CONTRIBUTIONS OF THE ROYAL ONTARIO MUSEUM
DIVISION OF ZOOLOGY AND PALAEONTOLOGY

No. 42

A STUDY OF THE PHYLOGENY OF THE GENERA OF THE TRIBE COCCINELLINI (COLEOPTERA)

by

W. Y. Watson

TORONTO
1956

(The institutional heading has been changed owing to the reorganization of the Museum. The series will be continued unbroken.)

The present study carried out in the Royal Ontario Museum, Division of Zoology and Palaeontology, under the direction of Dr. F. A. Urquhart, Curator of the Department of Entomology, fulfils in part the requirements for a degree of Doctor of Philosophy of the University of Toronto.

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This paper attempts to show the relationships of the genera of the tribe Coccinellini (sens. Korschefsky). It is based on a study of adult anatomy, geographic distribution, and, to a lesser extent, upon fossil evidence. It is hoped that this paper will induce others to attempt similar studies on other groups in the family Coccinellidae. The family as a whole, being both interesting and economically important, poses many problems of relationships and of geographic distribution.

The work done in connection with this paper would have been considerably more difficult had it not been for the assistance given by the following workers and institutions: Mr. W. J. Brown, Department of Agriculture, Ottawa, Canada; Mr. R. A. Crowson, The University, Glasgow, Scotland; Dr. F. E. Vesey-Fitzgerald, Northern Rhodesia; Dr. H. B. Leech, California Academy of Science, San Francisco, California; Dr. R. Paulin, Tananarive, Madagascar; British Museum (Natural History), London, England; National Museum, Paris, France; Institute of the Belgian Congo, Brussels, Belgium; The Australian Museum, Sydney, Australia; College of Agriculture, Rehovat, Israel. Thanks are due also to Mr. R. D. Pope, B.M. (N.H.), for searching some of the literature for me, and to Dr. E. M. Walker and Dr. F. A. Urquhart both of whom examined the manuscript. Finally, thanks also to the Director, Forest Biology Laboratory, Sault Ste. Marie, Canada, who has provided the space and time to carry out this work.

Historical Review

Linnaeus (1758) used but one genus in which to place all of his Coccinelline species. Since that time, with the accumulation of material, there has been a vast increase in the number of recognized genera until, today, more than 30 genera are recognized in the tribe Coccinellini alone. To deal with this ever-increasing number of names, systems of classification were set up which served simply to keep order in a regime which was fast becoming chaotic. With the advent of the evolutionary theory it was possible for these systems to take on new meanings. Unfortunately, characters upon which these classifications were based often lacked evolutionary significance, so that systematic studies had to be made to complement taxonomic studies. The present work is the result of a systematic investigation of the genera of the tribe Coccinellini (sens. Korschefsky) designed to accompany and augment recent taxonomic work.

Only a few of the great number of taxonomists who have contributed to the study of the Coccinellidae have continued their work into the systematic field. Wilson (1926) pointed out the composite nature of the tribe Coccinellini and suggested several important changes, not the least among which was the suggestion that *Megilla* (=*Coleomegilla*) was more closely related to *Coccinella* than to *Hippodamia.* Dobzhansky (1927) dealt with some of the genera of the tribe and attempted to arrange them in a phylogenetic sequence; this paper will be dealt with more fully later on.

Böving (1917), Gage (1920), and Strouhal (1926), working with larval forms, outlined the relationships of the tribes within the family and, in some cases, tried to establish the affinities of the Coccinellidae with the other families of beetles. Rarely do any of these authors suggest intra-tribal relationships. Böving does imply that the Hippodamiini and the Coccinellini, as recognized by some earlier authors (Casey, Leng), are not valid tribes and should be amalgamated.

Among the taxonomists the earliest to contribute substantially to the study of the tribe Coccinellini was Mulsant. His publications of 1846 and 1850 showed an obvious attempt to recognize as many of the logical divisions in the group as possible. He split the genera into five groups and included in them many genera not now associated with the Coccinellini. The Hippodamiares corresponded rather closely with the more recently used tribe, Hippodamiini, with the exception of *Adonia* and *Anisosticta* which were put in the Coccinelliares. This latter group, along with the Halyziares, corresponded roughly with the Coccinellini, and included also many genera now placed in the Psylloborini. Finally the Cariares, in part like the modern Synonychini, contained *Isora* and *Pelina,* two genera now considered to be part of the Coccinellini.

Thompson (1866) grouped all the subdivisions of Mulsant's work into the tribe Coccinella. Du Val (1868) removed all the major groups in this part of the Coccinellidae and recognized but four genera, *Hippodamia, Anisosticta, Coccinella,* and *Micraspis;* the genus *Coccinella* included fourteen of the Mulsant genera.

Crotch (1873, 1874) grouped all the divisions of Mulsant into the Coccinellides. At the same time many of the older genera were suppressed and many new ones erected. *Adonia* and *Hemisphaerica* were synonyms of *Hippodamia; Propylaea* and *Coelophora* were related to *Harmonia* and *Coccinella.* Gemminger (1876) adhered to the arrangement proposed by Crotch but committed many of the genera to synonymy.

Chapuis (1876) restored much of the work of Mulsant. *Anisosticta* was related to *Megilla* and *Naemia,* giving the Hippodamites a very modern appearance. *Adonia* was still placed with *Coccinella.* Gorham (1887–89) elevated the divisions of Mulsant to subfamilies. In the Hippodamiides were *Megilla, Naemia* and *Hippodamia; Adonia* was considered a synonym of *Hippodamia.* The Coccinellides contained

Coccinella and *Adalia,* and the Halyziides included the Halyziares and the Cariares.

Weise (1892) moulded the categories of Mulsant into a relatively modern system. Three tribes were erected, following the example of Chapuis. In the first, Hippodamiini, there were four genera, *Hippodamia, Adonia, Anisosticta,* and *Semiadalia;* this was the first time *Adonia* and *Anisosticta* had been placed together. The other tribes were Coccinellini and Synonychini.

Casey (1899) used the tribe Hippodamiini after the manner of Chapuis and Gorham, and included *Anisosticta,* as well as two new genera, *Paranaemia* and *Macronaemia.* The Coccinellini embraced all the other genera including those which Weise placed in the Synonychini. A third tribe, Psylloborini, was erected to contain *Psyllobora* and *Thea.* Leng (1903) recognized the first two tribes of Casey but not the third. Leng (1920) reversed this on the strength of the larval work done by Böving (1917) and Gage (1920). The Hippodamiini and Coccinellini were combined in the Coccinellini and the Psylloborini was recognized as a valid tribe. Jacobson (1916) uses the term Anisostictina as synonymous with Hippodamiini and placed in it *Hippodamia, Anisosticta, Semiadalia, Naemia, Adonia,* and *Aphidecta.*

Mader (1926–27), investigating the palaearctic Coccinellidae, recognized two tribes. In the Hippodamiini he included the same genera as did Jacobson, with the addition of *Spiladelphia.* In the Coccinellini were the Psylloborini of Casey and the Micraspini of earlier authors. Korschefsky (1932) has combined the Hippodamiini and the Coccinellini, and has removed the Psylloborini and the Micraspini.

THE ANATOMY OF THE ADULTS OF THE GENUS *Anatis*

(Plates I and II)

The anatomy of few adult Coccinellidae has been examined critically (e.g. Sweetman, 1930; Verhoeff, 1895). More often a detailed investigation of certain regions or structures has been made (e.g. Dobzhansky, 1927; Ehara, 1952; Landis, 1936; McKenzie, 1936; Pradhan, 1938; Wilson, 1926). Other information about the Coccinellidae may be found in general works covering the whole of the beetles (e.g. Sharp and Muir, 1912; Stickney, 1921). As a result, the anatomy of this family of beetles is not well known. Therefore, as a basis for further discussion, the skeletal anatomy of *Anatis* adults was examined.

The genus *Anatis* consists of three species (McKenzie, 1936). *Anatis ocellata* (L.) is found in the palaearctic regions, *A.o. mali* (Say), *A. quindecimpunctata* (Say), *A. rathvoni* LeC., and *A.r. lecontei* Casey are found in various parts of the nearctic region.

Individuals of this genus are large, almost round, and with black markings on a basic colour which ranges from ivory-white (*quindecim-*

punctata) to deep mahogany (*mali*). All but *lecontei* have a series of black dots on the elytra; usually a humeral spot, a scutellar spot, and two rows of three or four spots on each elytron; *lecontei* has a black margin around the elytra but no spots. Although the design of the pronotum is variable there is usually a large M-shaped discal marking, two small median basal spots, and wide white lateral margins each with a black spot in the posterior third; again *lecontei* differs in having the lateral margins broadly black. The venter of all species is mainly black, with the abdomen having slightly fulvous margins in *A.o. mali.* The shape of the elytra varies among the species. *A. rathvoni* has much expanded elytra which are almost angulate in the middle, *A. quindecimpunctata* and *A.o. mali* have elytra which are broadly rounded but not angulate, and *A. ocellata* has slightly elongate elytra, appearing narrower than the other species.

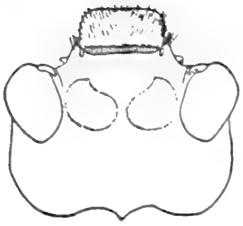
Head

Capsule. The head capsule is quadrate when viewed from above (Figure 1). In profile (Figure 2), it is deepest in the occipital third and gradually tapers to the labrum. Posteriorly the capsule is dorsally bi-emarginate, terminating medially in a blunt point. Ventrally (Figure 3), the occiput has a single, central emargination. Anteriorly, the fronto-clypeus (FC) is produced slightly on either side of the labrum (Lr) thus making the anterior edge of the fronto-clypeus emarginate. A frontal bar extends across in front of the compound eyes, separating them from the antennaria.

PLATE I

Anatis ocellata mali Say

FIGURES 1–21: **1**, Head capsule, dorsal view. **2**, Head capsule, lateral view: CE, compound eye; GS, genal sutures; Ge, gena; Gu, gula; Lr, labrum; Mc, mandicoria; Prc, paracoila; Prt, pretentorium; Psc, postcola. **3**, Head capsule, ventral view: as in Fig. 2; Pt, paratentorium; Pst, postentorium. **4**, Antenna. **5**, Mandible, inner face: At, apical teeth; Ps, prosteca; r, retinaculum. **6**, Mandible, outer face: v, vesicle. **7**, Maxilla: G, galea; C, cardo; L, lacinia; S, stipes; P, palpus; Co, condyle. **8**, Labium: Li, ligula; M, second submental plate; P, palpus; Pc, palpicoria; Prm, mentum. **9**, Hypopharyngeal basket: La, labium. **10**, Cervical sclerites: D, dorsal sclerite; V, ventral sclerite. **11**, Pronotum. **12**, Prosternum: Bs_I, basisternum; Fc_1, furcasternum; Pl, pleuron; Psp, prosternal spine; Sp, spiracle. **13**, Pterothorax, dorsal aspect: Psc_2, Psc_3, prescutum of meso- and meta-thorax; $Ptsc_3$, postscutum of metathorax; Sct_2, Sct_3, scutum of meso- and meta-thorax; l, "i"-strut to epipleuron. **14**, Pterothorax, lateral aspect: Epm_2, Epm, epimeron of meso- and meta-thorax; Eps_2, Eps, episternum of meso- and meta-thorax; St_2, St_3, meso- and meta-sternum; i, strut. **15**, Pterothorax, ventral aspect: Bs_2, Bs_3, meso- and meta-basisternum; Fc_2, Fc_3, meso- and meta-furcasternum; Mcl, mesocoxal lines. **16**, Mesothorax, anterior aspect: N, notum; Pl_3, pleurite of mesothorax; F, furcal arm. **17**, Metathorax, posterior aspect: Ph, phragma; Pl_3, pleurite of metathorax; Met_3, metendosternite. **18**, Elytra articular sclerites, I, II, and III. **19**, Hind wing articular sclerites, I, II, and III. **20**, Elytron, inner surface: Epp, epipleuron. **21**, Elytron, outer surface.



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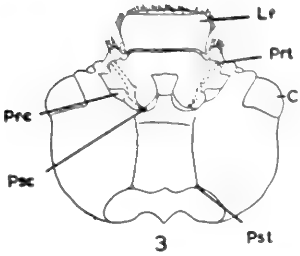

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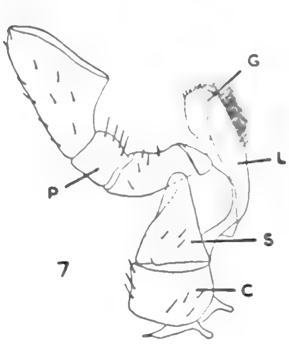

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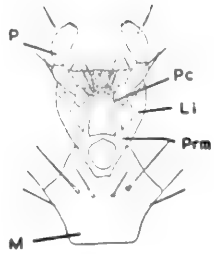

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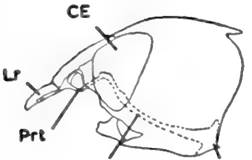

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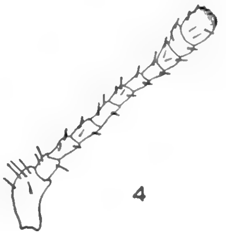

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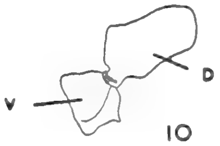

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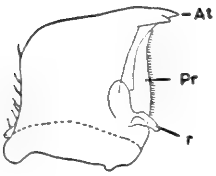

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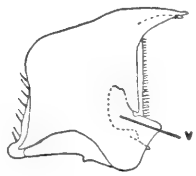

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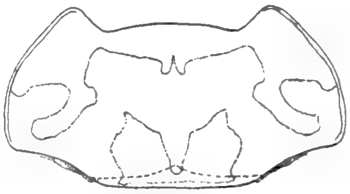

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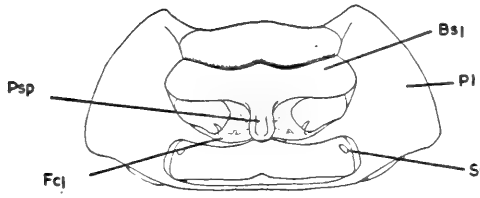

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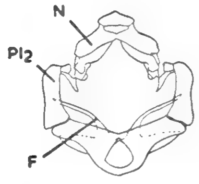

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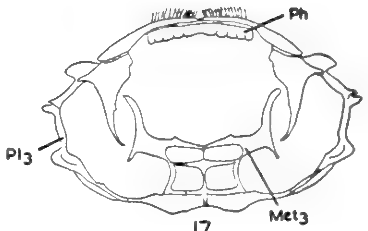

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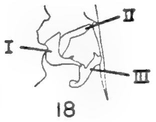

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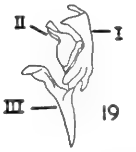

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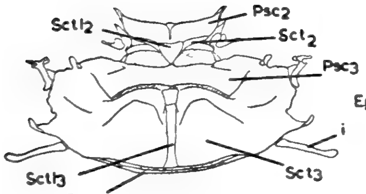

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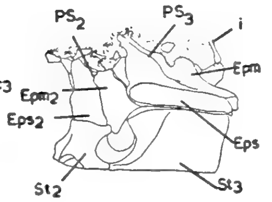

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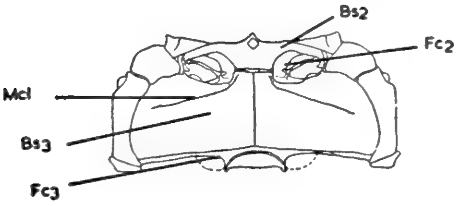

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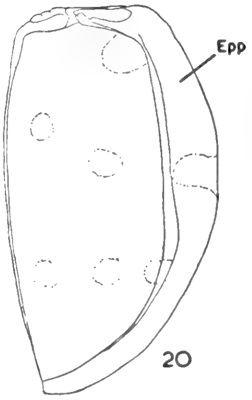

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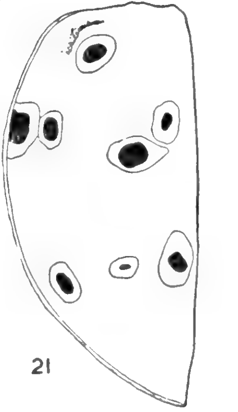

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Ventrally (Figure 3) the head capsule is composed of the ventral extensions of the gena (Ge) and a wide gula (Gu). At the anterior end of the gula is a small primary subdivision of the submentum (see discussion of the labium). When the maxillae and the mandibles are removed, the edges of the cibarial space are exposed. The posterior edge of this space forms a narrow shelf-like paracoila (Prc). The lateral edges of the cibarium form the postcola (Psc) on which are found the points of articulation of the maxillae. Anterior to these are the irregular mandacoria.

