

AN ABSTRACT OF THE THESIS OF

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Title: THE MORPHOLOGY AND TAXONOMIC SIGNIFICANCE OF THE
MALE GENITALIA OF COENONYCHA (COLEOPTERA,
SCARABAEIDAE)

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The genus Coenonycha contains 30 described species of small to medium sized scarabs. They are found in the arid and semi-arid regions of western United States and northern Baja California. The adults feed at night on several genera of xerophylous plants.

An examination of the male genitalia of the 19 long-winged species indicates that the internal sac possesses characters which are stable within a species and are, therefore, taxonomically useful. These structures are a dorsal, toothed, knob-like sclerite and from one to four spinose fields on the enlarged portion of the sac. Variation in these structures within a species occurs in the number of teeth on the knob and spines in the fields.

Sixteen new species of Coenonycha were discovered in the course of this study. They are indicated by letter in the text and phenetic tree and will be described elsewhere.

The male genitalic structures of the 19 long-winged species are described in detail and illustrated. A key to these species, using primarily the basal knob and spinose fields is included. In addition, a key (modified from Cazier and McClay, 1943) to all the described species of Coenonycha, using characters such as color, pilosity, clypeal reflection and pronatal punctation is provided.

A key to the North American genera of Macroductylini using the parameres, basal piece, basal apodeme, genital segment, and internal sac shows the diversity of genitalic structures in the tribe. Coenonycha, Dichelonyx, and Gymnopyge are presently placed with Macroductylus and Isonychus in the Macroductylini. Based on genitalic, larval, spiracular, and adult external morphological structures, Coenonycha, Dichelonyx, and Gymnopyge should be separated from the Macroductylini and placed in the tribe Dichelonychini.

The Morphology and Taxonomic Significance
of the Male Genitalia of Coenonycha
(Coleoptera, Scarabaeidae)

by

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THE MORPHOLOGY AND TAXONOMIC SIGNIFICANCE
OF THE MALE GENITALIA OF COENONYCHA
(COLEOPTERA, SCARABAEIDAE)

INTRODUCTION

It has been known for many years that the male genitalic structures of scarab beetles have taxonomic value. The value may be primary, that is, the only means of separating the species, or secondary, as a reinforcement of other characters used to define the species.

The papers illustrating or discussing genitalic characters of scarabs are too numerous to list, but a few are representative of the rest. Among those authors who have made note of the genital structures, most have illustrated but not discussed the parameres (Blaisdell, 1930; Brown, 1929; Cartwright, 1939, 1944; Davis, 1920; Frey, 1962, 1966, 1967a, 1967b; Sanderson, 1940); others have discussed these structures but not illustrated them (Dawson and McColloch, 1924). A few authors have studied the structure of the male genitalia in more detail and have used the genital sac as a character of taxonomic significance. For example, Sanderson (1939) illustrated not only parameres and basal apodeme, but also the internal sac and genital armature of three species of Phyllophaga. Luginbill and Painter (1953) used aedeagal characters to separate some species in a key to Phyllophaga, while Chapin (1932a), in his key to Strategus,

separated two of three species using these structures. Böving (1942) used male and female genitalic structures in his key to 21 species groups of Phyllophaga. Frey (1965a, 1965b), Chapin (1935), and Howden (1960) illustrated armature on the distal portion of the protrusible membranous aedeagus.

Brown (1946) stated that the male copulatory organ and internal sac are very useful in separating species of Canthon but not in the two species of Dichelonyx examined. Cornell (unfinished dissertation) studied the male genitalia of Dichelonyx, presented a key to the species using genitalic characters and illustrated the genital armature.

Cazier (1937) synonymized four species of Phobetus on similarities of the parameres, and in 1939 synonymized ten of Casey's species in the Phileurini on the similarity of the genitalic structures.

Reinhard (1939) described four subspecies of Phyllophaga tristis (F.) using characters of the internal sac in addition to other characters.

To my knowledge, there are no publications treating the male genitalic structures at the familial, subfamilial, or tribal levels.

The genus Coenonycha is one of 54 genera from the Western Hemisphere placed in the Macroductylini (Blackwelder, 1944; Arnett, 1968). It contains some 30 described species of small to medium sized, nocturnal scarabs. In the Macroductylini, more work has been done on the genitalic structures of Macroductylus and Isonychus than on other genera (Frey, 1964b, 1965a, 1966, 1967b; Carrillo, 1960). In

the case of Coenonycha, although the parameres were mentioned by Cazier and McClay (1943), and Howden (1969), their value in taxonomy was not discussed in detail. Ritcher (personal communication) studied the structures of the internal sac of most species of Dichelonyx and 13 species of Coenonycha in detail. He concluded that the genital armature may be useful in the species classification and suggested it as a thesis topic.

This study of the 19 species of Coenonycha with fully developed hind wings is the first in depth treatment of the taxonomic usefulness of the male genitalia in this genus. The long-winged species were studied because all these species were usually well represented in collections. The three described species in the genus which were not examined are brachypterous. The object of the study was to ascertain if the structures of the internal sac could be used in the species classification and also provide clues to affinities between species, species groups, and genera. In the course of this study, 16 new species were found, which will be described later. These are indicated by letters in the text and figures.

Historical Review

The genus Coenonycha was erected by Horn (1876) to include Dichelonycha rotundata Le Conte (1956) and two brachypterous species, C. socialis Horn and C. ovipennis Horn. No genotype was designated.

In the next 60 years, only three additional species were described: C. parvula Fall, 1901; C. clementina Casey, 1909; and C. stohleri Saylor, 1935. In 1937, Cazier described two new species, C. tingi Cazier and C. testacea Cazier, and suggested efficient methods of collecting specimens and discussed host plants.

Cazier and McClay, in their 1943 revision of the genus, increased the number of nominate species to 28. In addition, they discussed phylogeny, distribution, and speciation in the genus and presented a key to the adults. Since 1943, only two new species have been described, C. pascuensis Potts, 1945; and C. rufobrunnae Howden, 1969. By 1970, the genus contained 30 nominate species.

Little is known about the larvae of Coenonycha. Cazier and McClay (1943), and Potts (1945) mention the finding of larvae on the roots of the same plants from which the adults were taken. Ritcher (1944) characterized larvae of the genus based on two species and presented a key for distinguishing Dichelonyx and Coenonycha larvae.

Distribution of the Described Species in the Genus Coenonycha

The genus Coenonycha is a western North American group, occurring from Washington south to Baja California and east into Idaho, Utah, and Arizona. The majority of the species (23) occur in California, but three are found in Nevada, two in Washington, two in Baja California, and one each in Utah, Arizona, Oregon, and Idaho.

Members of the genus inhabit desert, semi-arid chaparral or ever-green woodland habitats.

C. purshiae has the widest distribution for a single species. It occurs from east central Washington to southwestern Oregon, then east and south through north eastern California to Nevada, near Reno. Within this range, C. purshiae is known to occur on two host plants, Ceanothus cuneatus and Purshia tridentata.

C. pallida has the widest distribution of the desert inhabiting species in the United States, occurring in the Mohave Desert.

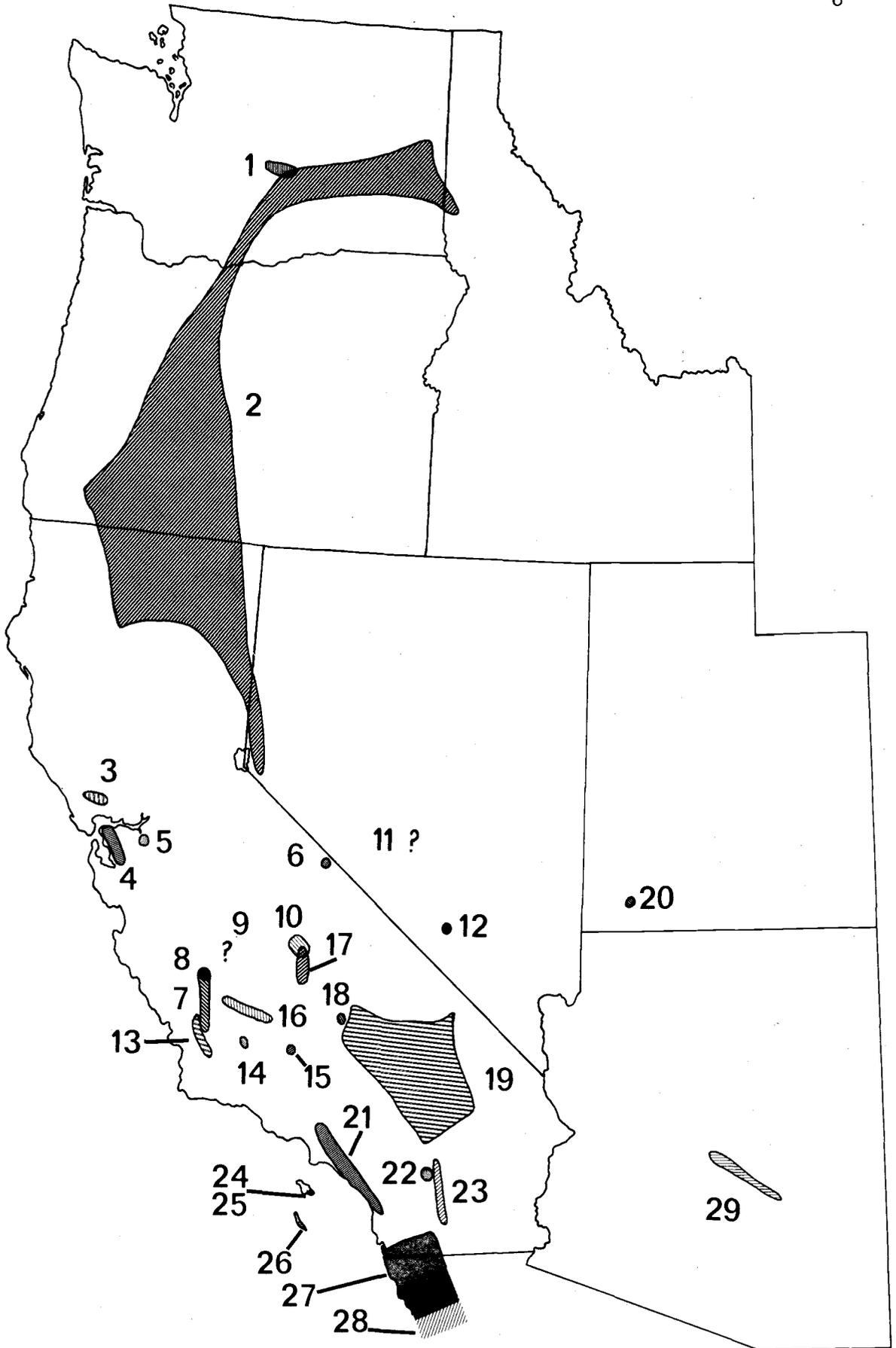
The following species occur sympatrically: C. tingi and C. fuga, on Adenostoma fasciculatum at Napa, California; C. fulva and C. clypeata on Santa Catalina Island, California; C. hageni on Eriogonum fasciculatum and C. ampla on Juniperus californica at Coalinga, California; and C. fusca and C. scotti at Kaweah, California.

Of the 11 species having brachypterous adults, C. parvula has the widest distribution. Eight of the 11 brachypterous species are known only from single localities.

In several instances, civilization has encroached on the habitats where Coenonycha has been collected, and significantly reduced or eliminated them. The habitat of C. stohleri is now in the Las Vegas Gunnery and Bombing range, and the locality of C. ovatis is now predominantly agricultural. Highways, agriculture, and industry appear to be the major causes of habitat modification in California.

Figure 1. Distribution of the genus Coenonycha in western North America.

