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Relationships of Palearctic and Nearctic Genera of Alticinae

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ABSTRACT. — Study of the 30 Palearctic and approximately 43 Nearctic genera of Alticinae reveals some relationships previously undetected. Examination of external and internal morphology, including male and female genitalia and the metafemoral spring, indicate synonymy or close relationship of a few Palearctic and Nearctic genera. Certain closely related genera are studied: *Orestioides Orestia*, *Hornaltica-Ochrosis*, *Macrohaltica-Altica*, *Kuschelina-Capraitia* and *Oedionychus*, *Asphaera-Omophoita*. Results suggest that *Orthaltica* is not an Alticinae.

Zoogeographic patterns of genera are also useful in evaluation of possible relationships.

As with most large families of insects the Chrysomelidae fauna of the Palearctic Region is better known than any other major biogeographic region of the world. This is certainly the case at the generic level. This is because of a historical preponderance of Palearctic entomologists since the time of Linnaeus, and the fact that the diversity is lower there relative to other major regions. The Nearctic Region is probably the next best known for chrysomelid faunistics and systematics, and although it is considerably less understood than the Palearctic at the species level, the genera are well known. There is also evidence of a Palearctic and Nearctic faunal connection through Laurasia during the Tertiary and across the Bering Straits during the Quaternary. Therefore, it seems reasonable to begin to assess some of the relationships of Palearctic and Nearctic Alticinae, possibly as an introductory phase to understanding phylogenetic relationships.

There are 30 truly Palearctic genera of Alticinae (Furth, 1982) and approximately 43 genera in North America north of Mexico (Nearctic). Most of these genera have distinctive external morphology, which has traditionally facilitated the definitive separation of these genera. A variety of external characters in addition to color have been used to distinguish the Palearctic and Nearctic genera of Alticinae, such as: metatibial and metatarsal morphology; tubercle and suture development on the frons; number and relative size of antennal segments; punc-

tation of elytra, pronotum, or head; transverse or longitudinal pronotal impressions; elytral striae; etc. Each genus usually feeds on a restricted number of foodplant families, which often further accentuates the distinctiveness of alticine genera. Although the hosts of several genera are still unknown, foodplant families are relatively better known in the Palearctic and Nearctic Regions than in other regions of the world.

Not until the beginning of this century were any internal structures used in alticine systematics. At first, a few male aedeagus figures were published for species separation, and this became increasingly common, especially in the 1940s and 1950s (e.g., Heikertinger, Blake, etc.). Spett and Lewitt (1926) made the first study of the female reproductive system, including the spermathecae. This latter study illustrated some differences among chrysomelid subfamilies and genera; however, their sample of alticine genera was quite incomplete. It was not until recently (Samuelson, 1966; Kevan, 1967; Leonardi, 1970, 1972; Seeno and Andrews, 1972; Furth, 1979, 1980; etc.) that female spermathecae became widely used for species separation within genera. Even though both male aedeagus and female spermatheca are now commonly used for distinguishing species, no attempt has been made to characterize the internal sexual structures at the generic level. The present study is an initial attempt to characterize the genera of Palearctic and Nearctic Alticinae based on internal structures, including the aedeagus and spermatheca. Of course, it will require examination and study of many species in each genus in order to develop a true generic characterization of these genitalia for the Alticinae.

I first suspected that another internal character, the metafemoral spring, of Alticinae demonstrated intergeneric differences (Furth, 1976). Upon further study I discovered these differences to be significant and characterizable into morphological groups for the Palearctic genera (Furth, 1980, 1982). In these previous papers I derived a terminology for the anatomical characteristics of the metafemoral spring, which are also used in the present study for illustrating potential relationships of genera (see Furth, 1982, figure 1).

Because the Palearctic Alticinae fauna has been thoroughly studied, the genera are well established, and there has been little splitting of genera. The Nearctic fauna is less firmly established, and several genera have been recently split into two or more genera, often based only on a few (sometimes of dubious value) morphological characters. Some of these changes are questionable and need to be studied in more depth. There is at least one case of splitting a genus, existing in both the Palearctic and Nearctic Regions, solely on the basis of its geography. These generic level questions and relationships will be considered in the present paper as well as the definition of the subfamily Alticinae.

