

SYSTEMATIC RELATIONSHIP OF THE GENUS *RHAEBUS* (COLEOPTERA: BRUCHIDAE)

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Abstract.—Morphological characteristics of the five species in the genus *Rhaebus* and of the final larval instar of *Rhaebus mannerheimi* Motschulsky are used to justify the inclusion of this genus in the family Bruchidae rather than in the Chrysomelidae wherein it has been placed in the past. The singular nature of certain traits of the genus, however, requires that it be relegated to a separate subfamily, the Rhaebinae.

Rhaebus, which includes five species, occurs only in central Asia and breeds in the drupes of the relict plant genus *Nitraria* L. (Zygophyllaceae). The genus was described in Curculionides by Fischer von Waldheim (1824), but subsequent authors have placed it in the Chrysomelidae as well, and one worker even related it to the Oedemeridae. Most recent authorities, however, recognize that its roots are near the common ancestor of Bruchidae and the sagrine Chrysomelidae, but opinions differ as to which family it should be assigned. We herein present evidence from adult and larval morphology and behavior that we believe supports assignment of this genus to the Bruchidae. At the same time, we recognize its distinctiveness by keeping it in a monotypic subfamily, the Rhaebinae (Chapuis, 1874, as Rhaebites).

For behavioral characteristics, we drew freely from Luk'yanovich (1939), and Luk'yanovich and Ter-Minassian (1957). An ongoing but unpublished morphological and phylogenetic study by Kingsolver is the basis for relating *Rhaebus* to other genera in both the Bruchidae and the Chrysomelidae. Likewise, an ongoing study of immature forms of Bruchidae by Pfaffenberg is the basis for the larval section of this paper. Because characteristics of the larval forms of *Rhaebus* have virtually been ignored, a discussion of the relationships based on the first comprehensive description of the final larval instar of *R. mannerheimi* Motschulsky is especially pertinent.

The family Bruchidae is singular in the Coleoptera in that, with the exception of adults feeding on nectar and pollen, it is totally geared to a spermatophagous mode of development. Oviposition occurs on the surface of the seed envelope of the host plant, or on the seed itself. The first instar larva has legs, is motile, and is uniquely equipped with a toothed pronotal plate that is thought to assist the larva in eclosion and in boring through the epidermis of the fruit or seed. This plate is lost with the first molt, and the larva becomes apodal, or nearly so, feeding entirely within the seed. Pupation occurs with few exceptions inside the feeding excavation after the larva has drilled an escape tunnel for the adult to the surface of the seed leaving only a thin cap of epidermis for the adult to penetrate. Adults harden in the pupal chamber before emerging. This suite of characteristics indicates a long period of evolution of the seed feeding habit.

Luk'yanovich (1939) recorded perhaps the most comprehensive observations of behavior of *Rhaebus*. He found that females of *R. mannerheimi* glued eggs rather indiscriminately in crevices, in feeding excavations, and upon or beneath the calyx of the developing drupe of *Nitraria schoberi* L., on its unopened buds and parts of the flower, and on the surfaces of thin branches. Although this randomness of site is not characteristic for most bruchids, it may illustrate the process of selection for oviposition directly on fruits by ancestral bruchids.

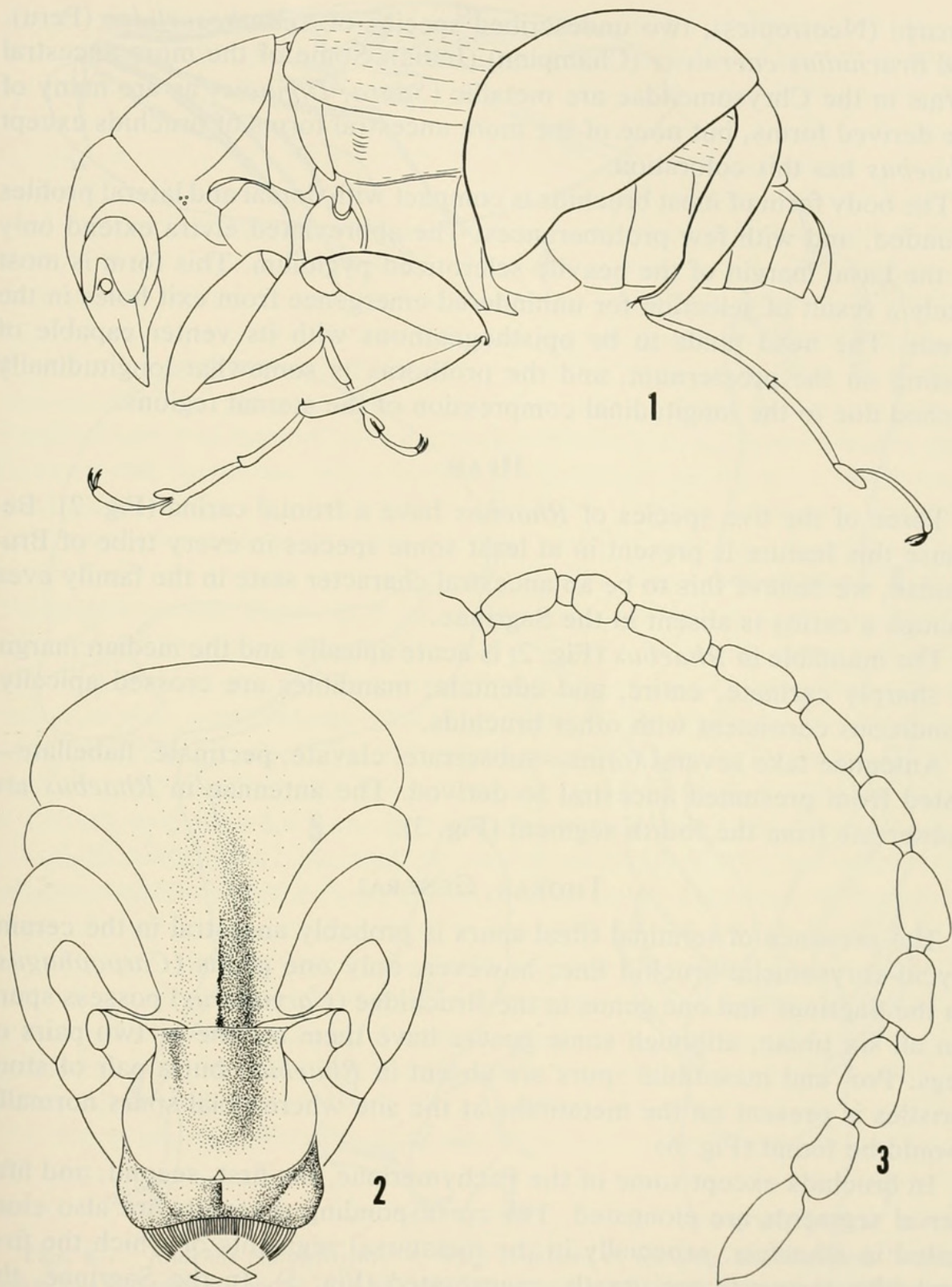
First instar larvae of *Rhaebus* are not known, but later instar larvae are typically bruchid in form and habit even to the extent that they bore an escape tunnel for the adult. Luk'yanovich (1939) thought that the rather elongated and loosely organized form of the adult results from the necessity of the yet soft imago having to squeeze through a disparately small opening bored by the larva. Final hardening of the adult body occurs after emergence from the drupe. Nearly all other bruchids harden in the pupal chamber.

