Bionomics of Nearctic Species of Aclypea Reitter: Phytophagous "Carrion" Beetles (Coleoptera: Silphidae)

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Abstract.—Diagnoses, distributions, notes on bionomics, and a key for identification are presented for the two Nearctic phytophagous "carrion" beetles Aclypea opaca (L.) and A. bituberosa (LeC.). A brief discussion of the possible evolutionary history of the genus in the Nearctic region is given.

Recent studies on the biology, distribution and systematics of the Silphidae of Canada and Alaska (Anderson, 1981) have revealed problems concerning the identity and distribution of two Nearctic species of the genus *Aclypea*. The latest reviews (Hatch, 1957; Miller and Peck, 1979) have indicated that two species live in North America; the primarily Palearctic *A. opaca* (L.), 1758, and the Nearctic *A. bituberosa* (LeConte), 1859. Adults of the two species are morphologically very similar. We have found the characters in keys that attempt to separate the species (Arnett, 1944; Hatch, 1927; Horn, 1880; Portevin, 1926) to be vague or imprecise. Thus, there has been a problem in distinguishing them and in accurately documenting their distributions and habits in North America.

Adult Aclypea can be recognized by the following generic characters: labrum deeply emarginate, with the inner faces of the emargination swollen; eyes relatively small, and not bounded posteriorly by a row of erect setae. The genus is represented by approximately 27 species, distributed throughout the Holarctic region, some members of which have been previously assigned to the genera Blitophaga Reitter and Silpha L. (Portevin, 1926; Hatch, 1927, 1928; and others). We use Aclypea rather than Blitophaga following Seidlitz (1883:311) as first reviser in accordance with article 24 (a) (i) in the International Code of Zoological Nomenclature.

The vast majority of the species are found in the Palearctic region, and no attempt is made here to treat them. We have found that the two Nearctic forms can be distinguished as follows:

1a. Genitalia of both sexes thinly sclerotized (light brown in color); pronotum often with impunctate area on anterior third behind eye; elytra with punctures shallow, the distance behind punctures rarely less than the width of a puncture (Fig. 3); isodiametric microsculpture of pronotum and elytra distinct (Fig. 3); generally smaller in size (12–15 mm). Distribution in Nearctic restricted to Alaska and extreme northwest N.W.T.
A. opaca (Linn.)

1b. Genitalia of both sexes thickly sclerotized (dark brown in color); pronotum never with impunctate area behind eye, although other impunctate areas may be present; elytra with punctures deep, the distance between the punctures often less than the width of a puncture (Fig. 4); isodiametric microsculpture usually indistinct (Fig. 4); larger in size (14–17 mm). Widespread in western North America ... A. bituberosa (LeConte)

Aclypea opaca (Linnaeus), the Beet Carrion Beetle (Figs. 1, 3, 5)

Silpha opaca Linnaeus, 1758:361.

Diagnosis.—Color blackish to brown, usually clothed with yellow hairs dorsally. Pronotum with anterior margin usually narrow (Fig. 1), lateral margins not distinctly raised; with occasional impunctate areas present behind eyes. Elytra with punctures shallow, distance between them rarely less than their width (Fig. 3). Isodiametric microsculpture of pronotum and elytra distinct. Genitalia in both sexes thinly sclerotized, light brown in color. Smaller in size, 12–15 mm in length. Synonymies are in Portevin (1926) and Hatch (1928).

Variation.—Variation in this species appears to occur primarily in the pattern of the impunctate areas on the pronotum. Some specimens of A. opaca possess impunctate areas on the pronotum in the anterior third directly behind the eyes in addition to other impunctate areas which may be present near the midline. These impunctate areas behind the eyes are not found in A. bituberosa, although other impunctate areas may be present.

There is little structural variation in other characters in the material that we have examined.

Distribution.—The species is known to us to occur in North America through very few specimens from Alaska and the Northwest Territories (Fig. 5). It has previously been recorded from various localities in the United States (Horn, 1880; Hatch, 1927), but these appear (based on our re-examination of available specimens) to be misidentifications of *A. bituberosa. Aclypea opaca* also occurs throughout the northern areas of the Palearctic region (Hatch, 1928).

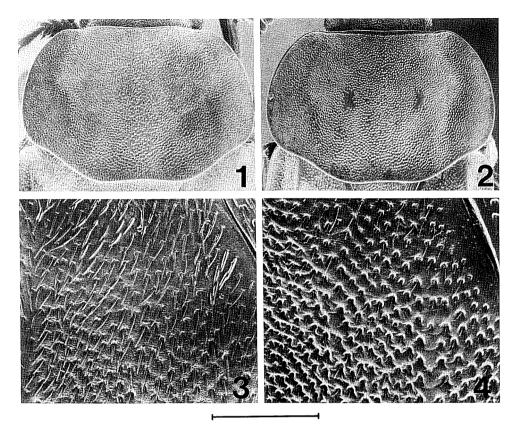
Material examined.—(24 specimens with the following data; abbreviations of collections in Arnett and Samuelson, 1969).