- | | |
|-------------------------|---|
| 1. <u>C. globosa</u> | 16. <u>C. crispata</u> |
| 2. <u>C. purshiae</u> | 17. <u>C. scotti</u> |
| 3. <u>C. tingi</u> | 18. <u>C. mediata</u> |
| 4. <u>C. fuga</u> | 19. <u>C. pallida</u> |
| 5. <u>C. pascuensis</u> | 20. <u>C. utahensis</u> |
| 6. <u>C. bowlesi</u> | 21. <u>C. parvula</u> |
| 7. <u>C. ampla</u> | 22. <u>C. acuta</u> |
| 8. <u>C. hageni</u> | 23. <u>C. lurida</u> |
| 9. <u>C. saylori</u> | 24. <u>C. clypeata</u> |
| 10. <u>C. fusca</u> | 25. <u>C. fulva</u> |
| 11. <u>C. ovipennis</u> | 26. <u>C. clementina</u> |
| 12. <u>C. stohleri</u> | 27. <u>C. rotundata</u> |
| 13. <u>C. testacea</u> | 28. <u>C. rufobrunnae</u> |
| 14. <u>C. barri</u> | 29. <u>C. rubida</u> |
| 15. <u>C. ovatis</u> | - <u>C. socialis</u> ,
Guadaloupe Island,
Baja California - not
figured. |



Host Associations of *Coenonycha* Species

Cupressaceae

Juniperus californicus Carr. : C. ampla.

Fagaceae

Quercus sp. : New species C.

Polygonaceae

Eriogonum fasciculatum Benth. : C. hageni, C. testacea.

Chenopodiaceae

Atriplex spinifera Macbr. : C. barri.

Lauraceae

Persea sp. : New species P.

Rosaceae

Adenostoma fasciculatum H. and A. : C. fuga, C. tingi.

Adenostoma sparsifolium Torr. : C. acuta.

Prunus fasciculatum (Torr.) Gray : C. sp.

Purshia tridentata (Pursh) D. C. : C. purshiae.

Leguminosae

Lupinus sp. : C. sp.

Rhamnaceae

Ceanothus cuneatus (Hook.) Nutt. : C. purshiae.

Ceanothus integerrimus H. and A. : C. sp.

Ceanothus sp. : New species C.

Compositae

Artemesia tridentata Nutt. : C. mediata.

Artemesia sp. : C. pallida.

Chrysothamnus nauseosus (Pall.) Britton : C. sp.

Gutierrezia microcephala (D. C.) Gray : C. sp.

Hymenoclea sp. : New species I, New species G.

It is reasonable to assume that the larvae of this genus can be found on the roots of or in the vicinity of the host plants of the adults. This is particularly true of the brachypterous species. In areas of dense and varied plant associations, adult Coenonycha can be found on a variety of plants, but it is not to be assumed that the larvae can be found on a similar variety of plant roots.

METHODS

In this study, the male genitalia were mounted on glass slides. This allowed the structures to be examined and compared with a minimum expenditure of time. It also reduced the possibility of damage to the adult specimens through repeated handling. The alternatives to slide mounting genitalia are either placing dissected structures in micro vials or leaving them extruded in situ. The methods employed to extract the genital capsule are different for live specimens than for pinned specimens or for specimens preserved in alcohol. The use of live specimens results in better preparations.

Dissection

Live Specimens

The male, with venter up and head to the left, is held on the dissecting stage of a microscope by the thumb and index finger of the left hand. Gentle pressure is applied in a caudad direction by the index finger to the area directly behind the metathoracic legs. This steady pressure will usually extrude the genital capsule. If too much pressure is applied, the male will die before extruding the capsule, or, if the parameres extrude, the sac may not. Often the sac becomes only partially extruded and it is necessary to apply pressure to the sac itself to complete the process. Care is taken to avoid rupturing the sac. After the capsule has been extruded, it is left in situ and the

beetle placed in a vial of 70 percent ethyl alcohol to which a drop of glycerine has been added.

The value of "squeezing" live specimens is obvious. The time involved in the dissection is reduced, and the sac can be mounted whole on a slide, showing the position of the armature in situ.

The above technique does not work on dead specimens or specimens placed briefly in an ethyl acetate killing jar, because (I assume) it depends upon the muscles of the beetle to extrude the capsule. Specimens placed in ethyl acetate fumes appear to lack sufficient muscular control to effect extrusion. The method that should be used, to extract the genitalia of freshly killed or stunned specimens, is the same as for pinned material, except for the relaxing process.

Pinned Specimens

Pinned material is placed in nearly boiling water until pliable. The time required, a maximum of three minutes, varies from beetle to beetle. The specimens should be tested by applying gentle pressure to the legs and noting their flexibility. If the abdominal contents are not relaxed, the beetle should be returned to the water bath for a few minutes.

The relaxed specimen is held, with the venter up and head to the left, between the thumb and index finger of the left hand and positioned for viewing under a dissecting microscope. An insect pin, bent at the

tip, is held in the right hand and used to remove the genital capsule. Initially, the membrane between the basolateral margin of the pygidium and the anteriolateral aspect of the last abdominal sternite is ruptured, facilitating the removal of the genital capsule between the two sclerites. The pin is then inserted into the abdominal cavity between the anus and the genital segment. The capsule is hooked by the pin between the basal piece and the parameres and withdrawn from the abdomen. The genital segment is usually removed with the capsule.

Specimens in Alcohol

The dissected genital structures are placed in a weak solution of potassium hydroxide (KOH) in a numbered spot plate and left for at least 24 hours. Use of hot KOH requires less time. When the membranes of the capsule are softened, the structures are placed in 70 percent ethyl alcohol. Using fine pointed forceps, and a sharp fine-pointed scalpel, the sac is removed from beneath the basal piece, if still in the inverted condition, or separated from the parameres if everted. The inverted sac can occasionally be everted manually. This is done before the sac is separated from the basal piece. As this procedure is difficult, it was not used to any extent.

If the sac is not everted it is removed with the apodemes and "horseshoe-shaped" sclerite and placed in a dish of alcohol. Using a stainless steel insect pin and a scalpel, the sac is cut its entire length.

To do this, the pin is inserted through the narrow basal opening of the sac and used as a cutting surface for the scalpel. Because the knob assumes a dorsal position in the everted sac, the sac is cut along the ventral midline. Also, the median ventral surface is free of fields and is ideal for bisection. Cutting the sac in this manner results in an equal amount of tissue on either side of the knob and gives a better view of the asymmetrical arrangement of the fields. The pin is moved the length of the sac until the apex is reached. If an apical field of spines is present, care is taken not to destroy it. When the sac is correctly bisected, it will lie flat.

The sac is then placed in a vial of 70 percent ethyl alcohol and shaken well to dislodge any foreign particles. A glass slide is prepared with a drop or two of Hoyer's mounting medium in the center and placed under a dissecting microscope. Next, the sac is removed from the alcohol and placed on absorbent paper to rid it of excess moisture. It is then positioned on the slide, armature up and basal portion to the left. A drop of Hoyer's is placed on the underside of the cover slip and the latter positioned over the sac. Gentle pressure is applied to the cover slip, forcing the sac to flatten and any bubbles present to move to the edge of the cover slip. The slide is then numbered and placed in a drying oven set at 31^oC.

The parameres, basal piece, and genital segment were placed on slides in preliminary dissections. Later, material examined in this

study was placed in micro vials. The procedure for mounting these structures is essentially the same as for the sac. The membrane connecting the ventral aspects of the parameres is severed to enable them to lie flat. Connective tissue and muscle are removed from the genital segment and the basal piece. The structures are placed in a vial of alcohol and agitated to remove any particles of dirt.

Small balls of high quality, gray, modeling clay are placed on the slide in a triangle to act as supports for the cover slip. A drop or two of Hoyer's is placed on the slide within the triangle. If the Hoyer's touches the clay before the cover slip is pressed into position, the clay will not adhere to the slide. The parameres, basal piece, and genital segment are placed dorsal side down in the Hoyer's. Bubbles often appear between the parameres and beneath the basal piece and genital segment. These are removed prior to placement of the cover slip. The cover slip, with a drop of Hoyer's, is positioned over the clay balls and pressed down. Frequently, when the cover slip is pressed down, the Hoyer's does not reach the edges of the cover slip. More mountant is then added at the edge of the cover slip and excess added to allow for shrinkage during drying.

When slides are made using "squeezed" specimens, the genitalic structures are removed from the beetle and the latter pinned. The sac and apodemes are separated from the median orifice and placed in 70 percent ethyl alcohol. If the sac is pliable, it need not be placed in

KOH. The contents of the sac are removed so that the opposite side of the sac can be seen in the finished slide. The sac is mounted using the same technique mentioned previously for the bisected sac, i. e., without clay balls. If the sac is mounted with the parameres and basal piece still attached, it is necessary to use the clay balls to elevate the cover slip. Preparation of a slide in this manner retains the relationship of the sac to the more basal genital structures.

COMPARATIVE MORPHOLOGY OF THE MALE GENITALIA
AND TAXONOMIC AFFINITIES OF THE NORTH
AMERICAN MACRODACTYLINAE GENERA

Structure and Description of the
Male Genitalia in *Coenonycha*

The male genitalia are composed of four basic structures; the basal apodeme, parameres, aedeagus or internal sac, and the genital segment (Tuxen, 1956) (Figures 14, 18).

The basal apodeme (ba) is a rectangular sclerite, in dorsal view, articulating at its apicolateral angles with the bases of the parameres. Posteriorly the apodeme is slightly convex mesad. In ten of the described species, there is a median strut or ridge the length of the ventral midline. Four additional species have the strut extending only half the length of the basal apodeme, while in 14 species, it is completely lacking. The posterior end of the basal apodeme is arcuately emarginate, often more darkly pigmented than the rest of the basal apodeme, with the space between the emargination and the bases of the parameres covered by a connecting membrane. The anterior margin is truncate or asymmetrically emarginate. The condition of the genitalia is unknown in three species.

The basal piece (bp) articulates with the basal apodeme at the basolateral angles. Medially, the two halves of the basal piece are connate, the line of fusion evident.

The parameres, evenly pigmented light fulvous to dark reddish

brown, curve lateroventrally and medially from the anteriolateral margins of the basal piece, terminating in ventrally directed, acute, setose apices. The anterior margins of the parameres are obtusely dentate medially (the "Antp" of Böving, 1942).

The membranous aedeagus or internal sac (is) is ventrad of the basal apodeme. When inverted, it is surrounded by a muscular sheath attached to the basal apodeme. When extruded (Figure 18), the internal sac passes through the median orifice and the opening formed by the curve of the parameres.

On the narrower basal portion of the sac are two dorsal slender apodemes (ap), and a ventral "sclerite shaped like a horseshoe" (Vaurie, 1958) (vs). This sclerite is V-shaped in Coenonycha, with the arms directed anteriorly. Other than these structures, the membrane is bare.

On the larger caudal portion of the sac are many minute spinules which vary in size and shape. At the base of the caudal portion is a sclerotized knob (bk) with teeth-like spines. Ventrad of the knob the sac is enlarged and covered with many, frequently pigmented, spinules. On the caudal portion itself are sclerotized spinose areas termed "fields" (Brinck, 1956) (fs) which vary in number from one to four in the genus. Of the 30 described species in the genus, 13 have one field, 12 have two fields, one has three, and one has four fields. The spines comprising the fields are either slender, stout, squat, or squamose

(Figures 33-36) and weakly to strongly pigmented.

Ventrad of the sac, and lying longitudinally, is the genital segment (gs), composed of the ninth abdominal pleurites. The genital segment is a V- or Y-shaped sclerite (Jeannel, 1944), the sclerotic annulus of Snodgrass (1935), with a weakly sclerotized triangular median plate, the lateral portions of the plate with two or three rows of setae apically. The lateral arms of the segment extend posteriorly and bend mesad apically. The anterior arm is much broader and shorter than the lateral arms and may appear to be absent. When extruded, the parameres and internal sac pass between the anus and the genital segment.

Generic Relationships

In general appearance, the genitalia of Coenonycha and Gymnopyge males are quite similar (Figures 27, 28), but Gymnopyge lacks spinose fields on the sac and teeth on the basal knob. Also, the parameres of Gymnopyge have neither subapical hairs nor acute apices. Both Coenonycha and Gymnopyge are uniformly colored dorsally and inhabit semi-arid and arid regions. However, adults of Gymnopyge are diurnal.