METHODS

The present study involved examination and comparison of the male aedeagus, female spermatheca, and metafemoral spring of representatives of the 43 Nearctic genera and several other genera, especially from the Neotropics. Also, for many Palearctic genera the aedeagus and spermatheca were not known and had to be examined. The aedeagus and spermatheca preparations were done by removing the abdomen and boiling it for about two minutes in water, then removing the desired structure under a dissecting microscope. The metafemoral spring of the Palearctic genera (29 of 30) has already been studied (Furth, 1980, 1982), and readers are referred to these publications for further information and comparisons. Preparation of the metafemoral spring was made by placing a metafemur in hot 10% KOH for several minutes to digest the attached musculature, then dissecting out the spring under the dissecting microscope. In all cases the internal structures were then placed into a depression slide with glycerine and illustrated using a camera lucida attachment for the Wild M5 dissecting microscope. Detailed measurements were made for each structure as well as for the whole specimen. For each genus at least three dissections were made (one for each structure), usually all from a single species, but in many cases more than one species per genus were examined. The drawings produced were then enlarged using a Goodkin Viewer and then retraced.

RESULTS AND DISCUSSION

Palearctic/Nearctic Confusions

At the beginning of this study there were several pairs of genera that were suspected of being synonymous. Some of these were suspect based on rather superficial examination of their habitus, my familiarity with the Palearctic fauna, as well as the previous use of apparently rather weak characters for their separation from related genera. One case causing confusion resulted from the extensive splitting of various Nearctic genera into several genera.

Orestioides was established by Hatch (1935), who stated that it was most closely related to *Orestia* by virtue of the sub-moniliform antenna and to *Crepidodera* (= *Asiolestia*) based on the form of the prosternum. *Oestioides robusta* (LeConte) and *O. pallida* (Fall) do have sub-moniliform antennae similar to *Orestia* and have less prominent prosternal meso-lateral carinae than most *Orestia*, however, these differences are quite subtle and are not adequate basis for considering these two North American species as belonging in separate genera. Other aspects of the prosternum are not significantly different. Examination of the male aedeagus (Fig. 1a), female spermatheca (Fig. 1b), and metafemoral spring (Fig. 1c) of *Orestioides* indicates no significant differences

between *Orestioides* Hatch and *Orestia* Germar. The spermatheca is quite similar to certain European species, and the metafemoral spring is identical. Also, like most species of Palearctic *Orestia*, *Orestioides* is found at high altitudes (Hatch, 1985). *Orestioides* is, therefore, synonymous with *Orestia*. It is suggested that, because of its disjunction from species of Europe, North Africa, and the Near East, *Orestioides* be considered as a subgenus of *Orestia* in order to preserve the shared phylogenetic origin (*sensu* Scherer, 1973).

Macrohaltica Bechyné and *Altica* Mueller were suspected of being synonymous because of the apparent establishment of the former based primarily on its larger size (Bechyné, 1957:57). Later Bechyné (1959:305) designated *Macrohaltica* as a new genus using a more detailed description even though this genus was originally mentioned earlier, including a brief description and data on five species (Bechyné, 1957:57). Nevertheless, according to the International Code of Zoological Nomenclature (Articles 13b and 68a), the earlier reference (Bechyné, 1957) did not qualify as an original designation of *Macrohaltica* because there was no type species designation; it was made later (Bechyné, 1959:305). This confusing situation also exists for a few other genera mentioned in both of these publications by Bechyné. Bechyné (1959:305) compared *Macrohaltica* and *Altica*, and stated that *Macrohaltica* has many hairs on the posterior border of elytra (sometimes on disk) with numerous setiferous punctures apically; the labrum has six dorsal setiferous pits, variably positioned. *Altica* has the elytra posteriorly bare with only up to three setiferous punctures near apical border; and labrum with four fixed dorsal setiferous pits; and further stated that *Macrohaltica* are but large *Altica* from the Neotropical Region. Examination of several species of Neotropical *Macrohaltica* compared to *Altica* from various regions, indicates that the elytral hairs and labrum pits are quite variable and not reliable characters. However, examination of the aedeagus and metafemoral spring clearly indicates the distinctiveness between *Macrohaltica* (Figs. 2a, 2c) and *Altica* (Figs. 3a, 3c). This is in contrast to Scherer (1962, 1983) who lumped *Macrohaltica* and several other genera with *Altica*.

