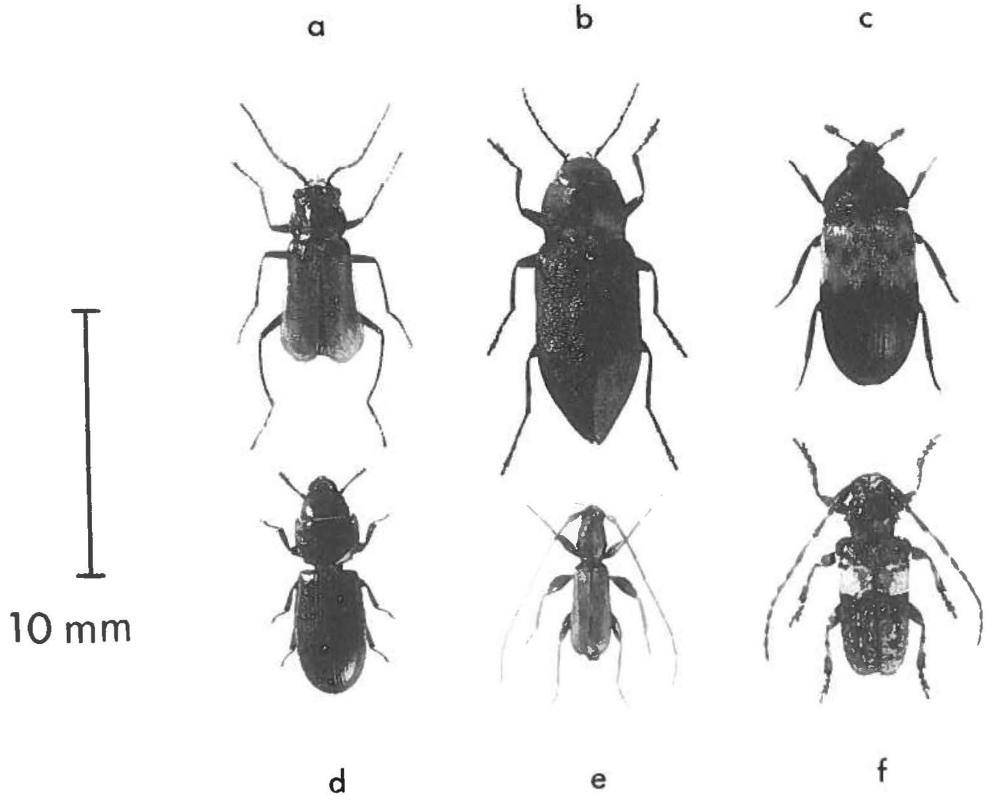


Fig. 51.
a: *Malachius aeneus* (L.) (p. 49); b: *Melanophila acuminata* (Degeer) (p. 42); c: *Dermestes lardarius* L. (p. 48); d: *Tenebroides mauritanicus* (L.) (p. 49); e: *Gracilia minuta* (F.) (p. 57); f: *Pogonocherus fasciculatus* (Degeer) (p. 59).

canus, is also brachypterous. As mentioned, *Micralymma brevilingue* is a likely candidate for having survived part of the Pleistocene in Greenland, but how and when the other two species have succeeded in getting to Greenland is really enigmatic.

Turning now to the palaearctic group of mainly subarctic to low arctic species, the discussion quoted above (Jensen, Henriksen, Lindroth, and others) shall not be repeated here, but is of course the basis for a reconsideration of the problems.

The possibilities of passive dispersal from Europe by means of wind, ocean currents or birds have been extensively discussed by Lindroth (1931, 1957; also by Elton 1925, Brændegaard 1928, Wolf 1937, and Kryger & Schmiedeknecht 1938). Bristowe (1925) thought that the entire invertebrate fauna of Jan Mayen could have come with driftwood from Scandinavia and Siberia.

As disposed nowadays, both the prevailing wind and the ocean currents of the North Atlantic would favour a passive transport in the opposite direction (i.e., from west to east); and especially regarding the Coleoptera, none of these means of dispersal have been credited any significance. On the other hand, a number of recent studies have shown that a large number of insects, including several species of Coleoptera, may be blown by the wind for considerable distances, e.g. to constitute "fall out" on glaciers (Gressitt & Yoshimoto 1974, Edwards 1987).

Regarding transport with driftwood and similar objects, both the very long duration of a voyage following the backward curling of the North Atlantic Drift northwards to about 80°N and then southwest along the East Greenland coast, and the protracted exposure to salt water and a very cold climate, renders this invasion route absolutely improbable. It should be remembered that a prolonged exposure to the salinity of ocean water causes lethal desiccation in most terrestrial organisms (Palmen 1944, Lindroth et al. 1973, Coope 1986).

Nonetheless, the proposal put forward by Coope (1969, 1970, 1979, 1986) of a Lateglacial passive spread over the North Atlantic from northwestern Europe to the North Atlantic Islands, including Greenland, appears to present the best solution to the enigmatic existence in these islands of fairly uniform biota of a marked palaearctic affinity (see Bengtson 1981). Coope envisages a situation which occurred twice, before and after the Younger Dryas episode, when the Gulf Stream had another course than today, turning westwards just before entering the Norwegian Sea, and passing the Faeroes and Iceland to southernmost Greenland (Jansen et al. 1983). At the same time there was a very low surface salinity in the North Atlantic, caused by masses of fresh meltwater from the rapidly shrinking ice sheet in Scandinavia (see Ruddiman & Mc Intyre 1981). Violent spring floods in Doggerland would carry to sea large quantities of fjord ice and river ice loaded with soil and

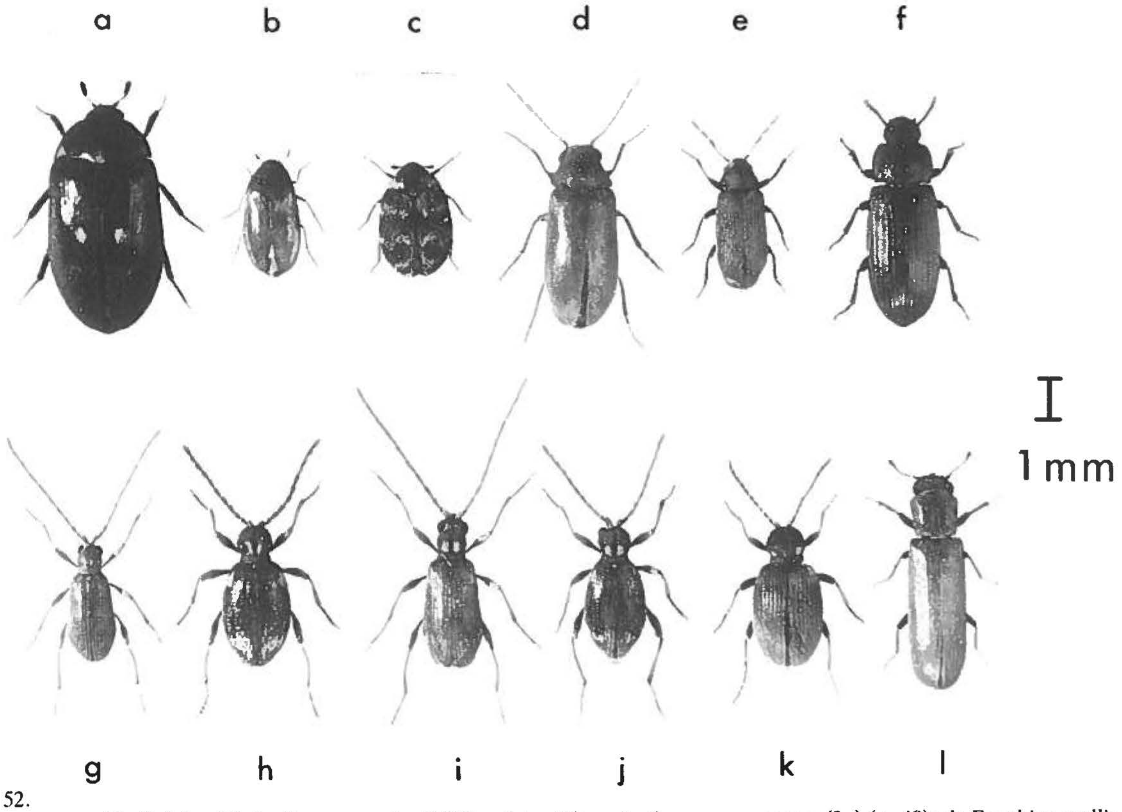


Fig. 52.
a: *Attagenus pellio* (L.) (p. 48); b: *Reesa vespulae* (Milliron) (p. 48); c: Anthrenus museorum (L.) (p. 48); d: *Ernobius mollis* (L.) (p. 48); e: *Anobium punctatum* (Degeer) (p. 48); f: *Tribolium destructor* Uyttenboogart (p. 57); g,h: *Ptinus fur* (L.) ♂,♀ (p. 49); i,j: *Ptinus raptor* Sturm ♂,♀ (p. 49); k: *Ptinus tectus* Boieldieu (p. 49); l: *Lyctus brunneus* (Stephens) (p. 48).

plant debris, also containing, e.g., insects in their cold resistant hibernating stages.

This means of transport would, of course, carry circumpolar as well as palaearctic species to the islands, and consequently circumpolar species have not necessarily invaded Greenland from North America. Moreover, since the combination of the deflected Gulf Stream and the fresh meltwater floating on the North Atlantic occurred during two relatively warm climatic periods, the flora and fauna available for transport was not arctic, but subarctic-temperate, which provides an explanation of the puzzling southern character of the coleopterous faunas of the North Atlantic islands.

It is, however, not quite enough to be brought safely to, for example, Greenland during the Lateglacial. The deflected Gulf Stream would most likely deposit any transported goods somewhere along the southernmost shore of the east coast, which at present, as probably also in the Lateglacial, is a highly inhospitable place, where establishment of temperate species would be almost excluded. An ocean current around Kap Farvel and continuing some way up the west coast, like today, must be a necessary prerequisite for a successful colonization by most of the present-day beetle fauna. Still, it is highly impressive that, e.g., the famous *Bembidion grapii*, in which only one third of the Greenlandic individuals are macropterous, has been able to extend its occurrence northwards to the head of Ukkusissat Fjord on the west coast, and to Mørkefjord on the east coast (map p. 11) during the 10000 years since its assumed arrival somewhere in southernmost Greenland. Here the possibility of wind dispersal during winter, as suggested by McAlpine (1965), could be taken into consideration.

The deterioration of climate during the Younger Dryas probably caused most of the early colonizers to succumb, so that the lasting colonization must have taken place just following this cold period, i.e., about 10000 to 9500 B.C. (see the discussion by Buckland et al. 1986).