Coenonycha differs from Dichelonyx in that the genital segment is V-shaped, while it is rectangular in Dichelonyx. The most outstanding feature on the internal sac of most Dichelonyx is the presence

of one or more hook- or spoon-shaped sclerites. The parameres of Dichelonyx lack subapical hairs. Species of Coenonycha are non-metallic dorsally, setose ventrally, not scaly; inhabit semi-arid, not boreal, habitats, and are nocturnal, not diurnal as are species of Dichelonyx.

Macroductylus and Isonychus vary markedly from the genera mentioned previously. The lateral margins of the basal apodeme in Macroductylus and Isonychus are strongly sinuate or expanded, not straight. Also, the dorsal surface of the internal sac lacks a raised sclerite, and the genital segment is Y-shaped, not V- or U-shaped.

Gymnopyge, Coenonycha, and Dichelonyx should probably be removed from the Macroductylini and placed in the Dichelonychini (Ritcher, 1966). In addition to their genitalic similarities, these three genera have chelate claws, large prominent eyes, and the last abdominal spiracle is in the fifth visible abdominal sternite which is not fused with the propygidium. Isonychus and Macroductylus lack these characters. In addition, the general body forms of these two genera are not like those of the other genera. Ritcher (1966, 1969) has also found larval and spiracular differences to support such a division.

Key to the North American Genera of
Macroductylini Using Genitalic Structures

1. Lateral margins of basal piece straight; dorsal surface of internal sac usually with a raised knob, spoon or hook-like sclerite 3

Lateral margins of basal piece sinuate or greatly expanded anteriorly, not straight (Figures 37, 38); dorsal surface of internal sac without a raised knob or hook-like sclerite..... 2
2. Parameres with hairs on subapicolateral aspects; parameres and basal piece forming a nearly complete circle (Figure 38) Macroductylus

Parameres with hairs on subapicolateral aspects; parameres and basal piece not forming a circle, basal piece visible laterally anterior to the parameres (Figure 37) Isonychus
3. Parameres with subapicolateral hairs (Figure 27); internal sac with fields of spines and a knob-like toothed sclerite (Figures 39-60) Coenonycha

Parameres without subapicolateral hairs; internal sac variable, not as above 4
4. Internal sac usually with a hook or spoon-shaped sclerite; genital segment almost rectangular (Figure 16); anterior margin of basal piece evenly emarginate medially (Figure 29) Dichelonyx

Internal sac with a rounded knob-like sclerite; genital segment V-shaped (Figure 15); anterior margin of basal piece truncate (Figure 28) Gymnopyge

Key to the Described Species of *Coenonycha*
Using Non-genitalic Structures

(Modified from Cazier and McClay, 1943)

1. Metathoracic wings fully developed; metasternum at narrowest point between middle and hind coxae distinctly longer than the length of the hind coxal plate (Figure 2) 12
 Metathoracic wings reduced in size and shape; metasternum, at narrowest point between middle and hind coxae, shorter than or subequal to the length of the hind coxal plates (Figures 3, 4) 2
2. Head and pronotum densely pilose throughout parvula
 Head and pronotum glabrous or very sparsely pilose laterally 3
3. Elytra with surface between punctures alutaceous throughout, opaque 4
 Elytra with surface between punctures, if evident, smooth, shining or with only the depressed areas faintly alutaceous 5
4. Pronotum with side margins markedly sinuate before apex; females larger in size than males and with nine-segmented antennae; Guadalupe Island socialis
 Pronotum with side margins straight or scarcely sinuate before apex; females equal in size to males and with ten-segmented antennae; San Clemente Island clementina
5. Scutellum broader than long, side margins subparallel to apical third, apical margin evenly rounded, not pointed globosa

- Scutellum longer than broad, side margins evenly rounded to the bluntly pointed apex 6
6. Elytra with punctures obscure, disk with rugose area; color black stohleri
- Elytra with punctures distinct, disk without rugose area, color testaceous or dark brown 7
7. Anterior clypeal angles dentate; side margins of pronotum subangulate medially, rather strongly converging anteriorly 8
- Anterior clypeal angles evenly rounded; side margins of pronotum evenly, obtusely rounded, not strongly converging anteriorly 10
8. Metathoracic wings without expanded anal membrane, anal veins represented only as basal vestiges, elytra subovate ovatis
- Metathoracic wings with expanded anal membrane, anal veins represented by well-developed 2dA and 3dA; elytra elongate 9
9. Pronotum with punctures large, separated by about their own widths on the disk; color dark brown tingi
- Pronotum with punctures small, separated by about twice their own width on the disk; color testaceous crispata
10. Elytra moderately pilose; metathoracic wings reduced to narrow vestiges, lacking anal area ovipennis
- Elytra sparsely pilose; metathoracic wings reduced but with a distinct anal area which has two or three veins 11

11. Metathoracic wings with apical portion of remigium reduced abruptly and transversely at or slightly beyond stigmal area; basal portions of either R_3 or M_1 evident; clypeal suture distinct throughout; elytra subovate saylori
- Metathoracic wings with apical portion of remigium normal in shape but reduced in size, not abruptly and transversely cut; R_3 and M_1 not present; clypeal suture obscured medially by dense, deep punctation; elytra elongate mediata
12. Anterior clypeal margin more widely reflexed than side margins, edge of anterior margin not continuing on the same level as edge of side margins, abruptly elevated at angles (Figure 9) 16
- Anterior reflexed clypeal margin equal to or less than side margins, edge of anterior margin continuing on the same level as edge of side margins, or depressed below level of side margins, at most, slightly elevated at angles (Figure 10) 13
13. Front of head, clypeus and entire dorsal pronotal surface pilose clypeata
- Front of head, clypeus and dorsal pronotal surface subglabrous, pile confined to lateral portions when present 14
14. Pronotum with discal punctures large, separated by about twice their own widths; anterior pronotal angles sharply produced forward; elytra clothed with long erect hair rubida
- Pronotum with discal punctures small, separated by about three to four times their own widths; anterior pronotal

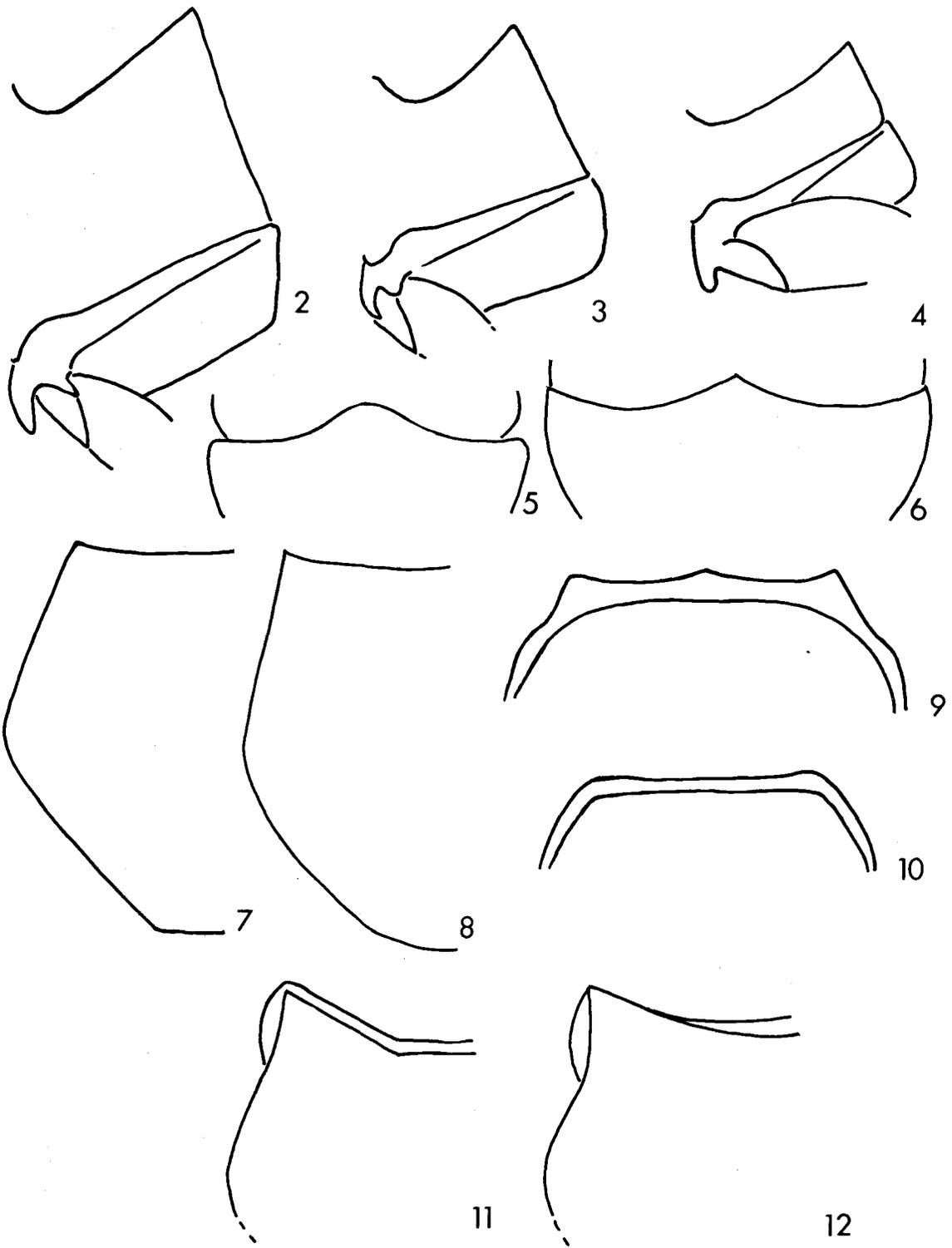
- angles not produced forward; elytra glabrous or clothed
with short, recumbent hair 15
15. Dorsal color usually dark brown to piceous; clypeal angles
not dentate fusca
- Dorsal color dark testaceous; clypeal angles weakly
dentate utahensis
16. Dorsal surface entirely or in greater part testaceous
(generally pale testaceous) or pale yellow 17
- Dorsal surface entirely or in greater part reddish brown
to piceous 22
17. Upper surface uniformly testaceous or pale yellow 18
- Upper surface with piceous areas interspersed 21
18. Clypeal suture obscured medially by dense punctation; side
pronotal margins obtusely angulate medially bowlesi
- Clypeal suture distinct; side pronotal margins obtusely
rounded medially, not rounded as above 19
19. Pronotum with side margins straight behind middle
(Figure 7), narrowly converging to base; elytra
proportionally long lurida
- Pronotum with side margins evenly rounded behind
middle (Figure 8); elytra not proportionally long 20
20. Pale yellow dorsally, clypeal suture narrowly emarginate
medially (Figure 6), anterior clypeal angles scarcely
dentate; anterior clypeal margin weakly emarginate
medially pallida
- Pale testaceous dorsally; clypeal suture broadly
arcuately emarginate (Figure 5); anterior clypeal angles

- only slightly elevated; anterior clypeal margin
straight pascuensis
21. Anterior third of clypeal surface rugose at middle;
clypeal suture weakly arcuately emarginate medially;
anterior clypeal margin weakly emarginate but not
sinuate testacea
- Anterior third of clypeal surface punctate and generally
alutaceous; clypeal suture broadly, strongly emarginate
medially; anterior clypeal margin shallowly sinuately
emarginate medially barri
22. Elytra densely covered with long hairs 23
Elytra sparsely covered with short hairs 26
23. Anterior pronotal margin abruptly angulate forward at
about lateral one third (Figure 11) acuta
- Anterior pronotal margin evenly rounded laterally,
angles not greatly produced forward (Figure 12) 24
24. Pronotal disk punctures large; clypeus strongly constricted
anteriorly; elytra dark brown scotti
- Pronotal disk punctures small; clypeus not strongly
constricted anteriorly; elytra fulvous to piceous 25
25. Elytra fulvous; clypeal suture weakly emarginate medially;
pronotal punctures separated on disk by two to three
times own width fulva
- Elytra piceous; clypeal suture moderately emarginate
medially; pronotal punctures separated on disk by one and
one-half times own width hageni

26. Elytral color reddish brown 28
 Elytral color brown to piceous 27
27. Pronotal disk punctures separated by three to four times
 own width; dorsal color piceous; clypeal suture strongly
 arcuately emarginate medially; anterior pronotal angles
 not prominently produced forward fuga
 Pronotal disk punctures separated by one and one-half
 to two times own width; dorsal color dark brown; clypeal
 suture obtusely sinuate medially, anterior pronotal
 angles acute, prominently produced forward ampla
28. Anterior clypeal angles elevated; anterior clypeal margin
 sinuate medially; pronotal disk punctures separated by
 own width 29
 Anterior clypeal angles not elevated; anterior clypeal
 margin straight or only weakly emarginate medially;
 pronotal disk punctures separated by one and one-half
 to two times own width rotundata
29. Clypeal suture moderately evenly emarginate; lateral
 pronotal margin evenly arcuate behind middle rufobrunnae
 Clypeal suture strongly curved toward base medially;
 lateral pronotal margin evenly rounded behind middle,
 obtusely angulate medially purshiae

Figure

- 2 Metasternum longer than length of hind coxal plate, C. ampla.
- 3 Metasternum and hind coxal plate, C. mediata.
- 4 Metasternum shorter than length of hind coxal plate, C. parvula.
- 5 Clypeal suture broadly arcuately emarginate medially, C. pascuensis.
- 6 Clypeal suture narrowly emarginate medially, C. pallida.
- 7 Pronotum with side margins straight behind middle, C. lurida.
- 8 Pronotum with side margins evenly rounded behind middle.
- 9 Anterior reflexed clypeal margin wider than side margins.
- 10 Anterior reflexed clypeal margin equal to or less than width of side margins.
- 11 Anterior pronotal margin abruptly angled forward at lateral third, C. acuta.
- 12 Anterior pronotal margin not abruptly angled forward at lateral third.