Macrohaltica ambiens (LeConte), *M. bimarginata* (Say), *M. prasina* (LeConte), and *M. subplicata* (LeConte) are listed in Wilcox (1975), but these actually belong to the true *Altica*, based on the present study of internal structures. Presumably, *Macrohaltica* (*sensu stricto*) is limited to the Neotropical Region. It should be pointed out that the accuracy of Nearctic *Altica* species names and their systematics are presently suspect.

Another possible case of Palearctic/Nearctic generic synonymy was *Ochrosis* Foudras and *Hornaltica* Barber. The two species of *Hornaltica* found in eastern North America were considered to be *Ochrosis* by Heikertinger and Csiki (1940). Indeed, superficial examination of external characters indicates close similarity. Internally, the aedeagus

and metafemoral spring are also quite similar among the species of these two genera (Figs. 4a, 4c, 5a, 5c). However, closer study of external aspects reveals *Hornaltica* differs from *Ochrosis* because of distinctly impressed dorsal frontal lines (none in *Ochrosis*) and a distinct pronotal transverse depression (faint and not very evident in *Ochrosis*). Furthermore, the female spermathecae are quite different (Figs. 4b, 5b).

Another problematic group that involves both Palearctic and Nearctic taxa is the genus *Oedionychus* Berthold *sensu lato* (with globose last metatarsal segments), which contains only two western Mediterranean species and many Nearctic and Neotropical species. In the New World this group has been divided into many genera (tribe Oedionychini) by Bechyné. Many of these genera present taxonomic problems, and placement of many species in these genera is still uncertain (Scherer, 1983). Virkki (this Symposium) has spent many years studying the cytogenetic system of the Oeionychina (subtribe) and has found some genetic relationship among certain genera. Seeno and Wilcox (1982) divide most of this group into two tribes.

The Palearctic *Oedionychus* (*s.s.*) is similar to its New World relatives in many traits, including internal structures. Examination of the aedeagus (Fig. 6a), spermatheca (Fig. 6b), and the metafemoral spring (Furth, 1982, fig. 11) of *Oedionychus* demonstrates the relatedness of it to its New World counterparts (Figs. 6-10); in fact, for certain comparisons it is difficult to characterize generic level differences.

There are two genera (*Kuschelina* Bechyné and *Capraitia* Bechyné) of the Oedionychini that are found in the USA which are difficult to distinguish from each other or from *Oedionychus s.s.* All three genera have as follows: short, broad, and thickened aedeagus with a basolateral acutely-angled notch, when viewed ventrally (Figs. 6a, 7a, 8a); oval spermathecal pump with palmate appendix (Figs. 6b, 7b, 8b); similarly shaped metafemoral spring (spring morpho-group 5, see Table 2) — all indicating relatedness within the Oedionychini.

Two other genera of Oedionychini, *Omophoita* Chevrolat and *Asphaera* Chevrolat, each with some species in the southern USA, are often confused and not clearly separable, except on rather insignificant color/pattern bases. These two genera also indicate great similarity of the aedeagus (Figs. 7a & 8a), spermatheca (Figs. 7b & 8b), and metafemoral spring (Figs. 7c & 8c). Seeno and Wilcox (1982) place these two genera together in a separate tribe from the three mentioned in the above paragraph. All are clearly related but there is a significant difference in the form of the metafemoral spring of the two groups (Furth, 1982, fig. 11; this paper, Figs. 7c, 8c, 9c, 10c). The only thing that is clear about these apparently related groups of genera is that they are in need of special study, possibly involving comparative biological or biochemical aspects.

What constitutes Alticinae?

The genus *Orthaltica* Crotch was considered by Scherer (1974) to contain several synonymous generic names, i.e., *Livolia* Jacoby from the African, Oriental, and Australian Regions, and *Leptotrichaltica* Heikertinger from North America. Scherer based this proposed synonymy mainly on the absence of the metafemoral spring (extensor apodeme) in all three genera. Scherer (1974) also mentioned that only the North American species (*Orthaltica* s.s. and *Leptotrichaltica*) have an asymmetrical aedeagus, a character rare in the Alticinae.