PHYSICAL CHARACTERISTICS OF ADULT *RHAEBUS*

Species of *Rhaebus* are small, metallic beetles, 3–5 mm long, with somewhat elongated bodies (Fig. 1). In some of their characteristics, they show definite affinities with the subfamily Pachymerinae (Bruchidae), but some others point to an independent line of development. Each of the body regions will be discussed in detail. From an unpublished study of characteristics showing evolutionary trends within Bruchidae and comparison of bruchids with presumed ancestral forms in the Chrysomelidae and Cerambycidae, the ancestral and derived status of a number of characters in *Rhaebus* can be determined with some confidence.

GENERAL COMMENTS

A metallic body color is unusual in bruchids and is known elsewhere in the family only in a few unrelated species, e.g., *Meibomeus cyanipennis*



Figs. 1-3. *Rhaebus mannerheimi*. 1, Habitus, lateral aspect. 2, Head, frontal aspect. 3, Antenna.

(Sharp) (Neotropics), two undescribed species of *Acanthoscelides* (Peru), and *Bruchidius caeruleus* (Champion) (India). Some of the more ancestral forms in the Chrysomelidae are metallic (*Sagra*, *Donacia*) as are many of the derived forms, but none of the more ancestral forms of bruchids except *Rhaebus* has this coloration.

The body form of most bruchids is compact with dorsal and lateral profiles rounded, and with few protuberances. The abbreviated elytra extend only to the basal margin of the heavily sclerotized pygidium. This form is most likely a result of selection for unhindered emergence from exit holes in the seeds. The head tends to be opisthognathous with its venter capable of resting on the prosternum, and the prothorax is somewhat longitudinally arched due to the longitudinal compression of the sternal regions.

HEAD

Three of the five species of *Rhaebus* have a frontal carina (Fig. 2). Because this feature is present in at least some species in every tribe of Bruchidae, we believe this to be an ancestral character state in the family even though a carina is absent in the Sagrae.

The mandible in *Rhaebus* (Fig. 2) is acute apically and the median margin is sharply carinate, entire, and edentate; mandibles are crossed apically, conditions consistent with other bruchids.

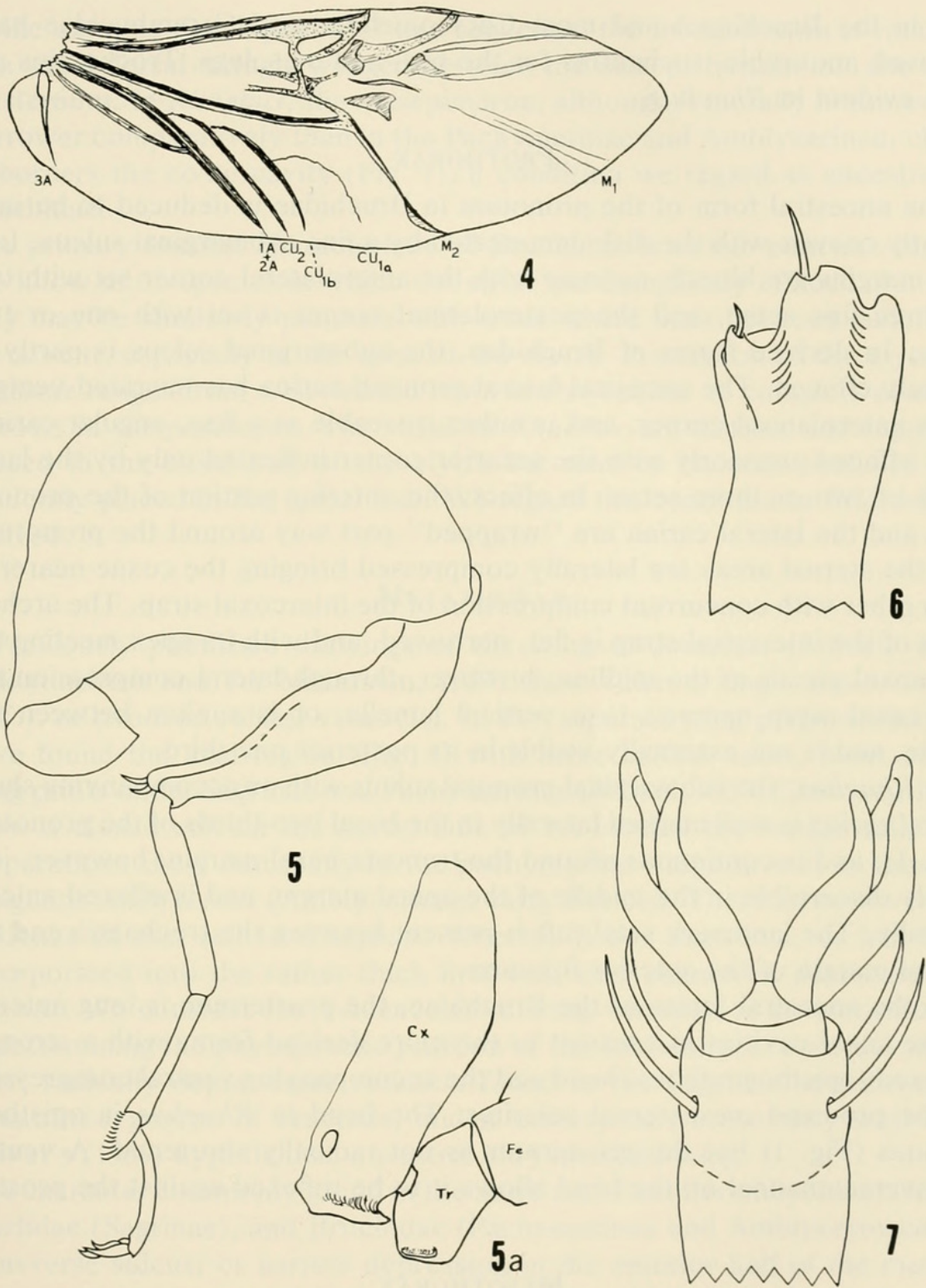
Antennae take several forms—subserrate, clavate, pectinate, flabellate—listed from presumed ancestral to derived. The antennae in *Rhaebus* are subserrate from the fourth segment (Fig. 3).