As in many of the specialized Coleoptera, head sutures are much reduced. Stickney (1921) found some evidence of epicranial sutures in *Hippodamia convergens*. Similar evidence is present in *Anatis* for there is a short suture (Es) extending along the lower edge of the compound eye between it and its antennarium (An). Ventrally, the gular suture (GS) appears as a thin line on each side extending from the edge of the cibarial space to the edge of the occiput. The posterior ends of the sutures are moderately invaginate forming the metatentorinae. A slight transverse suture separates the gula from the submentum. Dorsally, the labrum is separated from the fronto-clypeus by a well-defined suture.

The labrum is an oblong sclerite separated from the head capsule by a narrow membranous anteclypeus (Ac) (preclypeus of some authors). The anterior edge of the labrum is rounded, whereas the sides are divergent. When viewed laterally the labrum is convex along the dorsal edge. At the posterior corners short projections extend beneath the clypeus and connect with the hypopharyngeal bridge. The internal surface of the labrum is flat.

The arrangement and distribution of the punctures and setae are variable. Ventrally, both are lacking, there being but a few transverse lines marking the gular surface. Dorsally, however, there are fine punctures, separated by slightly more than their own width, scattered irregularly over the whole surface. Setae can be found scattered generally over the whole surface of the capsule and the labrum. These are most noticeable along the edge of the clypeus, at the summits of the fronto-clypeal prominences, and along the edges of the labrum.

Large, irregularly-shaped compound eyes (CE) occupy the greater part of the lateral walls of the capsule. The irregularity is further increased by the emargination of the front edge of the eyes by the frontal bar. In *Anatis* the facets are numerous and small. The surface of each eye is smooth.

Antennae. Each antenna is slightly longer than the head. Each arises from an oval antennarium situated between the compound eye and the corner of the labrum. A membrane connects the basal segment with the head capsule. Each antenna is composed of eleven segments which are of different shapes. The first segment is quite large and swollen, the second is much shorter, but still somewhat thicker than the succeeding ones. Segments three to five are each slightly longer than segment two; each is cylindrical. Segments six to eight are nearly equal in length, shorter than preceeding segments, slightly expanded distally, and each bears a slight projection at the outer distal angle. The ninth segment is equal to the eighth in length but expands distally as the first segment of the club; the distal angle of this segment is protuberant. The tenth segment is slightly shorter than the ninth but of the same general shape. Its distal angle is even more projecting than that of the ninth and the distal margin is oblique. The eleventh segment is longer and wider than the tenth and is bluntly rounded.

Tentorium. There is a greatly reduced tentorium (Figures 2, 3) in *Anatis.* It appears as a slender rod on either side of the hypopharynx. Each rod is narrow, unsclerotized, and dorsally curved. Since this condition is so far removed from that found in the orthopteroid insects (Kellogg, 1902) the term *paratentorium* (Pt) is proposed. Each part of the paratentorium is attached to the head capsule in two places, posteriorly at the end of the gular sutures and anteriorly on the sclerotized bar between the antennaria and the mandibular socket. The pretentorinae (Prt) are not visible externally and there are no superior tentorinae. The metatentorinae are seen as external invaginations at the ends of the gular sutures. Internally the end of the paratentorium extends dorsally along each side of the occiput.

Mandibles. The mandibles are heavily sclerotized, triangular structures which are concave on their buccal surfaces. The mesodistal angles of each bears two long teeth, which may be blunt or broken in older specimens. The mesal margin bears, basally, a short tooth and a knob-like structure which together form the retinaculum (r). Along the mesal margin between the base of the teeth and the retinaculum is a membranous prostheca (Pr) which forms, with the body of the mandible, a trough through which the food is sucked. At the basal end of the trough in the body of the mandible, is an oval vesicle (v) which opens into the trough. The use of this vesicle has not yet been established. The lateral margin of the mandible is broadly rounded and bears a fringe of long hairs on the basal half. The basal condyle is large and rounded whereas the second condyle, situated about two-thirds of the way between the basal condyle and the retinaculum, is a small dome-like structure (Figures 5, 6).

Maxilla. The maxilla (Figure 7) is a complete, moderately sclerotized structure. The cardo (C) is hemispherical and bears basally an expanded, tripartite, articular condyle. Distally the cardo articulates with an elongate stipes (S), which is subdivided into three parts, each supporting one of the distal structures. The lacinia (L) is elongate, loosely joined to the stipes, and bears apically a cluster of coarse, elongate setae, some of which may also be found along the free edge. The galea (G) is short and apically rounded. A few short hairs are found at the edge of the domelike summit, whereas the greater part of the setal mass is made up of long slender setae. The maxillary palpus (P) has four segments; the first is short, slender, and cylindrical; the second is thicker, elongate, and slightly curved; the third is small and cylindrical; the fourth is very large and securiform with an elongate oval apex, the surface of which is covered with very short setae. Long setae are found in several places on the maxilla, but their positions are apparently not constant.

Labium. The primary submental plate (Sm_1), usually referred to as the submentum (Walker, 1931), is a small sclerite with slightly diverging lateral margins and with the anterior margin wider than the posterior one. The secondary submental plate (Sm_2), usually called the mentum, is a quadrate sclerite with projecting, angulate sides and a slightly expanded apex. The true mentum (Prm), usually referred to as the prementum, consists of two parts, a posterior portion which takes the form of a deeply emarginate yoke of heavily sclerotized material and a more weakly sclerotized anterior portion, the two portions being separated by a membrane. The posterior portion bears the ligula (Li) and the anterior portion the palpi (P). The ligula is a broad, fleshy structure lying dorsal to and connected with the labium. It is expanded at the apex and is marked, over its free surface, with fine reticulations. The palpi (P) arise close together from large palpacoria. Each palpus is composed of three segments. The first is very small and cylindrical with an oblique apical margin. The second is two and one-half times as long as the first and is slightly swollen internally. The third segment is longer than the second, somewhat fusiform, and has a blunt apex which is covered with short setae like those found at the apex of the maxillary palpi.

Hypopharynx. Within the head capsule, arising from the submentum, is a complex hypopharyngeal basket (Figure 9). When viewed from the side it is seen that this structure arises as a central column from which there are four projections. One of these is directed posteriorly and is apparently not attached to any other structure. The other three are directed anteriorly. The most ventral of these is slender and attenuate, and is attached to one of the subdivisions of the stipes. The second projection is heavier at the base than the first but narrows gradually to a point; it is attached to the mandible. The third projection is, again, slender and is attached to the corner of the labrum. From above, the hypopharyngeal basket is roughly H-shaped. In function this structure probably replaces the tentorium of other insects as well as providing some support for the mouth-parts and the labrum.

Cervical Sclerites

Embedded in the cervical membrane on either side of the neck region are two small cervical sclerites (Figure 10). The more dorsal (D) of these is moderately sclerotized and is about twice the size of the ventral sclerite. It is oblong and has a rounded free end. At the short line of junction between it and the ventral sclerite, the dorsal one is more heavily sclerotized and is constricted. The ventral sclerite (V) is subquadrate and is divided by a fold from the point of articulation with the dorsal sclerite to the anterior end. The ventro-posterior angle is produced into a small point. The cervical sclerites are not attached, except by a membrane, to any other structure (see Martin, 1916; Crampton, 1917; Snodgrass, 1935).

Thorax

Prothorax. Dorsally (Figure 11) there is a single, large sclerite, the pronotum, which is twice as wide as long and is widest slightly behind the middle. The anterior border is emarginate, forming a recess for the head, the lateral margins are rounded and narrowly flattened, and the posterior margin is straight in the middle half and broadly excavate in the lateral angles. The anterior apices are acutely rounded, whereas the posterior ones are broadly rounded and oblique. Internally from the posterior margin is a phragmal fold lying parallel to the surface of the pronotum. A fringe of long hairs is present on each of the postero-lateral excavations.

Of the sternal sclerites (Figure 12), the large basisternum (Bs_I)is the most extensive. It is wide and short, and is separated from the pleural region by a suture on either side. Centrally the basisternum extends posteriorly between the coxal cavities as a prosternal spine (Psp). In *Anatis* this spine is slightly raised in the centre and has a shallow marginal groove around the apex. The anterior margin of the basisternum is broadly rounded in the middle and bears a fringe of short hairs. The very narrow furcasternum (Fc_1) lies behind the coxal cavities and joins the basisternum on the lateral margins of the spine. Laterally, the furcasternum is fused with the pleuron and bears, internally, a pair of furcal arms.

The pleurites of the prothorax are undefined in the adult, remaining in the undeveloped condition found in the larval stage. From the work of Snodgrass (1935) one would infer that most of the pleural region is made up of the episternum. Such an inference is probably correct since no structure corresponding to the epimeron could be found in any of the insects examined. This region (Pl) extends from the lateral margin of the pronotum to the basisternum in front of the coxae and as a narrow extension covering the lateral portion of the furcasternum behind the coxae. In the membrane between the prothorax and the mesothorax is a pair of large spiracles. Although associated with the prothorax, these spiracles are considered to be mesothoracic in origin (Snodgrass, 1909).

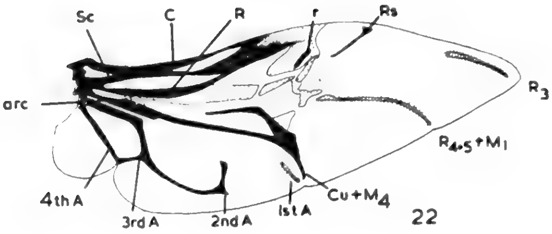
Mesothorax. The mesothorax is a very narrow segment more or less closely applied to the metathorax. Dorsally (Figure 13) it is visible only as a small triangular scutellum ($Sctl_2$) between the bases of the elytra. When the elytra are removed, the mesothorax is seen as two distinct sections. In front of the raised scutellum is a broad prescutum (Psc_2) which is sharply pointed at each antero-lateral corner. The prescutum is marked medially by a long, narrow groove. The scutum (Sct_2) is a narrow sclerite almost hidden in the posterior margin of the prescutum. Laterally it supports the wing processes. The anterior process is small, blunt, and hooked at the anterior end of the scutum. The posterior process is small, nearly flat, and lies at the level of the anterior margin of the scutellum.

The mesothoracic pleurites (Figure 14) are almost identical in size and shape. The episternum (Eps_2) is quadrate; its ventral margin is contiguous with the margin of the sternum whereas the dorsal end bears a rounded projection behind which lies the upper extension of the epimeron. At the antero-dorsal angle is a small L-shaped sclerite which is equivalent to the parapterum (Snodgrass, 1909). At the posterior sternal angle is a small internal condyle for the lateral articulation of the coxa. A well-defined pleural suture (PS_2) separates the pleural sclerites. The epimeron (Epm_2) is, like the episternum, quadrate but not regular in outline. The antero-ventral angle projects slightly into the coxal cavity. The posterior sternal margin lies against the metathoracic episternum. Dorsally the anterior angle lies beneath the head of the episternum and appears again posterior to the parapterum; this is the wing process of the pleuron.

The mesosternum (Figure 15) is a short, wide sclerite extending between the episterna in front of the coxae and projects as a broad, flat extension between the coxal cavities. The sternum is divided into a basisternum (Bs_2) and a furcasternum (Fc_2). The basisternum is that area which can be seen externally, whereas the furcasternum is hidden and forms the anterior edge of the mesocoxal basin. Internally the furcasternum bears a pair of divergent furcal arms (Figure 16F). The anterior edge of the basisternum is declivous and is marked by a shallow, central, triangular pit for the reception of the tip of the prosternal spine.

Metathorax. The metathorax is large and similar in some respects to the mesothorax. The notum (Figure 13) is divided into three sections, the prescutum, scutum, and scutellum. The prescutum (Psc_3) is a narrow, strap-shaped sclerite, fused with the scutum at each side but separated from it along the median part of the anterior margin. The scutum (Sct_3) is the largest of the three parts and is divided by a recurved fold, the W-suture of Snodgrass, which is found only in the anterior half of the scutum. Laterally, the scutum is produced into two wing processes. The scutellum ($Sctl_3$) is very narrow and is expanded as a short sclerite along the posterior margin of the scutum. A very narrow postscutum ($Ptsc_3$) lies just posterior to the margin of the scutellum and is separated from it by a narrow membrane. From the ends of the postscutum narrow sclerotic pieces (i) extend ventrally to connect with the epimeron on each side. From the posterior edge of the postscutum a broad phragma (Ph) (Figure 17) extends internally and ventrally. This phragma is marked by several ridges from the free edge nearly to the base, giving the structure the appearance of a draped curtain. More laterally the same sclerite bears two long phragmata which are broad at their bases but become narrower as they extend ventrally. The pleurites (Figure 14) are complex, elongate sclerites lying for the most part in a horizontal position. The epimeron (Epm) is narrow and is seen as a triangular plate at the lateral edge of the hind coxa in the undissected specimen. When the elytra are removed the rest of the epimeron can be seen extending from the coxa to the base of the wing where it is produced as a wing process. From the dorsal edge of the epimeron is a round flange, the pre-epimeron, behind which is the i-strut joining the epimeron with the postscutum. The deep L-shaped pleural suture (PS) extends from the wing base to the coxal cavity, turning, as it does so, through a complete right angle. In front of and ventral to this suture lies the episternum (Eps). This sclerite is divided into two parts, the more dorsal of which is moderately sclerotized and hidden beneath the folded elytra. The parapterum of the metathorax is fused to the end of this sclerite thereby extending to the episternum part of the function of the wing process. The ventral sclerite of the episternum lies along the whole length of the sternum and is visible when the elytra are closed. The visible part has its edges parallel or slightly divergent posteriorly. At the ventro-posterior corner of the episternum is a small lateral articulation of the coxa.