Key to the Long-Winged Males of *Coenonycha*
Using Mainly Genitalic Structures

1. Aedeagal sac with one strongly sinuate linear field
across the dorsum of the sac and one or two apical
fields; field spines squat (Figure 36) testacea

- Aedeagal sac without a strongly sinuate linear field
across dorsum of sac; apical field present or absent;
fields one to four in number; spines variable 2

2. Sac with four fields of stout, darkly pigmented
spines (Figure 52) rotundata

- Sac with one or two fields, spines variable 3

3. Sac with one field; if field apical then not triangular 4

- Sac with two fields, or if only one present, then field
triangular, apical 10

4. Elytra pale testaceous 5

- Elytra dark testaceous to piceous 6

5. Field wider than long; spines distinctly pigmented; knob
strongly sinuate dorsally pallida

- Field about as long as wide; spines weakly pigmented;
knob evenly elevated or only weakly sinuate dorsally lurida

6. Elytra dark testaceous or testaceous with piceous areas interspersed 7
- Elytra reddish brown to piceous 8
7. Basal knob elevated anteriorly; darkly pigmented basad of teeth; field two or three rows wide barri
- Basal knob small, weakly elevated and pigmented; field of one or two rows of stout spines utahensis
8. Field spines long, stout; teeth nine, clustered on cephalic surface of knob; field spines dark fulvous; field several spines wide rubida
- Field spines squat; teeth on cephalic and dorsal surface of knob; field spines fulvous; field one row wide 9
9. Field of six to nine spines, apical; knob evenly elevated, weakly pigmented purshiae
- Field of more than nine spines, may appear broken into two fields, not apical; knob distinctly elevated, moderately pigmented fusca
10. Elytra testaceous, linear field weakly sinuate 11
- Elytra reddish brown to piceous; linear field variable 12
11. Linear field on sac clavate anteriorly; darkly pigmented; field spines moderately long bowlesi

- Linear field not clavate anteriorly; weakly pigmented; field
composed of one or two rows of stout spines pascuensis
12. Apical field triangular, spines squat 13
- Apical field not triangular, spines stout 14
13. Basal knob hemispherical; teeth on right anterior half of
knob clypeata
- Basal knob triangular; teeth on dorsal median surface
of knob fulva
14. Teeth one to three; basal knob medium sized 15
- Teeth four or more; if less than four, then knob long, at least
three times longer than high 17
15. Teeth three, one may be reduced, on basal knob; pronotal
disk punctures large scotti
- Teeth two on basal knob; pronotal disk punctures small 16
16. Linear field long, narrow; length ratio about 3:1 fuga
- Linear field short, broad; length ratio about 4:3 hageni
17. Sac with apical field 18
- Sac without apical field; field spines stout, compact, fields
parallel; length ratio about 5:1 rufobrunnae

18. Basal knob darkly pigmented; apical field large; spines
 stout, many 19
- Basal knob weakly pigmented; apical field small; spines
 nearly squamose, few species A
19. Teeth dorsal on basal knob; length ratio almost 1:1;
 knob twice as long as high ampla
- Teeth cephalic on basal knob; length ratio about 5:1; knob
 at least three times longer than high acuta

Description of the Genitalia

Coenonycha acuta Cazier

Description:

Parameres: Fulvous, inner edge of parameres and posterior margin of basal piece dark fulvous. Subapicolateral hairs long, pale yellow. Median fusion line of basal piece about 0.2 mm long.

Basal Apodeme: Widest posteriorly. Anterior margin truncate, right side slightly shorter; posterior emargination moderately, broadly, obtusely angulate medially. Strut absent. Pale fulvous, v-shaped area anterior to posterior emargination fulvous, lateral margin of apodeme dark fulvous.

Internal Sac: Basal knob long, more than three and one-half times longer than high, evenly elevated, fulvous anteriorly, testaceous posteriorly, with three to five prominent, stout, dark fulvous teeth on the cephalic surface. Sac with two fields; linear field, on right lateral margin of posterior one-half of sac, paralleling apical field distally, composed of two rows of slender, darkly pigmented spines; apical field, on dorsal midline, ovoid, spines stout, dark fulvous.

V-shaped Sclerite: Arms slightly more than one-half the length of the sclerite. Median line lacking. Yellowish, arm apices dark reddish brown.

Variation:

The number of prominent teeth on the basal knob varies from three to five.

Discussion:

The genital armature of Coenonycha acuta is quite similar to that of C. parvula, a brachypterous species, but can be separated from the latter by the shorter linear field (about one-half as long), the lighter, unevenly pigmented basal knob, and the darker basal apodeme. Considering the external characters also, however, C. acuta is more closely related to C. fulva (Figure 61). C. acuta can be separated from C. fulva by the long narrow basal knob, the long, well pigmented linear field, and the ovoid apical field.

Coenonycha ampla Cazier

Description:

Parameres: Fulvous. Subapicolateral hairs long, yellow.

Median fusion line of basal piece about 0.25 mm long.

Basal Apodeme: Sides subparallel. Anterior margin truncate, right side slightly shorter; posterior emargination obtusely angulate medially. Strut extending one-third the lateral length. Testaceous, border of posterior emargination, strut, and lateral margins fulvous.

Internal Sac: Basal knob long, about twice as long as high (Figures 19, 40), fulvous (dark fulvous basad of teeth), with seven to ten stout, fulvous teeth on dorsal surface. Sac with two fields; linear field, on right dorsolateral margin just posterior to knob and extending to just past middle of sac, composed of two to three rows of stout, dark fulvous spines; apical field (Figure 54) on dorsal midline, ovoid, composed of many stout, dark fulvous spines.

V-shaped Sclerite: Arms slightly more than half the length of the sclerite. Median line evident, sclerite emarginate posteriomesad. Yellow, arm apices dark reddish brown.

Variation:

The number of teeth on the basal knob varies from seven to ten.

Discussion:

Coenonycha ampla appears to be most closely related to C. hageni (Figure 61), with which it occurs sympatrically. It can be distinguished from C. hageni by the larger, more darkly pigmented basal knob, and by the strut on the basal apodeme.

Coenonycha barri Cazier

Description:

Parameres: Dark fulvous, posterior margin of basal piece dark brown. Subapicolateral hairs long, very pale yellow. Median fusion line of basal piece about 0.25 mm long.

Basal Apodeme: Widest posteriorly. Anterior aspect asymmetrically emarginate, right side shorter; posterior emargination moderately, evenly rounded medially. Strut lacking. Pale testaceous, large v-shaped area anterior to posterior emargination and apicolateral angles moderately fulvous.

Internal Sac: Basal knob somewhat rectangular and elevated anteriorly (Figure 41), fulvous (area basad of spines dark fulvous), with four, prominent, stout, dark fulvous teeth on dorsocephalic surface. Sac with a linear field, on the right lateral margin equidistant between the knob and apex of sac, composed of two or three rows of stout, fulvous spines.

V-shaped Sclerite: Arms nearly three-fifths the length of the sclerite. Median line lacking. Yellowish, arm apices dark reddish brown.

Variation:

None.

Discussion:

Coenonycha barri is related to C. crispata and C. ovatis, two brachypterous species. Based on the shape of anterior margin of the basal piece, C. barri appears to be closely related to C. crispata (Figure 61). In C. ovatis, the margin is strongly, truncately produced medially. The shorter and narrower basal knob, darker parameres, and the absence of a strut on the basal apodeme distinguish C. barri from C. crispata.

Coenonycha bowlesi Cazier

Description:

Parameres: Dark fulvous, posterior margin of basal piece dark reddish brown. Subapicolateral hairs long, pale yellow. Median fusion line of basal piece about 0.25 mm long.

Basal Apodeme: Widest anteriorly. Anterior margin asymmetrically emarginate, right side shorter; posterior emargination moderately, obtusely angulate medially. Strut extending to about anterior one-fifth of apodeme. Pale testaceous, broad u-shaped area anterior to posterior emargination, lateral margins, and strut fulvous.

Internal Sac: Basal knob long, evenly elevated, sloping more gradually posteriorly than anteriorly, yellowish (area basad of teeth fulvous), with five prominent stout, fulvous teeth on anterior dorsal surface. Sac with two fields; linear field, on right dorsolateral margin near hind margin of knob, curving laterally posteriorly and almost reaching apex of sac, composed of moderately long, fulvous spines, clavate anteriorly, about five spines wide, narrowing to one row posteriorly; apical field to the left of the dorsal midline small, irregular, spines almost nub-like, fulvous.

V-shaped Sclerite: Arms three-fifths the length of the sclerite. Median line lacking. Testaceous, arm apices reddish brown.

Variation:

None.

Discussion:

Coenonycha bowlesi appears to be most closely related to species E (Figure 61). It differs from species E by the clavate linear field, well pigmented basal knob and field spines, and the larger size.

Coenonycha clypeata McClay

Description:

Parameres: Fulvous, apices darker. Subapicolateral hairs long, pale yellow. Anterior margin of basal piece slightly produced medially. Median fusion line about 0.2 mm long.

Basal Apodeme: Widest anteriorly. Anterior margin truncate, right side slightly shorter; posterior emargination moderately, evenly, rounded medially. Strut absent. Pale testaceous, broad v-shaped area anterior to posterior emargination and lateral margins fulvous.

Internal Sac: Basal knob long, hemispherical (Figure 42), dark reddish brown, with ten or more squat, reddish brown teeth on the anteriolateral half of the right side. Sac with two fields; linear field, on right dorsolateral margin just anterior to middle of sac, composed of a single row of seven, stout spines, moderately pigmented; apical field, on dorsal midline, triangular, composed of five large, squat, moderately pigmented spines.

V-shaped Sclerite: Arms one-half the length of the sclerite. Median line evident. Yellowish, arm apices dark reddish brown.

Variation:

Only one specimen was examined.

Discussion:

The genital armature of Coenonycha clypeata is very similar to that of C. fulva. C. clypeata may be distinguished by the shape of the basal knob. When external characters are considered, in addition to the genitalic characters, C. clypeata appears more closely related to C. clementina and C. socialis (Figure 61), both brachypterous species.

Coenonycha fuga Cazier

Description:

Parameres: Dark fulvous, tips almost brown. Subapico-lateral hairs long, yellow. Median fusion line of basal piece about 0.2 mm long.

Basal Apodeme: Widest anteriorly. Anterior margin truncate; posterior emargination shallowly, broadly, obtusely angulate medially. Strut weak, extending to lateral two-fifths of apodeme. Light fulvous, narrow v-shaped area anterior to posterior emargination and lateral margins dark reddish brown.