Later, Scherer (1982) proposed creating subgenera for geographical components of *Orthaltica* (*s.l.*) based on similarities of frontal punctation and pronotal front angles. However, this would split up the *Livolia/Micrepitrix* (all with symmetrical aedeagus) into two or three subgenera, including the North American *Orthaltica* which are different in several basic characters. The historical zoogeographical explanation (Scherer, 1982) for this scenario also seems overly complicated.

The present study concerns North American *Orthaltica* (*sensu* Scherer, 1974) and concentrates on the aedeagus, spermatheca, and a search for any vestiges of a metafemoral spring. As mentioned above the aedeagus of North American *Orthaltica* is asymmetrical (Fig. 11a; Scherer, 1974, fig. 1). The spermatheca of North American *Orthaltica* (Fig. 11b) is also quite aberrant compared to most alticine genera because of its very different proportion of the pump, receptacle, and ductus.

As the Greek derivation of the name Alticinae implies, it has long been known that flea beetles jump, some genera obviously better than others. Traditionally, the greatly enlarged metafemora have been the only characters which separate them from the Galerucinae. Some galerucines have slightly swollen metafemora, and in some alticines they are less swollen. However, when Maulik (1929) discovered the jumping apparatus to be a chitinized structure in the metafemora of Alticinae, this added hard-core evidence for the separation of these two chrysomelid subfamilies. Many subsequent chrysomelid workers have referred to the presence or absence of this structure (metafemoral spring *sensu* Furth, 1982) as the distinguishing characteristic between Alticinae and Galerucinae (Heikertinger, 1948; Barth, 1954; Mohr, 1960; Wilcox, 1965; Wisner, 1970; Scherer, 1971; Furth, 1980, 1982). Thus, it seems somewhat inconsistent to consider a chrysomelid genus, such as *Orthaltica*, as Alticinae if it completely lacks the metafemoral spring or even any vestige of one. If such a chitinous structure would be lost or atrophied, we would expect to find some genera in the world with rudimentary indications or vestiges of this jumping apparatus. Yet, *Orthaltica*, though without a metafemoral spring, has been considered as a flea beetle genus and placed in the middle of Alticinae classification (Scherer, 1974, 1982; Seeno and Wilcox, 1982).

An assymetrical aedeagus is extremely rare in Alticinae, occurring only in *Chaloenosoma* Jacoby from the Orient, which is placed near the beginning of the Alticinae classification (Seeno and Wilcox, 1982) and has a rather "primitive" metafemoral spring (Furth, unpublished). However, an assymetrical aedeagus is very common within the Galerucinae. It would seem more feasible for galerucine species/genera to evolve pronotal impressions (possibly for internal muscle attachment) or frontal punctures (possibly sensory) than for alticine species/genera to evolve an assymetrical aedeagus (reproduction) or lose the metafemoral spring (locomotion and escape).

Therefore, it is suggested that, primarily because of the absence of any vestige of the typical Alticinae metafemoral spring and secondarily because of the galerucine-like assymetrical aedeagus and unusual spermatheca, at least the North American species of *Orthaltica* (*s.s.*) and possibly all species of *Orthaltica* (*s.l.*) should be withdrawn from the Alticinae and placed into the Galerucinae. Considerable research, including biological, is still needed on the components of *Orthaltica* (*sensu* Scherer, 1974) in order to understand their proper relationships and phylogenetic placement. The few other genera of "Alticinae" that are reported to lack the metafemoral spring need to be studied in much greater detail.

Metafemoral Spring Morpho-groups

Readers are referred to explanations of metafemoral spring morphology and morpho-group description and arrangement in previous publications (Furth, 1980, 1982). Table 1 shows the Palearctic metafemoral spring morpho-groups from Furth (1982) with the addition of the final Palearctic genus, *Cardax*, and with the genera alphabetized in each group.

Table 2 illustrates the metafemoral spring morpho-groups of all genera recorded in the continental U.S.A. by Wilcox (1975), with the exception of *Hypolampsis* Clark and *Phaedromox* Clark which are both probable mistaken records. The reader is referred to Wilcox (1975) for generic authorship. It should be noted that 15 genera from the Palearctic are also present in the Nearctic. There is not room for extensive discussion of Table 2 beyond what has already been mentioned above. However, the following metafemoral spring relationships are of special note relative to their traditional classification (Wilcox, 1975): *Acrocyum* near to *Blepharida*; most of the Group 2 members are related to *Altica*; the increase in the Nearctic Region of the number of genera in Group 3 with *Phyllotreta*, including *Systema*, *Dysphenges*, *Lupraea* (the introduced *Agasicles* also falls into this group); the Oedionychini genera all are in Group 5 (*Omophoita* and *Alogoasa* are also in this group).