THORAX, GENERAL

The presence of terminal tibial spurs is probably ancestral in the cerambycid-chrysomelid-bruchid line; however, only one genus (*Carpophagus*) in the Sagrae and one genus in the Bruchidae (*Caryoborus*) possess spurs on all six tibiae, although some genera have them on one or two pairs of legs. Pro- and mesotibial spurs are absent in *Rhaebus*, but a pair of stout bristles is present on the metatibiae at the site where tibial spurs normally would be found (Fig. 6).

In bruchids except some of the Pachymerinae, the first, second, and fifth tarsal segments are elongated. The corresponding segments are also elongated in *Rhaebus*, especially in the metatarsal segments of which the first and fifth segments are greatly exaggerated (Fig. 5). In the Sagrae, the tarsal segments are not elongated.

A consistent characteristic throughout the Bruchidae (except in *Rhaebus*) is the presence of a basal angulate lobe on the ventral side of each tarsal claw (appendiculate claw). Appendiculate claws do not occur in the Sagrae. In *Rhaebus*, however, the claw is split, with the mesal hook of each claw nearly as long as the lateral hook (Fig. 7). Whether this represents an



Figs. 4–7. *Rhaebus mannerheimi*. 4, Wing venation. 5, Metaleg, lateral aspect. 5a, Right metacoxa and metatrochanter, caudal aspect showing pincerlike structure. 6, Metatibia, apex, ventral aspect. 7, Tarsal claw, dorsal aspect. (cx = Coxa, Tr = Trochanter, Fe = Femur).

intermediate step between an unmodified form of claw (Sagrinae) and the appendiculate form of other bruchids, or is an extension of the basal lobe found in other bruchids, cannot be determined at present.

All Bruchidae (except in tribes Bruchini, Bruchidiini, and Acanthosceli-

dini in the Bruchinae) and most Chrysomelidae and Cerambycidae have exposed, moveable trochantins for the pro- and mesolegs. Trochantins are fully evident in *Rhaebus*.

PROTHORAX

The ancestral form of the pronotum in Bruchidae is deduced to be only slightly convex with the disk demarcated by a fine submarginal sulcus. Lateral margins are bluntly carinate with the anterolateral corner set with two or three fine setae, and the posterolateral corner is set with one or two setae. In derived forms of Bruchidae, the submarginal sulcus is partly to entirely effaced. The ancestral lateral pronotal carina has migrated ventrad at its anterolateral corner, and is either traceable as a fine, angular carina, or is effaced anteriorly with the anterior corner indicated only by the landmark of two or three setae. In effect, the anterior portion of the pronotal disk and the lateral carina are "wrapped" part way around the pronotum, and the sternal areas are laterally compressed bringing the coxae nearer to each other with concurrent compression of the intercoxal strap. The archaic form of the intercoxal strap is flat, narrowed, and with its apex meeting the postcoxal pieces at the midline; however, through lateral compression the intercoxal strap narrows to a vertical lamella, or is sunken between the coxae, and is not externally visible in its posterior one-third.

In *Rhaebus*, the submarginal pronotal sulcus with an accompanying sharp lateral carina is well marked laterally in the basal two-thirds of the pronotum (Fig. 1), and is continuous around the truncate basal margin; however, it is barely discernible in the middle of the apical margin, and is effaced anterolaterally. The landmark setal tuft is present between the trochantin and the lateral margin of the anterior foramen.

In the ancestral forms of the Bruchidae, the prosternum is long anterior to the coxal cavities in contrast to the more derived forms with a strongly reflexed (opisthognathous) head and the accompanying ventral compression of the pro- and mesosternal sclerites. The head in *Rhaebus* is opisthognathous (Fig. 1) but the prosternum is not radically shortened. A ventral transverse channel on the head allows it to be reflexed against the prosternum.

MESOTHORAX

The visible pleural sclerites are the mesepisternum and mesepimeron separated by the pleural sulcus. In the more generalized bruchids, and in the Sagrinae, the mesepimeron is elongate trapezoidal with the mesal end forming part of the mesocoxal cavity. The mesal end is about one-half the width of the dorsal end. In some of the more derived bruchids (Bruchinae), as the thoracic compression evolves, the mesepisternum encroaches on the mesepimeron at its mesal end and gradually separates it from the coxal cavity.

In the extreme development of this sequence, the mesepimeron is reduced to a small dorsal triangle wedged between the mesepisternum and the metepisternum. In *Rhaebus*, the mesepimeron, although it mesally is somewhat narrower comparatively than in the Pachymerinae and Amblycerinae, clearly borders the coxal cavity (Fig. 1), a condition we regard as ancestral in Bruchidae.

A primary familial characteristic of Bruchidae is striate-punctate elytra. We know of no species in which the striae are completely effaced although they may be shallowly punctate with areas where lines between punctures are absent, especially at the apex of the elytra. Punctuation of the elytra in Sagrinae ranges from well-defined rows in *Polyoptilus* to complete absence of rows in *Carpophagus*. The striae in *Rhaebus* are distinct and regularly spaced in the basal half of the elytra but tend to become confused and randomly placed in the apical half. We regard this condition in *Rhaebus* as derived.

METATHORAX

Previously published drawings of the wing of *Rhaebus* (Jolivet, 1957; Luk'yanovich and Ter-Minassian, 1957) show either a single anal vein (L. & T.), or two free cubital veins (J.). In two separate wing preparations, we have found the anal region (Fig. 4) with three cubital veins. Most of the wing prints of the Sagrinae and Pachymerinae (Jolivet, 1957; Crowson, 1946) show a closed cell on the dorsal side of 1A labeled the wedge cell. Our preparations show that many of the pachymerine wings as well as those of the genus *Amblycerus* (Amblycerinae) carry this cell. There is, however, no evidence of this cell in *Rhaebus*. Whether it has been lost, or has been incorporated into the rather thick first anal vein cannot be determined at present. We consider the evidence from wing venation to be inconclusive in determining the phylogenetic position of the subfamily. It does not, however, radically depart from venation found in the Sagrinae and the more generalized groups of bruchids, and it corresponds reasonably well with Jolivet's (1957) hypothetical ancestral chrysomeloid wing.