The broad, slightly convex sternum (Figure 15) is transversely marked by a fine suture just in front of the posterior coxae, which divides the sternum into two sclerites, the basisternum (Bs_3) and a narrower, posterior furcasternum (Fc_3). The basisternum is marked in the anterior half on each side by a ridge, the mesocoxal ridge (Mcl), extending from the inner corner of the mesocoxal cavity almost to the edge of the sternum slightly in front of the mid-point. The mesocoxal plate is concave; its purpose is to receive the femur of the middle leg when this is drawn against the body. The furcasternum forms the anterior wall of the metacoxal basin. Between the coxae, the furcasternum is broadly emarginate to accommodate the first abdominal segment. Internally from the furcasternum is a pair of furcal arms



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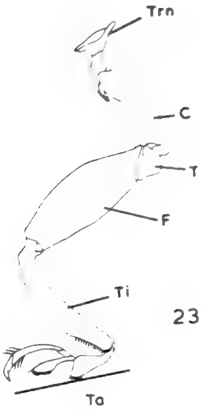

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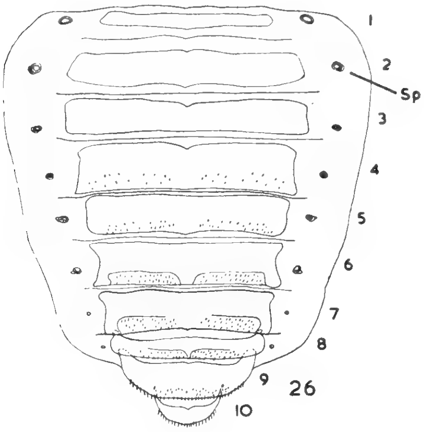

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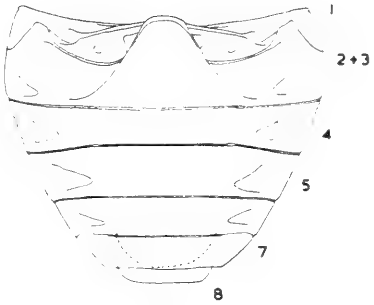

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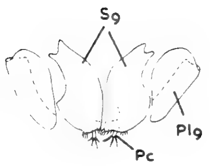

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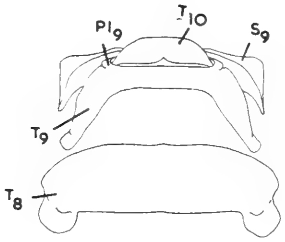

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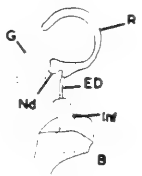

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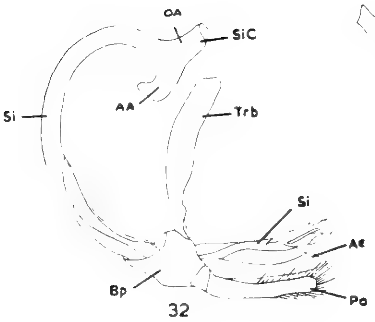

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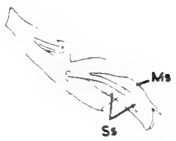

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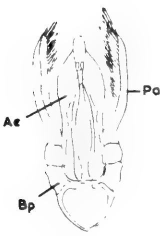

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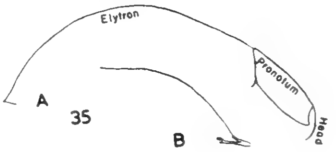

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(Figure 17, Met_3) which are broadly united along the central line. This metendosternite consists of a thin base from which a lateral projection arises on either side bearing dorsal and ventral arms. The dorsal arms are closely associated with the ventral extensions of the postscutum. At the base of each dorsal arm there is a minute projection, the base of the anterior tendon, which projects forward (Crowson, 1938). The coarse intersegmental membrane arises from the base of the metendosternite.

Articular sclerites of the wing. There are three articular sclerites at the bases of both the elytron and the hind wing. Those of the elytron (Figure 18) are small, whereas those of the hind wing (Figure 19), being involved in much greater physical stress, are larger. At the base of the elytron the first and second (I, II) sclerites are fused into a single L-shaped structure. The third (III) is small, quadrate, and closely applied to the pleural parapterum. The sclerite is long and lies almost touching the lateral margin of the scutum. The second sclerite (II) is also elongate and lies against the posterior end of the first; it is slightly arcuate. The third (III) arises at the posterior end of the second and projects as a slender rod in the direction of the hind margin of the wing.

Thoracic Appendages

Elytron. The elytron (Figures 20, 21) is a large, convex structure (see also Figure 35 A, B) lying over the whole of the abdomen; in some gravid females the terga of the seventh and eighth segments may be exposed. The sutural margin is almost straight in the basal two-thirds and is slightly divergent towards the apex. The anterior margin is truncate and the inner corner is obtuse where it fits against the scutellum. The lateral margin is narrowly expanded and is strongly curved from the humeral angle to the apex. This curvature is more noticeable in *Anatis rathvoni* than in the other species; in this species

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PLATE II

Anatis ocellata mali Say

FIGURES 22–35: **22**, Hind wing (veins designated by the Comstock-Needham system). **23**, Foreleg: Trn, trochantin; C, coxa; T, trochanter; F, femur; Ti, tibia; Ta, tarsus. **24**, Hind leg: legend as in Fig. 23. **25**, Pretarsal claw, hind leg. **26**, Abdomen, dorsal view: 1–10, segments: sp, spiracle. **27**, Abdomen, ventral view: 1–8, segments. **28**, Segment 9, female, ventral aspect: Pl_9, pleuron; So, sternum; Pc, pseudocercus. **29**, Genital segments, male, dorsal aspect: T_8-T_{10}, terga; Pl_9, pleuron of ninth segment; S_9, ninth sternum. **30**, Ninth segment, male, ventral aspect: Apo, apodeme; S_9, ninth sternum. **31**, Spermatheca and accessory organs: B, bursa; ED, efferent duct; G, accessory gland; Inf, infundibulum; Nd, nodus; R, ramus. **32**, Male genitalia: AA, adjacent arm; Ae, aedeagus; Bp, basal plate; OA, opposite arm; Pa, paramera; S, sipho; SiC, siphonal capsule; Trb, trabes. **33**, Apex of sipho: Ms, membranous sac; Ss, sclerotic spicules. **34**, Genitalia without sipho or trabes, dorsal aspect: legend as in Fig. 32. **35**, Outline of: A, body, lateral aspect; B, elytron, cross section.

there is a decided angle just before the middle of each margin. At the humeral angle is a prominent humeral callus. The surface of the elytron is finely and evenly punctate, the punctures being separated by their own width. Ventrally, the surface is relieved by a narrow sutural margin, a complex anterior margin bearing the articular surfaces for the wing sclerites, and a wide lateral margin (epipleuron). This last is flat for most of its length but becomes convex in the apical third and closely united with the body of the elytron. This flat shelf is widest in the middle. Along the internal edge of the epipleuron is a declivous fold which disappears in the apical third.

Hind wing. The hind wing (Figure 22) has a sinuous anterior margin, an acute apex, and a gently curving hind margin which is slightly indented at the apices of the veins. This is most noticeable in the anal region where there is a well-defined cleft separating the anal lobe from the rest of the wing membrane. Although much reduced, the venation is still quite complex; it is of the typical cucujoid type with median and recurrent veins. Despite the fact that some of the veins are absent, their former course is marked by a series of deeply pigmented areas or flecks (Crowson, 1952). The venation can be more easily associated with the interpretation of Forbes (1922) than with that of Graham (1922).

The anterior edge of the wing is thickened by the costa (C) which extends as far as the hinge. Behind the costa, and joined with it for part of its length, is the subcosta (Sc); this vein is thickened at its outer end. In the basal area, the radius (R) extends from the base of the wing and, sweeping forward, joins the subcosta at the hinge. At about one-third of its length, the radius gives rise to a series of patches which together make up the basal part of the radial sector. This series of patches continues as a well-defined vein (Rs) behind the hinge to the margin of the wing in front of the apex. In the hinge itself is a small vein often bearing two or three setae; this vein may be considered as the radial cross-vein (r) between the radius and the radial sector. In the apex is a long pigmented area which, if produced, would join the radial sector at about the same point as does the radial cross-vein; this vein is R_3.

Half-way along the radius between its base and that of the radial sector is a short, oblique cross-vein, the arculus (arc.). From near the radial end of the arculus arises a short stub which, if produced, joins the free end of the central vein, the median recurrent. In its outer portion the median vein turns away from the radius to join the cubitus (Cu) as M_4. In the outer membrane of the wing at the level of the median is a second elongate patch. This may be produced to meet the median and hence may be considered as a remnant of M_1 but since there is also some evidence of a connecting vein between this and the radial sector, R_{4+5} must be included with M_1.

Passing behind the arculus is the cubitus which turns sharply to the margin of the wing where it joins with M_4 to become M_4+Cu. Immediately behind and contiguous with the cubitus at its base is the base of the first anal vein. The central portion of this vein has been lost but the apex appears just posterior to the M_4+Cu complex. The base of the second anal vein (2nd A) is present, lying directly behind the base of the first anal. Like the first, the central portion of this vein is missing. The vein reappears however, lying in an antero-posterior direction in the anal membrane and joins a marginal vein near the edge of the wing. The third anal vein (3rd A) lies behind and is contiguous with the base of the second anal vein from which it turns sharply to the margin of the wing. About half-way to the margin of the wing this vein divides into two branches, one away from the body (3rd A_1) and one towards the body (3rd A_2). The first branch joins the apex of the 2nd anal vein and together the two veins continue for a short distance beyond this junction as 2nd A+3rd A_1. The fourth anal vein (4th A) is short and lies obliquely across the anal lobe. This vein extends to the margin of the wing where it is joined by the 3rd A_2.

Legs. The structure of the three pairs of legs (Figures 23, 24) is very similar. The trochanter (T) is cuboid and broadly abuts the end of the femur. The femur is broadest in its distal half and bears a shallow groove along the inner surface. The tibia (Ti), which is almost as long as the combined lengths of the femur and trochanter, is slender and cylindrical. It is weakly expanded across the apex where there is a short groove on the outer side. A row of coarse setae is borne along the outer apical margin and across the apex where there is also a pair of stout, short spines. The tarsus (Ta) is composed of four segments; the first is long, slightly excavate at the apex and is covered ventrally with coarse, short setae; the bilobed second segment, shorter than the first, is expanded distally, and its surface too is covered with coarse setae. At the basal end of the broad excavation on the second segment arises the narrow, short, cylindrical third segment. From the apex of this segment arises the long, curved fourth segment. The fourth segment is conical, broadest at the apex, and bears at its apex the much reduced pretarsus. In *Anatis* this pretarsus consists of a pair of tarsal claws (Figure 25) and the membrane which connects them. Each claw is broad at the base and tapers to a curved point; each bears a large basal tooth.

The greatest anatomical difference in the legs is to be found in the size and shape of the coxae. The coxae of the first pair of legs are slender and quadrate with emarginate antero-lateral borders. The lateral articulation of each is joined to a small hook-like trochantin (Tr) which in turn connects with the pleural region of the prothorax. The coxae of the middle legs are globular. In the hind leg the coxa is stout, elongate, and has a wide base. In its posterior margin is a deep groove for the reception of the femur.

Abdomen

Pregenital segments. Segments one to eight are completely represented dorsally (Figure 26) and are fairly homogeneous in structure. The terga are weakly sclerotized, oblong plates separated by wide intersegmental membranes. The terga of the first three segments are shorter than the others. Segments four to eight bear setiferous areas in the posterior half of each segment, these areas being well-defined in segments five to seven. Lateral to the sclerotized terga are broad, membranous pleural sheets in which the segmentation is almost absent. Simple annular spiracles are present on all these segments; those of the first segment are somewhat larger than the others and lie close to the metepimeron. The spiracles of segments two to six are small and circular, whereas those on segment seven are minute and, although joined by a large tracheal trunk to the other spiracles, are not likely functional.

Ventrally (Figure 27) the abdominal segments are completely sclerotized. Segment one has been reduced to a narrow margin fused with the anterior edge of the first visible segment which is composed largely of segments two and three, the remnant of two being hidden for the most part by the metacoxae. This first visible segment is projected forward in the middle of the anterior margin between the coxae as a broad rounded lobe. The lateral surfaces of the segment are marked by oblique lines (metacoxal lines) which enclose the metacoxal plates. These lines, one on each side of the segment, begin in the inner corners of the coxal cavities and extend almost to the posterior margin of the segment half-way between the mid-line and the lateral edge. Hence these lines are considered to be incomplete. A complete line is one which forms a complete arc terminating at the outer edge of the coxal cavity, e.g. in *Hippodamia.*

The sterna of segments four to seven are alike in structure; each is narrower than the one before. The eighth sternum is much narrower than the seventh and lies partly dorsal to it; the intersegmental connections extend almost to the sixth sternum internally.

Genital Segments. The ninth and tenth segments of the abdomen are considered to be the genital segments. The structure of these segments is different in each sex.

Female. The ninth and tenth segments (Figures 26, 27) of the female are dissimilar. The ninth segment resembles the eighth but lacks the membranous pleural plates found in the latter, having instead well-defined sclerotic plates. The sternum (Figure 28) of this segment is divided into two arcuate plates, each having a bifurcate base, and bearing a pseudocercus (pc). In *Anatis* the pseudocerci are elongate and bear several long, stiff hairs. The tenth segment consists principally of a small tergum, the anterior corners of which are produced under the ninth segment; also, the anterior border of this segment is emarginate medially. There are no pleura. The sternum of this segment, if present, is reduced to a narrow membrane between the anus and the gonopore. The ninth and tenth terga and the ninth substernum bear fringes of setae.

Male. The ninth tergum (Figure 29) is sclerotized. Its anterior corners are produced to the front of the eighth tergum and its anterior margin is straight. The lateral margins of this tergum are directed ventrad and the pleural sclerites are fused with the posterior edge of this folded portion. The sternum (Figure 30) of the ninth segment is membranous and, from the membrane, a long apodeme projects forward into the body cavity. The tenth segment, like that of the female, is simply a narrow rounded tergum, the anterior border of which is emarginate. There are no pleura and the sternum, if present, is membranous.

Genitalia

Only those structures which are sclerotized, or partly so, will be considered here.

Female. The female genitalia (Figure 31) lie within the posterior half of the abdomen and consist of a spermatheca, an infundibulum surrounding the ductus, and a bursa. The spermatheca is a slender arcuate cylinder composed of three parts; a ramus, a nodus, and a base. The ramus (R) is a long, free, arcuate structure which is bluntly rounded at the distal end and usually annulate, at least in the central portions. It has been shown (Camargo, 1937) that, in some genera at least these annulations are actually on a cylinder within the ramus. The nodus (Nd) is cylindrical and short providing an entrance for the spermathecal glands (G). The base (B) has a nipple-like projection from which arises the efferent duct (ED). Around this duct is a chitinous collar covering the distal half of the ductus before it enters the bursa. This collar is the infundibulum (Inf) and is thick, with its base expanded in the form of a triangular plate applied to the surface of the bursa. The bursa is a long membranous sac without armature on the walls.

Male. The complex male genitalia (Figures 32, 33, 34) lie in the left side of the abdomen and consist essentially of two tubes, one moving back and forth within the other, the latter of which is capable of limited movement in the same direction.