Introductions by man

About half the species of Coleoptera recorded from Greenland are without doubt human introductions, most of them members of the cosmopolitan, synanthropic fauna (see the survey in Table 13 and Figs 51–55).

Regarding what is here considered the indigenous fauna, the possibility of importation by the Norsemen

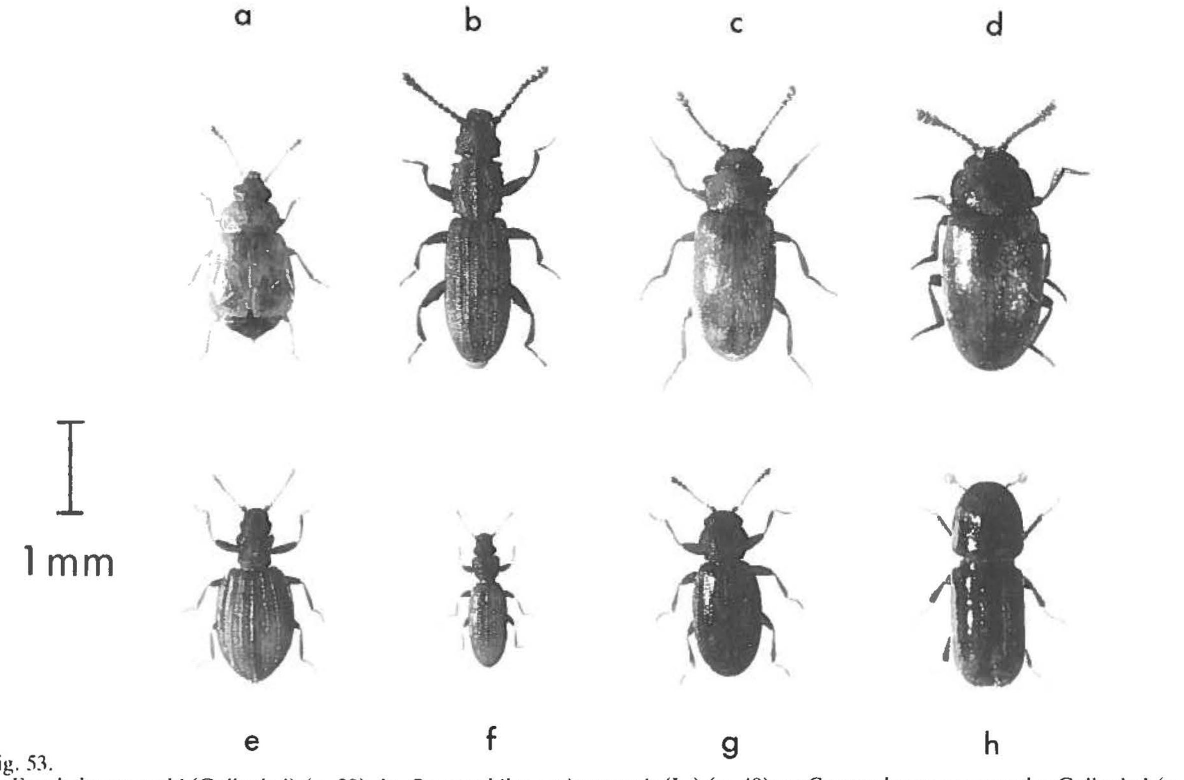


Fig. 53.
a: *Eusphalerum sorbi* (Gyllenhal) (p. 29); b: *Oryzaephilus surinamensis* (L.) (p. 49); c: *Cryptophagus acutangulus* Gyllenhal (p. 49); d: *Cryptophagus lapponicus* Gyllenhal (p. 50); e: *Thes bergrothi* (Reitter) (p. 56); f: *Dienerella filum* (Aubé) (p. 56); g: *Corticaria serrata* (Paykull) (p. 56); h: *Pityogenes chalcographus* (L.) (p. 68).

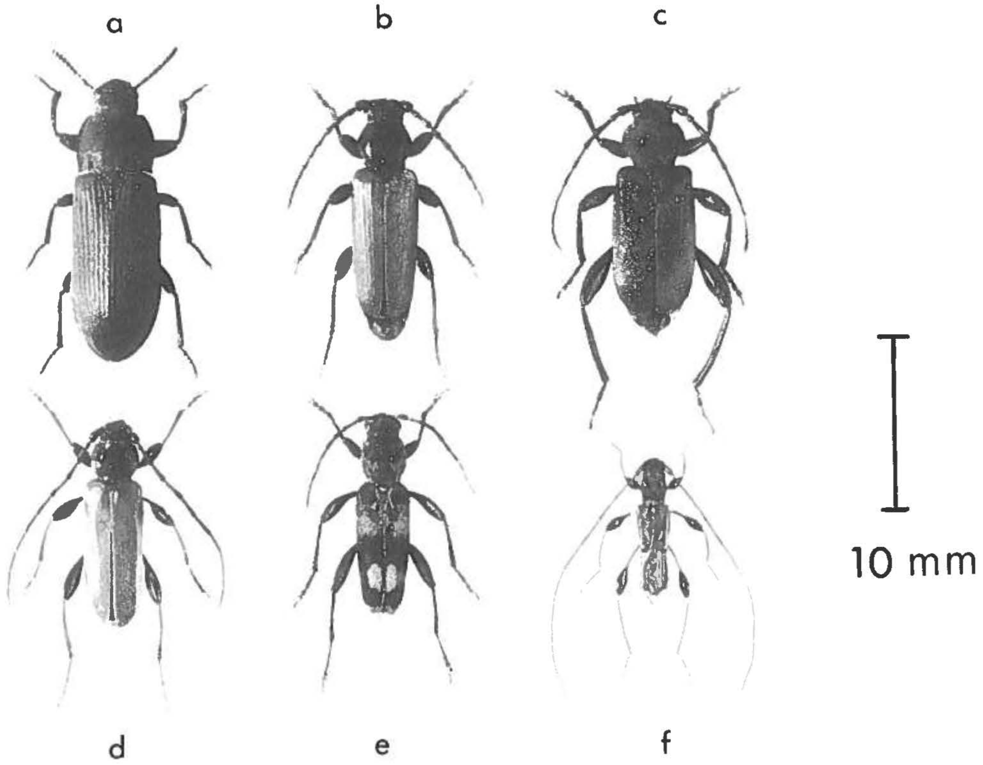
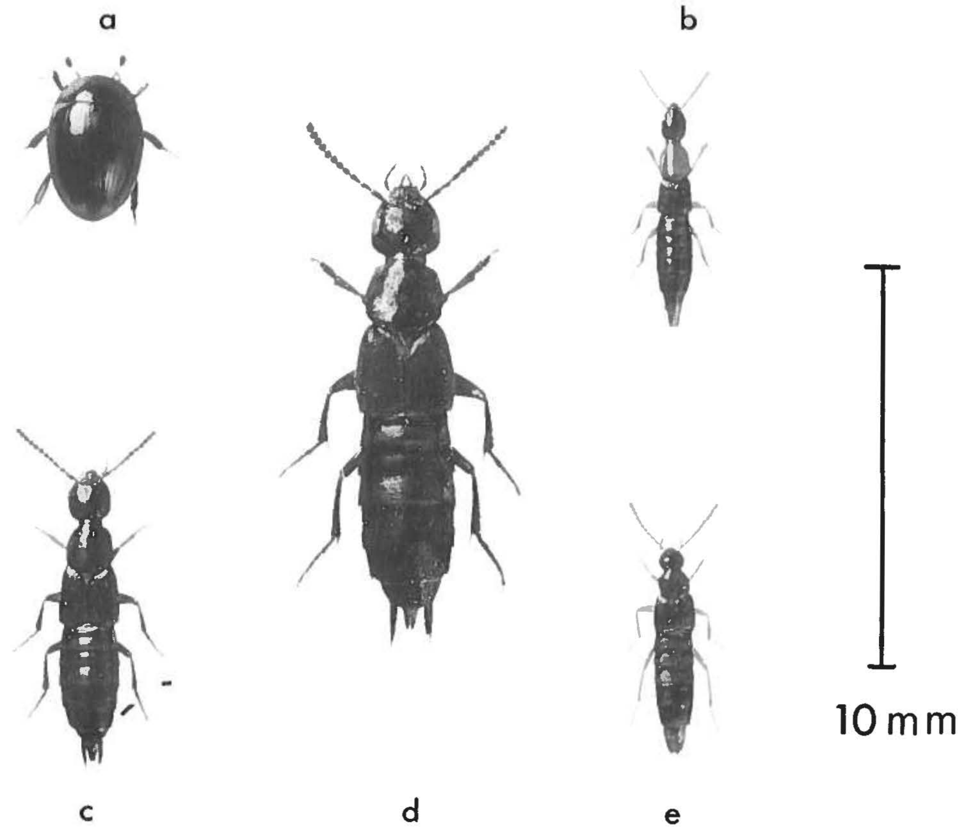


Fig. 54.
a: *Tenebrio obscurus* F. (p. 57); b: *Tetropium castaneum* (L.) (p. 57); c: *Callidium violaceum* (L.) (p. 59); d: *Phymatodes testaceus* (L.) (p. 59); e: *Xylotrechus colonus* (F.) (p. 59); f: *Molorchus minor* (L.) (p. 59).

Fig. 55. a: *Cercyon obsoletus* (Gyllenhal) (p. 23); b: *Othius angustus* Stephens (p. 28); c: *Philonthus cephalotes* (Gravenhorst) (p. 24); d: *Philonthus politus* (L.) (p. 24); e: *Ocalea picata* (Stephens) (p. 36).



(Jensen 1928: 15) cannot be totally rebutted. However, Norse introductions are difficult to detect among the circumpolar species when an occurrence in Greenland fits naturally into the general distribution of a species.

Among the palaearctic species only those largely confined to the old Norse settlements (Nanortalik and Qaqortoq/Julianehåb Districts, Godthåbsfjord) need consideration – species belonging to the subarctic-southern low arctic fauna element (p. 71): *Lathrobium fulvipenne*, *Omalium excavatum*, *Atheta vestita*, and *Nephus redtenbacheri*.

These species are in common with Iceland, and Lindroth's arguments against their possible introduction (pp. 81–83) still appear valid*). It must also be remembered that they could as well belong to the group of suggested Lateglacial invaders treated above (p. 86). Vibe (1953a, 1953b) pointed out that during the entire period from the start of Danish colonization in 1721 till now, with increasing traffic and trade with Europe, not a single instance of an introduced insect species established outdoors in Greenland has been reported. Why should the vikings have been so much more capable of introducing insects?