A character commonly found in the more ancestral Cerambycidae, Chrysomelidae (Sagrinae), and Bruchidae (Pachymerinae and Amblycerinae) is a transverse sulcus, or narrow depression in the anterior half of the metepisternum. In many cases, this connects mesally with a fine sulcus extending parallel to the mesopleural-metapleural sulcus and is mirrored on the metasternum by a similar sulcus, an extension of the postmetacoxal sulcus. These parallel sulci have been termed "parasutural sulci" by Kingsolver (1965), and have been found even in the fossil genus *Oligobruchus* Kingsolver (Florissant). In *Rhaebus*, the transverse sulcus is a poorly defined depression and traces of parasutural sulci are present. We consider the condition in *Rhaebus* to be derived.

In all Bruchids except *Rhaebus*, the metatrochanter is a small, triangular piece joined diagonally to the base of the metafemur and is fitted proximally with a condyle rotating in a foramen at the proximal end of the coxa. In *Rhaebus*, however, the trochanter is enlarged ventrally into a blunt triangular process (Fig. 5). In addition, the proximal end of the metacoxa is produced caudally into a short, lamelliform plate which at one point in the rotation of the trochanter in relation to the coxa forms a pincerlike structure opposing the trochanteral plate (Fig. 5a). The function of this unusual structure is unknown. This development is not found in other Bruchidae nor in Sagrinae and is obviously a derived condition probably peculiar to *Rhaebus*.

In most species of Bruchidae, the metafemur in both sexes is strongly expanded dorsoventrally, but in certain genera (e.g., *Conicobruchus*, *Kytorhinus*, *Megacerus*), it is slender, and in the Amblycerinae it is slightly incrassate. In addition to the expanded condition, the ventral margin of the femur, with some exceptions is armed with one or more spines (incidentally a primary source of subfamilial and generic characters). Both the expanded condition of the metafemur and the presence of ventral armature are commonly found in the Sagrinae, but it is yet unclear whether an expanded femur is ancestral in Bruchidae and Sagrinae because both groups also include forms with slightly expanded or "normal" femora. The males of the five species of *Rhaebus* exhibit a wide range of femoral expansion. The metafemur of *R. solskyi* Kraatz and *R. lukjanovitschi* Ter-Minassian is simple and not expanded dorsoventrally and is armed with a ventral row of fine spines; *R. gebleri* Fischer has slightly thickened femora with ventral spines; and *R. mannerheimi* Motschulsky and *R. komarovi* Luk'yanovich have greatly expanded femora without spines (Fig. 5). In the females of these species, the metafemora are not or are only slightly thickened.

Concurrent with the apparent developmental sequence from a slender to an expanded femur in *Rhaebus* is a derived condition of the metatibia in the male. In *R. solskyi* and *lukjanovitschi*, the tibia is slightly bowed, slender, and simply produced at the apex; in *R. gebleri*, it is slightly thickened medially, but with a simple apex; in *R. mannerheimi*, the tibia is asymmetrically thickened medially (Fig. 5) and somewhat spatulate and tricuspidate apically. We have not seen specimens of *R. komarovi*, but the original description and illustration indicate that the tibia is similar to that of *R. mannerheimi*.

The concurrent derived conditions in the femur and tibia in *Rhaebus* strongly suggest that femoral expansion is an independent evolutionary line in this genus; however, the tendency for thickened femora is probably inherent in the Sagrinae-Bruchidae line.

Chapuis (1874) was led to suggest a relationship between *Rhaebus* and the genus *Oedemera* (Oedemeridae) because of the remarkably similar development of the male hind leg in the two groups.

Crowson (1946) compared the metendosternite of *Rhaebus* with those of some of the Sagrinae and with other Bruchidae and concluded that this structure is "essentially bruchid."