Internal Sac: Basal knob trapezoidal, posterior margin sloping more gradually than anterior margin (Figure 21), dark yellow, with two large, stout, fulvous teeth on the median dorsal surface. Sac with two fields; linear field, on right dorsolateral margin equidistant between knob and apical field, slender, composed of two rows of stout, fulvous spines; apical field, on dorsal midline, ovoid, composed of many stout, fulvous spines.

V-shaped Sclerite: Arms slightly more than one-half the length of the sclerite. Median line evident, the halves of the sclerite seemingly separated. Yellowish, arm apices dark reddish brown.

Variation:

The number of teeth on the basal knob may be reduced to one.

Discussion:

Coenonycha fuga is most closely related to the brachypterous C. tingi (Figure 61), but can be distinguished from the latter by the two teeth on the basal knob.

Coenonycha fulva McClay

Descriptions:

Parameres: Dark fulvous. Subapicolateral hairs long, pale yellow. Median fusion line of basal piece about 0.2 mm long.

Basal Apodeme: Widest anteriorly. Anterior margin truncate, right side slightly shorter; posterior emargination moderately, obtusely angulate medially. Strut absent. Pale testaceous, u-shaped area anterior to posterior emargination and apicolateral angles fulvous.

Internal Sac: Basal knob almost triangular (Figure 43), moderately fulvous, with four prominent, squat, dark fulvous teeth on the median dorsal surface. Sac with one or two fields; linear field (Figure 56), when present, on right lateral margin on anterior half of sac, composed of about five slender, fulvous spines; apical field (Figure 57) on dorsal midline, triangular, composed of six or seven large, squat or very stout, fulvous spines.

V-shaped Sclerite: Arms not quite three-fourths the length of the sclerite. Median line evident, the halves of the sclerite nearly separated. Yellowish, arm apices dark reddish brown.

Variation:

The lateral field, when present, is composed of four or five slender spines. The number of spines in the apical field varies from six to seven.

Discussion:

Coenonycha fulva is most closely related to C. clypeata, but can be distinguished from the latter by the subtriangular basal knob, and the reduced, sometimes absent, linear field. Considering external characters, however, C. fulva is more closely related to C. scotti (Figure 61). From the latter, C. fulva can be separated by the position of the teeth on the basal knob, the narrow linear field, and the triangular apical field.

Coenonycha fusca McClay

Description:

Parameres: Fulvous, basal piece, except for posterior margin, yellowish. Subapicolateral hairs long, pale yellow. Anterior margin of basal piece weakly produced medially. Median fusion line about 0.25 mm long.

Basal Apodeme: Posterior margin twice as wide as anterior margin. Anterior margin asymmetrically emarginate, right side slightly shorter; posterior margin evenly, shallowly emarginate medially. Strut nearly reaching the anterior margin. Pale yellow, the area anterior to the posterior emargination, apicolateral angles, and the strut light fulvous.

Internal Sac: Basal knob elevated cephalad, sloping caudad (Figure 24), pale yellow, with five large, squat, dark fulvous teeth on the cephalic margin. Sac with a linear field (Figure 55) on the left dorsolateral margin about equidistant between hind margin of knob and apex of sac, composed of one row of squat, pale fulvous spines.

V-shaped Sclerite: Arms slightly less than two-thirds the length of the sclerite. Median line lacking, represented only by a narrow anterior emargination. Yellowish, arm apices medium reddish brown.

Variation:

None.

Discussion:

Coenonycha fusca is most closely related to species A (Figure 61), from Auburn, California, but is distinguished from it by the absence of the apical field on the sac. C. fusca can be separated from C. purshiae by the more prominent teeth on the basal knob, the longer field of squat spines, the lighter parameres, and the shorter basal apodeme.

Coenonycha hageni Cazier

Description:

Parameres: Fulvous, tips slightly darker. Subapicolateral hairs long, yellow. Anterior margin of basal piece weakly produced medially. Median fusion line about 0.2 mm long.

Basal Apodeme: Widest posteriorly. Anterior margin truncate; posterior emargination moderately, evenly rounded medially. Strut absent. Pale testaceous, lateral margins and area anterior to posterior emargination weakly fulvous.

Internal Sac: Basal knob rectangular (Figure 44), dark fulvous, with three prominent, darkly pigmented teeth on the upper cephalic margin. Sac with two fields; linear field, on right dorsolateral margin just anterior to apical field, on posterior one-half of sac, composed of three rows of stout, dark fulvous spines; apical field, on dorsal midline, ovoid, composed of stout, dark fulvous spines.

V-shaped Sclerite: Arms slightly more than one-half the length of the sclerite. Median line lacking. Yellow, arm apices moderate red brown.

Variation:

None.

Discussion:

Coenonycha hageni is most closely related to C. ampla (Figure 61), occurring sympatrically with it. C. hageni can be distinguished from C. ampla by the reduced number of teeth on the basal knob and the absence of a strut on the basal apodeme.

Coenonycha lurida Cazier

Description:

Parameres: Pale fulvous. Subapicolateral hairs long, sparse, pale yellow. Anterior margin of basal piece evenly, shallowly produced medially. Median fusion line less than 0.2 mm long.

Basal Apodeme: Sides subparallel. Anterior margin truncate; posterior emargination moderately, obtusely angulate medially. Strut lacking. Pale yellow, apicolateral angles slightly darker.

Internal Sac: Basal knob long (Figure 45), about the times longer than high, rather evenly elevated, weakly pigmented, with several stout, fulvous teeth on the dorsal surface. Sac with one quadrate field (Figure 58), on dorsal surface just behind middle of sac; field about as long as wide, composed of weakly pigmented, squamose spines.

V-shaped Sclerite: Arms slightly less than four-fifths the length of the sclerite. Median line evident, the halves separated. Yellowish, arm apices dark reddish brown.

Variation:

The number of teeth on the basal knob varies from seven to thirteen. The large teeth vary from six to eight in number.

Discussion:

The less sinuate and more weakly pigmented basal knob, the smaller, quadrate field, and the shorter and lighter parameres will distinguish Coenonycha lurida from C. pallida.

Coenonycha pallida Cazier

Description:

Parameres: Fulvous, posterior margin of basal piece and inner surface of parameres dark reddish brown. Subapicolateral hairs long, pale yellow. Median fusion line of basal piece about 0.25 mm long.

Basal Apodeme: Widest posteriorly. Anterior margin truncate; posterior emargination shallowly, obtusely angulate medially. Strut absent. Pale testaceous, posteriolateral margins, and u-shaped area anterior to posterior emargination fulvous.

Internal Sac: Basal knob long (Figures 22, 46), about seven times longer than narrowest height, sinuate, elevated anteriorly and posteriorly, narrowed behind middle, pale testaceous, yellower basad of teeth, with seven large, stout, dark fulvous teeth on the dorsal surface (smaller teeth may be present posteriorly). Sac with one rectangular field (Figure 60), on dorsal surface, about one knob length behind the basal knob, of squamose, moderately fulvous spines; field wider than long.

V-shaped Sclerite: Arms slightly longer than one-half the length of the sclerite. Median line evident, sclerite halves distinct. Yellow, arm apices reddish brown.

Variation:

The number of teeth on the basal knob varies from five to eight.

Discussion:

Coenonycha pallida is most closely related to C. lurida (Figure 61), but can be distinguished from the latter by the more sinuate basal knob, larger and more rectangular field, and the darker coloration of the field, parameres, and basal apodeme.

Coenonycha pascuensis Potts

Description:

Parameres: Dark fulvous, anterior median margin of basal piece diagonally to parameres testaceous. Subapicolateral hairs long, pale yellow. Anterior margin of basal piece extending as a truncate median projection. Median fusion line about 0.4 mm long.

Basal Apodeme: Posterior margin twice as wide as anterior margin. Anterior margin truncate; posterior emargination obtusely angulate medially. Strut extending almost to anterior margin.

Testaceous, v-shaped area anterior to posterior emargination, strut, and apicolateral angles fulvous.

Internal Sac: Basal knob long, elevated anteriorly (Figure 47), very weakly pigmented, with four squat, moderately pigmented teeth on the dorsocephalic surface. Sac with two fields; linear field, extending from right dorsolateral margin just anterior of middle of sac and reaching almost to apex on left dorsolateral margin, sinuate, composed of one or two rows of stout, fulvous spines; apical field, to the right of dorsal midline, ovoid, composed of squat, fulvous spines.

V-shaped Sclerite: Arms one-half the length of the sclerite. Median line absent. Yellowish, arm apices pale fulvous.

Variation:

None.

Discussion:

The genital armature of Coenonycha pascuensis is similar to that of C. testacea, but can be distinguished from C. testacea by the less sinuate linear field and the longer basal knob. In general appearance, C. pascuensis is more closely related to C. pallida (Figure 61), but can be distinguished from the latter by the evenly elevated basal knob, the position of the teeth on the knob, the number of fields, and the shape of the spines.

Coenonycha purshiae Cazier

Description:

Parameres: Dark reddish brown, posterior margin of basal piece dark brown. Subapicolateral hairs long, pale brown. Anterior margin of basal piece weakly produced medially as a truncate projection. Median fusion line about 0.33 mm long.

Basal Apodeme: Posterior margin twice as wide as anterior margin. Anterior margin asymmetrically emarginate, right side shorter; posterior emargination moderately rounded medially. Strut extending the length of the apodeme. Fulvous, area anterior to posterior emargination to lateral margins, and strut dark reddish brown.

Internal Sac: Basal knob ovoid, light fulvous, with several stout, fulvous teeth on the dorsal surface. Sac with one linear field (Figure 51), on right dorsolateral margin of posterior one-third of caudal portion of sac, composed of a single row of six or more squat, fulvous spines.

V-shaped Sclerite: Arms less than one-half the length of the sclerite. Median line lacking. Yellow, arm apices reddish brown.

Variation:

The number of teeth on the basal knob varies from one to nine, the usual number five or six. The number of spines in the field varies from six to nine, the usual number is eight.

Discussion:

The ovoid basal knob, reduced field of squat spines, and the darker parameres serve to distinguish Coenonycha purshiae from C. fusca.

Coenonycha rotundata (Le Conte)

Description:

Parameres: Fulvous. Subapicoltaeral hairs long, pale yellow. Anterior margin of basal piece produced medially as a truncate projection. Median fusion line about 0.25 mm long.

Basal Apodeme: Widest posteriorly. Anterior aspect asymmetrically emarginate, right side shorter; posterior emargination moderately, evenly rounded medially. Strut nearly reaching anterior emargination. Pale testaceous, strut and posterior half of lateral margins fulvous.

Internal Sac: Basal knob ovoid, distally elevated and rounded, sloping anteriorly (Figure 23), testaceous, with five prominent, stout, fulvous teeth on the cephalic sloping surface. Sac with four fields (Figure 52); the longest linear field three times longer than the two median fields, the fourth field one-half the length of the longest. The fields are arranged two to the right and two to the left of the dorsal midline. The longest field on the left lateral and the medium field on the right lateral margins, the shorter fields in between.

V-shaped Sclerite: Arms more than half the length of the sclerite. Median line lacking. Yellowish, arm apices reddish brown.

Variation:

Only one specimen was examined.

Discussion:

Coenonycha rotundata appears to be most closely related to C. rufobrunnae (Figure 61), but is distinguishable from the latter by the larger basal knob, longer, more prominent teeth, and the greater number of fields on the sac. From species F (Figure 61), C. rotundata can be distinguished by the fewer number of teeth on the basal knob and the darker elytral color.

Coenonycha rubida McClay

Description:

Parameres: Dark fulvous. Subapicolateral hairs long, yellow. Anterior margin of basal piece slightly produced medially as a rounded projection. Median fusion line about 0.25 mm long.

Basal Apodeme: Widest posteriorly. Anterior margin asymmetrically emarginate, right side shorter; posterior emargination strongly angulate medially. Strut extending to about one-half the lateral length of the apodeme. Testaceous, apicolateral angles dark fulvous.