Table 1. Palearctic Alticinae metafemoral spring morpho-groups

GROUP 1:	GROUP 4:
Arrhenocoela	Longitarsus
Blepharida	
Hermaeophaga	GROUP 5:
Mantura	Argopus
Orestia	Anthobiodes
Podagrica	Aphthona
	Chaetocnema
GROUP 2:	Heyrovskya
Altica	Oedionychus
Asiorestia	Sphaeroderma
Cardax	
Crepidodera	GROUP 6:
Derocrepis	Apteropeda
Epitrix	Batophila
Hippuriphila	Dibolia
Lythrarina	Psylliodes
Minota	
Mniophila	
Ochrosis	
GROUP 3:	
Phyllotreta	

Zoogeographical Affinities

Tables 3 and 4 indicate the primary zoogeographical affinities of the Palearctic and Nearctic genera of Alticinae, respectively. In some cases there is a secondary or tertiary affinity indicated. There are 15 genera present in both the Palearctic and Nearctic faunas and 10 have a cosmopolitan distribution. In the Palearctic Region (Table 3) there are 10 endemic genera with almost all but one of the rest having at least partial Palearctic affinity (see Table 3 for percentage affinity).

In the Nearctic Region (Table 4) there are only six endemic genera and 11 genera with at least partial Nearctic affinity. However, the largest number of genera (15 = 35%) are of Neotropical affinity, apparently indicating the most recent connection between the faunas of North and South America rather than with any other region. This predominance of Neotropical genera in the Nearctic may indicate an increase in temperature and humidity to the north after North and South were rejoined. Of course, some of this influence is due to the proximity of the southern U.S.A. (e.g. Texas) to the Neotropics. Only two genera are truly Holarctic, possibly from the time of the Bering land bridge. Another two genera apparently have an older Mesozoic/Tertiary Laurasian connection through their present-day Holarctic/Ethiopian affinity.

Table 2. Nearctic Alticinae metafemoral spring morpho-groups

GROUP 1:	GROUP 3:	GROUP 5:
Acrocyum	Dysphenges	Aphthona
Blepharida	Glenidion	Asphaera
Mantura	Lupraea	Capraita
Orestioides	Pachyonychus	Chaetocnema
(=Orestia)	Phydanis	Euplectroscelis
Pseudorthygia	Phyllotreta	Glyptina
	Pseudolampsis	Kuschelina
GROUP 2:	Systema	Pachyonychis
Altica	GROUP 4:	Sphaeroderma
Crepidodera	Longitarsus	GROUP 6:
Derocrepis		Argopistes
Disonycha		Dibolia
Epitrix		Distigmoptera
Hemiglyptus		Psylliodes
Hippuriphila		
Hornaltica		
Luperaltica		
Lysathia		
Macrohaltica		
Monomacra		
Phrynocephala		
Strabala		
Syphrea		
Trichaltica		

The Palearctic and Nearctic genera of Alticinae have a moderately strong relationship, because, other than the few genera that show some Holarctic affinities, many of the 10 cosmopolitan genera are actually primarily Holarctic. These two Regions probably have a stronger relationship than any other pair of major biogeographic regions in the world; however, this study only concentrated on 63 of the more than 450 genera worldwide; so, there is still a lot to do even at the generic level in order to begin to understand flea beetle systematics and phylogeny.

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Table 3. Zoogeographical affinities of Palearctic Alticinae

PALEARCTIC	COSMOPOLITAN	PALEARCTIC	HOLARCTIC
Anthobiodes	Altica	Argopus	Hippuriphila
Apteropeda	Aphthona	Mniophila	Orestia
Arrhenocoela	Chaetocnema	Ochrosis	= 6.7%
Asiorestia	Crepidodera	= 10%	
Batophila	Dibolia		HOLARCTIC/
Cardax	Epitrix	ETH./PALEARCTIC	ETHIOPIAN
Heyrovskya	Longitarsus		
Lythraria	Phyllotreta	Podagrica	Derocrepis
Minota	Psylliodes	= 3.3%	Mantura
Oedionychus	Sphaeroderma		= 6.7%
= 33.3%	= 33.3%	PAL./ETH./	
		ORIENTAL	ETHIOPIAN/
		Hermaeophaga	NEARCTIC
		= 3.3%	Blepharida
			= 3.3%