The more movable part is the sipho (Si), an elongate, arcuate tube, the free end of which is expanded into a siphonal capsule (SiC). In *Anatis* this capsule has two arms, one opposite (extending away from the sipho), one adjacent (lying towards the sipho). The opposite arm is short, narrower at the distal end than at the base, and is somewhat excavate. The adjacent arm is hooked at the distal end and has a slight prominence where it joins the sipho. In the middle third the sipho is open forming a trough with thinly sclerotized sides and a sclerotized rod closing it dorsally. The trough is closed again in the slender apical third at the end of which is an expanded, complex membranous sac (Figure 33). The end of the sipho is emarginate and somewhat longer dorsally than ventrally, and from the irregular margin so formed the membranous sac arises. Laterally the sac is supported by slender, sclerotized spicules and dorsally it is bounded by a thinly sclerotized hood which also extends around the sides of the sac.

The more immobile parts of the genitalia (Figure 34) consist of a basal plate, median lobe or aedeagus, paramera or lateral lobes, and the trabes, a heavy median piece articulating with the basal plate ventrally. The basal plate (Bp), from which the other pieces arise, forms a collar through which the sipho moves. This plate is elongate dorsally and bends around to form a broad side wall on either side of the siphonal orifice. Ventrally, the side walls are connected by a slender isthmus making the basal plate complete. Medially the basal plate joins the median lobe or aedeagus (Ae). This lobe is hollow and the ventral surface is incomplete so that the sipho may be thrust through the median lobe during copulation. In *Anatis ocellata mali* Say the median lobe narrows to a short, slender, blunt apex. In *Anatis rathvoni* Lec. the aedeagus has slightly divergent sides to about two-thirds of its length from the base and then narrows abruptly and forms a slender blunt point. In *Anatis o. ocellata* L. the aedeagus is widest in the middle where it is about half as wide as in *A. o. mali.*

In *A. o. mali* the ventral surface of the apex of the median lobe bears a pair of oval pads. The open ventral surface is partly covered by a pair of membranous folds, the ventral alae. In the undissected specimens, the sipho occupies this space so that the ventral alae are pushed outward to form a V-shaped trough over the end of the sipho.

On either side of the median lobe, and articulating by broad acetabula with the basal plate, are the paramera. These are thick, slightly curved structures which are slightly longer than the median lobe in *A. ocellata.* In *A. rathvoni* the paramera are equal in length to the median lobe, and in *A. quindecimpunctata* they are slightly shorter than the median lobe. In all the species the paramera bear fringes of long hairs on the apices. Setae may also be found on the ventral, and to a lesser extent, on the dorsal crest of the paramera.

The trabes (Trb) is long and paddle-shaped, and arises from between the lateral walls of the basal plate behind the isthmus. There is a curious twist of about 90° in the blade of the trabes forming a crest along the posterior edge (compare also Figures 36 and 41).

In function the sipho is the actual intromittent organ, the median lobe serves as a guide, and the paramera as the claspers for grasping the sides of the female abdomen. The trabes is apparently the fulcrum for the attachment of the muscles required to move the sipho. The paramera have their own sets of motor muscles internally.

Comparative Anatomy

Most of the structures in the members of the Coccinellini reveal variations in form which indicate quite clearly possible directions of evolution. These directions are indicated most clearly by the structures discussed in this section. It must be borne in mind that other structures could also be used which would indicate similar evolutionary trends.

Male Genitalia (Plates III-V)

Paramera. The paramera may be short (less than two-thirds the length of the aedeagus) or they may be long, as they are in most genera. In *Hippodamia* (Figures 39, 63), *Coccinella* (Figures 45, 68), and *Semiadalia* (Figures 36, 59), the paramera are short and thick with nearly parallel sides and rounded apices. The fringe of hairs extends further towards the base of the upper edge (in the figures) except in *Hippodamia* where there are a few more hairs on the lower side. In *Semiadalia* the upper edge is slightly angulate. *Adonia* (Figures 37, 60) and *Aphidecta* (Figures 57, 74) have short paramera but differ from the genera mentioned above. In *Adonia* the paramera are tubular, curved a little dorsally, and each bears a patch of hairs near the apex. In *Aphidecta* the paramera are very short and conical with an acute apex, and with a fringe of hairs extending well along the dorsal edge and only slightly along the ventral edge.

Of those genera which have long paramera some are straight. In *Synharmonia* (Figures 58, 76) and *Harmonia* (Figures 46, 71) the paramera have broad bases. *Synharmonia* has a fringe of hairs along both edges with a group of setae at the apex. *Harmonia* has a swollen apex with a fringe of long hairs arranged about it; the hairs do not extend basally along the shaft. In *Eriopis* (Figures 44, 56), *Hysia* (Figures 47, 78), *Neopalla* (Figures 56, 77), and *Neocalvia* (Figures 52, 79) the paramera have narrow bases. In *Eriopis* the fringe of hairs is extensive along the dorsal edge and on the apex but does not appear along the ventral edge. *Neocalvia* has a short fringe of long hairs around the apex and along the dorsal edge. In *Hysia* the fringe extends for a short distance along the ventral edge as well. In *Neopalla* the hairs are very long, denser at the apex, and extend a long way towards the base dorsally and ventrally.

The genus *Ceratomegilla* (Figures 38, 61) has long, tubular paramera which are a little swollen at the apices and are directed ventrally. The fringe of hairs extends over the apex and slightly along the dorsal


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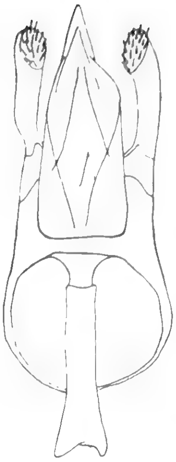
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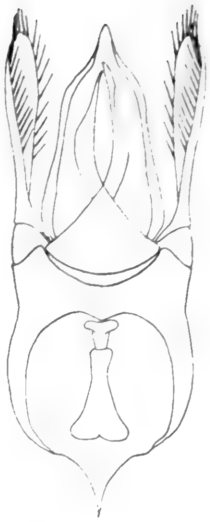
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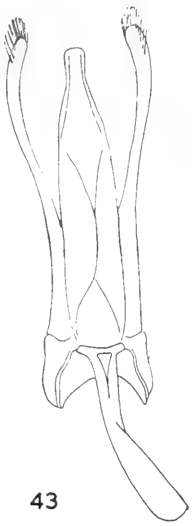
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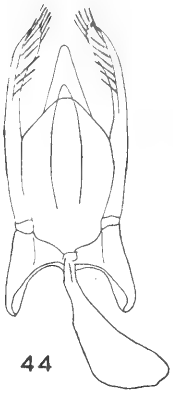
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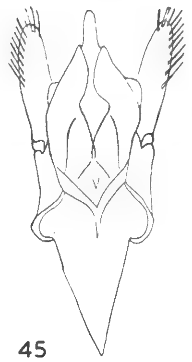
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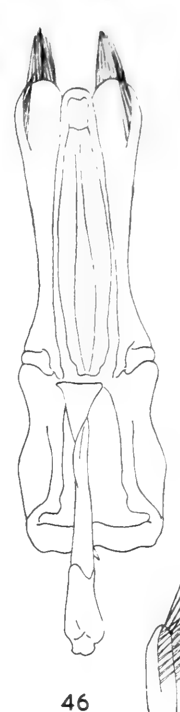
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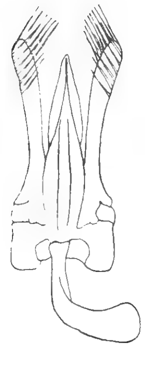
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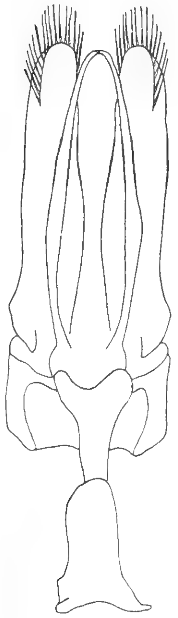
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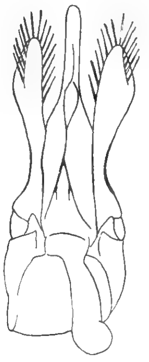
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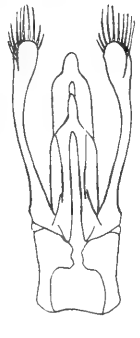
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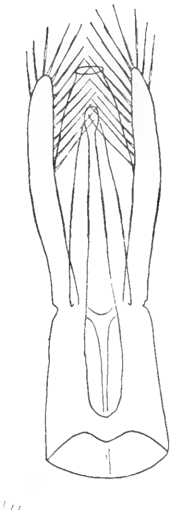
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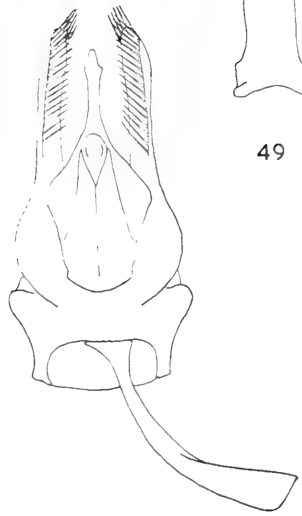
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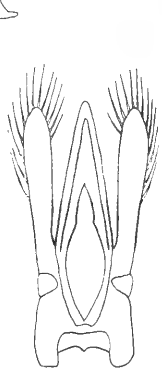
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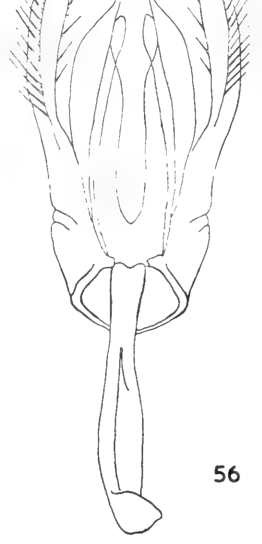
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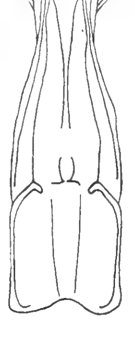
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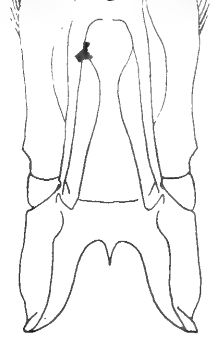
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edge. *Macronaemia* (Figures 49, 64) has paramera which are bent dorsally so that the dorsal edge is angulate, a condition not found in other genera. In this genus the fringe of hairs is restricted to the narrow apex and for a short distance along the two edges.

The remaining genera have long, curved paramera. In *Coleomegilla* (Figures 40, 69) and *Naemia* (Figures 41, 66) the curvature is dorsal and is restricted to the apical third. In these two genera the fringe of hairs extends over the apex and for a short distance along the ventral edge, while along the dorsal edge the fringe is very sparse and continues almost to the base. In *Paramaemia* (Figures 43, 67) the curvature is continuous to the base but the fringe of hairs is like that in *Naemia. Anisosticta* (Figures 42, 62) has a fairly sharp dorsal curvature, and the fringe of hairs extends over a much greater distance along the ventral edge than in the previous genera. In *Isora* (Figure 75) and *Adalia* (Figures 50, 73) the paramera are curved dorsally from the base and then slightly recurved. This is much more pronounced in *Adalia.* The fringe of hairs is shorter in *Adalia* than in *Isora,* where they extend for a much greater distance along the dorsal edge.

Basal plate and trabes. The basal plate varies in size among the genera of this tribe. In some genera, e.g. *Neomysia* (Figure 53) it is very broad, whereas in other genera, e.g. *Hysia* (Figure 47) the plate is narrow and elongate. In most genera the anterior margin of the plate is simple, e.g. *Adonia* (Figure 37), whereas in others, e.g. *Coccinella* (Figure 45) and *Hippodamia* (Figure 37), the margin forms a spinous process. This process, however, is variable, for many of the Old World species of *Coccinella* lack the spine. The same sort of variability is seen among the species of *Hippodamia.*

The trabes may be thick and in one plane throughout its length and may have a swollen, slightly emarginate apex, as in *Ceratomegilla* (Figure 61), *Adonia, Hippodamia* (Figure 39), and *Semiadalia.* The distal portion of the trabes is twisted through 90° in all the rest of the genera, except *Adalia.* With this twist the trabes becomes spatulate

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PLATE III

Aedeagus, dorsal aspect, without sipho

FIGURES 36–58: **36**, *Semiadalia notata* Laich; **37**, *Adonia variegata* Goeze; **38**, *Ceratomegilla ulkei* Crotch; **39**, *Hippodamia convergens* Guérin; **40**, *Coleomegilla cubensis* Timberlake; **41**, *Naemia seriata* Melsheimer; **42**, *Anisosticta* sp.; **43**, *Paranaemia vittigera* Mannerheim; **44**, *Eriopis connexa* Germar; **45**, *Coccinella transversoguttata* Fald.; **46**, *Harmonia quadripunctata* Herbst; **47**, *Hysia endomycina* Boisduval; **48**, *Mysia oblongoguttata* (Linnaeus); **49**, *Macronaemia episcopalis* Kirby; **50**, *Adalia bipunctata* (Linnaeus); **51**, *Calvia decimguttata* (Linnaeus); **52**, *Neocalvia anastomozans* Crotch (after Camargo); **53**, *Neomysia* sp.; **54**, *Anisocalvia duodecimmaculata* Gebl.; **55**, *Propylaea quatordecimpunctata* (Linn.); **56**, *Neopalla hydropicta* (Muls.); **57**, *Aphidecta obliterata* (Linnaeus); **58**, *Synharmonia conglobata* (Linnaeus).