CANADA. Northwest Territories. Aklavik, 10.VIII.31, O. Bryant, 1 (CASC). UNITED STATES. Alaska. Circle, 3.VII.58, G. E. Ball, dry field, 1 (UASM); Fairbanks, 26.VI–1.VII.79, B. Wright, 1 (NSMC); Fort Yukon, 17.VI.16, Harrington, 2 under logs (USNM); 11.VI.16, Evans, 1 (USNM); Kussiloff (Kasilof), VII.98, Evans, 1 (USNM); Palmer, 15.VII.79, 1.VI.80, 25.VII.80, 1.VIII.80, 13.VIII.82, 3.IX.82, D. P. Bleicher, baited cone traps 8 (University of Alaska).

OTHER COUNTRIES. 8 specimens from Northern and Central Europe.

Bionomics.—Like other *Aclypea*, the species in Europe is phytophagous on various Chenopodiaceae, and has also been recorded as a pest of sugar beets (Martin, 1945; Heymons et al., 1929).

The natural history has been well documented by Heymons et al. (1929) and Martin (1945) in Europe. According to these authors, adults overwinter and emerge in the spring when the sugar beets are germinating. Larvae appear about two weeks later and feed externally on the young shoots and leaves. When mature, the larvae



Figures 1–4. 1. Dorsal view of pronotum of *Aclypea opaca* (Northwest Territories: Aklavik); scale line = 2.3 mm. 2. Dorsal view of pronotum of *Aclypea bituberosa* (Saskatchewan: Kenosee); scale line = 2.7 mm. 3. Dorsal view of base of left elytron of *Aclypea opaca* (Northwest Territories: Aklavik); scale line = 0.7 mm. 4. Dorsal view of base of left elytron of *Aclypea bituberosa* (Alberta: Calgary); scale line = 0.9 mm.

move into the soil to pupate. Adults emerge 10-15 days later and also feed on the plants, but not as extensively as the larvae.

Although recorded as a pest of sugar beets in North America (Cooley, 1906, 1917; Forbes and Hart, 1900), data presented here make it very likely that these records were misidentifications of A. bituberosa. There appears to be no indication that A. opaca is a pest of any cultivated crops within the extent of its known distribution in North America. In fact, we know of no reliable data on native host plant relationships in North America.

Our Nearctic records indicate that adults are active from June through August.

Aclypea bituberosa (LeConte), the Spinach Carrion Beetle (Figs. 2, 4, 5)

Silpha bituberosa LeConte, 1859:6.

Diagnosis.—Color blackish to brown, usually clothed with yellow hairs dorsally, although these are often abraded. Pronotum with anterior margin thicker than in

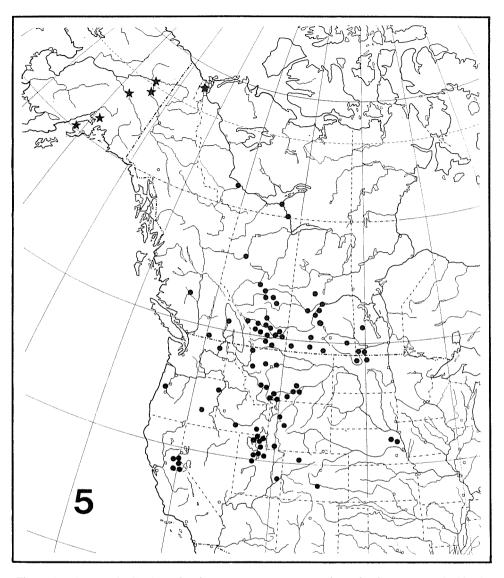


Figure 5. Known distribution of Aclypea opaca (stars) and Aclypea bituberosa (dots) in North America.

A. opaca (Fig. 2), lateral margins distinctly elevated; with occasional impunctate areas, but not with any behind eyes. Elytra with punctures deep, often confluent, especially towards base (Fig. 4). Microsculpture of pronotum and elytra not distinct. Genitalia in both sexes thickly, darkly sclerotized. Larger in size, 14–17 mm in length.

Variation.—Although all prairie specimens of A. bituberosa are structurally similar, examination of the few available specimens of A. bituberosa from montane localities indicates a smaller overall size and a much less convex elytra than those from the lowland prairie areas. In these montane forms, the genitalia tend to be

as heavily sclerotized as in all other A. bituberosa. However, the punctures of the elytra tend to become smaller and shallower, thus approaching the state in A. opaca. The punctures at the base of the elytra, although still large and deep, are rarely confluent.