Table 4. Zoogeographical affinities of Nearctic Alticinae

NEARCTIC	NEOTROPICAL	NEARCT./	HOLARCTIC	COSMOPOLITAN
Glyptina	Acrocyum	NEOTROP.	Hippuriphila	Altica
Hemiglyptus	Asphaera	Capraita	Orestioides	Aphthona
Luperaltica	Disphenges	Disonycha	(=Orestia)	Chaetocnema
Pachyonychis	Euplectroscelis	Distigmoptera	= 4.7%	Crepidodera
Pachyonychus	Glenidion	= 7%		Dibolia
Hornaltica	Lysathia		HOLARCTIC/	Epitrix
= 14%	Macrohaltica	NEOTROP./	ETH.	Longitarsus
	Monomacra	NEARCTIC		Phyllotreta
	Phrynocephala		Derocrepis	Psylliodes
	Phydania	Kuschelina	Mantura	Sphaeroderma
	Pseudolampsis	Lupraea	= 4.7%	= 23%
	Pseudorthygia	Systema		
	Strabala	= 7%		PAN-TROPICAL
	Syphraea			Argopistes
	Trichaltica	ETH./		= 2.3%
	= 35%	NEARCTIC		
		Blepharida		
		=2.3%		

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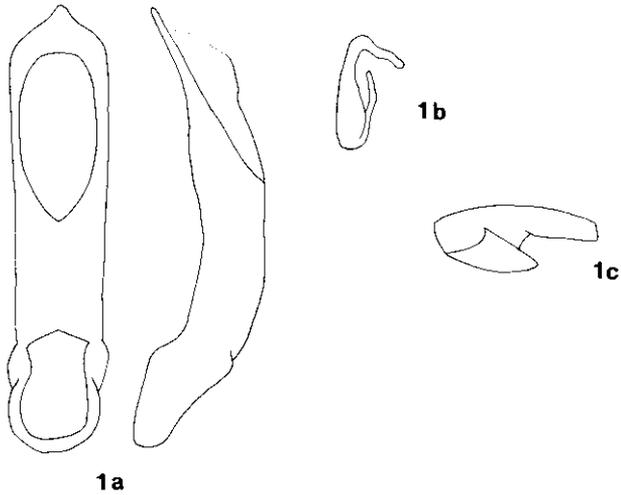


Fig. 1. *Orestioides* (= *Orestia*) *robusta* (LeConte). **a**, aedeagus (left = ventral view, right = lateral view) [0.98 mm long]; **b**, female spermatheca [0.30 mm = length, not including ductus]; **c**, metafemoral spring [0.33 mm = length].

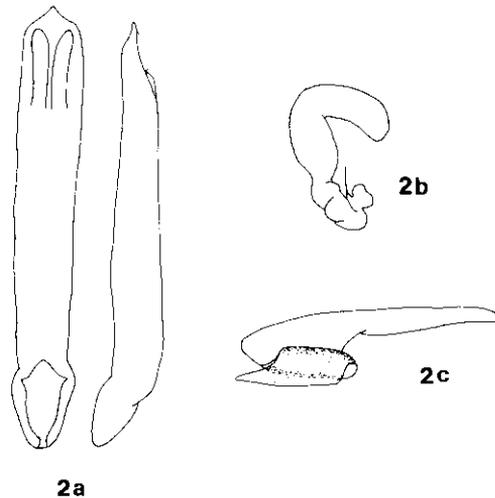


Fig. 2. Figs. **a** & **b**, *Macrohaltica jamaicensis* (Fabricius): **a**, aedeagus [3.65 mm]; **b**, spermatheca [0.41 mm]. Fig. **c**, *Macrohaltica* sp. metafemoral spring [1.11 mm].