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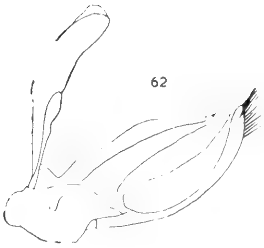
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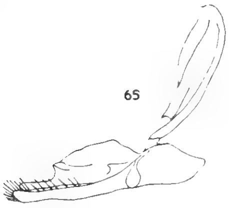
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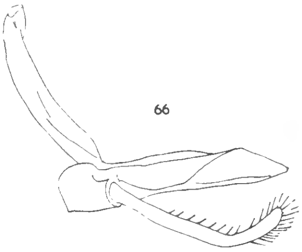
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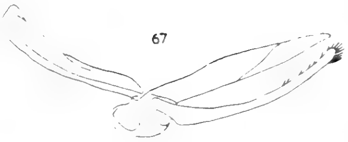
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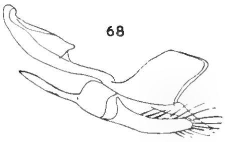
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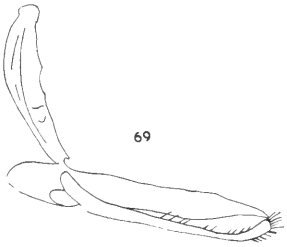
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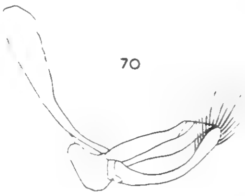
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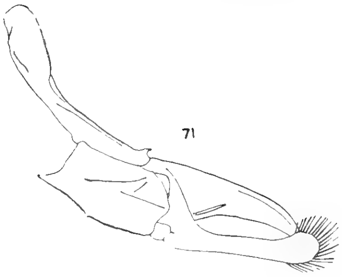
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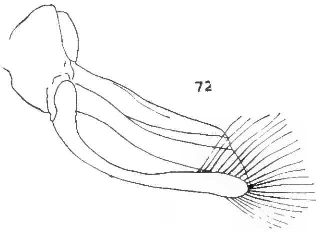
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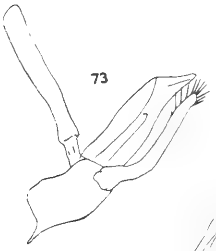
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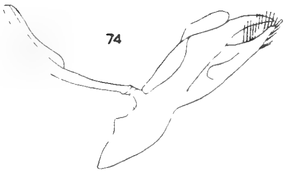
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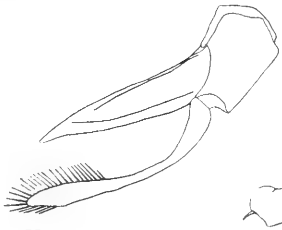
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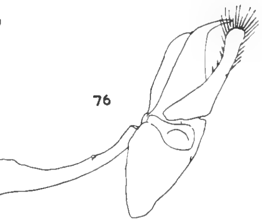
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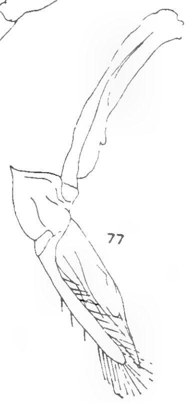
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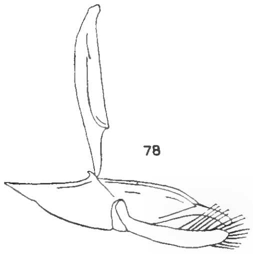
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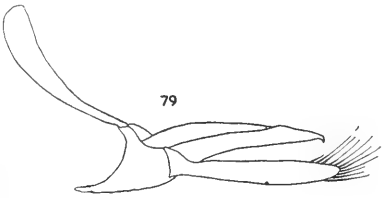
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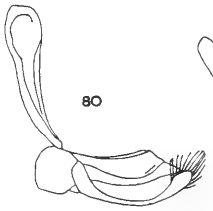
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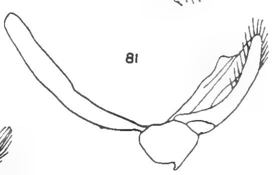
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and thin with a crest extending for much of its length. The genus *Adalia* exhibits a form of trabes which is cylindrical, peg-like, and has a basal constriction. Apically this structure is expanded into a rounded knob.

Aedeagus. The aedeagus may be of two types. It may be slender and elongate, e.g. *Coleomegilla* (Figure 69), or thickened and high-crowned, e.g. *Semiadalia* (Figure 59). Those genera which have a thickened aedeagus usually have well developed ventral alae. *Ceratomegilla* is an exception, having well-developed ventral alae but a narrow aedeagus. On the other hand, *Adonia* has a thick aedeagus but weak, membranous ventral alae. High membranous ventral alae are also found in members of the genus *Coccinella.*

Where the aedeagus is narrow, the ventral alae are always membranous. There is some variation in the direction of the apex of the median lobe. In most genera the apex is straight but in *Anisosticta* (Figure 62) it is directed dorsally, and in *Neocalvia* (Figure 79) and *Synharmonia* (Figure 75) it is directed ventrally.

In most of the genera the aedeagus gradually narrows to a slender, rounded apex, e.g. *Naemia.* In other genera the broadest part of the aedeagus is in the middle, e.g. *Neopalla, Coccinella.* In still others, the aedeagus has almost parallel sides, e.g. *Synharmonia, Calvia.*

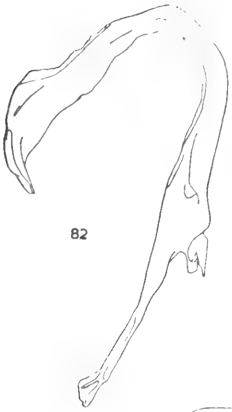
The form of the apex is variable. In *Hippodamia, Adonia,* and *Eriopis* it is very sharp, in *Anisocalvia* it is sharp but has a long narrow shaft which widens just before the apex, and in *Aphidecta, Synharmonia,* and *Naemia* it is emarginate. In most of the other genera the aedeagal apices are narrow, bluntly rounded at the end of a short shaft which is narrower than the rest of the aedeagus.

The aedeagus of *Ceratomegilla* is, in many ways, one of the most complex to be found in any members of this tribe. The margins are deeply concave in the basal half, swollen at the centre, and then quickly narrowing to a moderately long, sinuately margined apical shaft.

PLATE IV

Aedeagus, lateral aspect, without sipho

FIGURES 59–81: **59**, *Semiadalia notata* Laich; **60**, *Adonia variegata* Goeze; **61**, *Ceratomegilla ulkei* Crotch; **62**, *Anisosticta* sp.; **63**, *Hippodamia convergens* Guérin; **64**, *Macronaemia episcopalis* Kirby; **65**, *Eriopia connexa* Germar; **66**, *Naemia seriata* Melsheimer; **67**, *Paranaemia vittigera* Mannerheim; **68**, *Coccinella transversoguttata* Fald.; **69**, *Coleomegilla cubensis* Timberlake; **70**, *Mysia oblongoguttata* (Linnaeus); **71**, *Harmonia quadripunctata* Herbst; **72**, *Neomysia* sp. **73**, *Adalia bipunctata* (Linnaeus); **74**, *Aphidecta obliterata* (Linnaeus); **75**, *Isora anceps* Mulsant; **76**, *Synharmonia conglobata* (Linnaeus); **77**, *Neopalla hydropicta* (Muls.); **78**, *Hysia endomycina* Boisduval; **79**, *Neocalvia anastomozans* Crotch (after Camargo); **80**, *Calvia decimguttata* (Linnaeus); **81**, *Propylaea quatordecimguttata* (Linn.).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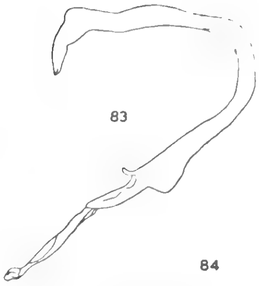
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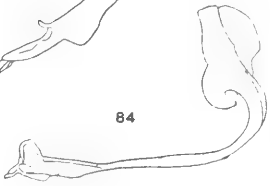
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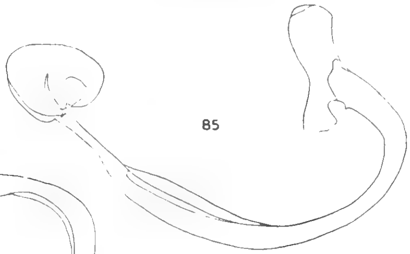
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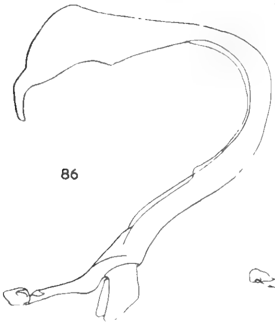
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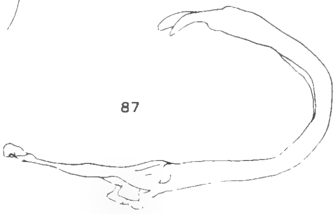
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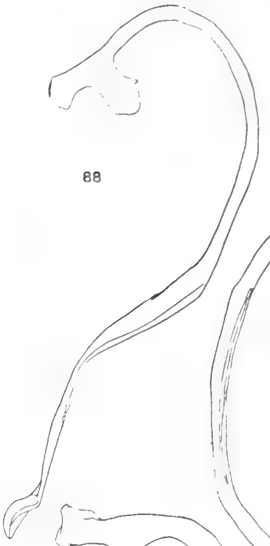
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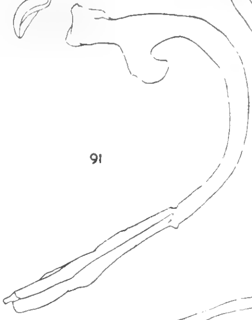
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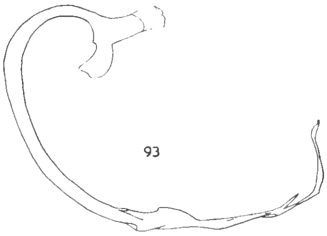
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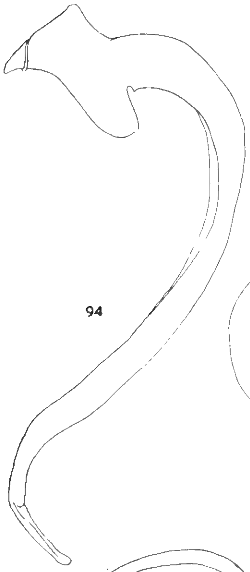
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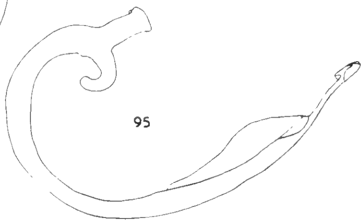
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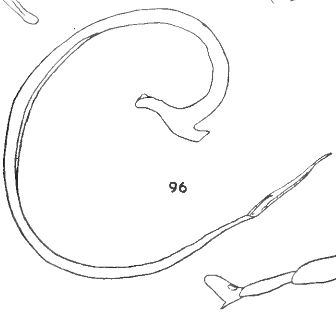
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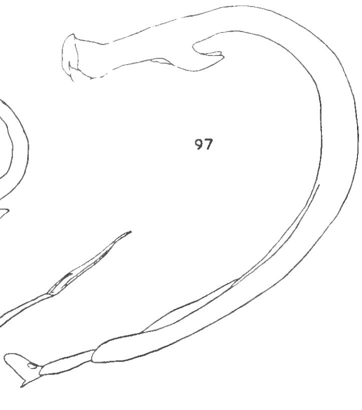
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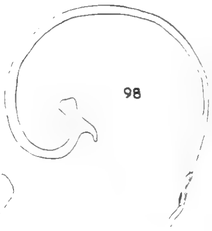
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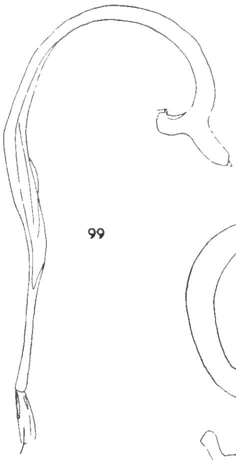
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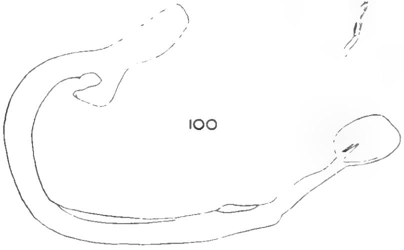
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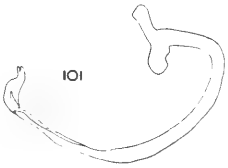
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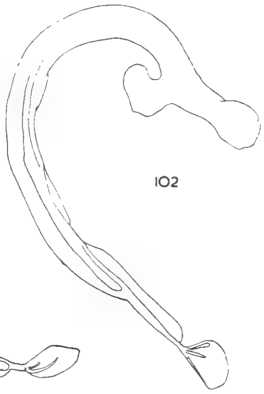
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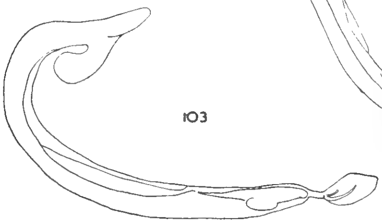
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Sipho. Among the genera of this tribe there are two, and possibly three, distinct types of sipho, easily separable by the shape of the siphonal capsule. In *Semiadalia* (Figure 82), *Adonia* (Figure 83), *Hippodamia* (Figure 86), and *Ceratomegilla* (Figure 87) the capsule is flattened and spatulate with, usually, a bifurcate apex. The capsule may be bent at right-angles to the sipho as in *Adonia,* or it may be a continuation of the sipho itself as in *Ceratomegilla.* In all these genera the sipho is sharply angulate with a straight (*Semiadalia, Adonia*) or slightly angulate (*Hippodamia*) apex. The base of the apical third is complicated by the presence of ventral valves of which there may be as many as three pairs. In *Adonia* these valves are mere triangular projections, but in the other genera they are well-developed, flap-like valves. The apex of the sipho is complex and supports, at its tip, a small membranous sac which has several supporting, chitinous rods.

A second type is that found in *Coccinella* (Figure 84) in which the siphonal capsule has a large, lunate crest along its dorsal edge. The bipartite capsule has a large opposite arm and a short, sharply curved adjacent arm. The sipho is sharply turned and is straight in the apical third. At the apex there is a complex sac on which there is a high dorsal prominence.

All the other genera which were examined in this tribe have a simple, bipartite siphonal capsule and, in most, the arms of the capsule are easily recognizable. In *Anisosticta* (Figure 90) and *Macronaemia* (Figure 94), the capsule is large, with the arms losing their definition. In *Neomysia* (Figure 98), the opposite arm is reduced to a small, narrow protuberance.

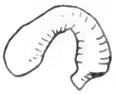
At the base of the adjacent arm in some genera is a small hook *Adalia* (Figure 85), and *Paranaemia* (Figure 92). In *Neopalla* this projection has moved to a position on the adjacent arm.

In *Adalia, Hysia* (Figure 100), *Synharmonia* (Figure 102), and *Neocalvia* (Figure 103), the apex is inflated into a large, membranous sac. In the other genera the apex is either slightly inflated or is slender.