But, in fact, they were. Recent archaeological investigations have shed a highly interesting light on the insect fauna associated with the Norse settlements in the Nuuk/Godthåb District (Buckland et al. 1983, Buckland 1986, in litt.). In excavated farms from Nipaatsoq and Kilaarsarfik were found both ubiquitous, indigenous species and synanthropic species associated with rural culture. These included a number of species which were here recorded from Greenland for the first time – and which probably later died out when the Norsemen disappeared: *Othius angustus, Philonthus politus, Philonthus (?) cephalotes, Ocalea (?) picata, Atomaria* sp.

Quedius mesomelinus and *Xylodromus concinnus*, contrary to the other species, apparently managed to survive to the present day, but may now have become extinct. These species may have survived the disappearance of the Norse culture by switching over to a life associated with the eskimo turf huts, which have now largely disappeared, at least in southern Greenland.

Also *Eusphalerum sorbi* belongs to these old introductions, but has presumably been reintroduced recently. *Latridius minutus* may or may not belong to the indigenous fauna (p. 55) but was probably also introduced with the Norsemen.

*) Lindroth (1957: 267) also included *Atheta fungi* and *Quedius boops* in his list of species "which may have been brought over, by pure chance". The first-mentioned turned out to be the circumpolar *Q. fellmanni*, which appears to have a Greenlandic distribution restricted to the Norse settlements (map p. 27). The Greenlandic species formerly considered *A. fungi* is in fact the newly described *A. groenlandica* Mahler (p. 39).

Conclusions about origin

A survival from the Tertiary through the entire Pleistocene of any Greenlandic beetle is highly improbable. A few, hardy species might have existed in refugia from the Eem Interglacial during the last glaciation. One purely nearctic and one holarctic species undoubtedly have come to Greenland from North America during the Holocene, most probably during the Lateglacial Hypsithermal, and the same may be true for two more, "western" holarctic species, absent from Europe. The remainder of the species most likely are Lateglacial invaders from western Europe.

The Norsemen were responsible for a number of introductions, of which only very few, partly synanthropic forms, have survived to the present day. If some of the palaearctic species here considered indigenous have in fact been imported by vikings, this possibility is restricted to only a couple of species.

Final conclusions

Danks (1981a: 247) enumerated the characteristics of the Greenlandic insect fauna as "1) The prevalence of circumpolar (or at least holarctic) species; 2) the nearctic rather than palearctic affinities of a majority of the fauna that is not holarctic; 3) the significance within Greenland of north-south differences in range type; 4) the substantial proportion of the North American *high* arctic fauna that occurs in northern Greenland; 5) the relative paucity of low arctic, subarctic and boreal elements that might be expected in southern Greenland; 6) the frequent occurrence, in the south, of introduced species, many of which are palearctic".

Considering the Coleoptera of Greenland, it appears that none of these points really applies.

The number of circumpolar + holarctic species (11 + 5) is almost equalled by the number of palaearctic species (13 + 1) if the amphiatlantic *Micralymma marinum* is considered introduced to North America (Larsson & Gigja 1959). The purely nearctic element is represented by only one species (but possibly the "endemic" *Atheta groenlandica* will prove to be nearctic).

Only one species, the high arctic *Gnypeta cavicollis*, appears to have a southern limit in Greenland.

Of the seven species of beetles (apart from introductions) reported by Danks from high arctic North America, only two are found in high arctic Greenland (*Hydroporus morio, Micralymma brevilingue*), but two more merely identified to genus (*Gnypeta* sp., *Atheta* sp.) might be in common. One remarkable difference between the two high arctic faunas is the occurrence in northeastern Canada of *Amara alpina* (Paykull), which is absent from Greenland (p. 82); another is the extension into high arctic Greenland of a number of species (*Bembidion grapii, Colymbetes dolabratus, Byrrhus fasciatus, Coccinella transversoguttata*) which in North America are confined to low arctic and subarctic environments.

The Greenlandic beetle fauna is chiefly made up of low arctic and subarctic species.

It is not evident, nor very likely, that any of the Greenlandic beetles today living in the open have been introduced by man. Exceptions are probably a few partly synanthropic species (*Cercyon obsoletus, Quedius mesomelinus, Omalium excavatum, Latridius minutus*).

G. R. Coope has presented an inspiring and well-founded theory of a Lateglacial colonization of the North Atlantic islands from Northwestern Europe by the soil-bound biota, including most Coleoptera. This theory offers a solution to the problems concerning the strong palaearctic influence in the Greenlandic Coleoptera, and also explains the southern character of the fauna.

Acknowledgements

My sincere thanks are extended to the Danish Natural Research Council for a grant (J.No. 11–5435) which enabled me to work for half a year on this project.

I am moreover indebted to a number of colleagues who have contributed information and/or have placed material at my disposal:

P.C. Buckland, Department of Geography, University of Birmingham, U.K.; G.R. Coope, Department of Geological Sciences, University of Birmingham, U.K.; M.J. Cotton, Beaumont College, Lancaster, U.K.; S.A. Elias, University of Colorado, Boulder, Colorado, U.S.A.; P. Jeppesen, ZMUC, Denmark; P.J. Johnson, University of Idaho, Moscow, Idaho, U.S.A.; J. Madsen, Naturhistorisk Museum, Århus, Denmark; J.V. Matthews, Geological Survey of Canada, Ottawa, Ontario, Canada; P. Nielsen, ZMUC, Denmark; D. & J. Stroud, School of Biological Sciences, University College of Wales, Aberystwyth, U.K.; C. Vibe, ZMUC, Denmark.

I am indebted to my old friend, T. Christensen, Institute of Thallophytes, University of Copenhagen, for a translation from Latin.

Finally, I extend my sincere thanks to the following friends and colleagues at the ZMUC, for their help:

H. Enghoff, N.P. Kristensen and U. Røen, for reading and commenting on parts of the manuscript; E. Asmussen, for a translation from Russian; M. Bevort, for word-processing the manuscript; E. Bonde, for serigraphic reproduction of drawings; G. Brovad, for photography; O. Martin, for various practical and professional assistance; M.E. Petersen, for correction of the English text; B.W. Rasmussen, for SEM-photography.

Last, but not least, I wish to thank R. Nielsen, scientific illustrator at the ZMUC, for an excellent collaboration and for the enormous work put into the beautiful drawings of all the beetles indigenous to Greenland.

References

Literature consulted but not referred to in the text is marked with an asterisk.

Andersen, J. 1970. The larvae of *Pelophila borealis* Payk., *Nebria gyllenhali* Schnh. and *N. nivalis* Payk. (Coleoptera, Carabidae). – Astarte 3: 87-95.

– 1982. Contribution to the knowledge of the distribution, habitat selection and life history of the riparian beetles in Norway. – Fauna norvegica (B) 29: 62-68.

– 1984. A re-analysis of the relationships between life cycle patterns and the geographical distribution of Fennoscandian carabid beetles. – Journal of Biogeography 11: 479-489.

Angus, R.B. 1973. Pleistocene *Helophorus* (Coleoptera, Hydrophilidae) from Borislav and Starunia in the Western Ukraine, with a reinterpretation of M. Lomnicki's species, description of a new Siberian species, and comparison with British Weichselian faunas. – Philosophical Transactions of the Royal Society of London, Series B, 265 (869): 299-326.

Arnett, R.H. (ed.) 1983. Checklist of the Beetles of North and Central America and the West Indies. North American Beetle Fauna Project. Volumes 1-10. – Flora & Fauna Publications, Gainesville, Florida, U.S.A. 2173 pp.

Asahina, E. 1966. Freezing and frost resistance in insects. – In: Merryman, H.T. (ed.). Cryobiology: 451-486. – Academic Press, London & New York.

Aurivillius, C. 1883. Insektlifvet i arktiska länder. – In: Nordenskiöld, A.E. (ed.). Studier och forskningar föranledda af mina resor i höga Norden: 403-459. – F. & G. Beijers Förlag, Stockholm.

– 1900. Lepidoptera och Coleoptera insamlade under professor A.G.Nathorst's arktiska expeditioner 1898 och 1899, under den svenska expeditionen till Beeren Eiland 1899 och under konservator G. Kolthoff's expedition till Grönland 1900. – Öfversigt af Kungliga Vetenskaps-Akademiens Förhandlingar 1900, 10: 1135-1144.

Bakken, H. 1985. Cold hardiness in the alpine beetles *Patrobus septentrionis* and *Calathus melanocephalus*. – Journal of Insect Physiology 31 (6): 447-453.

Balfour-Browne, F. 1934. Systematic notes upon British aquatic Coleoptera. Part V. – The Entomologist's Monthly Magazine 70: 247-255.

– 1936. Systematic notes upon British aquatic Coleoptera: additional correction. – The Entomologist's Monthly Magazine. 72: 257.

– 1938. Systematic notes upon British aquatic Coleoptera 1. Hydradephaga; being a corrected and revised edition of a series of papers which appeared in the E.M.M., from 1934-1936. – Nathaniel Lloyd & Co., London. 96 pp.

– 1940. British Water Beetles, Volume I. – The Ray Society, London. 375 pp.

– 1950. British Water Beetles, Volume II. – The Ray Society, London. 394 pp.

– 1958. British Water Bettles, Volume III. – The Ray Society, London. 210 pp.

Bangsholt, F. 1983. Sandspringernes og løbebillernes udbredelse og forekomst i Danmark ca. 1830-1981 (Coleoptera: Cicindelidae and Carabidae). Dansk Faunistisk Bibliotek 4. – Scandinavian Science Press. København. 271 pp.

Becker, P. 1975. Island colonization by carnivorous and herbivorous Coleoptera. – The Journal of Animal Ecology 44: 893-906.

Belicek, J. 1976. Coccinellidae of Western Canada and Alaska with analyses of the transmontane zoogeographic relationships between the fauna of British Columbia and Alberta (Insecta: Coleoptera: Coccinellidae). – Quaestiones Entomologicae 12: 283-409.

Bell, J.E. 1981. An annotated list of invertebrates collected from Equalungmiut Nunaat. – In: Fox, A.D. & Stroud, D.A. (eds.). Report of the 1979 Greenland White-fronted Goose Study Expedition to Eqalungmiut Nunaat, West Greenland: 227-229. – Greenland White-fronted Goose Study, Aberystwyth.

Bengtson, S.-A. 1980. Species assemblages and coexistence of Faroe Island ground beetles. – Entomologica Generalis 6(2/4): 251-266.

– 1981. Terrestrial invertebrates of the Faroe Islands: III. Beetles (Coleoptera): Check-list, distribution, and habitats. – Fauna norvegica (B) 28 (2): 52-69.

Bengtson, S.-A., Enckell, P.H., Erikstad, K.E. & Solhöy, T. 1983. Geography of leg-colour dimorphism in the carabid beetle *Nebria gyllenhali* in Iceland and on the Faroe Islands. – Entomologica scandinavica 14 (1): 57-66.