These patterns of morphological variation appear correlated with a change to montane-alpine habitats and may have an ecogenotypic or ecophenotypic basis. Possibly there is a continuous morphocline between the northern A. opaca and the southern A. bituberosa through these intermediate montane populations. This would indicate probable conspecificity but our collection data presently indicate the existence of a geographic zone where neither species occurs. However, until more representatives of this genus become available from this area (i.e., provided the known distribution is a collecting artifact) we think it best to continue to recognize the two forms as distinct species.

Distribution.—In Canada, the species is found throughout the provinces of Alberta, Saskatchewan and Manitoba, extending northward into the southern Northwest Territories (Fig. 5). It appears to be found primarily in open grassland or prairie habitats, although some specimens have been collected in interior valleys and alpine habitats in British Columbia. In the United States it occurs throughout the northern midwest into the western coastal and Rocky Mountain states.

Material examined.—(278 specimens examined and other literature records.) Only generalized locality and seasonality data (when available) are given here. Full data are available from the authors. Specimen numbers are given only if the record is based on more than one. Material is in the following collections: AMNH, CASC, CDFA, CNCI, DZEC, FMNH, LACM, MCZC, SBPC, UASM, UBCZ, UICM, USNM (abbreviations follow Arnett and Samuelson, 1969); the collections of the Canadian Department of Agriculture at Lethbridge, Saskatoon, and Winnipeg; the Saskatchewan Provincial Museum; the Universities of Manitoba and Saskatchewan; and J. L. Carr collection, Calgary.

CANADA. *Alberta*. Brooks, August, 3. Calahoo, July. Calgary, May, 20; June, 2; July. Diamond City (Farstad, 1949). Drumheller, June. Gorge Creek (50 mi W Calgary), June, 29; July, 23. Grand Prairie, July. High River, April. Holden, May, 3. Hussar, May, 2. Leduc, June. Lethbridge, April, 3; May, 2; June, 2. Medicine Hat, April; May, 6; June, 5. Millarville, May. Ralston, May, 2. Raymond, July, 2. Sherwood Park (suburb of Edmonton), April, 4; May, 5; September. Tilley, June, 3. Viking (MacNay, 1954). *British Columbia*. Chilcotin, April, October. Manning Prov. Park (Nicomen Ridge, 6600'), July. Vernon, May, 2. *Manitoba*. Grandview, May, 3. Lauder, May. *Northwest Territories*. Fort Resolution, June, 2; July. Fort Smith, May, 9; June, 11; July, 21; August, October. Fort Simpson, June, July, August. *Saskatchewan*. Big River, July. Chaplin, July. Dundurn, April. Fort Walsh, July. Gravelbourg, July. Kenosee, June. Moosomin, July. Norbery, May. Prince Albert (MacNay, 1954). Rockglen, July. Rosthern, June, 2. Saskatoon, March, April, May, July, October, November.

UNITED STATES. *California*. Alpine Co., Ebbetts Pass, July; Sonora Pass, June, 2. Eldorado Co., Echo Lake, 7400'; July. Tallac, July. Mono Lake (1880 Horn record, in MCZ). Tuolumne Co., no other data; Yosemite National Park, Mt. Lyell, August (see Miller and Peck, 1979, for full data). *Colorado*. Craig, May, 6200'. Custer Co., no other data. *Idaho*. Buhl, no other data. Downey, June. *Kansas*. No locality, Forbes and Hart (1900); this could be an error resulting from the type collection which was made in Wyoming, then in "Kansas Territory."

Montana. Billings (Cooley, 1912, 1916); April, May. Bozeman, March, 2; April, 2; May, June. Butte, no date. Cartersville, July. Edgar, May, 2. Gallatin Co., April, 4800'; May, 4; June. Glacier Park, no date. Huntley, April, May. Jefferson Co., April, May, 18. Rapelje, October. Ravalli (Pepper, 1951). Teton Co., no date. Yellowstone Park, June. Nebraska. Norfolk and West Point (Cooley, 1917). North Dakota. Bottineau, June, 3; July. Maxbass, July. Oregon. Malheur Lake and Snake River (Hatch, 1957); Alpine, June. Utah. Benson, March. Davis Co., May. Hooper, June. Logan, April. Logan Canyon, June. Moab, May. Orme, June. Ogden, May. Petersboro, June. Provo, April, May. Salt Lake City, May. Trenton, June. Vernon, May (most records from McComb and Knowlton, 1950). Washington. Okanogan, Slate Peak, 6500', August. Wyoming. Fort Bridger (Holotype 8952 in MCZ). Pinedale (20 mi NE), 10,400', August, 4. Togwotee Pass, 9600', August.