PLATE V

Sipho, lateral aspect

FIGURES 82–103: **82**, *Semiadalia notata* Laich; **83**, *Adonia variegata* Goeze; **84**, *Coccinella transversoguttata* Fald.; **85**, *Adalia bipunctata* (Linnaeus); **86**, *Hippodamia convergens* Guérin; **87**, *Ceratomegilla ulkei* Crotch; **88**, *Coleomegilla cubensis* Timberlake; **89**, *Naemia seriata* Melsheimer; **90**, *Anisosticta* sp.; **91**, *Eriopis connexa* Germar.; **92**, *Paranaemia vittigera* Mannerheim; **93**, *Calvia decimguttata* (Linnaeus); **94**, *Macronaemia episcopalis* Kirby; **95**, *Aphidecta obliterata* (Linnaeus); **96**, *Mysia oblongoguttata* (Linnaeus); **97**, *Harmonia quadripunctata* Herbst; **98**, *Neomysia* sp.; **99**, *Propylaea quatordecimpunctata* (Linn.); **100**, *Hysia endomycina* Boisduval; **101**, *Anisocalvia duodecimmaculata* Gebler; **102**, *Synharmonia conglobata* (Linnaeus); **103**, *Neocalvia anastomozans* Crotch (after Camargo).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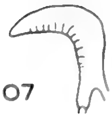
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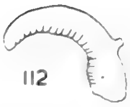
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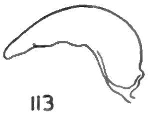
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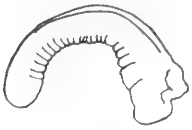
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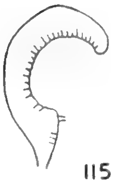
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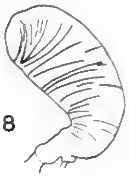
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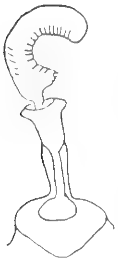
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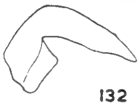
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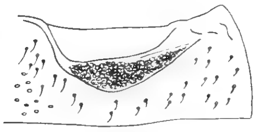
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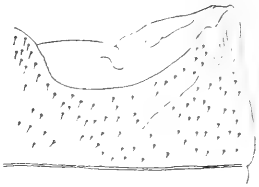
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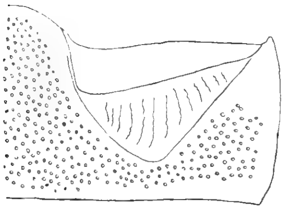
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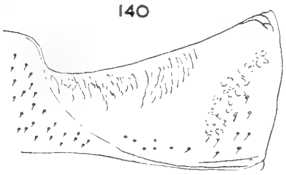
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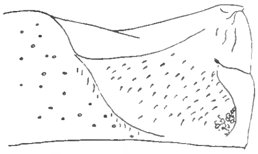
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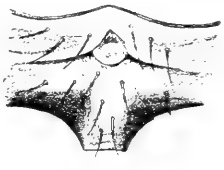
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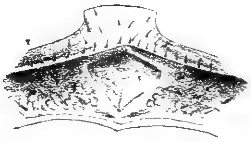
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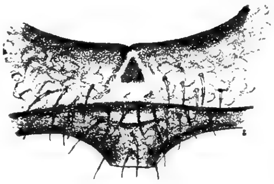
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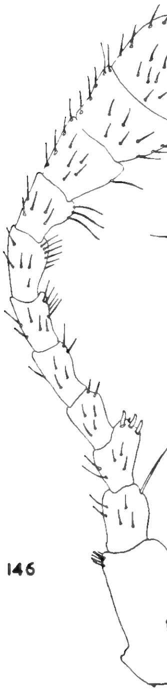
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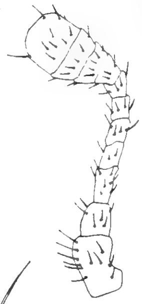
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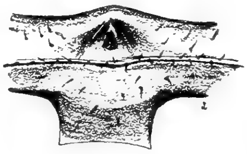
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In *Harmonia* (Figure 97) and *Aphidecta* (Figure 95), there is a low, dorsal crest in the middle third of the sipho.

The sipho may be strongly curved as in *Neomysia* (Figure 96), straight in the apical half as in *Eriopis* (Figure 91), or gently curved as in *Coleomegilla* (Figure 88) and *Naemia* (Figure 89), or it may be sharply curved as in *Macronaemia* and *Anisosticta.*

Female Genitalia (Plate VI, Figures 104–121)

In the spermatheca the only change is a gradual straightening of the ramus as seen in *Macronaemia* (Figure 105), *Myrrha* (Figure 118), and *Bulaea* (Figure 117). In these genera the apex of the ramus is usually rounded. In *Adalia* (Figure 100) and *Anisosticta* (Figure 111), the apex is short but sharp, whereas in *Megillina* (Figure 107) and *Sospita* (Figure 113) the apex is long and pointed. In this last genus the annulations are missing from the ramus.

Some genera show a much more deeply arched ramus than usual,

PLATE VI

Spermatheca

Figures 104–121: **104**, *Eumegilla conterminata* Mulsant; **105**, *Macronaemia episcopalis* Melsheimer; **106**, *Coleomegilla maculata* De Geer; **107**, *Megillina voeltkowi* Weise; **108**, *Hippodamia convergens* Guérin; **109**, *Anatis ocellata mali* Say; **110**, *Adalia bipunctata* (Linnaeus); **111**, *Anisosticta* sp.; **112**, *Adaliopsis alpina* Villa; **113**, *Sospita vigintiguttata* (Linnaeus); **114**, *Neopalla lebasi* (Muls.); **115**, *Neocalvia anastomozans* Crotch (after Camargo); **116**, *Anisocalvia quatordecimguttata* Gebler; **117**, *Bulaea lichatschovi* Hummel; **118**, *Myrrha octodecimguttata* (Linnaeus); **119**, *Neomysia* sp.; **120**, *Calvia oblongoguttata* (Linnaeus); **121**, *Coccinella transversoguttata* Fald.

Figure 122: *Hippodamia convergens* Guérin; first segment, hind tarsus, male.

Figure 123: *Adonia variegata* Goeze; first segment, hind tarsus, male.

Figures 124–128, Hind femur: **124**, *Coleomegilla maculata* De Geer; **125**, *Eumegilla conterminata* Mulsant; **126**, *Hippodamia tredecimpunctata* (Linn.); **127**, *Coccinella transversoguttata* Fald.; **128**, *Harmonia quadripunctata* (Linnaeus), also hind tibia (right).

Figures 130–139, Pretarsal claws: **130**, *Adalia bipunctata* (Linnaeus); **131**, *Calvia quatordecimguttata* (Linn.); 132, *Propylaea quatordecimpunctata* (Linn.); **133**, *Hysia endomycina* Boisduval; **134**, *Neopalla hydropicta* (Muls); **135**, *Adonia variegata* Goeze; **136**, *Hippodamia tredecimpunctata* (Linn.); **137**, *Neomysia* sp.; **138**, *Eriopis connexa* Germar; **139**, *Naemia seriata* Melsheimer.

Figure 140: *Macronaemia episcopalis* Melsheimer, mesocoxal plate.

Figures 141–145, Metacoxal plate: **141**, *Ceratomegilla ulkei* Crotch; **142**, *Coleomegilla cubensis* Timberlake; **143**, *Bulaea lichatschovi* Hummel; **144**, *Propylaea quatordecimpunctata* (Linn.); **145**, *Neopalla hydropicta* (Muls.).

Figures 146–149, Antenna: **146**, *Semiadalia notata* Laich; **147**, *Tyttahaspis sedecimpunctata;* **148**, *Coleomegilla maculata* De Geer; **149**, *Myrrha octodecimguttata* (Linnaeus).

Figures 150–156, Anterior face of mesosternum: **150**, *Coleomegilla cubensis* Timberlake; **151**, *Hippodamia convergens* Guérin; **152**, *Semiadalia notata* Laich; **153**, *Neopalla hydropicta* (Muls.); **154**, *Tyttahaspis sedecimpunctata* (Linn), lateral view of anterior face; **155**, *Sospita vigintiguttata* (Linnaeus); **156**, *Bulaea lichastschovi* Hummel.

e.g. *Calvia* (Figure 120), *Anisocalvia* (Figure 116), and *Neomysia* (Figure 119). *Neocalvia* (Figure 115) presents a wide curvature that is not as deep as in *Calvia. Adalia* has a ramus which is straight in the middle third, from which both the apex and the nodus are sharply curved. *Eumegilla* (Figure 104) has a sharply curved ramus, but the apex is greatly swollen.

The form of the nodus is variable. In some genera (*Megillina, Coleomegilla, Anisosticta*) it is barely distinguishable from the body, whereas in other genera (*Adalia, Neopalla, Coccinella, Anatis*) the nodus is quite large.

Infundibula are present in *Coccinella* (Figure 121), *Anatis,* and *Hippodamia.* In *Coccinella* and *Anatis* the infundibulum is a complicated structure, whereas in *Hippodamia* it is reduced to a slender sclerotized column surrounding the lower portion of the ductus.

Leg Structures (Plate VI, Figures 122–139)

Even though the structure of the legs is fairly constant throughout the members of this tribe, there are certain differences which appear to be of importance. These differences are apparent in the form and extent of the grooves on the femur and tibia. Also, in the genera *Adonia* (Figure 123; compare with Figure 122) and *Semiadalia* the first segment of the fore tarsus and the middle tarsus in the males is strongly dilated. In *Calvia* and *Anisocalvia* the width of the tibia is a little greater than usual. Differences that are present are usually found on all legs but in some cases are more marked in the front pair.

In one group of genera the femoral grooves are less noticeably margined. They may be long and shallow, e.g. *Coleomegilla* (Figure 124), *Paranaemia;* or all but absent, e.g. *Eumegilla* (Figure 125); or they may be deep but without sharp edges (*Naemia, Macronaemia, Megillina*). In all these forms, except *Megillina,* the groove of the tibia is very slight or is entirely missing. In *Coleomegilla* and *Paranaemia* the tibia has a long flattened area. In *Coleomegilla* this is more developed in the hind leg where there is also a long, low carina. In *Eumegilla* there is a sharp, high ridge along the outer edge of the fore tibia which is not so well marked in the other legs.

Ceratomegilla and *Hippodamia* (Figure 126) have long femoral grooves which do not continue on to the trochanter. In *Semiadalia* and *Adonia* there is a similar situation, but in *Adonia* the high outer crest is not as sharp as in the other three genera. The tibial groove in all these genera is short.

The remaining genera may be divided into two groups on the basis of the extent of the inner border of the femoral groove. In one group this border is sharp and complete on the femur whether or not it continues on to the trochanter. In the other smaller group the ridge is not complete or, if it is, it is low, rounded, and does not possess a sharp crest.

In the first group *Coccinella* (Figure 127), *Synharmonia, Neomysia,* and *Harmonia* have on each femur a deep groove which continues onto the trochanter but there is a decided break in the groove between the femur and the trochanter. Also, in the tibia of these genera there is a short groove but a long carina (Figure 129) extending the length of the segment. *Cissella* differs in having a second long carina on the tibia which touches the first in several places. *Hysia, Agrabia,* and *Adalia* (Figure 128) all have typical femoral grooves but the tibia differ in having along the outer side a long flat area extending the length of the segment. This is far more extensive in *Adalia* than in other genera. By far the largest group of genera have legs with deep femoral grooves and short, deep, tibial grooves which are apical. In this group are *Isora, Myrrha, Buprestodera, Aphidecta, Anisosticta,* and *Adaliopsis. Tytthaspis* differs in having edges of the femoral grooves very high on one side and so slender as to give the trochanter a wafer-like appearance. In *Bulaea* the tibial groove is long, narrow, and deep.

In the second group the tibia is slightly wider than in the first group, and the inner margin of the femoral groove is rounded. *Anatis* (Figure 24) and *Calvia,* as well as *Anisocalvia* and *Propylaea,* have femoral grooves continuing on to the trochanter. In *Calvia* the tibial groove is shallow but quite long. This is true also of *Propylaea* which has as well a long carina on one side. In *Anatis* the groove is short but the carina is present, the inner femoral ridge with a high carina, giving the tibia a triangular cross-section.

Pretarsal claws. There are four variations in the form of the pretarsal claws among the genera of this tribe. The commonest form of the pretarsal claws has a large basal tooth. In this group are *Semiadalia, Aphidecta, Adalia,* (Figure 130), *Coccinella, Halyzia, Spiladelphia, Myrrha, Sospita, Calvia* (Figure 131), *Propylaea* (Figure 132), *Coleomegilla, Hysia* (Figure 133), *Harmonia, Agrabia, Neopalla* (Figure 134). A second group in which the claw tooth arises from near the middle of the claw includes *Anatis* and *Mysia.* A third group, in which the claw and the tooth are combined, giving a decidedly bifid appearance to the claw, includes *Adonia* (Figure 135), *Hippodamia, Eriopis* (Figure 138), and *Neomysia* (Figure 137). In the fourth group may be placed those genera which have simple tarsal claws. In this group are included *Anisosticta, Naemia* (Figure 139), *Macronaemia, Bulaea, Cisseis,* and *Paranaemia.* In some individuals of *Naemia* a minute basal tooth may be found.

Mesocoxal Plates (Plate VI, Figure 140)

In the majority of genera the mesocoxal plate is completely bounded by a mesocoxal line. In those genera which have lost the capacity to retract their legs tightly against the body these plates have been lost. Among such genera are *Hippodamia, Semiadalia, Adonia, Ceratome-*

gilla, Coleomegilla, Naemia, and *Paranaemia.* It is of interest to note that *Anisosticta* and *Macronaemia* have mesocoxal plates which in *Anisosticta* are simply punctate and in *Macronaemia* (Figure 140) are rugosely striate.

Metacoxal Plates (Plate VI, Figures 141–145)

There are three types of metacoxal plates found among the genera of this tribe. First, there are those plates which are unbounded by metacoxal lines, but which are defined, usually, by being concave. Second, there are plates which are completely bounded by metacoxal lines, the arcs so formed being either shallow or quite deep and extending almost to the hind margin of the segment. Finally, there are plates which are incomplete, only the inner portion being limited by a raised line. In these forms the line attains the hind margin of the segment and either ends there or continues parallel with the edge of the segment until it attains the lateral margin of the abdomen. When this condition is found there is often a false line extending from the inner arc obliquely to the outer edge of the coxal cavity.

In the first group there are four genera. In *Eriopis* there is a small, but deep, concave plate. In *Paranaemia* and *Coleomegilla* (Figure 142) the plate is very shallow. And in *Eumegilla* very little good evidence of a plate can be found.

Adonia, Ceratomegilla (Figure 141), *Isora,* and *Hippodamia* all have shallow metacoxal arcs and small plates. *Macronaemia* also has shallow arcs but these are not quite complete, ending a little short of the coxal cavity. *Adalia* and *Adaliopsis* have deeper arcs extending into the posterior quarter of the segment before turning again to the coxal cavity. In the genus *Bulaea* (Figure 143) the arc is apparently incomplete, attaining the hind margin of the segment and becoming contiguous with it. From the point where this arc joins the hind margin, a definite line, the outer arc of the metacoxal line, extends to the outer end of the coxal cavity. In *Buprestodera* the inner arc is contiguous with the segmental margin for a short distance before turning forward, whereas the outer arc is quite straight. This development is carried further in *Sospita* where the outer arc is reduced to an obsolescent line.

The third group, in which the plates are incomplete, may be divided into those genera which have a false line and those which do not. Among those genera which lack false lines *Agrabia* has the inner arc stopping anterior to the hind margin of the segment. *Calvia* and *Anisocalvia* have inner arcs which meet the segmental margin at about one-half the distance between the mid-line and the lateral edge of the segment. In *Propylaea* (Figure 144) the inner arc does not meet the edge of the segment until almost the lateral edge of the abdomen.

In the rest of the genera the false line is present in some degree. In

Tytthaspis the inner arc is much like that in *Propylaea* and the false line extends from the mid-point of the inner arc to the outer edge of the coxal cavity. In *Myrrha* the inner arc does not reach the hind margin of the segment, and the false line extends from near the posterior end of the inner arc to near the outer end of the coxal cavity.

The other genera have inner arcs which meet the hind margin and are contiguous with it to the edge of the abdomen. In *Coccinella* and *Synharmonia* the false line is very short and is in the posterior part of the plate where the arc meets the segmental margin. In *Anatis* the short false line is found only near the outer corner of the coxal cavity and is longer than in *Coccinella*. In *Neomysia* and *Neopalla,* (Figure 145) the false line is quite long but touches neither the inner arc nor the end of the coxal cavity.