Bengtson, S.-A., & Erikstad, K. E. 1984. Wing polymorphism in Amara quenseli (Schönherr) (Coleoptera: Carabidae) in Iceland. - Entomologica scandinavica 15: 179-183.

Bennike, O. 1984. Skov-tundra i Nordgrønland i Plio-Pleistocæn – plantegeografiske implikationer. – Dansk geologisk Forening, Årsskrift for 1984 :111-112.

Bennike, O. & Böcher, J. (in press). Forest-tundra neighbouring the North Pole: Plant and insect remains from the Plio-Pleistocene Kap København Formation, North Greenland. – Arctic.

*Bertrand, H. 1931. Notice sur les larves Dytiscides de la collection Meinert. – Entomologiske Meddelelser 17: 286-305.

Blackwelder, R.E. 1973. Family 27. Staphylinidae. – In: Arnett (1983). Checklist of the Beetles of North and Central America and the West Indies 2. The Rove Beetles and Related groups. 167 pp. – Flora & Fauna Publications, Gainesville, Florida, U.S.A.

Blair, K.G. 1930. Coleoptera from Greenland. Oxford University Greenland Expedition, 1928. – The Annals and Magazine of Natural History, Tenth Series, 5: 394-400.

Böcher, J. 1971. Preliminary studies on the biology and ecology of *Chlamydatus pullus* (Reuter) (Heteroptera: Miridae) in Greenland. – Meddr Grønland 191 (3): 1-29.

– 1976. Population studies on *Nysius groenlandicus* (Zett.) (Heteroptera: Lygaeidae) in Greenland, with particular reference to climatic factors, especially the snow cover. – Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 139: 61-89.

– (in press) Boreal insects from northernmost Greenland: palaeo-entomological evidence from the Kap København Formation (Plio-Pleistocene), Peary Land. – Fauna norvegica (B) 36.

Böcher, J. & Enghoff, H. 1984. A centipede in Greenland: *Lamyctes fulvicornis* Meinert, 1868 (Chilopoda, Lithobiomorpha, Henicopidae). – Entomologiske Meddelelser 52: 49-50.

Böcher, T. W. 1938. Biological distribiutional types in the flora of Greenland. A Study on the flora and plant-geography of South Greenland and East Greenland between Cape Farewell and Scoreby Sound. – Meddr Grønland 106 (2): 1-339.

– 1956. Area-limits and isolations of plants in relation to the physiography of the southern parts of Greenland. – Meddr Grønland 124 (8): 1-40.

– 1963a. Phytogeography of Greenland in the light of recent investigations. – In: Löve, A. & Löve, D. (eds.). North Atlantic Biota and Their History: 285-295. – Pergamon Press, Oxford.

– 1963b. Phytogeography of Middle West Greenland. – Meddr Grønland 148 (3): 1-289.

– 1979. Birch woodlands and tree growth in southern Greenland. – Holarctic Ecology 2: 218-221.

– 1981. Hovedtræk af Grønlands plantegeografi. – In: Nørrevang, A. & Lundø, J. (eds.). Danmarks Natur 11, Grønland: 350-364. – Politikens Forlag, København.

Böcher, T.W., Holmen, K. & Jakobsen, K. 1959. A synoptical study of the Greenland flora. – Meddr Grønland 163 (1): 1-32

Böcher, T.W., Holmen, K. & Jakobsen, K. 1968. The Flora of Greenland. – P. Haase & Søn, Copenhagen. 312 pp.

*Bøgvad, R. 1940. Quaternary geological observations etc. in South-East and South Greenland. – Meddr Grønland 107 (3): 1-42.
Brændegaard, J. 1928. Araneina. – In: Spärck, R. & Tuxen, S.L. (eds.): The Zoology of the Faroes 2, Part 2 (47): 1-28. – Andr. Fred. Høst & Søn, Copenhagen. 28 pp.
– 1938. Aeronautic spiders in the Arctic. – Meddr Grønland 119 (5): 1-9.
– 1946. The spiders (Araneina) of East Greenland. A faunistic and zoogeographical investigation. – Meddr Grønland 121 (15): 1-128.
Brændegaard, J., Henriksen, K.L. & Spärck, R. 1935. Insects and Arachnids. – Meddr Grønland 104 (16): 1-18.
Brinck, P. 1940. Beitrag zur Kenntnis der Wasserkäfer Grönlands – Opuscula Entomologica 5: 37-41.
– 1966. Animal invasion of Glacial and Late Glacial terrestrial environmants in Scandinavia. – Oikos 17: 250-266.
Brinck, P. & Wingstrand, K.G. 1951. The mountain fauna of the Virihaure area in Swedish Lapland. – Lunds Universitets Årsskrift, N.F.Avd.2, 46 (2): 1-173.
Bristowe, W. S. 1925. The fauna of the arctic island of Jan Mayen and its probable origin. – The Annals and Magazine of Natural History, Ninth Series, 15(88): 480-485.
Brockmann-Jerosch, H. 1907. Die Flora des Puschlav und ihre Pflanzengesellschaften. – Die Pflanzengesellschaften der Schweizeralpen I. Leipzig.
*Brødsgaard, C., Bonde, J. & Madsen, H. 1984. Arktiske biller med speciel henblik på de grønlandske arters forhold. – Unpublished thesis, University of Copenhagen. 119 pp.
Brown, W.J. 1932. New species of Coleoptera. – Canadian Entomologist 64: 3-12.
– 1937. The Coleoptera of Canada's eastern arctic. – Canadian Entomologist 69: 106-111.
– 1962. A revision of the forms of *Coccinella* L. occurring in America north of Mexico (Coleoptera: Coccinellidae). – Canadian Entomologist 94: 785-808.
Brundin, L. 1934. Die Coleopteren des Torneträskgebietes. Ein Beitrag zur Ökologie und Geschichte der Käferwelt in Schwedisch-Lappland. – Lund. 436 pp.
– 1940. Zwei neue nordische *Atheta*-Arten aus der *islandica*-Gruppe (Col. Staphylinidae). Vorläufige Mitteilung. – Entomologisk Tidskrift 61 (3-4): 131-133.
– 1943. Zur Kenntnis einiger in die *Atheta*-Untergattung *Metaxya* M.& R. gestellten Arten (Col. Staphylinidae). – Lunds Universitets Årsskrift N.F.Avd. 2, 39 (4): 1-38.
– 1953. Die palaearktischen Arten der *Atheta*-Untergattung *Dimetrota* Muls. et Rey (Col., Staphylinidae). Eine systematische Studie. – Arkiv för Zoologi 5 (7): 369-434.
Bryan, M.S. 1954. Interglacial pattern spectra from Greenland. – Studies in Vegetational History in honour of Knud Jessen 29th November 1954. – Geological Survey of Denmark, II. Series 80: 65-72.
Buckland, P.C., Sveinbjarnardóttir, Savory, D., McGovern, T.H., Skidmore, P., Andreasen, C. 1983. Norsemen at Nipaitsoq, Greenland: A palaeoecological investigation. – Norwegian Archaeological Review 16 (2): 86-98.
Buckland, P.C., Perry, D.W., Gislason, G.M., Dugmore, A.J. 1986. The pre-Landnam fauna of Iceland: a palaeontological contribution. – Boreas 15: 173-184.
Campbell, J.M. 1980. Distribution patterns of Coleoptera in Eastern Canada. – Canadian Entomologist 112: 1161-1175.
Carpenter, G.D.H. 1938. Notes on insects collecteed in West Greenland by the Oxford University Greenland Expedition, 1936. - The Annals and Magazine of Natural History, Eleventh Series, 1: 529-553.
Coope, G.R. 1969a. The contribution that the Coleoptera of Glacial Britain could have made to the subsequent colonisation of Scandinavia. – Opuscula Entomologica 34: 95-108.
– 1969b. Insect remains from Mid Weichselian deposits at Peelo, The Netherlands. – Mededelingen Rijks Geologische Dienst, Nieuwe Serie 20: 79-83.
– 1970. Interpretations of Quaternary insect fossils. – Annual Review of Entomology 15: 97-120.
– 1977. Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage.- Philosophical Transactions of the Royal Society of London B 280: 313-340.
– 1979a. The Carabidae of the Glacial Refuge in the British Isles and their Contribution to the Post Glacial Colonization of Scandinavia and the North Atlantic Islands. – In: Erwin, T.L., Ball, G.E., Whitehead, D.R.(eds.). Carabid Beetles, their Evolution, Natural History, and Classification: 407-424. – Dr. W. Junk Publishers; the Hague, Boston, London.
– 1979b. Late Cenozoic fossil Coleoptera: Evolution, biogeography, and ecology. – Annual Review of Ecology and Systematics 10: 247-267.
– 1986. The invasion and colonisation of the North Atlantic islands: a palaeoecological solution to a biogeographic problem. – Philosophical Transactions of the Royal Society of London B 314: 619-635.
Corbet, P. S. 1972. The microclimate of arctic plants and animals, on land and in fresh water. – Acta Arctica 18. 43 pp.
Cotton, M.J. 1979. Records of insects from North-East Greenland. – The Entomologst's Monthly Magazine 113: 213-217.
Cuellar, O. 1977. Animal parthenogenesis. A new evolutionary-ecological model is needed. – Science 197, 4306: 837-843.
Danks, H.V. 1978. Modes of seasonal adaptation in the insects. I. Winter survival. – Canadian Entomologist 110: 1167-1205.
– 1981a. Arctic arthropods. A review of systematics and ecology with particular reference to the North American fauna. – Biological Survey Project, Entomological Society of Canada. 608 pp.
*– 1981b. Bibliography of the Arctic Arthropods of the Nearctic Region. – Entomological Society of Canada. 125 pp.
Degerbøl, M. 1937. A contribution to the investigation of the fauna of the Blosseville Kyst, East Greenland, with special reference to zoogeography. – Meddr Grønland 104 (19): 1-36.
Deichmann, H. 1895. III. Østgrønlandske Insekter. Korte Bemærkninger om Insektlivet. – In: Den østgrønlandske Expedition, udført i Aarene 1891-92 under Ledelse af C.Ryder. Tredie Del. – Meddr Grønland 19: 97-104.
Den Boer, P. J., Van Huizen, T. H. P., Den Boer-Daanje, W., Aukema, B. & Den Bieman, C. F. M. 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae). – Entomologia Generalis 6 (2/4): 107-134.
Downes, J.A. 1962. What is an arctic insect? – Canadian Entomologist 94: 143-162.
– 1964. Arctic insects and their environment. – Canadian Entomologist 96: 279-307.
– 1965. Adaptations of insects in the Arctic. – Annual Review of Entomology 10: 257-274.
– 1966. The Lepidoptera of Greenland; some geographic considerations. – Canadian Entomologist 98: 1135-1144.
Edwards, J. S. 1987. Arthropods of alpine aeolian ecosystems. – Annual Review of Entomology 32: 163-179.
Eldholm, O. & Thiede, J. 1979. Cenozoic continental separation between Europe and Greenland. – Palaeogeography, Palaeoclimatology, Palaeoecology 30: 243-259.
Elias, S. A. 1984. Coleoptera from two subarctic localities in Canada with ecological notes and six new distribution records. - The Coleopterists Bulletin 38 (2): 142-144.
Elton, C. S. 1925. The dispersal of insects to Spitzbergen. – Transaction of the Entomological Society of London. 1925, I- II: 289-299.
Erwin, T., Whitehead, D. R., & Ball, G. E. 1977. Family 4. Carabidae, The Ground Beetles. – In: Arnett, R. H. 1983 (ed.). Checklist of the Beetles of North and Central America and the West Indies 1. The Ground Beetles, Water Beetles,