ABDOMEN

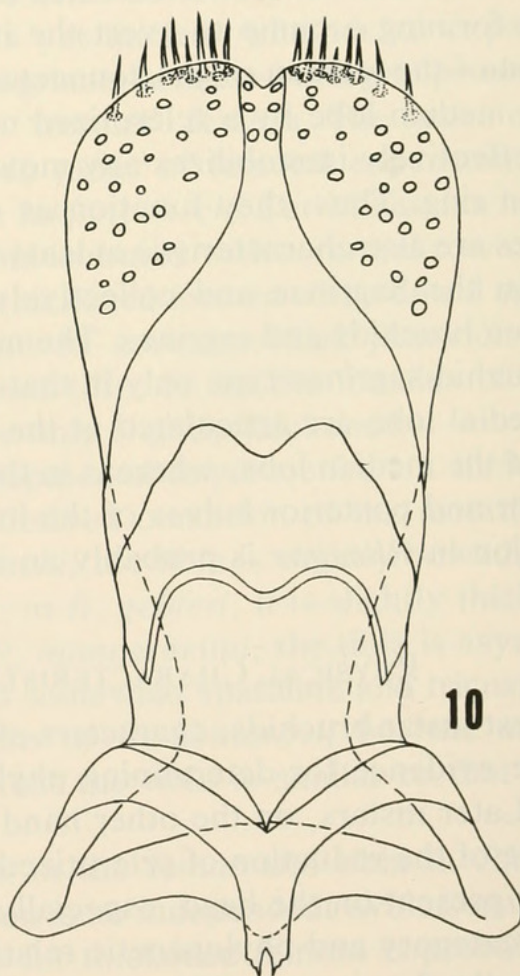
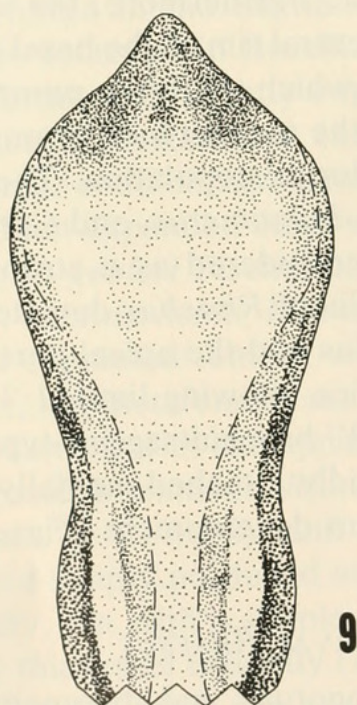
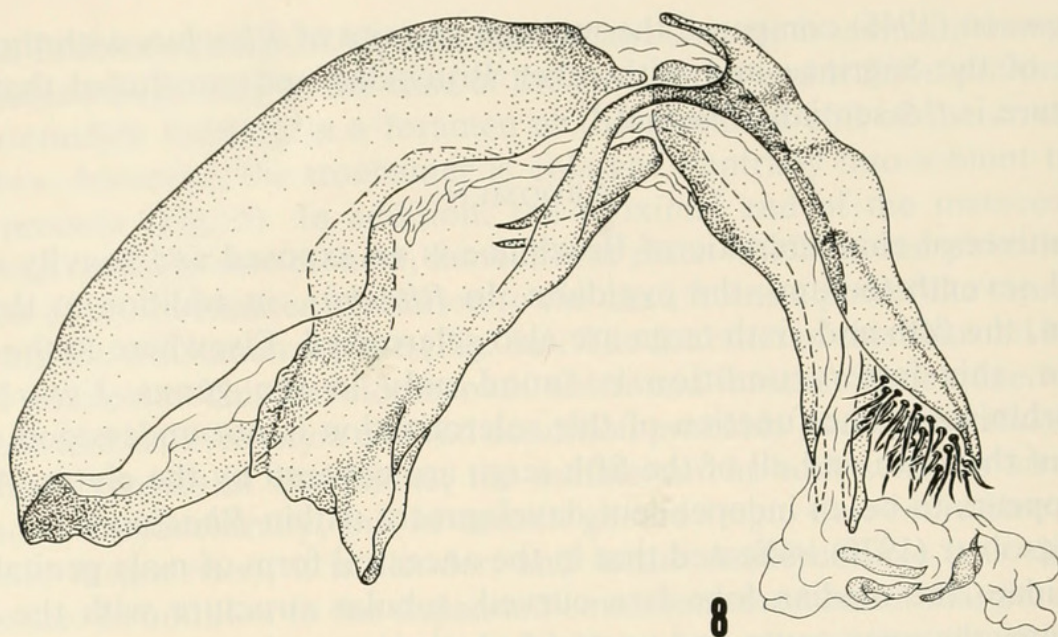
A universal characteristic of Bruchidae is an exposed and heavily sclerotized seventh tergum—the pygidium. In *Rhaebus*, in addition to the pygidium, the fifth and sixth terga are also sclerotized. Elsewhere in the Bruchidae, this latter condition is found only in the genus *Kytorhinus* (Kytorhinae). The function of this sclerotization is not understood since most of the sixth and all of the fifth terga are covered by the elytra. Again this appears to be an independent development within *Rhaebus*.

Kingsolver (1970) indicated that in the ancestral form of male genitalia in Bruchidae, the median lobe is a curved, tubular structure with the base cucullate, the apex acute and unmodified, the internal sac armed with variously formed sclerites, the lateral lobes present and fused basally, and the ventral tegminal strut connected to the cucullus by densely placed muscle bands forming a pump to evert the internal sac. Furthermore, the ventral portion of the tegmen ring is connected to the ventral rim of the basal orifice of the median lobe by a sclerotized membrane which, with the pump muscles, effectively immobilizes any movement of the median lobe through the tegmen ring. Thus, they function as one unit during copulation. These attributes are also characteristic at least for *Sagra*, *Megamerus*, and *Carpophagus* in the Sagrinae and collectively can be considered as a strong link between bruchids and sagrae. The male genitalia of *Rhaebus* deviate from the bruchid-sagrae type only in that the cucullus and the apical portion of the median lobe are articulated at the basal orifice allowing limited "bending" of the median lobe, whereas in the "normal" bruchid-sagrae type, the anterior and posterior halves of the lobe are rigidly attached medially. The condition in *Rhaebus* is probably an independent development (Figs. 8, 9, 10).

PHYSICAL CHARACTERISTICS OF LARVAL *RHAEBUS*

In first instar bruchids, characters of head, pronotum, and abdomen offer reliable evidence for determining phylogenetic affinities above the species level. Later instars, on the other hand, are much less useful in this respect because of the reduction of sclerotized parts. Useful specific characters are usually present on the head, especially in the mouthparts, but indicators of higher category and phylogenetic relationships are less evident.

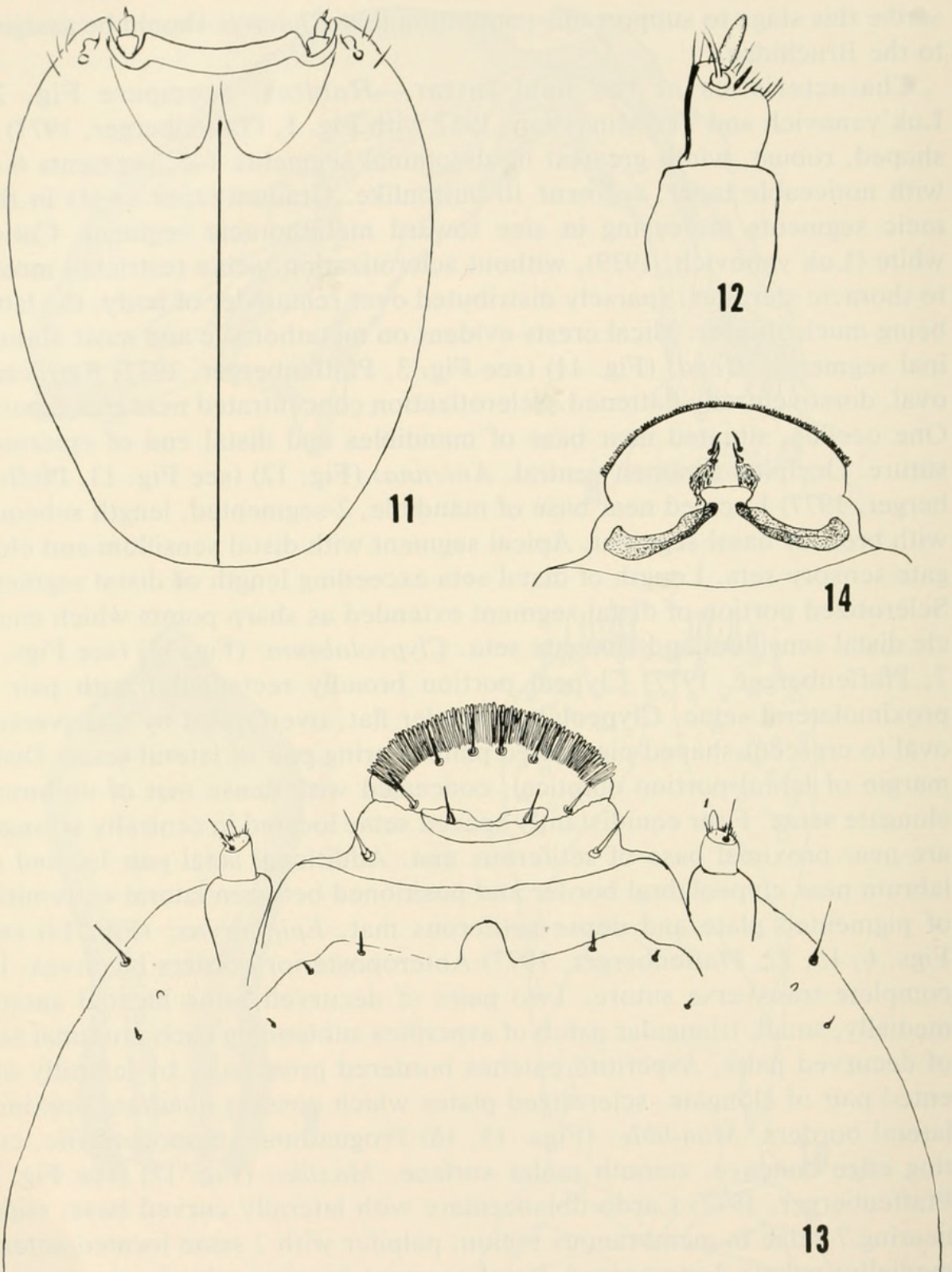
Since the first instar of *Rhaebus* has not yet been seen by us, its possible contribution to the phylogenetic position of this genus remains to be determined. Characteristics of the final larval instar of *Rhaebus mannerheimi*, however, are consistent with those of other Bruchidae. We therefore de-