Internal Sac: Basal knob hemiovoid, highest near middle (Figures 26, 48), yellowish, with nine stout, prominent, dark fulvous teeth on the cephalic margin. Sac with one linear field, on right dorsolateral margin, slightly closer to apex of sac than to knob, composed of several rows of long, stout, dark fulvous spines.

V-shaped Sclerite: Arms slightly more than one-half the length of the sclerite. Anterior emargination and posterior median margin narrow, acute. Median line lacking. Yellowish, arm apices light reddish brown.

Variation:

None.

Discussion:

Coenonycha rubida does not appear to be closely related to any of the described species, but it does have some resemblances to C. rotundata (Figure 61). From C. rotundata, C. rubida can be distinguished by the different shape of the basal knob, the reduced number of fields on the sac, the darker parameres, and the shorter strut on the basal apodeme.

Coenonycha rufobrunnae Howden

Description:

Parameres: Dark fulvous. Subapicolateral hairs long, yellow. Anterior margin of basal piece weakly produced medially. Median fusion ling of basal piece about 0.25 mm long.

Basal Apodeme: Widest posteriorly. Apodeme asymmetrically emarginate anteriorly, right side longer; posterior emargination strongly rounded medially, narrow v-shaped area anterior to posterior emargination darker, strut fulvous.

Internal Sac: Basal knob ovoid (Figures 25, 49), elevated anteriorly, weakly pigmented, with eight large, squat, fulvous teeth on the dorsal and cephalic margins. Sac with two fields (Figure 53); longer linear field, on right dorsolateral margin equidistant between knob and apex of sac, composed of two rows of stout, moderately pigmented spines; the smaller field laterad and mesad of the first field composed of less than ten stout, fulvous spines.

V-shaped Sclerite: Arms almost three-fourths the length of the sclerite. Median line evident only as an anteriomedian emargination. Yellow, arm apices reddish brown.

Variation:

Only one specimen was available for study.

Discussion:

From C. rotundata, Coenonycha rufobrunnae can be separated by the less elevated basal knob, squatter teeth, and the reduced number of fields on the internal sac.

Coenonycha scotti McClay

Description:

Parameres: Dark fulvous. Subapicolateral hairs long, yellow. Median fusion line of basal piece about 0.25 mm long.

Basal Apodeme: Widest posteriorly. Anterior margin truncate, right side slightly shorter; posterior emargination moderately, evenly rounded medially. Strut weak, extending less than one-half the length of the side. Testaceous, narrow v-shaped area anterior to posterior emargination and lateral margins fulvous.

Internal Sac: Basal knob elevated anteriorly (as in Figure 21), moderately fulvous, with two or three stout, dark fulvous teeth on the dorsocephalic margin. Sac with two fields; linear field, on right dorsolateral margin, extending from near hind margin of knob to near anterior margin of apical field, composed of two or three rows of stout, fulvous spines; apical field, on dorsal midline, ovoid, composed of stout, fulvous spines.

V-shaped Sclerite: Arms slightly more than half the length of the sclerite. Median line evident anteriorly. Yellowish, arm apices dark reddish brown.

Variation:

The number of prominent teeth on the basal knob varies from two to three.

Discussion:

Coenonycha scotti is similar to C. fuga, being distinguishable from the latter by having only three teeth on the basal knob. Considering external characters also, C. scotti is more closely related to C. fulva (Figure 61). From C. fulva it can be distinguished by the smaller basal knob, more definite linear field, the ovoid apical field, and the stout shape of the spines.

Coenonycha testacea Cazier

Description:

Parameres: Fulvous, posterior margin of basal piece, inner surface and tips of parameres dark fulvous. Subapicolateral hairs long, very pale yellow. Median fusion line of basal piece about 0.3 mm long.

Basal Apodeme: Posterior margin three times wider than anterior margin. Anterior aspect weakly emarginate, almost truncate, right side shorter; posterior emargination strongly, broadly, evenly rounded medially. Strut extending almost to anterior margin. Testaceous, shallow v-shaped area anterior to posterior emargination, strut, and apicolateral angles fulvous.

Internal Sac: Basal knob small, weakly elevated (Figure 20), testaceous, with five squat, fulvous teeth on the dorsal surface. Sac with two or three, usually three, fields; linear field, of large, squat, fulvous spines, strongly sinuate across dorsum of sac, the right arm extending anteriorly, the left arm posteriorly; apical field(s) ovoid, composed of stout, fulvous spines.

V-shaped Sclerite: Arms nearly three-fourths the length of the sclerite. Median line absent. Yellowish, arm apices dark reddish brown.

Variation:

The number of apical fields may be reduced to one.

Discussion:

The linear field on the internal sac in Coenonycha testacea is a direct modification of a two field condition, apparently the fields have joined medially, and the left anterior and right posterior arms have disappeared. C. testacea is most closely related to species G (Figure 61), but is distinguishable from the latter by the single, strongly sinuate field, the two apical fields, and the darker pigmentation anterior to the hind margin of the basal apodeme.

The original distribution (Cazier and McClay, 1943) included many populations of species with the two field condition. The modified field is found at the type locality north to Shandon and Creston, California (about 100 miles).

Coenonycha utahensis McClay

Description:

Parameres: Dark fulvous. Subapicolateral hairs long, pale yellow. Median fusion line of basal piece about 0.25 mm long.

Basal Apodeme: Widest posteriorly. Anterior margin asymmetrically emarginate, right side shorter; posterior emargination strongly, obtusely angulate medially. Strut extending the length of the apodeme. Pale fulvous, narrow v-shaped area anterior to posterior emargination scarcely darker than apodeme, strut and apicolateral angles dark fulvous.

Internal Sac: Basal knob small, weakly elevated and pigmented (Figure 50), with about four stout fulvous teeth on the dorsal surface. Sac with one linear field, on right dorsolateral margin equidistant between the hind margin of knob and apex of sac, composed of one to two rows of stout, fulvous spines.

V-shaped Sclerite: Arms slightly longer than half the length of the sclerite. Median line absent. Yellowish, arm apices pale reddish brown.

Variation:

None.

Discussion:

Coenonycha utahensis appears to be most closely related to species H (Figure 61), but can be distinguished from it by the apical field, narrower v-shaped sclerite, and the darker parameres.

TAXONOMIC VALUE OF THE MALE
GENITALIA IN COENONYCHA

Parameres:

The color of the parameres and the length of the basal fusion line vary within the genus, but not noticeably within a species. In some species, a median projection of the anterior margin of the basal piece is present.

Basal Apodeme:

The strut on the basal apodeme is present, absent, or only partially absent in the genus and exhibits not infraspecific variability. The general shape of the apodeme varies in width, being considerably narrower anteriorly in some species. The shape of the posterior emargination and the anterior margin are only secondarily useful taxonomically. Finally, the coloration of the basal apodeme varies considerably within the genus.

Internal Sac:

The size of the basal knob, degree of sclerotization, and the number, arrangement, and size of the teeth on the knob vary from species to species and are usually stable morphologically. The position of the basal knob on the internal sac does not vary.

The fields on the caudal portion of the sac can also be used to help separate species. Not only does the number of fields vary from

species to species, but the shape and position of the fields vary also. Finally, the size and shape of the spines comprising the fields can be used in an evaluation of the species. The size and shape of the minute spinules on the caudal portion of the sac may prove, with additional study, to be of some taxonomic value.

V-shaped Sclerite:

The horseshoe-shaped sclerite, which in Coenonycha is more v-shaped than in Diplotaxis (Vaurie, 1958), has several characters, which may have some taxonomic value. The length of the sclerite, the length of the arms, the presence or absence of the median line, and the color of the arm apices vary to some degree from species to species.

Intraspecific variation of these characters is very low in the genus. Where variation occurs, it is mentioned following the species descriptions of the genitalia.

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APPENDICES

Definition of Terms

Basal apodeme: the sclerite anterior to and articulating with the basal piece (apodeme of the phallobase, Snodgrass, 1935).

Basal knob or knob: the raised dorsal sclerite on the internal sac at the base of the swollen distal portion.

Basal piece: the proximal portion of the tegmen articulating with the basal apodeme and from which the parameres arise (the "piece basale," Jeannel, 1955; phallobase, Snodgrass, 1935).

Field length ratio: the length of the long linear field to the length of the shorter non-linear field.

Fields: a well defined area of pigmented spines on the distal portion of the internal sac.

Genital segment: a v-shaped sclerite composed of the ninth abdominal pleurites, orientated ventrad of the inverted internal sac (the sclerotic annulus, Snodgrass, 1935).

Internal sac: The membranous aedeagus of the male, which when inverted lies ventrad of the basal apodeme and dorsad of the genital segment (the "sac interne," Jeannel, 1955; "vesica," Snodgrass, 1935).

Parameres: the slender curved distal lateral portions of the tegmen, possessing subapical setae (the "lobe lateraux," Jeannel, 1955; the lateral lobes, Sharp and Muir, 1912).

Spines: the pigmented spines of the fields.

Teeth: the large spines of the basal knob.

Tegmen: the single or divided sclerite situated basally to penis (aedeagus) and often surrounding it when in repose; usually divided into basal piece and parameres (Sharp and Muir, 1912).

V-shaped sclerite: the ventrad sclerite on the narrow portion of the internal sac.

Figures 13-17. Genital segments.