and Related Groups. 68 pp. – Flora & Fauna Publications, Gainesville, Florida, U.S.A.
Fabricius, O. 1780. Fauna Groenlandica. – Hafniæ et Lipsiæ. 452 pp.
Feilberg, J. 1984. A phytogeographical study of South Greenland. Vascular plants. – Meddr Grønland, Bioscience 15: 1-72.
– 1985. Grønlands varme kilder – naturens egne mistbænke. – Forskning i Grønland 2/85: 10–22.
Fjellberg, A. 1972. Coleoptera from Hardangervidda. – Zoological Museum, University of Bergen. Fauna of the Hardangervidda No. 1. 74 pp.
– 1983. Three species of staphylinid Coleoptera new to Spitzbergen. – Fauna norvegica. (B) 30: 110-111.
Forsskåhl, B. 1972. The invertebrate fauna of the Kilpisjärvi area, Finnish Lapland, 9. Carabidae, with special notes on ecology and breeding biology. – Acta Societas pro Fauna et Flora Fennica 80: 99-119.
Fredskild, B. 1969. Nordboplanter – vikingernes ukrudt. – Tidsskriftet Grønland, April 1969: 97-106.
– 1973. Studies in the vegetational history of Greenland. Palaeobotanical investigations of some holocene lake and bog deposits. – Meddr Grønland 198 (4): 1-245.
Fredskild, B., Jacobsen, N. & Røen, U. 1975. Remains of mosses and freshwater animals in some holocene lake and bog sediments from Greenland. – Meddr Grønland 198 (5): 1-44.
Fredskild, B. & Røen, U. 1982. Macrofossils in an interglacial peat deposit at Kap København, North Greenland. – Boreas 11: 181-185.
Fristrup, B. 1943. Contributions to the fauna and zoogeography of Northwest Iceland. – Entomologiske Meddelelser 23: 143-173.
– 1981. Klimatologi. – In: Nørrevang, A. & Lundø, J. (eds.): Danmarks Natur 11, Grønland: 170-179. – Politikens Forlag, København.
Funder, S. 1979. Ice-age plant refugia in East Greenland. – Palaeogeography, Palaeoclimatology, Palaeoecology 28: 279-295.
– 1982. Planterefugierne i Grønland. – Naturens Verden 1982: 241-255.
Funder, S. & Hjort, C. 1980. A reconnaissance of the Quaternary geology of Eastern North Greenland. – Grønlands geologiske Undersøgelse Rapport 99: 99-105.
Funder, S., Bennike, O., Mogensen, G.S., Noe-Nygaard, B., Pedersen, S.A.S., & Petersen, K.S. 1984. The Kap København Formation, a late Cainozoic sedimentary sequence in North Greenland. – Grønlands Geologiske Undersøgelse Rapport 120: 9-18.
Funder, S., Bennike, O., Petersen, K.S., Pedersen, S.A.S., Mogensen, G.S. 1985a. Mudder, mos og muslinger nær Nordpolen. – Naturens Verden 1985: 226-245.
Funder, S., Abrahamsen, N., Bennike, O., Freyling-Hanssen, R.W. 1985b. Forested Arctic: Evidence from North Greenland. – Geology 13: 542-546.
Galewski, K. 1967. The description of pupae of *Colymbetes paykulli* Er. and *C. dolobratus* (Payk.) with a key to the identification of pupae of the European species of *Colymbetes* Clairv. (Coleoptera, Dytiscidae). – Annales Zoologici 24 (5): 367-374.
– 1968. The descriptions of larvae of *Colymbetes dolabratus* (Payk.) with keys to the identification of larvae of the European species of *Colymbetes* Clairv. (Coleoptera, Dytiscidae). – Annales Zoologici 26 (7): 227-238.
Gelting, P. 1934. Studies on the vascular plants of East Greenland between Franz Joseph Fjord and Dove Bay. – Meddr Grønland 101 (2): 1-337.
– 1941. Über Pleistozäne Pflanzenrefugien in Grönland. – Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 17: 74-96.
Gislén, T. & Brinck, P. 1950. Subterranean waters on Gotland with special regard to the Lummelunda Current. II. Environmental conditions, plant and animal life, immigration problems. – Lunds Universitets Årsskrift N.F.Avd.2, 46 (6): 1-81.
Glesener, R. T. & Tilman, D. 1978. Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in terrestrial animals. – The American Naturalist 112,986: 659-673.
Gressitt, J. L. & Yoshimoto, C. M., 1974. Insect dispersal studies in northern Alaska. – Pacific Insects 16 (1): 11-30.
Haarløv, N. 1942. A morphologic-systematic-ecological investigation of Acarina. – Meddr Grønland 128 (1): 1-71.
Hale Carpenter, G.D. & Holm, Å. 1939. Insects and Araneæ collected in the Kangerdlugsuak Region of East Greenland by the British Expedition, 1935-36. – The Annals and Magazine of Natural History, Eleventh Series, 3 (13): 60-80.
Hammer, M. 1944. Studies on the oribatids and collemboles of Greenland. – Meddr Grønland 141: 1-210.
– 1955. Some aspects of the distribution of microfauna in the Arctic. – Arctic 8 (2): 115-126.
Hansen, M. 1983. De danske arter af slægten *Helophorus* Fabricius 1775 (Coleoptera, Hydrophilidae). – Entomologiske Meddelelser 50 (2): 55-76.
– 1987. The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 18. – E. J. Brill/Scandinavian Science Press Ltd. Leiden-Copenhagen. 254 pp.
Hansen, V. 1951. Biller 14. Clavicornia 2 og Bostrychoidea. Danmarks Fauna 56. – G.E.C. Gads Forlag, København. 253 pp.
– 1965. Biller 21. Snudebiller. Danmarks Fauna 69. – G.E.C. Gads Forlag, København. 524 pp.
– 1968. Biller 24. Sandspringere og løbebiller. Danmarks Fauna 76. – G.E.C.Gads Forlag, København. 451 pp.
– 1973. Biller 10. Blødvinger, klannere m.m. Danmarks Fauna 44. – G.E.C. Gads Forlag. 344 pp.
Henriksen, K. L. 1924. The Canadian Arctic Expedition 1913-18. – Entomologiske Meddelelser 14: 235-239.
– 1933. Undersøgelser over Danmarks-Skånes kvartære Insektfauna. – Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 96, Festskrift 2: 77-355.
– 1937. Insects collected on the Fifth Thule Expedition. – Report of the Fifth Thule Expedition 1921-24. The Danish Expedition to Arctic North America in charge of Knud Rasmussen, ph.d. 2 (8): 1-34.
– 1939. A revised index of the insects of Grønland. – Meddr Grønland 119 (10): 1-112.
– 1973 (1930). Vandkalve- og hvirvlerlarverne. – In: V. Hansen. Biller 8. Vandkalve og hvirvlere. Danmarks Fauna 34: 150-226. – G.E.C. Gads Forlag, København.
Henriksen, K.L. & Lundbeck, W. 1917. Landarthropoder (Insecta et Arachnida). Conspectus Faunæ Groenlandicæ, Pars secunda. – Meddr Grønland 22: 481-823.
Hinton, H.E. 1945. A Monograph of the Beetles associated with Stored Products. 1. – British Museum (Natural History). London. 443 pp.
Holdhaus, K. & Lindroth, C.H. 1939. Die europäischen Koleopteren mit boreoalpiner Verbreitung. – Annales des Naturhistorischen Museums in Wien 50: 123-293.
Holm, Å. 1967. Spiders (Araneae) from West Greenland. – Meddr Grønland 184 (1): 1-99.
Holmen, K. 1957. The vascular plants of Peary Land, North Greenland. A list of the species found between Victoria Fjord and Danmark Fjord. – Meddr Grønland 124,9. 149 pp.
Holmen, M. 1987. The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark I. Gyrinidae, Haliplidae, Hygrobiidae and Noteridae. Fauna Entomologica Scandinavica 20. – E. J. Brill/Scandinavian Science Press Ltd. Leiden-Copenhagen. 168 pp.
Holmgren, A.E. 1872. Insekter från Nordgrönland, samlade af Prof.A.E. Nordenskjöld år 1870. Granskade och beskrifna af A.E. Holmgren. – Öfversigt af Kungliga Vetenskaps-Akademiens Förhandlingar 1872, 6: 97-105.