Figs. 8-10. *Rhaebus mannerheimi*, male genitalia. 8, Median lobe, lateral aspect. 9, Median lobe, dorsal aspect of apex. 10, Lateral lobes, dorsal aspect.

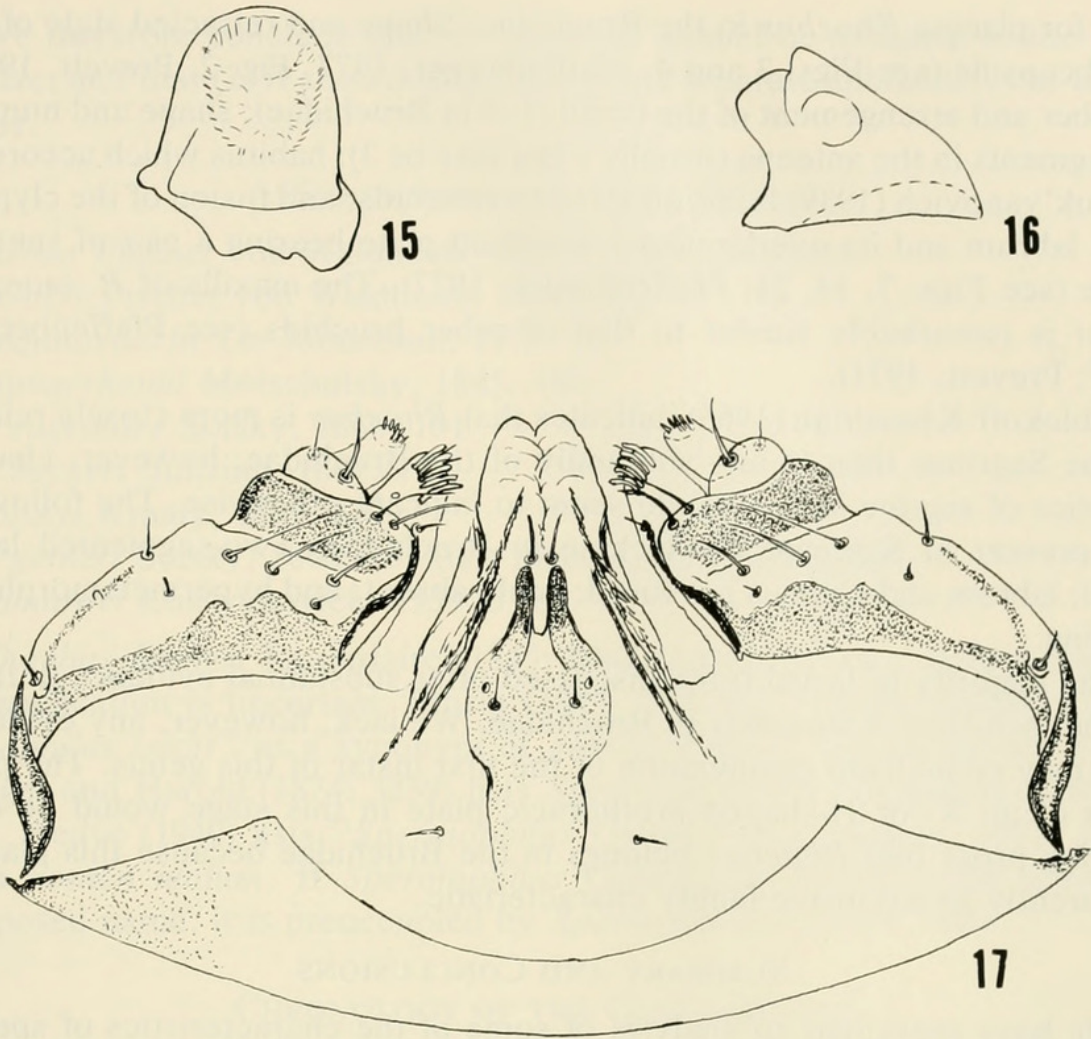
scribe this stage to support our contention that *Rhaebus* should be assigned to the Bruchidae.