Mesosternum (Plate VI, Figures 150–156)

There are five major variations in the form of the anterior face of the mesosternum. Generally these lead either to a flattening of the declivous face or, conversely, to a further increase in the angle of the face. At the same time the central pit may become obsolete or may be greatly enlarged and interfere with the posterior margin of the face.

Five genera, *Coleomegilla* (Figure 150), *Macronaemia, Paranaemia, Eriopis* and *Eumegilla* form a group in which the face of the mesosternum gradually becomes less steep and the limiting ridge gradually becomes obliterated. Accompanying this, the central pit is also lost. In *Coleomegilla* the face is moderately steep, the pit is deep, but the limiting ridge is absent. In *Paranaemia* and to a greater extent in *Macronaemia,* the face is slanting, the limiting ridge is low, and the pit is obsolescent. *Eumegilla* has a convexly curved face with no ridge and a very shallow pit. *Eriopis* has a more strongly curved face with no ridge and no central pit. In this genus the curvature of the face continues back onto the sternum giving the sternum a bulbous appearance.

In *Naemia* the face of the mesosternum is steep with a well-defined ridge, but the pit is much like that in *Coleomegilla.*

A second group of genera show a gradual flattening of the mesosternal face, but this does not lead to simplification as it does in the first group. Four genera comprise this group, *Ceratomegilla, Hippodamia* (Figure 151), *Adonia,* and *Semiadalia.* In *Ceratomegilla* the face is very gently sloping with a well-defined ridge and a small pit. *Hippodamia* is similar, but, in addition, has a deep groove just anterior to the ridge; there is also a rounded pit present. The genus *Semiadalia* shows an advanced condition of this by having the central portion containing the pit raised into a low hump. This is continued in *Adonia* in which the hump is greatly developed. In both *Semiadalia* and *Adonia* the plane of the face has become almost horizontal.


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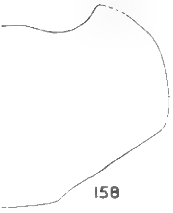
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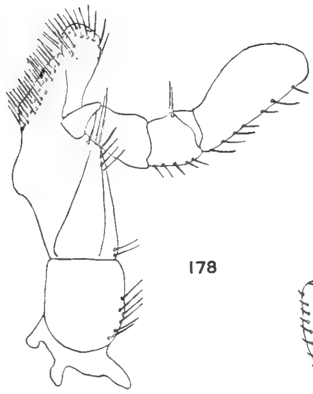
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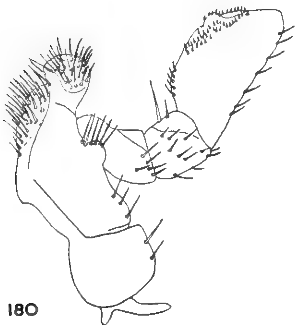
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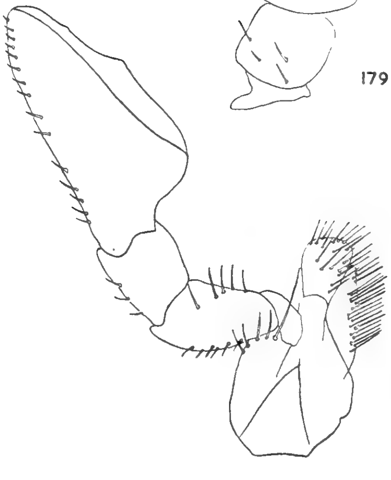
181

A small group of genera, *Coccinella, Harmonia,* and *Synharmonia,* have a slightly steeper mesosternal face. In *Synharmonia* the ridge is rather high and very slightly emarginate.

One group of genera have increasingly steeper mesosternal faces, and the central pits become very large and surrounded by a high ridge on all sides. Incorporated into the pit margin is the posterior ridge of the face which has become deeply emarginate in the centre (*Calvia, Propylaea, Neopalla*). A final form of this development is seen in *Neopalla* (Figure 153) in which the limiting ridge is very low, but the whole of the edge of the face has become emarginate to accommodate the large pit. *Propylaea* differs somewhat from the other genera because the face is shallow.

In *Myrrha, Isora, Bulaea, Aphidecta, Adaliopsis,* and *Sospita* (Figure 155) there is a very steep face. In one case, *Tytthaspis* (Figure 154), the face appears to be undercut. *Myrrha* has a slightly bulbous sternum behind the ridge and, in this respect, resembles *Harmonia. Isora* has a slight shelf dorsally. *Bulaea* has a very short, steep face. In *Aphidecta* the hind ridge is slightly emarginate in the centre and has a very small pit. *Sospita* and *Adaliopsis* have steep faces with very sharply defined ridges.

Anisosticta has a moderately shallow face with a thin, but well-defined, ridge and a small shallow pit.

Pronotum (Plate VII, Figures 157–171)

Although there are several variations in the form of the pronotal shield there is one form which predominates. This form is seen in *Adalia* (Figure 157). Slight variations of this are seen in *Myrrha* in which there are rounded lateral edges and an almost straight anterior margin. In *Harmonia* (Figure 158) the anterior emargination is shallow while in *Coccinella* and *Neomysia* it is quite deep.

Another group of genera have the hind margin more flattened. In

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PLATE VII

Outline of right half of pronotum

FIGURES 157–171: **157**, *Adalia bipunctata* (Linnaeus); **158**, *Harmonia quadripunctata* (Linnaeus); **159**, *Neocalvia anastomozans* Crotch (after Camargo); **160**, *Adaliopsis alpina* Villa; **161**, *Synharmonia conglobata* (Linnaeus); **162**, *Hysia endomycina* Boisduval; **163**, *Adonia variegata* Goeze; **164**, *Eumegilla conterminata* Mulsant; **165**, *Naemia seriata* Melsheimer; **166**, *Eriopis connexa* Germar; **167**, *Hippodamia convergens* Guérin; **168**, *Buprestodera mimetica* Sicard; **169**, *Tyttahaspis sedecimpunctata* (Linn.); **170**, *Semiadalia notata* Laich; **171**, *Isora anceps* Mulsant.

FIGURES 172–176, Prosternal spine: **172**, *Neopalla hydropicta* (Muls.); **173**, *Agrabia cyanoptera* Casey; **174**, *Coccinella transversoguttata* Linn.; **175**, *Anisosticta* sp.; **176**, *Isora anceps* Mulsant.

FIGURES 177–181, Maxilla: **177**, *Tyttahaspis sedecimpunctata* (Linn.); **178**, *Bulaea lichatschovi* Hummel; **179**, *Anisocalvia quatordecimmaculata* (Linn.); **180**, *Propylaea quatordecimpunctata* (Linn.); **181**, *Neomysia* sp.

Adaliopsis (Figure 160) and *Aphidecta* the central emargination is nearly straight while in *Neopalla, Calvia,* and *Synharmonia* (Figure 161) this margin is projected in the centre. The genus *Hysia* (Figure 162) is very similar, but the anterior margin, instead of being emarginate or nearly so, is almost bisinuate with the central portion being noticeably anterior to the apical angles.

A large group of genera differ from this pattern by having the apex slightly narrower than the base and the anterior margin often more sinuate than emarginate. In *Adonia* (Figure 163), and *Eumegilla* (Figure 164) the hind angles are rounded, while in all the rest of the genera they are slightly emarginate. *Eumegilla* is unique because the lateral margins are angulate in the middle. In the genera *Naemia* (Figure 165), *Coleomegilla, Ceratomegilla, Paranaemia,* and *Eriopsis* (Figure 166) the centre of the anterior margin is level with the apical angles. In *Eumegilla* the anterior margin is bisinuate with a narrow emargination in the centre. This angulation is seen to a lesser extent in *Bulaea* and *Anisocalvia.*

In one small series of genera the pronotum has straight lateral margins which converge at the apex. In *Anatis* these are not quite straight but are much more so than in any of the foregoing genera. In *Buprestodera* (Figure 168) the margin is straight but not so convergent anteriorly as in *Neocalvia* (Figure 169) or *Propylaea.* In all these genera the emargination of the anterior border is distinct.

A few genera cannot be placed in any of the previously mentioned groups. *Tytthaspis* (Figure 169), *Semiadalia* (Figure 170) and *Isora* (Figure 171) are such genera. In *Anisocalvia* as in *Isora* the widest part of the pronotum is across the middle.

Prosternal Spine (Plate VII, Figures 172-176)

The prosternal spine is smooth and unmarked by carinae in the following genera: *Adalia, Halyzia, Harmonia, Naemia, Paranaemia, Macronaemia,* and *Hippodamia.* In *Neopalla* the apex of the spine has a pair of short carinae (Figure 172). In all other genera examined carinae are present and are usually well-marked. These carinae are variable in their extent, some being continuous from the apex of the spine to the anterior margin of the sternum, other being very short and extending only to the anterior edge of the coxal cavities.

In *Myrrha* and *Neomysia* the lines are short and joined at the apex of the spine. In *Tytthaspis, Calvia,* and *Anisocalvia* the carinae are slender, well-marked, and extend forward only to the anterior edge of the coxal cavities (Figure 173). In *Coccinella* (Figure 174) the carinae are moderately long but are not well-marked. In *Semiadalia* and *Anisosticta* (Figure 175) the lines are short and follow the edge of the coxal cavities. In *Bulaea* and *Isora* (Figure 176) the carinae are long and extend well in front of the coxal cavities; they are slightly narrower in *Isora*. In *Coccinula* the carinae almost attain the anterior edge of the sternum (Dobzhansky, 1926). In *Adaliopsis* the spine is short and unlined but bears long hairs. In *Eriopis* the spine is very narrow and ends in an acute apex.

Antenna (Plate VI, Figures 146–149)

In the majority of the genera the antenna is of the form described in *Anatis* (p. 3). In some forms such as *Tytthaspis* (Figure 147) and *Coleomegilla* the club is very compact with the eleventh segment larger than the other segments of the club. In *Chelonites, Coccinella,* and *Adalia* the club is compact with the tenth segment much wider than long and truncate along the anterior (distal) border. In only one genus are any of the segments, other than those of the club, noticeably protuberant. In *Semiadalia* (Figure 146) it can be seen that the third segment is triangular and bears four or five spines on the projecting angle. The outer apical angles of the ninth and tenth segments project in such genera as *Anatis* and, to a lesser extent, in *Neomysia* and *Myrrha* (Figure 149).

Maxillae (Plate VII, Figures 177–181)

As in the case of the antenna the majority of the genera have maxillae of the form described for *Anatis* (p. 18). Some of the variations which occur are seen in *Tytthaspis* (Figure 177), *Bulaea* (Figure 178), and *Anisocalvia* (Figure 179).

The terminal segment of the palp is securiform in most of the genera. The regular outline may be interrupted in some genera such as *Propylaea* (Figure 180) and *Neomysia* (Figure 181). In *Bulaea* the apical segment is rather cylindrical with just a slight oblique truncation to the apex, thus forming an exception to the usual securiform shape.

Wing Venation

The wing venation is very constant among the genera of this tribe. There is only one real exception, *Eriopis,* in which the pigmentation of the hind wings is reduced to the point where the pigmented patches are absent and the veins are very pale in colour. A stage which might have led to this condition is found in *Macronaemia,* in which the pigmentation is light and the veins rather pale in colour.

Body Form

From the sub-ovoid form, as seen in *Adalia bipunctata,* several other body forms may be derived, perhaps the most striking of which is the elongate or sub-elongate form found in many genera. This form can be traced from genus *Adalia,* through *A. flavomaculata* which is more elongate than other *Adalia* species, and through the closely allied genus *Hysia.* The elongate Coccinelline beetles are found in the genera

Ceratomegilla, Hippodamia, Semiadalia, Adonia, Coleomegilla, Naemia, Paranaemia, Macronaemia, Eriopis and *Eumegilla.* In most of these forms the widest part of the elytra is just posterior to the middle. The margins of the elytra may be parallel in front of this point (*Macronaemia*) or they may be slightly convergent (*Eumegilla*). Different types of convergence can be found. In *Eumegilla* the margins of the elytra are rounded from the greatest width to the base, whereas in *Eriopis* the margins are straight over this same distance.

One group of genera including *Coccinella, Harmonia, Synharmonia,* and *Aphidecta* have retained the ovoid shape. In this group the main difference from *Adalia* is one of size. Only *Coccinella trifasciata* and *Coccinella fulgida* begin to approach the size of the species of *Adalia.* In the genus *Harmonia* are species which are elongate but which exhibit this in a manner different from the elongate forms mentioned before. In *Harmonia* the individuals are widest across or slightly behind the humeral angles. This width is retained in the basal half of the elytra.

The genus *Megillina* has the widest part of the elytra about two-thirds of the distance from the base to the apex. Behind this the margins quickly converge to a bluntly pointed apex. In front of the greatest width the anterior margins are rounded and gradually converge to a very wide anterior margin.

The remaining genera show a more decided roundness in shape. In *Isora* and *Bulaea* the form is almost circular. *Neopalla,* which is extremely large, is very round, and the widest point of the elytra is in the middle. This is more noticeable in *N. hydropicta,* in which species too, the margins of the elytra are angulate in the middle.

Size, as well as shape, must be considered. Of the elongate forms those of the genus *Macronaemia,* although closely allied to *Anisosticta,* are consistently smaller. At the other end of this series, specimens of *Eumegilla conterminata* are very large when considered with the rest of the elongate forms. In the rounded forms there is one series, *Anatis, Neomysia, Neocalvia, Neopalla,* in which there is a gradual increase in size. This can be correlated with an increase in complexity of the female spermatheca and an increase in size of the epipleura.

Several other genera show a considerable specialization among their members. In *Isora, Bulaea,* and *Buprestodera* a decrease in size is linked with a rather striking development of the pronotum. This is most conspicuous in *Bulaea* in which both the pronotum and prosternum have become anteriorly elongate and form a distinct tube within which the head may be drawn. Members of this genus also show an extreme flattening of the ventral surface.

On the basis of these data it is now possible to show relationships among the genera under discussion from which a proper phylogenetic sequence will automatically develop. This sequence will not necessarily be equivalent to a classification system. Classification systems are constructed principally for ease of handling specimens, and, to this end, keys and descriptions are made as clear as possible by using characters which are readily observable, but which may be rather trivial. Finally, however, having made identification by any means available, a true appreciation of the taxonomic categories can only be gained if their arrangement is based on a sound phylogenetic analysis.

In any phylogenetic study all the available evidence must be taken into consideration. In some groups of animals much more evidence is available than in other groups. In the ducks and geese, for example, studies on behaviour (Lorenz, 1941), as well as on anatomy and distribution, allow for a phylogenetic analysis unequalled elsewhere in biology, except perhaps in the study of man. In most animals such a vast amount of evidence is not available. It is necessary then to use what evidence there is as fully as possible. In insects, such as those we are studying here, the main bulk of data is derived from the anatomy of the skeletal structures. Care must be taken to use as many characters as possible in any analysis made, for almost as many sequences can be constructed as there are characters and these sequences will not necessarily be the same. For example, a sequence based on the form of the metacoxal plates will result in a generic arrangement which differs from a sequence based on the form of the tooth characters of the pretarsal claw. These single sequences do not, of themselves, contribute to any adequate analysis of the phylogenetic relationships of the genera. Only an analysis of the various characters in *relation to one another* will make for a proper understanding of the relationships.