Bionomics.—The habits of this species have been well documented by Cooley (1917). Adults and larvae are phytophagous, eating Chenopodium album (lamb's quarters, introduced), Monolepis nuttalliana (povertyweed) and other native Chenopodiaceae, as well as Solanum triflorum (nightshade) (Solanaceae) (Hatch, 1957; Cooley, 1917). They have also been recorded from squash, pumpkin, spinach, beet, wheat, radish, rhubarb, potato, lettuce, cabbage, rapeseed, and turnip (Cooley, 1906, 1916, 1917; MacNay, 1954, 1955; Forbes and Hart, 1900; Farstad, 1949, 1951) and are considered a pest of these crops in some areas. The species is in some North American texts on agricultural entomology (sometimes under the name Silpha opaca). We have found adults in montane meadows, where they were crawling along the ground and not in direct association with any single plant species. Adults could probably be collected in meadows and grassland areas by using large pans as unbaited pit traps.

Cooley (1917) has reported on the life cycle of the species in Montana, summarized as follows: Adults emerge very early in the spring, and lay eggs in the soil which hatch about 5 days later. Larvae eat leaves and young shoots of the young plants during the day, hiding in the soil during the night. The first larval instar lasts 5 days, the second also 5 days, and the third about 15 days. Pupation takes place in the soil and the adults emerge about three weeks later. These new adults feed, but do not lay eggs, returning to the soil to overwinter. Other rearing (Forbes and Hart, 1900) found larvae in June and July, with adults emerging in July. The above records show the adults to be active from March through November, with later dates usually being more northerly or at higher elevations.

IMMATURE STAGES

Aclypea larvae are easily distinguished from all other silphine larvae by the presence of a ventral as well as mesal serrate edge on the mandibles (Newton, pers. comm.). The side margins of the tergites, noted as pale by Hatch (1927) and used to distinguish Aclypea larvae from other silphine larvae, are black in some of the material that we have seen and hence this character is unreliable.

Third instar larvae of Nearctic Aclypea will key to Heterosilpha ramosa in Dorsey (1940) but can be distinguished from the latter by the aforementioned mandibular structure and by the following key:

1a. Maxillary apical palpomere approximately three times as long as wide; labial palp with the basal segment $1.5 \times$ the length of the apical segment H. ramosa

We are not presently able to distinguish the larvae of *A. opaca* from *A. bitu-berosa*. Although larvae and other immature stages of these two have been treated by Cooley (1917), Martin (1945), and Heymons et al. (1928), the descriptions in these papers and the key in Hatch (1927) are insufficient to provide reliable species identifications based on material that we have available.

EVOLUTIONARY CONSIDERATIONS

It has been long thought that A. opaca was introduced from Europe, probably with shipments of plants (Hatch, 1927, 1957; Forbes and Hart, 1900) and hence was not a regular member of our fauna. However, the apparent confinement of the species to the extreme northwestern corner of North America, and its wide-spread distribution in the northern Palearctic region would suggest recent dispersal via a Beringian land bridge connection. The direction of dispersal was probably from the Palearctic to the Nearctic, as it was for many large mammals and some other insects during the Quaternary, and as would be expected of a group whose highest diversity is centered in the Palearctic.

The marked similarity of the two species suggests that they are sister species, descended from a single common ancestor. However, we cannot now demonstrate this by synapomorphies. We suggest that this ancestor originated in the Palearctic and dispersed to the Nearctic across the Bering bridge in the Tertiary or Pleistocene. During a Pleistocene glacial some populations of the ancestor were isolated in localities south of the ice margin, and differentiated into A. bituberosa. North and west of the ice margin, in unglaciated refugia in Alaska and the Yukon, A. opaca retained intermittent contact with Palearctic conspecifics, or became extinct and has reoccupied the Nearctic in the Recent. The lack of far northern specimens of A. bituberosa indicates that it did not survive glaciation in the northern refugia, but only in areas south of the ice sheets. Subsequent reinvasion of previously glaciated land has therefore been from the south, resulting in the present distribution pattern.

Unfortunately, no fossil specimens of *Aclypea* have been recorded in North America which can test these evolutionary hypotheses.¹

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After this paper had gone to press, a single record of a fossil specimen of *Aclypea* was sent to us by Dr. R. E. Nelson, Colby College, Maine. The specimen was collected from deposits of age 16,640 years BP at Seattle, Washington, and is assignable to *A. bituberosa* based on elytral sculpture and punctation characteristic of that species. This discovery indicates that isolation and structural divergence of *A. bituberosa* did not occur in the glacial advance of the Late Wisconsinan.