Hughes, O. L., Harrington, C. R., Janssens, J. A., Matthews, J. V., Morlan, R. E., Rutter, N. W. & Schweger, C. E. 1981. Upper Pleistocene stratigraphy, paleoecology, and archaeology of the Northern Yukon Interior Eastern Beringia. 1. Bonnet Plume Basin. – Arctic 34,4: 329-365.
Iversen, J. 1952-1953. Origin of the flora of Western Greenland in the light of pollen analysis. – Oikos 4: 85-103.
Ives, J.D. 1974. Biological refugia and the nunatak hypothesis. – In: Ives, J.D. & Barry, R.G. (eds.). Arctic and Alpine Environments: 605-636. – Methuen, London.
Jansen, E., Sejrup, H.P., Fjæran, T., Hald, M., Holtedahl, K. & Skarbø, O. 1983. Late Weichselian paleoceanography of the southeastern Norwegian Sea. – Norsk Geologisk Tidsskrift 63: 117-146.
Jansson, A. 1926. Coleopteren aus dem Sarekgebiet. – Naturwissenschaftlische Untersuchungen des Sarekgebirges in Schwedisch Lappland 4 (9): 895-938.
Jansson, A. & Palm, T. 1936. Resultat av en coleopterologisk studieresa till nordvästra Jämtlands fjälltrakter. – Entomologisk Tidskrift 57: 180-226.
Jensen, A.S. 1928. Grønlands Fauna, et Forsøg på en Oversigt. Festskrift udgivet af Københavns Universitet i Anledning af Hans Majestæt Kongens Fødselsdag 26. September 1928. – København. 88 pp.
Jeppesen, P.C. 1986. Dytiscid beetles in Greenland, with description of the three larval stages of *Hydroporus melanocephalus* (Marsham, 1802). – Entomologica Basilensis 11: 67-79.
Johansen, F. 1911. Freshwater life in North-East Greenland. – Danmark-Ekspeditionen til Grønlands Nordøstkyst 1906-1908, 5 (6). Meddr Grønland 43: 321-327.
– 1921. Insect life on the western arctic coast of America. Part K, 3 (insects). Report of the Canadian Arctic Expedition 1913-18. – Ottawa. 61 pp.
Johansen, F. & Nielsen, J.C. 1910. The insects of the "Danmark" Expedition. Danmark-Ekspeditionen til Grønlands Nordøstkyst 1906-1908, 3 (2). – Meddr Grønland 43: 35-68.
Kaufmann, T. 1969. Life history of *Upis ceramboides* at Fairbanks, Alaska. – Annals of the Entomological Society of America 62 (4): 922-923.
– 1971. Hibernation in the arctic beetle *Pterostichus brevicornis* in Alaska. – Journal of the Kansas entomological Society 44: 81-92.
Kavanaugh, D.H. 1980. Insects of western Canada, with special reference to certain Carabidae (Coleoptera): Present distribution patterns and their origin. – Canadian Entomologist 112: 1129-1144.
King, P. E., Fordy, M. & Al-Khalifa, M. S. 1979. Observations on the intertidal *Micralymma marinum* (Strom) (Col., Staphylinidae). – Entomologist's monthly Magazine 115: 133-136.
Korotyaev, B.A. 1976. A review of weevils of the genus *Dorytomus* Germ. (Coleoptera, Curculionidae) of North-eastern Asia. – Revue d'Entomologie de l'URSS 55 (1): 124-136.
Koponen, S. 1978. Notes on herbivorous insects of the birch in southern Greenland. – Reports from the Kevo Subarctic Research Station 14: 13-17. (Annales Universitatis Turkuensis A, 2 (60)).
Krogerus, R. 1960. Ökologische Studien über nordische Moorarthropoden. Artenbestand, ökologischen Faktoren, Korrelation der Arten. – Societas Scientiarum Fennica, Commentationes Biologicae 21 (3): 1-238.
Kryger, J.P. & Schmiedeknecht, O. 1938. Hymenoptera. – In: Spärck, R. & Tuxen, S.L. (eds.). The Zoology of the Faroes, 2, Part 2 (43). – Andr. Fred. Høst & Søn, Copenhagen. 108 pp.
Lack, D. 1934. Some insects from the Scoresby Sound Region, East Greenland, with an account of the fauna of a nunatak. – The Annals and Magazine of Natural History, Tenth Series, 14 (84): 599-606.
Larsson, S.G., 1939. Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. – Entomologiske Meddelelser 20: 277-560.
– 1968. Løbebillernes larver. – In: V. Hansen: Biller 24. Sandspringere og løbebiller. Danmarks Fauna 76: 282-433. – G.E.C. Gads Forlag, København.
– 1959. Coleoptera 2. General remarks. – In: Frídriksson, Á. & Tuxen, S. L. (eds.). The Zoology of Iceland 3, Part 46b. – Ejnar Munksgaard, Copenhagen & Reykjavik. 85 pp.
Larsson, S.G. & Gigja, G. 1959. Coleoptera 1. Synopsis. – In: Frídriksson, Á. & Tuxen, S. L. (eds.). The Zoology of Iceland 3, Part 46a. – Ejnar Munksgaard, Copenhagen & Reykjavik. 218 pp.
Le Conte, J. L. 1878. 1. Descriptions of new species. – In: Hubbard, H. G. & Schwarz, E. A. 1878. The Coleoptera of Michigan: – Proceedings of the American Philosophical Society 17: 593-626.
Leng, C.W. & Mutchler, A.J. 1927. Supplement (I) 1919 to 1924 (inclusive) to Catalogue of the Coleoptera of America, north of Mexico. – New York. 78 pp.
de Lesse, H. 1950a. Notes zoologiques et botaniques sur l'Ouest de Groenland. Expeditions polaires francaises (Missions P.-E. Victor). – La Terre et la Vie 1950 (4): 175-201.
– 1950b. Coleoptéres du Gröenland. – l'Entomologiste 6: 73-76.
Lindberg, H. 1927. Zur Ökologie und Faunistik der subalpinen und alpinen Käferwelt in Enontekis-Lappmark. – Acta Societatis Fauna et Flora Fennica 56 (14): 1-51.
– 1933. Untersuchungen in N-Petsamo über die Käferfauna hochnordischer Biotopen. – Memoranda Societatis pro Fauna et Flora Fennica 9: 103-125.
Lindroth, C.H. 1929. Zur Land-Evertebratfauna Islands. II. – Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Sjätte Följden, Ser. B. 1 (6): 1-34.
– 1931. Die Insektenfauna Islands und ihre Probleme. – Uppsala. 589 pp.
– 1945a. Die fennoskandischen Carabidae. Eine tiergeographische Studie. I. Spezieller Teil. – Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Sjätte Följden, Ser. B. 4 (1). 709 pp.
– 1945b. Die fennoskandischen Carabidae. Eine tiergeographische Studie. II. Die Karten. – Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Sjätte Följden, Ser. B, 4 (2). 277 pp.
– 1949. Die Fennoskandischen Carabidae. Eine tiergeographische Studie. III. Allgemeiner Teil. – Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Sjätte Följden, Ser. B, 4 (3). 911 pp.
– 1953. Influence of Pleistocene climate changes on the insect fauna of Northern Europe. Transactions of the IXth International Congress of Entomology 2: 145-153. – Amsterdam.
– 1954. Experimentelle Beobachtungen an parthenogenetischem und bisexuellem *Otiorrhynchus dubius* Stroem (Col., Curculionidae). – Entomologisk Tidskrift 75 (2-4): 111-116.
– 1955. The carabid beetles of Newfoundland. – Opuscula Entomologica, Supplementum 12. 160 pp.
– 1957. The Faunal Connections between Europe and North America. – Almqvist & Wiksell, Stockholm. 344 pp.
– 1958. Istidsövervintrare bland djuren (Glacial hibernators among animals). – Naturvetenskapliga Forskningsrådet, Årbok 11: 134-151.
– 1960. Coleopteren – hauptsächlich Carabiden – aus dem Diluvium von Hösbach. – Opuscula Entomologica 25: 112-128.
– 1961a. Verbindungen und Barrieren in der zirkumpolaren Verbreitung der Insekten. – XI. Internationaler Kongress für Entomologie, Wien 1960, 1: 438-445.
– 1961b. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 2. – Opuscula Entomologica, Supplementum 20: 1-200.
– 1963a. The fauna history of Newfoundland. – Opuscula Entomologica, Supplementum 23. 112 pp.
– 1963b. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 3. – Opuscula Entomologica, Supplementum 24: 201-408.