Characteristics of the final instar.—*Habitus*: (compare Fig. 25, Luk'yanovich and Ter-Minassian, 1957 with Fig. 1, Pfaffenberger, 1977) C-shaped, robust, width greatest in abdominal segments 1–5, segments 6–10 with noticeable taper, segment 10 buttonlike. Gradual taper exists in thoracic segments increasing in size toward metathoracic segment. Cuticle white (Luk'yanovich, 1939), without sclerotization, setae restricted mostly to thoracic sternites, sparsely distributed over remainder of body, the latter being much shorter. Plical crests evident on metathoracic and most abdominal segments. *Head*: (Fig. 11) (see Fig. 3, Pfaffenberger, 1977) Retracted, oval, dorsoventrally flattened. Sclerotization concentrated near mouthparts. One ocellus, situated near base of mandibles and distal end of epicranial suture. Occipital foramen ventral. *Antenna*: (Fig. 12) (see Fig. 13, Pfaffenberger, 1977) Located near base of mandible, 2-segmented, length subequal with broader basal segment. Apical segment with distal sensillum and elongate sensory seta. Length of distal seta exceeding length of distal segment. Sclerotized portion of distal segment extended as sharp points which encircle distal sensillum and elongate seta. *Clypeolabrum*: (Fig. 13) (see Figs. 3, 7, Pfaffenberger, 1977) Clypeal portion broadly rectangular with pair of proximolateral setae. Clypeolabral border flat, overlapped by transversely oval to crescent-shaped pigmented plate bearing pair of lateral setae. Distal margin of labral portion elliptical, concealed with dense mat of uniformly elongate setae. Four equidistantly spaced setae located in centrally arranged arc near proximal base of setiferous mat. Additional setal pair located on labrum near clypeolabral border and positioned between lateral extremities of pigmented plate and dense setiferous mat. *Epipharynx*: (Fig. 14) (see Figs. 6, 15, 22, Pfaffenberger, 1977) Anteroposterior borders biconvex. Incomplete transverse suture. Two pairs of decurved setae located anteromedially, small, triangular patch of asperities subtending each proximal seta of decurved pairs. Asperite patches bordered proximally by laterally oriented pair of elongate, sclerotized plates which possess quadrate proximolateral borders. *Mandible*: (Figs. 15, 16) Prognathous, monocondylic, cutting edge concave, smooth molar surface. *Maxilla*: (Fig. 17) (see Fig. 9, Pfaffenberger, 1977) Cardo oblongate with laterally curved base; stipes bearing 7 setae in membranous region; palpifer with 2 setae located anteromedially; palpus 2-segmented, basal segment bearing pair of anteroventral setae, distal segment longer than wide and bearing 7 minute sensillae; mala with 5 anteroventral, spatulate setae, pair of small, pointed sensory setae located on anteromedial edge, sensory pore on ventrolateral aspect of mala. Single seta at anterior end of lacinia mobilis near base of mala. *Labium*: (Fig. 17) Palpi absent, submentum lacking, mentum longitudinally elongate



Figs. 11-14. *Rhaebus mannerheimi*, larva. 11, Head, dorsal aspect. 12, Antenna, dorsal aspect. 13, Labrum, dorsal aspect. 14, Epipharynx, ventral aspect.

(see Fig. 31D, Prevett, 1971), basal portion appearing as 2 posterolateral, sclerotized projections, flanked laterally by pair of sensory setae. Median aspect of mentum with pair of mediolateral setae isolated in membranous pockets, sensory pore located anterolaterally to each seta. Anterior aspects



Figs. 15–17. *Rhaebus mannerheimi*, larva. 15, Mandible, mesal face. 16, Mandible, dorsal aspect. 17, Labium and maxillae, ventral aspect.

of mentum prong-like (see Fig. 32B, Prevett, 1971) with pair of setae located near distal end of each pronglike projection, glossae partially fused. *Legs*: Absent (Luk'yanovich, 1939).

DISCUSSION OF LARVAL CHARACTERS

Features of *R. mannerheimi* which are peculiar to the Bruchidae include: Two pairs of short, decurved epipharyngeal setae; absence of labial palpi (according to Böving and Craighead (1931), these palpi are single segmented in *Pachymerus*, but this is in conflict with Pfaffenberger (1974) who found that labial palpi are absent); chaetotaxy associated with the mentum (see Prevett, 1971), hypermetamorphosis (Luk'yanovich 1939); the seed boring habit; and pupation within the excavated larval chamber. Emergence behavior as described by Luk'yanovich (1939) also appears similar to that of other bruchids.

The following characteristics of this instar individually are not exclusively those of bruchids; nevertheless, in combination, they offer substantial sup-

port for placing *Rhaebus* in the Bruchidae: Shape and retracted state of the head capsule (see Figs. 3 and 4, Pfaffenberger, 1977; Fig. 2, Prevett, 1971); number and arrangement of the ocelli (1–3 in Bruchidae); shape and number of segments in the antenna (usually 2 but may be 3); habitus which according to Luk'yanovich (1939) is identical to the bruchids; and fusion of the clypeus with labrum and its overlapping sclerotized plate bearing a pair of sensory setae (see Figs. 7, 14, 21, Pfaffenberger, 1977). The maxilla of *R. mannerheimi* is remarkably similar to that of other bruchids (see Pfaffenberger, 1977; Prevett, 1971).

Iablokoff-Khnzorian (1966) indicates that *Rhaebus* is more closely related to the Sagrinae than to any subfamily of the Bruchidae; however, characteristics of sagrine larvae would seem to indicate otherwise. The following are present in Sagrinae but lacking in Bruchidae: Two-segmented labial palpi; labrum and clypeus not fused; ocelli absent; and hypermetamorphosis lacking.

The majority of larval traits discussed offer substantial evidence in favor of the inclusion of *Rhaebus* in Bruchidae. We lack, however, any evidence that may come from examination of the first instar of this genus. The presence of an X- or H-shaped prothoracic plate in this stage would be convincing proof that *Rhaebus* belongs in the Bruchidae because this plate is apparently an exclusive family characteristic.

SUMMARY AND CONCLUSIONS

We have presented an analysis of some of the characteristics of species in the genus *Rhaebus* to give evidence for its proper placement in the beetle family Bruchidae.

We propose that the spermatophagous mode of life, the form of the male genitalia, subserrate antennae, presence of a frontal carina on the head, lateral carina on the pronotum, elytral striae, and structure of larval mouthparts are sufficient to assign *Rhaebus* to the Bruchidae and at the same time to exclude the genus from the sagrine Chrysomelidae.

We have concluded, however, that the split tarsal claws, enlarged metafemora (only in males), deeply emarginate eyes, wing venation, elongated metatrochanters, modified metacoxae, sclerotized fifth and sixth tergites, crossed tips of the mandibles, metallic body color, and random ovipositional behavior indicate a separate line of evolution probably early in the history of the family Bruchidae.

Within the Bruchidae, *Rhaebus* exhibits the following characters we believe to be ancestral in the family: Male genitalia lacking a ventral valve but having straplike lateral lobes, subserrate antennae, unmodified mesopleural sclerites, trochantins present on pro- and mesolegs, frontal carina present, parasutural sulci present, and larval labial palpi absent.