13. Macrodactylus uniformis

14. Coenonycha ampla

15. Gymnopyge sp.

16. Dichelonyx backii

17. Isonychus albicinctus

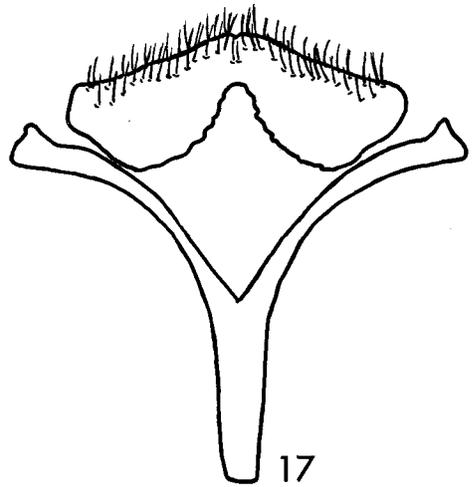
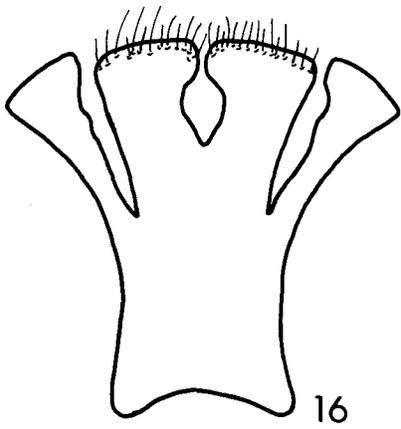
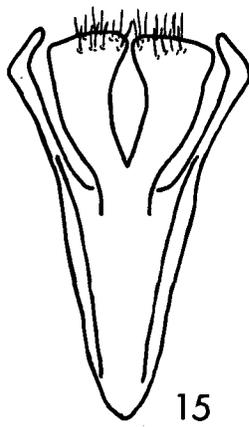
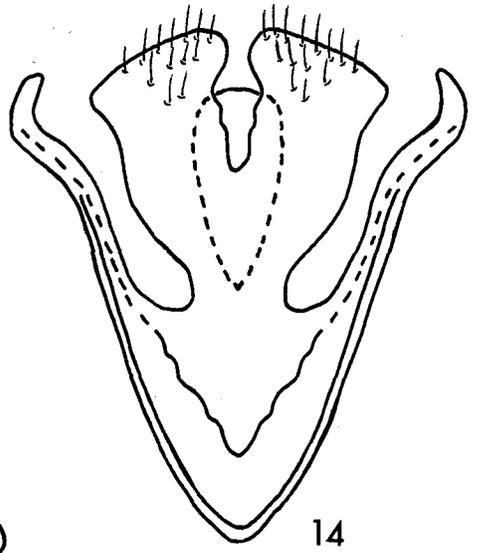
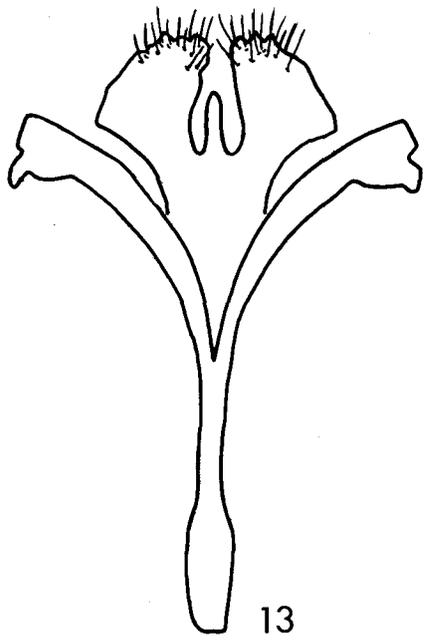
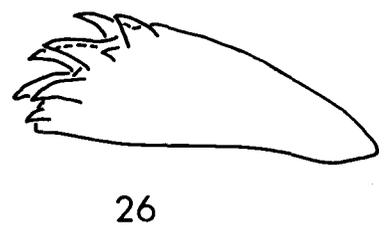
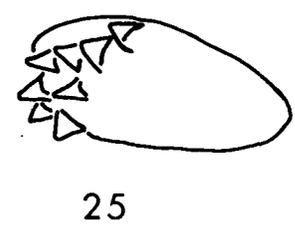
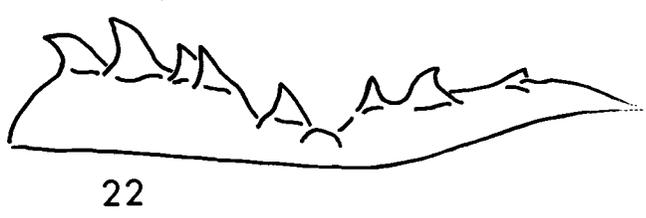
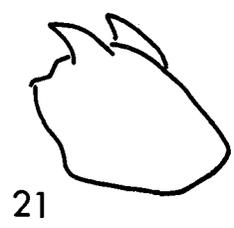
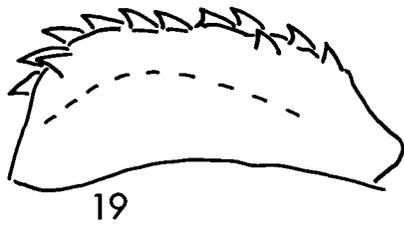
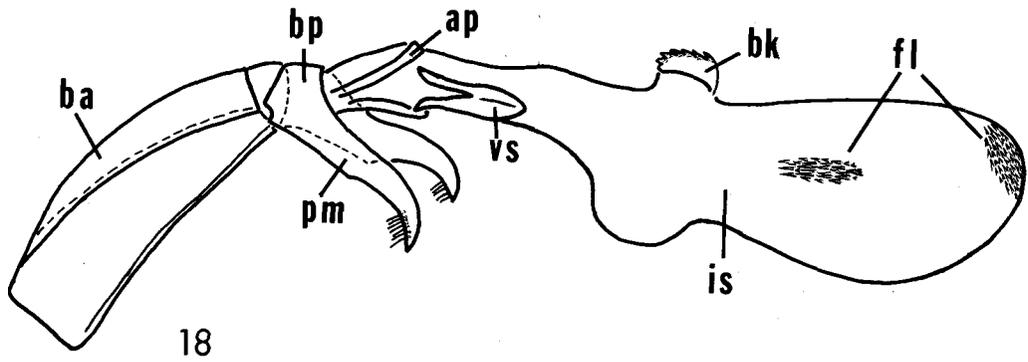


Figure 18. The genital structures of male Coenonycha, diagrammatic. (ap, apodeme of the internal sac; ba, basal apodeme; bk, basal knob; bp, basal piece; fl, field; is, internal sac; pm, paramere; vs, v-shaped sclerite)

Figures 19-20. Basal knobs.

19. C. ampla
20. C. testacea
21. C. fuga
22. C. pallida
23. C. n. sp.
24. C. fusca
25. C. rufobrunnae
26. C. rubida



Figures 27-29. Parameres and basal apodeme.

27. C. barri (ba, basal apodeme; bp, basal piece; pm, parameres).

28. Gymnopyge sp.

29. Dichelonyx backii

Figures 30-32. V-shaped sclerite.

30. C. hageni

31. Gymnopyge sp.

32. Dichelonyx backii

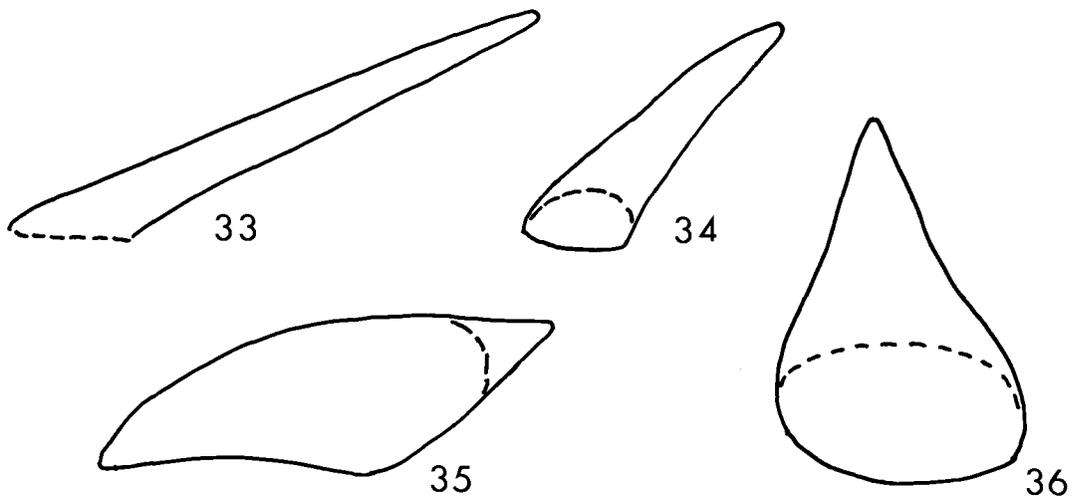
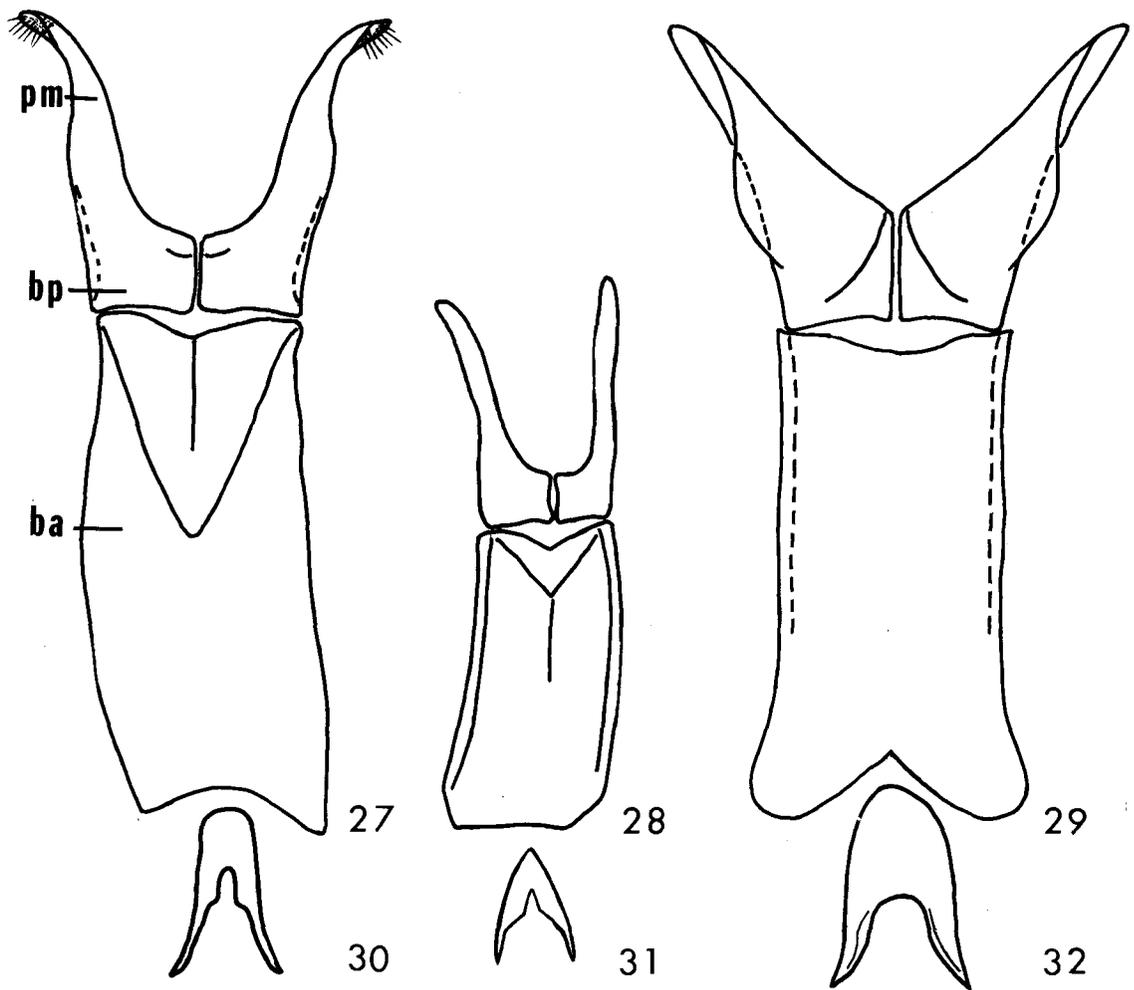
Figures 33-36. Field spines.

33. Slender spine

34. Stout spine

35. Squamose spine

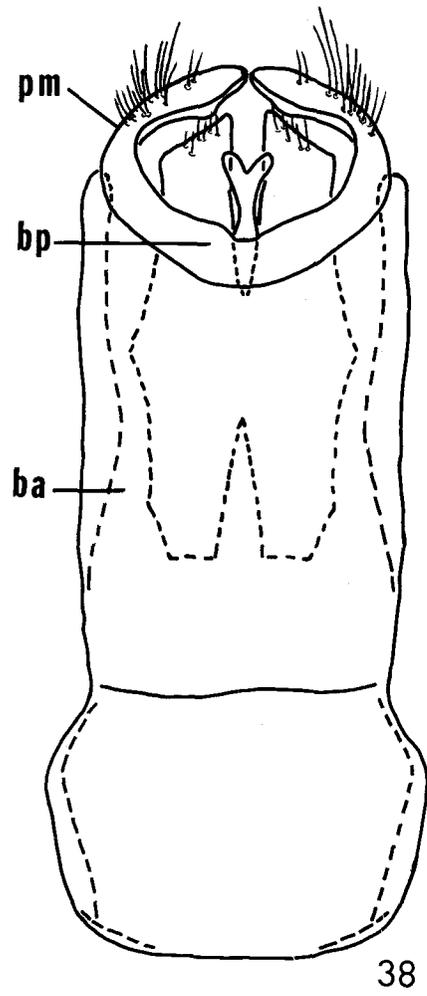
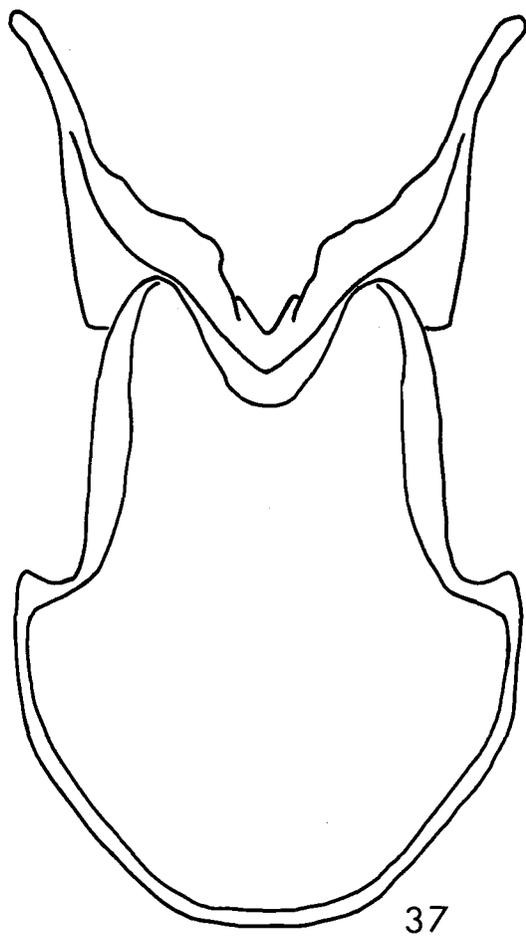
36. Squat spine



Figures 37-38. Parameres and basal apodeme.