– 1965. Skaftafell, Iceland, a living glacial refugium. – Oikos, Suppementum 6. 142 pp.
– 1968a. Distribution and distributional centers of North Atlantic insects. – Bulletin of the Entomological Society of America 14 (2): 91-95.
– 1968b. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 5. – Opuscula Entomologica, Supplementum 33: 649-944.
– 1969. The theory of glacial refugia. Comments on present opinions. – Notulae Entomologicae 49: 178-192.
– 1970. Survival of animals and plants on ice-free refugia during the Pleistocene glaciations. – Endeavour 29 (108): 129-134.
– 1979. The Theory of Glacial Refugia. – In: Erwin, T. L., Ball, G. E. & Whitehead, D. R. (eds.). Carabid Beetles, their Evolution, Natural History, and Classification: 385-394. – Dr. W. Junk Publishers; The Hague, Boston, London.
– 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark. – Fauna Entomologica Scandinavia 15 (1): 1-126. – E. J. Brill/Scandinavian Science Press Ltd., Leiden – Copenhagen.
– 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica 15 (2): 227-497. – E. J. Brill/Scandinavian Science Press Ltd., Leiden-Copenhagen.
Lindroth, C.H. & Coope, G.R. 1971. The insects from the interglacial deposits at Leveäniemi. – Sveriges Geologiska Undersökning, Ser. C 658. Appendix 2: 44-55.
Lindroth, C.H., Andersson, H., Bödvarsson, H. & Richter, S. H. 1973. Surtsey, Iceland. The development of a new fauna, 1963-1970. Terrestrial invertebrates. – Entomologica Scandinavica Supplementum 5. 280 pp.
Lomholdt, O., Nielsen, P. & Schnack, K. (eds.) 1984. Entomological literature. – Entomologiske Meddelelser 51 (1-2): 1-85.
Lundbeck, W. 1891. Entomologiske undersøgelser i Vest-Grønland 1889 og 1890. – Meddr Grønland 7 (4): 107-144.
– 1891-1892. Notitser om Grønlands entomologiske Fauna. – Entomologiske Meddelelser 3: 45-52.
– 1895. III. Østgrønlandske Insekter. Fortegnelse over de indsamlede Insekter. – In: Den østgrønlandske Expedition, udført i Aarene 1891-92 under Ledelse af C. Ryder. Tredie Del. – Meddr Grønland 19: 105-120.
– 1896. Coleoptera Groenlandica. – Videnskabelige Meddelelser fra dansk naturhistorisk Forening 1896: 196-219.
Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. – The Quarterly Review of Biology 59: 257-290.
MacLean, S.F. 1975. Ecological adaptation of tundra invertebrates. – In: Vernberg, E.J. (ed.). Physiological Adaptation to the Environment: 269-300. – Intext Educational Publications. New York.
Madsen, B.L. 1959. Limnologiske undersøgelser fra Sydvestgrønland. – Flora og Fauna 65 (3): 41-48.
Madsen, H. 1936. Investigations on the shore fauna of East Greenland, with a survey of the shores of the other arctic regions. – Meddr Grønland 100 (8): 1-79.
Madsen, J. 1981. Seasonal activity and abundance of some land invertebrates. – In: Fox, A.D. & Stroud, D.A. (eds.). Report of the 1979 Greenland White-fronted Goose Study Expedition to Eqalungmiut Nunaat, West Greenland: 222-227. – Greenland White-fronted Goose Study, Aberystwyth.
Mahler, V. 1988. A new species of *Atheta* Thomsom, 1858, from Greenland (Coleoptera, Staphylinidae, Aleocharinae). – Steenstrupia 14: 93–97.
Mäklin, F.W. 1881. Coleoptera insamlade under den Nordenskiöld'ska Expeditionen 1875 på några öar vid Norges nordvestkust, på Novaja Semlja och ön Waigatsch samt vid Jenisey i Sibirien. – Kungliga Svenska Vetenskaps-Akademiens Handlingar 18 (4): 1-48.
Manton, S.M. 1945. The larvae of the Ptinidae associated with stored products. – Bulletin of Entomological Research 35: 341-365.
Matthews, J.V. 1974. Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): Evolution of a tundra ecosystem. – Geological Society of America Bulletin 85: 1353-1384.
– 1975. Insects and plant macrofossils from two Quaternary exposures in the Old Crow-Porcupine Region, Yukon Territory, Canada. – Arctic and Alpine Research 7 (3): 249-259.
– 1977. Tertiary Coleoptera from the North American Arctic. – The Coleopterists' Bulletin 31 (4): 297-308.
– 1979a. Fossil Beetles and the Late Cenozoic History of the Tundra Environment. – In: Gray, J. & Boucot, A. J. (eds.). Historical Biogeography, Plate Tectonics, and the Changing Environment: 371-378. – Oregon State University Press.
– 1979b. Tertiary and Quaternary environments: Historical background for an analysis of the Canadian insect fauna. – In: Danks, K.V. (ed.). Canada and its insect fauna: 31-86. – Memoirs of the Entomological Society of Canada 108.
– 1980. Tertiary land bridges and their climate: Backdrop for development of the present Canadian insect fauna. – Canadian Entomologist 112: 1089-1103.
Matthews, J. V., Mott, R. J. & Vincent, J.-S. 1986. Preglacial and interglacial environments of Banks Island: Pollen and macrofossils from Duck Hawk Bluffs and related sites. – Géographie physique et Quaternaire 40,3: 279-298.
Mc Alpine, J. F. 1964. Arthropods of the bleakest barren lands: composition and distribution of the arthropod fauna of the Northwestern Queen Elisabeth Islands. – Canadian Entomologist 96: 127-129.
– 1965. Insects and related terrestrial invertebrates of Ellef Ringnes Island. – Arctic 18 (2): 73-103.
*Messersmith, D. H. 1982. Some Trichoptera, Coleoptera and Hymenoptera from Iceland and Greenland. – Fauna norvegica (B) 29: 17-18.
Miller, K. 1982. Cold-hardiness strategies of some adult and immature insects overwintering in interior Alaska. – Comparative Biochemistry and Physiology 73A (4): 595-604.
Morgan, A. 1969. A Pleistocene fauna and flora from Great Billing, Northamptonshire, England. – Opuscula Entomologica 34: 109-129.
Morgan, A. V. & Morgan, A. 1980. Faunal assemblages and distributional shifts of Coleoptera during the late Pleistocene in Canada and the Northern United States. – Canadian Entomologist 112: 1105-1128.
Munster, T. 1924. Report of the second Norwegian arctic expedition in the "Fram" 1898-1902. Coleoptera, supplement. – Norsk Entomologisk Tidsskrift 1: 297.
– 1925. Coleoptera. Report of the scientific results of the Norwegian expedition to Novaya Zemlja 1921. No. 30: 1-15. – Det Norske Videnskaps-Akademi i Oslo.
Nielsen, J. C. 1907. The insects of East-Greenland. – Meddr Grønland 29 (10): 365-414.
Nilsson, A. N. 1982. A key to the larvae of the Fennoscandian Dytiscidae (Coleoptera). – Fauna Norrlandica 2: 1-45.
Nurminen, M. 1970. Records of Enchytraeidae (Oligochaeta) from the west coast of Greenland. – Annales Zoologici Fennici 7: 199-209.
– 1973. Distributions of northern Enchytraeids (Oligochaeta). – Annales Zoologici Fennici 10: 483-486.
O'Brien, C. W. & Wibmer, G. J. 1982. Family 135. Curculionidae. Annotated checklist of the weevils (Curculionidae sensu latu) of North America, Central America, and the West Indies (Coleoptera: Curculionoidea). – In: Ross, H. A. (ed.) 1983. Checklist of the beetles of North and Central America and the West Indies 9. The Fungus Weevils, Bark Beetles, Weevils, and Related Groups. 240 pp. – Flora & Fauna Publications, Gainesville, Florida, U.S.A.
Oliver, D. R. 1963. Entomological studies in the Lake Hazen area, Ellesmere Island, including lists of species of Arachnida, Collembola, and Insecta. – Arctic 16 (3): 175-180.

– 1968. Adaptations of arctic Chironomidae. – Annales Zoologici Fennici 5 (1): 111-118.
*Oliver, D. R., Corbet, P. S., & Downes, J. A. 1964. Studies on arctic insects: the Lake Hazen project. – Canadian Entomologist 96 (1-2): 138-139.
Omer-Cooper, J. 1930. The British Species of *Gyrinus*. – The Entomologist's monthly Magazine 66: 64-75.
– 1931. *Gyrinus opacus* var. *lecontei* O.-C. (nec. Fall. 1921) = G. opacus var. *blairi* nom. nov. – The Entomologist's monthly Magazine 67: 239.
Omodeo, P. 1957. Lumbricidae and Lumbriculidae of Greenland. – Meddr Grønland 124 (6): 1-27.
Östbye, E. 1969. Records of Coleoptera from the Finse Area. – Norsk entomologisk Tidsskrift 16: 41-43.
Ostenfeld, C. H. 1926. The flora of Greenland and its origin. – Det Kongelige Danske Videnskabernes Selskab, Biologiske Meddelelelser 6 (3). 71 pp.
Ottesen, P. S. 1985. Diel activity patterns of South Scandinavian high mountain ground beetles (Coleoptera, Carabidae). – Holarctic Ecology 8 (3): 191-203.
Palmén, E. 1944. Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor. – Annales Zoologici Societatis Zoologicæ Botanicæ Fennicæ Vanamo 10 (1). 262 pp.
Palmgren, P. 1930. Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands. – Acta Zoologici Fennici 7: 1-209.
Paulian, R. 1941. Les premiers états des Staphylinoidea. – Mémoires du Muséum National d'Histoire Naturelle, Nouevelle Série (1). 361 pp.
Pearson, R. 1964. Alary polymorphism in *Bembidion grapei* Gyll. – The Entomologist's Monthly Magazine 100: 152-153.
Poppins, B. 1908. Zur Kenntnis der Staphyliden-Gattung *Micralymma* Westw. – Meddelanden från Societatis Fauna et Flora Fennica 35: 96-99.
– 1910. Die Coleopteren des arktischen Gebietes. – Fauna Arctica 5 (1): 289-447.
Porsild, M. P. 1932. Alien plants and apophytes in Greenland. – Meddr Grønland 92 (1): 1-85.
Refseth, D. 1980. Differences in seasonal activity pattern and breeding time of *Patrobus atrorufus* (Carabidae) in central Norway. – Holarctic Ecology 3: 87-90.
*Richard, P. W. & Harmston, F. C. 1972. Diptera and other arthropods of the Sukkertoppen Tasersiaq area. – Arctic 25 (2): 107-114.
Ring, R. A. & Tesar, D. 1980. Cold-hardiness of the arctic beetle, *Pytho americanus* Kirby, Coleoptera, Pythidae (Salpingidae). – Journal of Insect Physiology 26: 763-774.
– & – 1981. Adaptations to cold in Canadian Arctic insects. – Cryobiology 18: 199-211.
Røen, U. I. 1962. Studies on freshwater Entomostraca in Greenland II. Localities, ecology, and geographical distribution of the species. – Meddr Grønland 170 (2): 1-249.
– 1963. Nogle udbredelsestyper i den grønlandske ferskvandsfauna. – Tidsskriftet Grønland, oktober 1963: 361-374.
– 1981. Ferskvandsfaunaen. – In: Nørrevang, A. & Lundø, J. (eds.). Danmarks Natur 11, Grønland: 459-473. – Politikens Forlag, København.
Ruddiman, W. F. & McIntyre, A. 1981. The North Atlantic Ocean during the last deglaciation. – Palaeogeography, Palaeoclimatology, Palaeoecology 35: 145-214.
*Ryan, J. K. 1977. Appendix 7. Invertebrates of Truelove Lowland. – In: Bliss, L. C. (ed.). Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem: 699-703. – University of Alta Press, Edmonton.
Sahlberg, J. 1880. Bidrag till Nordvestra Sibiriens Insektfauna, Coleoptera, insamlade under expeditionerna till Obi och Jenessej 1876 och 1877. – Kungliga Svenska Vetenskaps-Akademiens Handlingar 17 (4): 1-115.
– 1901. Aleocharider insamlade i Polarregionerna af svenska expeditionerna 1883 och 1899. – Entomologisk Tidskrift 1901: 167-169.
Salomonsen, F. 1972. Zoogeographical and ecological problems in arctic birds. – In: Proceedings of the XVth International Ornithological Congress, The Hague, September 1970: 25-77. – E. J. Brill, Leiden.
– 1979. Ornithological and ecological studies in S. W. Greenland (59°46'–62°27' N. Lat.). – Meddr Grønland 204 (6): 1-214.
– 1981 (ed.). Grønlands Fauna. Fisk, Fugle, Pattedyr. – Gyldendal, København. 464 pp.
Schiødte, J. C. 1844-1845. Om Slægten *Micralymma*. – Naturhistorisk Tidsskrift 2 (1): 370-389.
– 1857. Tillæg Nr. 3. Udsigt over Grønlands Land-, Ferskvands- og Strandbreds-arthropoder. – In: Reinhardt, I., Schiødte, J.C., Mørch, O.M.L., Lütken, C.F., Lange, J. & Rink, H. Naturhistoriske Bidrag til en Beskrivelse af Grønland. Særskilt Aftryk af Tillæggene til Rink, H. Grønland, geografisk og statistisk beskrevet: 50-74. – København.
Seidenfaden, G. & Sørensen, T. 1937. The vascular plants of Northeast Greenland from 74°30' to 79°00' N lat. – Meddr Grønland 101 (4): 1-215.
Silfverberg, H. (ed.) 1979. Enumeratio Coleopterorum Fennoscandiae et Daniae. – Helsingfors. 79 pp.
Smetana, A. 1964. Paederinae and Staphylininae from Kodiak Island, Alaska (Col. Staphylinidae) (58th contribution to the knowledge of Staphylinidae). – Opuscula Entomologica 29: 34-40.
*– 1965a. Staphylinini und Quediini von Canada und Alaska (Col. Staphylinidae). – Acta Universitatis Lundensis II, 13: 1-18.
– 1965b. Staphylinini und Quediini (Col. Staphylinidae) von Newfoundland, Südost-Labrador und Nova Scotia (59. Beitrag zur Kenntnis der Staphyliniden). – Acta Entomologica Fennica 20: 1-60.
– 1971. Revision of the tribe Quediini of America north of Mexico (Coleoptera: Staphylinidae). Memoirs of the Entomological Society of Canada 79. – Ottawa. 303 pp.
Southwood, T. R. E. 1978. Ecological methods with particular reference to the study of insect populations. – Chapman & Hall, London. 524 pp.
Spärck, R. 1943. Zoogeographical remarks on the chironomid fauna of Greenland. – Entomologiske Meddelelser 23: 432-442.
Steel, W. O. 1958. Notes on the Omalinae (Col., Staphylinidae) (9). The genus *Micralymma* Westwood. – The Entomologist's monthly Magazine 94: 138-142.
– 1961. Notes on the Omaliinae (Col., Staphylinidae) (11). The genus *Micromalium* Melichar, with further notes on *Micralymma* Westwood. – The Entomologist's monthly Magazine 97: 237-239.
– 1970. The larvae of the genera of the Omaliinae (Coleoptera: Staphylinidae) with particular reference to the British fauna. – Transactions of the Royal entomological Society of London 122: 1-47.
Steinböck, O. 1943. Eigenheiten arktisch-alpiner Tierverbreitung. – Veröffentlichungen des Deutschen Wissenschaftlichen Instituts zu Kopenhagen. Reihe I: Arktis, 12: 1-11.
*Stephensen, K. 1921. Grønlands Dyreverden. – Meddr Grønland 50: 57-72.
Stoltze, M. 1981. Grønlandske vårfluers udbredelse og indvandringshistorie. – Unpublished thesis, University of Copenhagen. 16 pp.
*Strand, A. 1943. Die Käferfauna von Svalbard. – Norsk Entomologisk Tidsskrift 6: 53-69.
– 1946. Nord-Norges Coleoptera. – Tromsø Museums Årshefter, Naturhistorisk Avdeling Nr. 34, 67 (1): 1-629.
Strand, E. 1905. Coleoptera, Hymenoptera, Lepidoptera und Araneae. – Report of the Second Norwegian Arctic Expedition in the "Fram" 1898-1902, I, 3: 1-30.
Suomalainen, E. 1962. Significance of parthenogenesis in the evolution of insects. – Annual Review of Entomology 7: 349-366.
Suomalainen, E., Saura, A. & Lokki, J. 1976. Evolution of