We therefore conclude that (1) *Rhaebus* should be assigned to the Bruchidae, and that (2) it should be retained in a separate subfamily, the Rhaebinae.

SYNONYMICAL LIST OF SPECIES

- Rhaebus* Fischer von Waldheim, 1824: 178 (monotypic).
gebleri Fischer von Waldheim, 1824: 180.
lukjanovitschi Ter-Minassian, 1973: 76.
mannerheimi Motschulsky, 1845: 108.
sagroides Solsky, 1866: 181.
beckeri Suffrian, 1867: 141.
solskyi Kraatz, 1879: 277.
gebleri Solsky, 1866: 181 (not Fischer von Waldheim).
komarovi Luk'yanovich, 1939: 551.

Rhaebus fischeri Lacordaire (1845: 604) appears to be a valid name but its application is uncertain. Sturm (1843: 268) lists "*viridis* Gebler (*Spermophilus* (sic))" as a synonym of *gebleri* Fischer von Waldheim. Gemminger and Harold (1874: 3239) lists *Spermophilus* as a synonym of *Rhaebus*. Neave (1940) lists "*Spermophilus* Gebler (teste Scudder, 1882: 311)" as a *nomen nudum*. If *Spermophilus* Gebler were found to be a validly proposed name, it is preoccupied by *Spermophilus* Cuvier, 1824.

CHRONOLOGY OF THE GENUS *RHAEBUS*

This list is not exhaustive, but it contains the principal references in which the genus is listed and its family assignment. The family-group names Lariidae and Mylabridae are synonyms of Bruchidae, whereas Criocerides (-ites) and Sagrides (-inae) are in Chrysomelidae.

1824. Fischer von Waldheim, p. 178. Described *Rhaebus* in Curculionides with *gebleri*, new species, monotypic.
 1826. Schoenherr, p. 30. *Rhaebus* in Bruchides immediately following *Bruchus*.
 1830. Gebler, p. 143. *Rhaebus* placed in Tetramera, Curculionides, Orthoceri, immediately following *Bruchus* which is also placed in Curculionides.
 1833. Schoenherr, p. 2 (footnote). Removed *Rhaebus* from Bruchides to "Chrysomelinarum, probably near Sagra."
 1840. Laporte, p. 509. *Rhaebus* in Chrysomelines, tribe Eupoda, group Criocerites.
 1843. Sturm, p. 268. *Rhaebus* in Chrysomelina, Sagrida.
 1845. Lacordaire, p. 604. *Rhaebus* in tribe Criocerides in Phytophages (Chrysomelidae). Listed *R. fischeri* in text.

1845. Motschulsky, p. 99. *Rhaebus* in Chrysomelines. Described *R. mannerheimi* n. sp.
1848. Gebler, p. 5. *Rhaebus* in Chrysomelina following *Donacia*.
1866. Solsky, p. 181. Described *R. sagroides*, n. sp., but did not list family placement. Misidentified new species as *R. gebleri* Fischer von W. later described by Kraatz (1879) as *R. solskyi*.
1866. Lacordaire, p. 598. Stated that he was "forced" to keep *Rhaebus* in Chrysomelides.
1867. Suffrian, p. 143. *Rhaebus* a Criocerides genus. Described *R. beckeri*, n. sp.
1868. Stein, p. 123. *Rhaebus* in Criocerini in Chrysomelidae.
1868. Abeille, p. 120. *Rhaebus* in Criocerides in Phytophages.
1869. Motschulsky, p. 94. Synonymized *R. beckeri* and *R. sagroides* with *R. mannerheimi*. Did not give family placement.
1874. Chapuis, p. 51. *Rhaebus* in section Eupodes, Tribe Sagrides, Group VII Rhaebites. First usage of family group name based on *Rhaebus*.
1874. Gemminger and Harold, p. 3239. *Rhaebus* in Sagrinae.
1877. Stein and Weise, p. 173. *Rhaebus* in Sagrinae.
1879. Kraatz, p. 276. *Rhaebus* excluded from Chrysomelidae, placed near Bruchidae in an aberrant group not named. Proposed *S. solskyi* as a replacement name for *R. gebleri* Solsky, not Fischer.
1883. Heyden, Reitter, and Weiss, p. 179. *Rhaebus* in Rhaebini in Mylabridae.
- 1886a. Baudi, p. 385. *Rhaebus* in Rhaebini in Mylabridum.
- 1886b. Baudi, p. 7. *Rhaebus* in Rhaebini in Mylabridae.
1893. Erichson, p. 3. *Rhaebus* in Bruchidae. Mentioned *R. fisch.* (sic).
1901. Bedel, p. 342. *Rhaebus* in tribe Rhaebini in Lariidae.
1903. Everts, p. 523. *Rhaebus* mentioned in text describing the Bruchidae.
1905. Schilsky, pp. 1, 2. *Rhaebus* in Bruchidae.
1906. Heyden, Reitter, and Weiss, p. 586. *Rhaebus* in Rhaebini in Lariidae.
1913. Pic, p. 5. *Rhaebus* in Rhaebinae in Bruchidae.
1932. Bridwell, p. 102. Excluded *Rhaebus* from Bruchidae but did not place it.
1939. Luk'yanovich, p. 546. *Rhaebus* in Bruchidae. Described *R. komarovi*, n. sp.
1946. Crowson, p. 77. "*Rhaebus* unquestionably bruchid."
1955. Crowson, p. 77. "*Rhaebus* . . . certainly bruchid."
1957. Luk'yanovich and Ter-Minassian, p. 53. *Rhaebus* in Rhaebinae in Bruchidae.
1959. Monros, p. 75. Listed Rhaebites in Sagrinae but did not mention *Rhaebus*.

1966. Iablokoff-Khnzorian, p. 134. Included *Rhaebinae* and *Bruchinae* as subfamilies of *Chrysomelidae* (schema 1) and showed them on a common line emerging near the *Sagrinae*.
1967. Iablokoff-Khnzorian, p. 66. Illustrated male genitalia of *R. gebleri* and placed in *Chrysomelidae*, but noted that the systematic position of the genus is difficult to determine.
1967. Teran, p. 314, figs. 33–37. Illustrated male genitalia of *R. solskyi* and placed *Rhaebus* in *Bruchidae*.
1968. Bottimer, p. 1010. Followed Bridwell in excluding *Rhaebus* from *Bruchidae*.
1973. Ter-Minassian, p. 75. Placed *Rhaebus* in *Bruchidae*. Described *R. lukjanovitschi*, n. sp.

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