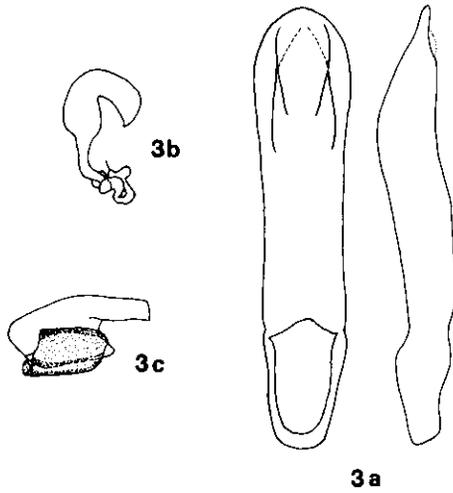


Fig. 3. *Altica oleracae* (Linnaeus). a, aedeagus [1.54 mm]; b, spermatheca [0.22 mm]; c, metafemoral spring [0.46 mm].

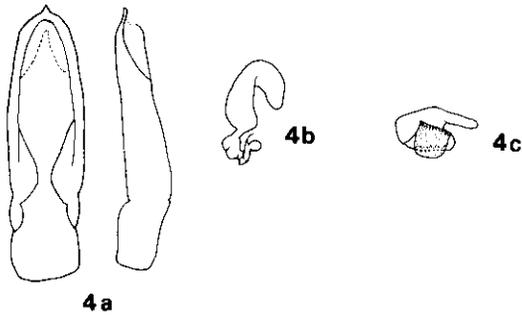


Fig. 4. *Hornaltica atriventris* (Melsheimer). a, aedeagus [0.61 mm]; b, spermatheca [0.17 mm]; c, metafemoral spring [0.20 mm].

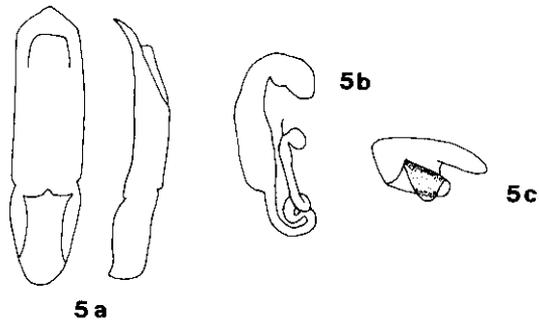


Fig. 5. *Ochrosis ventralis* (Illiger). a, aedeagus [0.56 mm]; b, spermatheca [0.28 mm]; c, metafemoral spring [0.22 mm].

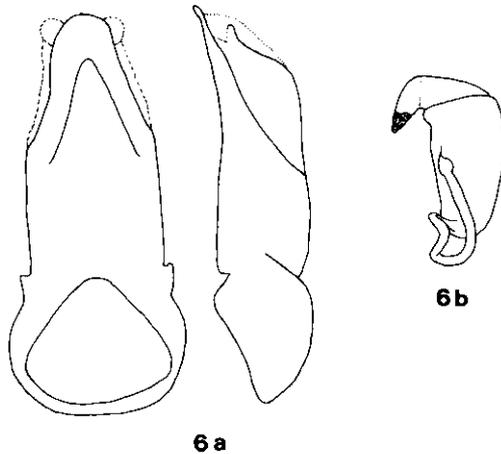


Fig. 6. *Oedionychus cincta* (Fabricius). a, aedeagus [2.13 mm]; b, spermatheca [1.11 mm].

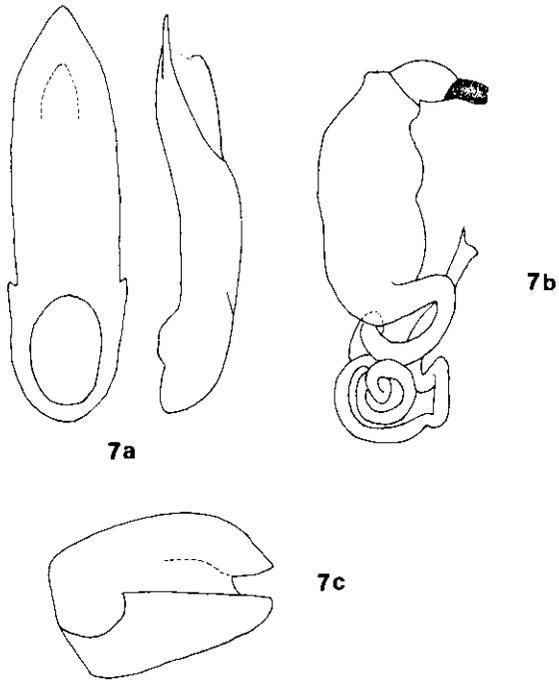


Fig. 7. *Kuschelina thoracica* (Fabricius). a, aedeagus [2.35 mm]; b, spermatheca, [1.02 mm]. Fig. c, *Kuschelina miniata* (Fabricius), metafemoral spring [0.76 mm].