parthenogenetic insects. – In: Hecket, M. K., Steere, W. C. & Wallace, B. (eds.). Evolutionary Biology 9: 209-257. – Plenum Press, New York & London.
Székessy, V. 1936. Revision der boreoalpinen Koleopteren auf vergleichend-anatomischer Grundlage. II. – Entomologisk Tidskrift 57: 97-126.
Thayer, M. K. 1985. *Micralymma marinum* (Stroem) in North America: biological notes and new distributional records (Coleoptera: Staphylinidae). – Psyche 92 (1): 49-55.
Thiele, H.-U. 1977. Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour. Zoophysiology and Ecology 10. – Springer-Verlag. Berlin, Heidelberg, New York. 369 pp.
*Thor, S. 1930. Beiträge zur Kenntnis der Invertebraten Fauna von Svalbard. – Skrifter om Svalbard og Ishavet 27: 1-156.
Topp, W. 1975a. Zur Larvalmorphologie der Athetae (Col., Staphylinidae). – Stuttgarter Beiträge zur Naturkunde, Ser. A, 268: 1-23.
– 1975b. Morphologische Variabilität, Diapause und Entwicklung von *Atheta fungi* (Grav.) (Col., Staphylinidae). – Zoologische Jahrbücher. Systematik, Ökologie und Geographie der Tiere 102: 101-127.
Vanhöffen, E. 1897. Die Fauna und Flora Grönlands. – Grönlands-Expedition der Gesellschaft für Erdkunde zu Berlin 1891-1893 unter Leitung von Erich von Drygalski II, 2: 1-383.
Weber, N. A. 195o. A survey of the insects and related arthropods of Arctic Alaska, Part I. – Transactions of the American Entomological Society 76: 147-206.
Wegmann, C. E. 1941. Geologische Gesichtspunkte zur Frage der Eiszeitüberdauerung von Pflanzen in Grönland. – Mitteilungen der Naturforschenden Gesellschaft Schaffhausen 17: 97-115.
Vepsäläinen, K. & Järvinen, O. 1979. Apomictic parthenogenesis and the pattern of the environment. – American Zoologist 19: 739-751.
West, A. 1937. Coleoptera. – In: Jensen, A.S., Lundbeck, W., Mortensen, T. & Spärck, R. (eds.). The Zoology of the Faroes 2 (1),40. – Andr. Fred. Høst & Søn, Copenhagen. 92 pp.
– 1942. Fortegnelse over Danmarks biller. – Entomologiske Meddelelser 21: 1-664.
Vibe, C. 1950. Some insects new to Greenland. – Entomologiske Meddelelser 25 (6): 419-420.
– 1953a. Grønlands zoogeografiske problemer. – Tidsskriftet Grønland 1953: 432-436.
– 1953b. The zoogeography of Greenland. – In: Proceedings of the XIV International Congress of Zoology, Copenhagen 5.-12. August 1953: 126-127.
– 1981. Lavere dyr i Grønland. – In: Nørrevang, A. & Lundø, L. (eds.). Danmarks Natur 11, Grønland: 542-550. – Politikens Forlag, Copenhagen.
Wolff, N. L. 1937. Lepidoptera. – In: Jensen, A.S., Lundbeck, W., Mortensen & T., Spärck, R. (eds.). The Zoology of the Faroes 2 (1), 34. – Andr. Fred. Høst & Søn, Copenhagen. 38 pp.
– 1964. The Lepidoptera of Greenland. – Meddr Grønland 159 (11): 1-74.

Taxonomical index

Synonyms in brackets.

(Surveys of indigenous species are found in Tables 6, 7 & 8; a survey of synanthropic and introduced species is found in Table 13; a survey of families is found in Table 5)

Instructions to authors

Two copies of the manuscript, each complete with illustrations, tables, captions, etc. should be sent to the Secretary, Kommissionen for videnskabelige Undersøgelser i Grønland. Manuscripts will be forwarded to referees for evaluation. Authors will be notified as quickly as possible about acceptance, rejection or desired alterations. The final decision on these matters rests with the editor.

Manuscripts corresponding to less than 16 printed pages (of 6100 type units) including illustrations are not accepted, unless they are part of a special theme issue. Manuscripts that are long in relation to their content will not be accepted without abridgement.

Manuscript

Language. – Manuscripts should be in English (preferred language), French or German. Authors who are not writing in their native language must have the language of their manuscript corrected before submission.

Place names. – All Greenland place names used in the text and in illustrations must be names authorised by The Greenlandic Language Committee. Authors are advised to submit sketch-maps with all required names to the Secretary for checking before the manuscript is submitted. Names of Greenland localities outside the area with which the paper is concerned should be accompanied by coordinates (longitude and latitude).

Title. – Titles should be as short as possible, with emphasis on words useful for indexing and information retrieval.

Abstract. – An abstract in English must accompany all papers. It should be short (no longer than 250 words), factual, and stress new information and conclusions.

Typescript. – Typescripts must be clean and free of handwritten corrections. Use double spacing throughout, and leave a 4 cm wide margin on the left hand side. Avoid as far as possible dividing words at the right-hand end of a line. Consult a recent issue for general lay-out.

Page 1 should contain 1) title, 2) name(s) of author(s), 3) abstract, 4) key words (max. 10), 5) author's full postal address(es). Manuscripts should be accompanied by a table of contents, typed on separate sheet(s).

Underlining should *only* be used in generic and species names. The use of italics in other connections can be indicated by a wavy line in pencil under the appropriate words.

Use at most three grades of headings, but do not underline. The grade of heading can be indicated in soft pencil in the left hand margin of one copy of the typescript. Avoid long headings.

References. – References to figures and tables in the text should have the form: Fig. 1, Figs 2–4, Table 3. Bibliographic references in the text are given thus: Shergold (1975: 16) ... (Jago & Daily 1974b).

In the list of references the following style is used:

Boucot, A. J. 1975. Evolution and extinction rate controls. – Elsevier, Amsterdam: 427 pp.

Sweet, W. C. & Bergström, S. M. 1976. Conodont biostratigraphy of the Middle and Upper Ordovician of the United States midcontinent. – In: Bassett, M. G. (ed.). The Ordovician System: Proceedings of a Palaeontological Association symposium, Birmingham, September 1974: 121–151. Univ. Wales Press.

Tarling, D. H. 1967. The palaeomagnetic properties of some Tertiary lavas from East Greenland. – Earth planet. Sci. Lett. 3: 81–88.

Titles of journals should be abbreviated according to the latest (4th) edition of the World List of Scientific Periodicals and supplementary lists issued by BUCOP (British Union-Catalogue of Publications). If in doubt, give the title in full.

Meddelelser om Grønland, Bioscience (Geoscience, Man & Society) should be abbreviated thus: *Meddr Grønland, Biosci. (Geosci., Man & Soc.)*

Illustrations

General. – Submit two copies of all diagrams, maps, photographs, etc., all marked with number and author's name. Normally all illustrations will be placed in the text.

All figures (including line drawings) must be submitted as glossy photographic prints suitable for direct reproduction, and preferably have the dimensions of the final figure. Do not submit original artwork. Where appropriate the scale should be indicated on the illustration or in the caption.

The size of the smallest letters in illustrations should not be less than 1.3 mm. Intricate tables are often more easily reproduced as text figures than by type-setting; when lettering such tables use "Letraset" or a typewriter with carbon ribbon.

Colour plates may be included at the author's expense, but the editor must be consulted before such illustrations are submitted.

Size. – The width of figures must be that of a column (76.5 mm), 1½ columns (117 mm) or a page (157 mm). The maximum height of a figure (including caption) is 217 mm. Horizontal figures are preferred. If at all possible, fold out figures and tables should be avoided.

Caption. – Captions to figures must be typed on a separate sheet and submitted, like everything else, in duplicate.

Proofs

Authors receive two page proofs. Prompt return to the editor is requested. Only typographic errors should be corrected in proof; the cost of making alterations to the text and figures at this stage will be charged to the author(s).

Twenty-five copies of the publication are supplied free, fifty if there are two or more authors. Additional copies can be supplied at 55% of the retail price. Manuscripts (including illustrations) are not returned to the author after printing unless specifically requested.

Copyright

Copyright for all papers published by Kommissionen for videnskabelige Undersøgelser i Grønland is vested in the commission. Those who ask for permission to reproduce material from the commission's publications are, however, informed that the author's permission must also be obtained if he is still alive.

Meddelelser om Grønland

Bioscience
Geoscience
Man & Society

Published by
The Commission
for Scientific
Research
in Greenland

AiO Print Ltd., Odense, Denmark