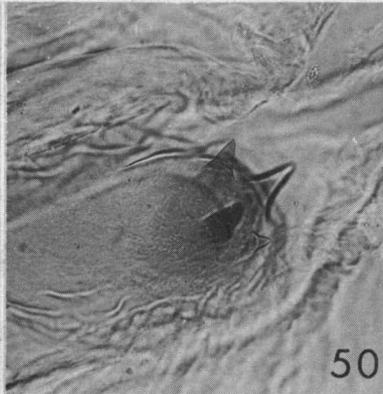
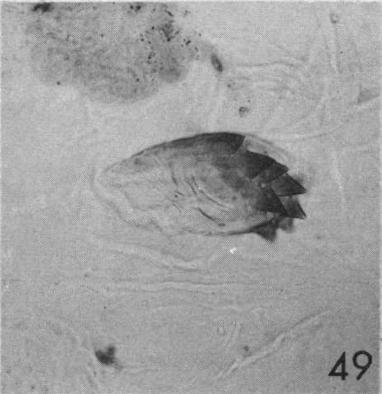
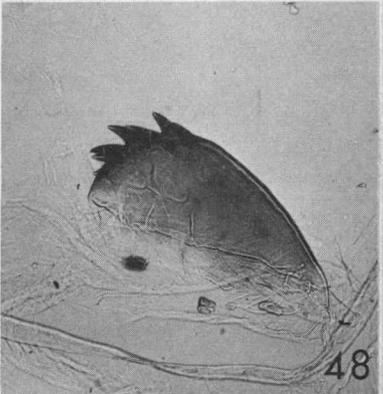
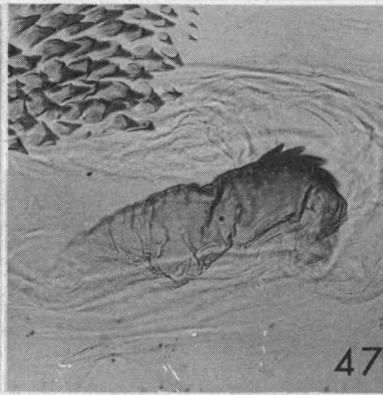
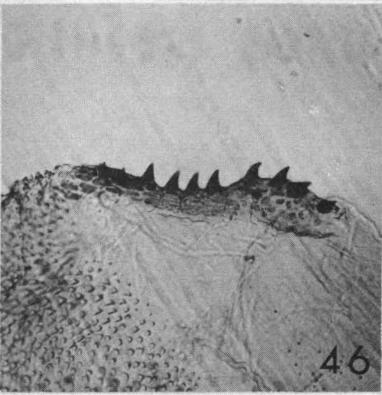
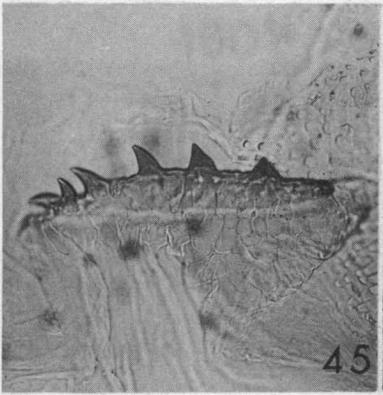
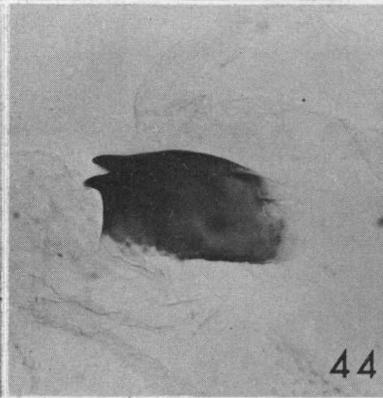
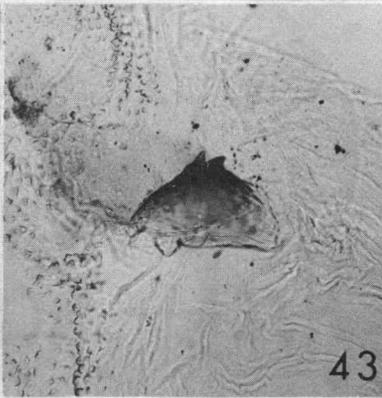
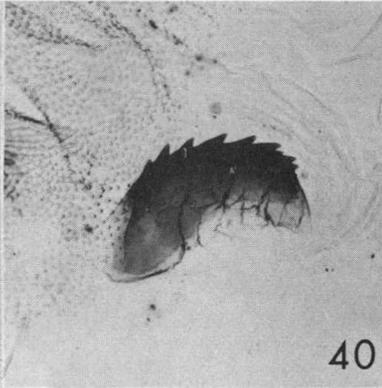
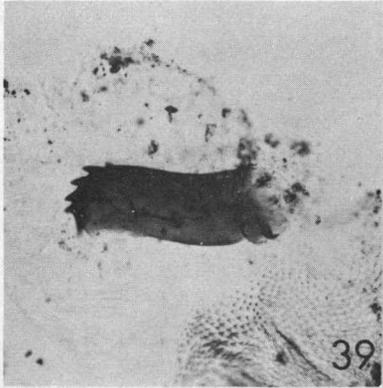
37. Isonychus albicinctus

38. Macrodactylus uniformis
(ba, basal apodeme; bp, basal
piece; pm, parameres)



Figures 39-50. Basal knobs.

39. C. parvula
40. C. ampla
41. C. barri
42. C. clypeata
43. C. fulva
44. C. hageni
45. C. lurida
46. C. pallida
47. C. pascuensis
48. C. rubida
49. C. rufobrunnae
50. C. utahensis



Figures 51-60. Fields.

51. C. purshiae
52. C. rotundata
53. C. rufobrunnae
54. C. ampla, apical field
55. C. fusca
56. C. fulva, linear field
57. C. fulva, apical field
58. C. lurida
59. C. mediata, apical field
60. C. pallida

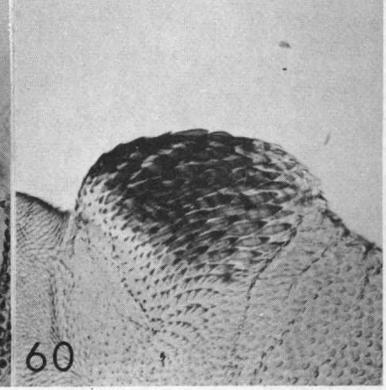
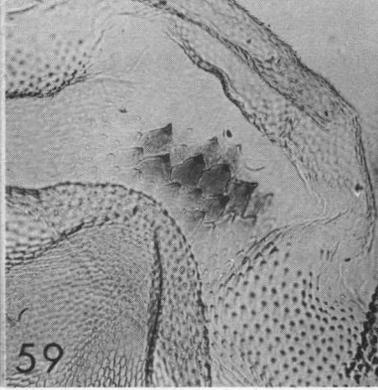
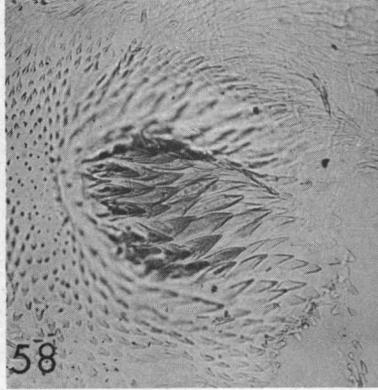
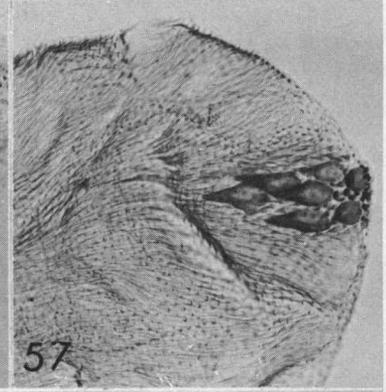
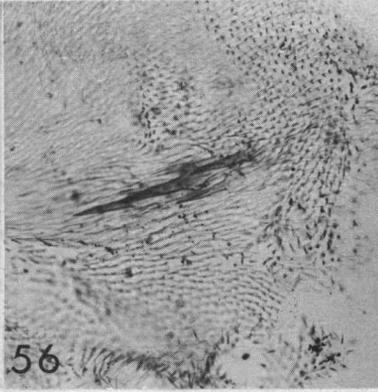
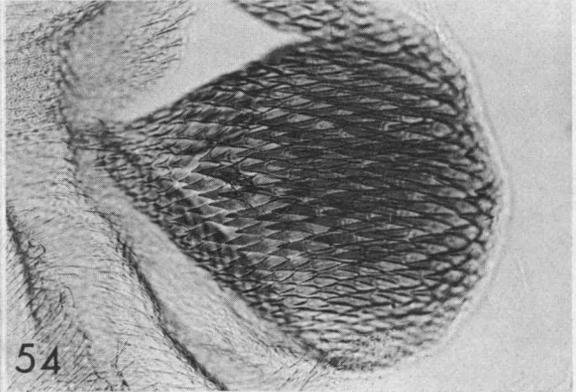
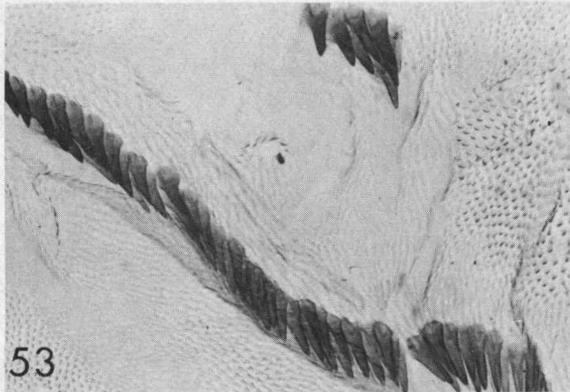
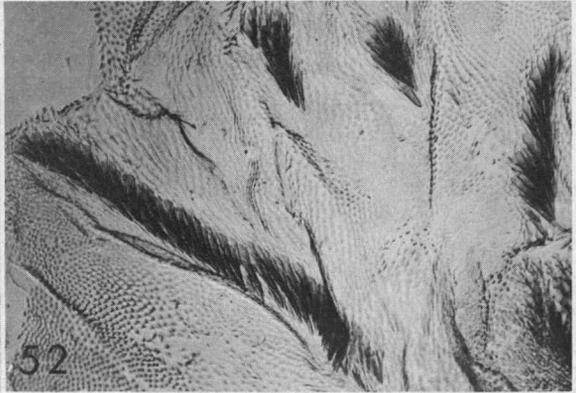
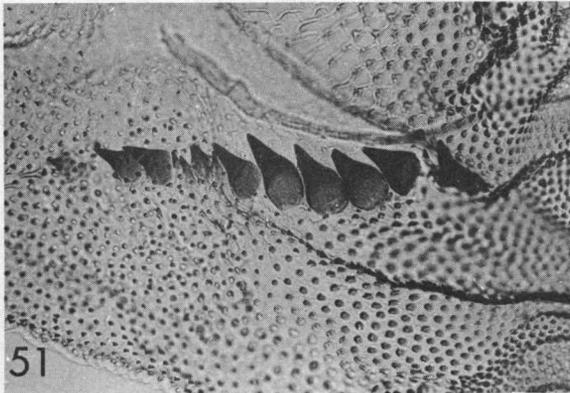


Figure 61. Phenetic relationships of species and species groups in the genus Coenonycha.