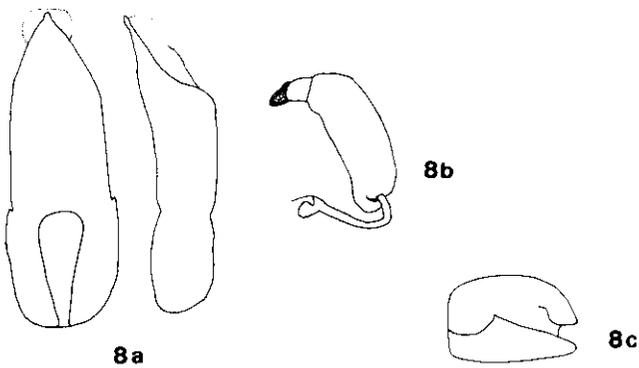


Fig. 8. *Capraitia quercata* (Fabricius). a, aedeagus [1.39 mm]; b, spermatheca [0.70 mm]; c, metafemoral spring [0.88 mm].

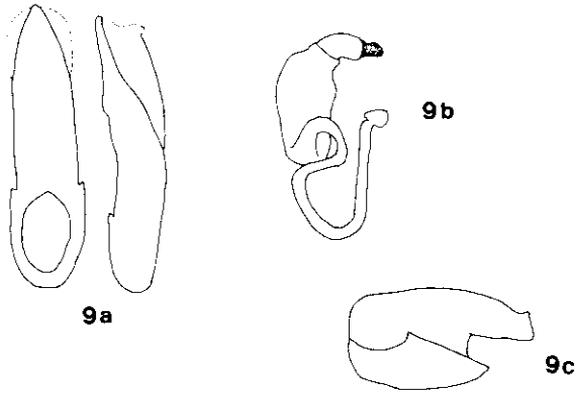


Fig. 9. *Omophoita aequinoctialis* (Linnaeus). a, aedeagus [2.35 mm]; b, spermatheca [0.57 mm]; c, metafemoral spring [0.80 mm].

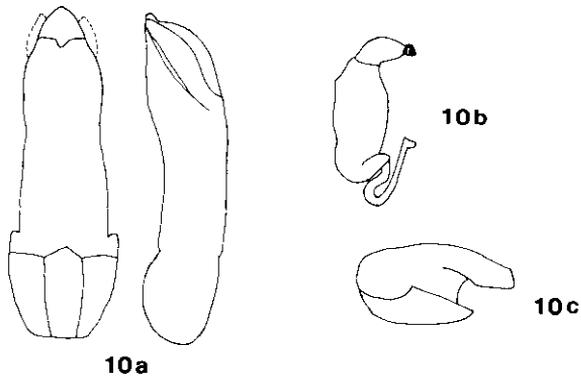


Fig. 10. *Asphaera abdominalis* (Chevrolat). a, aedeagus [2.58 mm]; b, spermatheca [1.28 mm]. Fig. c, *Asphaera lustrans* (Crotch), metafemoral spring [0.78 mm].

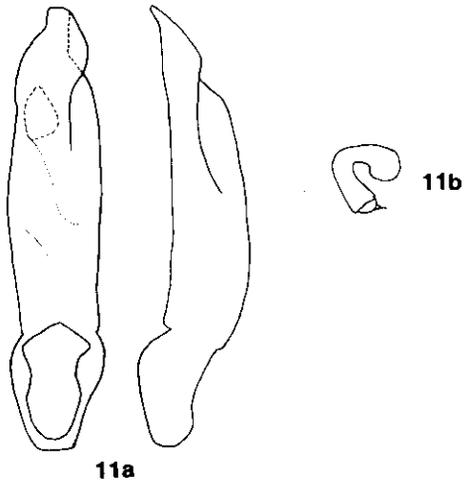


Fig. 11. *Orthaltica copalina* (Fabricius). a, aedeagus [0.92 mm]; b, spermatheca [0.13 mm].