One of the great problems in a study of this kind is the determination of the value of characters, e.g. which are the more primitive and which are the more advanced. In the present study three criteria were used to decide character value (Maslin, 1952). *First,* if a character was found generally throughout a group or in a large part of the group, that character was considered as being primitive (e.g. the gently curved sipho). *Second,* if a character in the group under study was found to be common to other groups known to be related, then such a character was considered primitive (e.g. the complete metacoxal plate in the Hyperaspini and Coccinellini). *Third,* if a character was found from which other characters could be derived in a logical sequence, such a character was considered as primitive (e.g. the cylindrical trabes of *Adalia*). By the use of these criteria, the structural characters were assessed as shown in the following list:

Primitive Characters	*Advanced Characters*
Obovoid form	Elongate form
Clavate antennae	Clubbed antennae
Truncate, cylindrical palpi	Securiform palpi

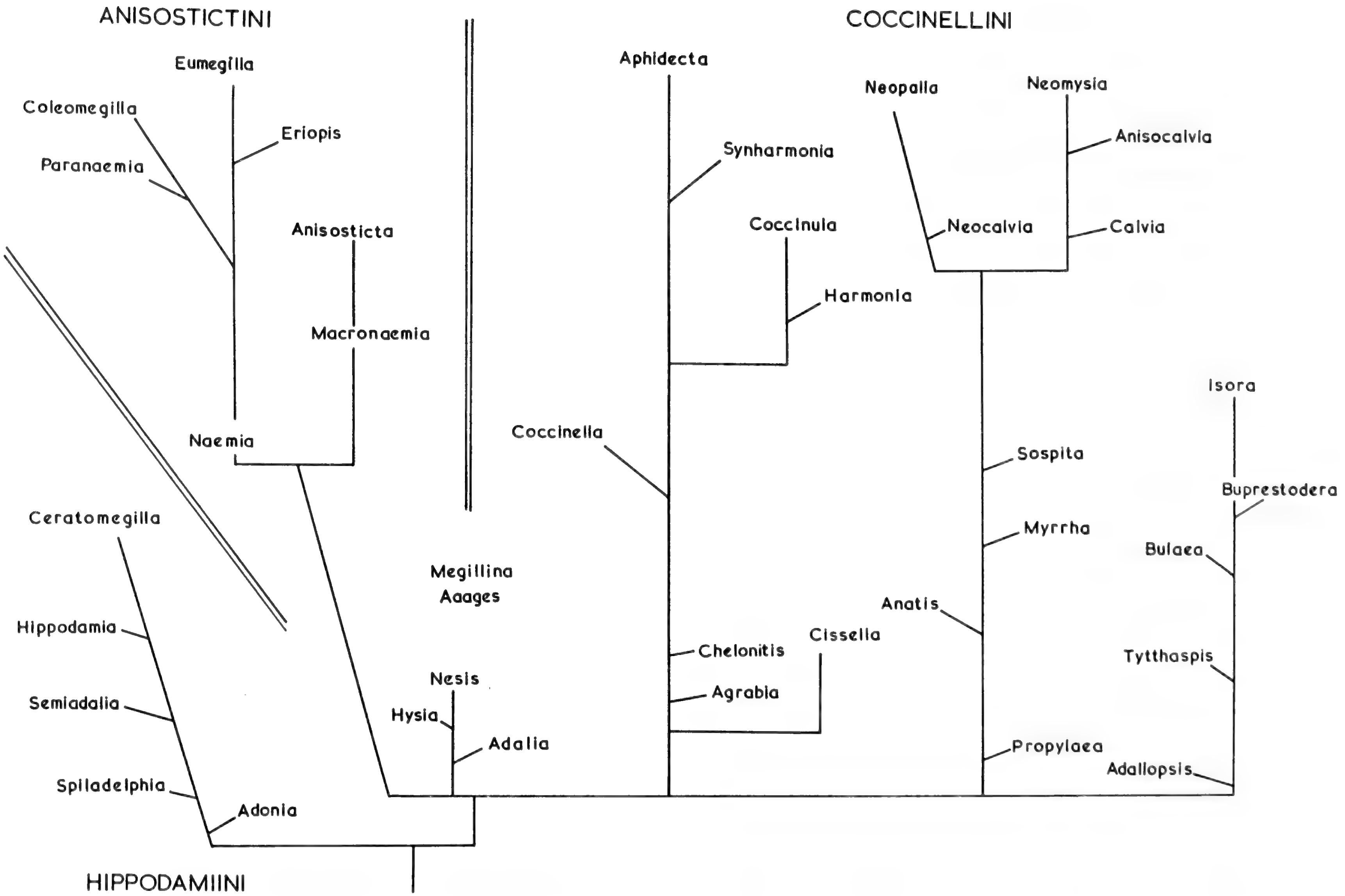

PLATE VIII

Phylogenetic arrangement of the genera in the tribes Hippodamiini, Anisostictini, and Coccinellini.

Deeply emarginate pronotum	Shallow emargination or none
Declivous mesosternal face	Round mesosternal face
Deep mesosternal pit	Shallow mesosternal pit or none
Mesocoxal plates present	Mesocoxal plates absent
Elytra with narrow epipleura	Elytra with wide epipleura
Hind wings with well-marked veins	Hind wings with ill-defined veins
Leg segments grooved	Leg segments not grooved
Pretarsal claws with a quadrate basal tooth	Pretarsal claws with teeth of other forms
Metacoxal plates complete	Metacoxal plates incomplete
Sipho curved, slender, elongate	Sipho of a different form
Capsule bipartite, simple	Capsule of a different form
Aedeagus simple, ventral alae not complex	Aedeagus and ventral alae complex
Spermatheca with a long slender ramus	Spermatheca with thick, ribbed ramus
Limbs withdrawn in death feint	Limbs not withdrawn in feint

The genus *Adalia* exhibits more primitive characters than any other genus. Two other genera, *Hysia* and *Nesis,* may be associated with *Adalia,* but both are more advanced. *Hysia* has become elongate and the trabes shows a tendency to twist; this genus can be related to some of the more elongate species of *Adalia* (*A. flavomaculata*). *Nesis* lacks the well-developed humeral calli that are found in *Adalia.*

Considering *Adalia* to represent the primitive form, it is found that two series of advanced genera can be derived. In one series of genera (*Adonia, Semiadalia, Hippodamia, Ceratomegilla,* and possibly *Spiladelphia*) the trabes is straight but has a flattened, rather than a cylindrical, apex. Within this series *Adonia* is, on the basis of male genitalia, most closely associated with *Adalia,* differing only in the blunt, rounded paramera. On the other hand, certain features such as the structure of the mesosternum and the sequence it forms with those of other genera would place *Adonia* as an advanced genus, possibly having arisen near the base of the rest of the series.

Of this series the rest of the genera may be easily related by the form of the male genitalia. The form of the aedeagus in *Semiadalia* shows some affinities with *Adalia,* as seen in the simple ventral alae and the spatulate paramera. The complexity of this structure increases in *Hippodamia,* where the ventral alae are highly developed but the aedeagus is similar to that found in *Semiadalia.* Finally, in *Ceratomegilla* the sides of the aedeagus are emarginate and the ventral alae are complex, and the paramera are long with small setaceous areas. Of these three genera *Ceratomegilla* shows the least specialization in the form of the mesosternum, but the form of the pretarsal claws of this genus is intermediate between that of *Semiadalia* and *Hippodamia.* In the arrangement of these genera, *Semiadalia* is considered to be more primitive than *Hippodamia. Ceratomegilla,* in spite of the mesosternal structure, must be considered as an advanced form because of the complex genital structure of the male. The genus *Spila-*

delphia has not been seen but, from its description, must be placed close to *Adonia*. *Adonia,* in turn, is related to *Adalia.*

The remaining genera, in which the trabes has been rotated through 90°, can be divided into several series which have as their final development, a decided change in body form. One of the more distinct series is that in which the body has become elongate. In body shape this series resembles *Hysia* very closely and probably arose near these forms. In this series are *Naemia, Eumegilla, Coleomegilla, Paranaemia, Anisosticta,* and *Macronaemia. Anisosticta* and *Macronaemia* are closely related and may be separated from the rest of the genera by the form of the siphonal capsule in the male and by the presence of metacoxal plates. The gradual flattening and simplification of the mesosternal face can be traced through *Naemia, Coleomegilla, Paranaemia, Eriopis,* and *Eumegilla. Coleomegilla* and *Paranaemia* must be related by the form of the apically emarginate aedeagus. *Eriopis* and *Eumegilla* both have distinctive body forms and must be considered among the most advanced of these genera. The loss of well-marked veins in the hind wings isolates *Eriopis* from other genera. The marked simplicity of the mesosternum places *Eumegilla* in a very advanced position.

This series arises near *Hysia* and is divided into two groups, one containing *Anisosticta* and *Macronaemia,* and the other *Naemia, Paranaemia, Coleomegilla, Eriopis,* and *Eumegilla.*

One group of genera retain the general body form of *Adalia* throughout, although the size is slightly larger. In this group are *Agrabia, Cisella, Coccinella, Harmonia, Synharmonia,* and *Aphidecta. Synharmonia* and *Harmonia* show a distinct relation to *Adalia* in the form of the paramera. In *Coccinella* the paramera have become short and straight, and in *Aphidecta* they are short and conical. *Synharmonia* and *Aphidecta* can be related by the form of the aedeagus which is deeply emarginate at the apex in both genera. In this respect *Harmonia* and *Coccinella* both have an aedeagus with a rounded apex, illustrating the affinities of these genera with *Adalia.* This rounded form in *Harmonia* may, however, be a final stage in the development of the emarginate form as found in *Synharmonia. Coccinella* must be isolated in this series by the form of the sipho. *Agrabia* has a body shape which would place it in this series and the tibiae are flat, resembling closely those of *Adalia. Cisella,* on the other hand, has a double carina on the tibia and simple claws, which at once removes this genus from any close connection with this series. *Harmonia, Coccinella, Synharmonia,* and possibly *Coccinula,* have deep femoral grooves and singly carinate tibia. In *Aphidecta* the tibia has a short apical groove and no carinae. In *Coccinella, Harmonia,* and *Synharmonia* the face of the mesosternum is quite steep with a large central pit. In *Aphidecta* also the face is steep, but the pit is small. In this genus, as well as in *Synharmonia,* the posterior margin of the mesosternal face is slightly emarginate.

These genera are all closely related, with the exception of *Cisella* which must be considered a specialized branch. The other genera, it is believed, are related in the following way: *Coccinella, Synharmonia,* and *Aphidecta* form a small series almost in a direct relation to *Adalia, Aphidecta* being the most highly developed. *Harmonia* and *Coccinula* are somewhat isolated from this line and arise in a very slightly advanced position from the point at which *Coccinella* arises. *Agrabia,* if it is related to these other genera, possibly arises somewhere between *Adalia* and *Coccinella.*

The next series of genera form a sequence, the end result of which is an extremely large size. Most of the genera can also be related by the form of the sipho, which is narrow and gently curved. The series begins with *Propylaea,* which is much like *Adalia* but exhibits the beginnings of a slight emargination of the posterior edge of the mesosternal face, a change becoming much more evident throughout the rest of the genera in the group.

More advanced than *Propylaea* are *Anatis, Sospita, Myrrha, Calvia,* and *Anisocalvia.* These genera differ from *Adalia* in several genital structures, prominent among which is the loss of the membranous sac at the end of the sipho. At the same time, the carinae of the prosternal spine have become enlarged and elongate. *Sospita* differs from the other genera in the form of the mesosternum and the spermatheca. *Calvia* and *Anisocalvia,* although closely related, are quite distinct on the basis of the male genitalia, that of *Anisocalvia* showing a much more advanced condition than that of *Calvia.*

Neomysia is related to the *Calvia-Anisocalvia* group. *Neocalvia* is somewhat removed from these genera on the form of the male genitalia and the pronotum, but is related to *Neopalla,* which is the extreme in body size, by the presence of a large, sharply curved sipho.

The increase in size, associated with an increase in the emargination of the anterior margin of the mesosternum, begins with *Propylaea* and includes in order *Sospita, Myrrha, Calvia, Anisocalvia, Anatis, Neocalvia,* and *Neopalla. Propylaea, Anatis, Myrrha,* and *Sospita* form a short linear series from *Adalia.* There are two groups of genera more advanced than these. *Calvia, Anisocalvia,* and *Neomysia* form one group which can be considered an extension of the more primitive genera. *Neocalvia* and *Neopalla* form the other group, which diverges from the rest on the basis of the male genitalia.

Finally, there is a series of genera in which there is a gradual decrease in size and an increase in roundness of form. From *Adalia* arises, first, *Adaliopsis* in which the metacoxal plates show a decided advance over those of *Adalia. Tytthaspis* resembles *Adaliopsis* in many ways and also shows an affinity to *Propylaea* in the last series. For this reason *Tytthaspis* is placed in a rather isolated position in this series.

The remaining three genera of this series, *Isora, Bulaea,* and *Buprestodera,* must be isolated from the rest of the series because of their size and form; they are all small and more nearly round than the other genera. At the same time *Buprestodera* cannot be too closely related to the other two genera because of its flat ventral surface, a character not found elsewhere in the tribe. And too, the head is much more deeply inserted in the prothorax in which both the notum and the sternum are prolonged in front. That *Buprestodera* is at all related to these other genera can be seen in other characters. The male genitalia are similar in all of them, the form of the metacoxal plates is the same in *Buprestodera* and *Bulaea,* and the shape of the legs is similar in *Buprestodera* and *Isora.*

Dobzhansky (1927) discusses some of the genera of this tribe and, in some ways, the results are much the same as those reached here. Group I of Dobzhansky includes *Megilla, Naemia, Paranaemia,* and *Eriopis,* and was considered as only distantly related to the genus *Coccinella* (sens. str.). On the other hand, group II included *Hippodamia, Adonia,* and *Semiadalia* and was closely related to the genus *Coccinella* because of the similarity between the genitalia of *Semiadalia* and *Coccinella undecimpunctata. Aphidecta* was considered to be isolated because of the form of the aedeagus. *Aaages,* possessing characteristics of the hippodamine genus, *Coccinella,* and the megilline genera, was considered as isolated because of the peculiar distribution of the setae on the paramera. *Anisosticta* was considered to be closely related to the genera *Bulaea* and *Coccinula.*

As outlined in the present study, the genera *Coccinella* and *Aphidecta* are placed in the same group, which is considered as the most primitive of all the groups. Despite the similarities that exist between the genitalia of *Semiadalia* and *Adonia* and some of the *Coccinella* species it is felt that the *Hippodamia* group is not closely related to *Coccinella.* In this group *Adonia* is considered as primitive and *Ceratomegilla,* a genus not considered by Dobzhansky, as most advanced. In the *Naemia* group, corresponding to the *Megilla* group of Dobzhansky, *Naemia* is primitive, leading to *Coleomegilla* in one direction and to *Anisosticta* and *Macronaemia* in another. *Anisosticta* should be placed with *Macronaemia* rather than with *Bulaea.* In general the structure of the genitalia of this group resembles that found in *Coccinella* more closely than does that found in the *Hippodamia* group.

The genus *Aaages,* because of its composite nature, must be isolated, though possibly included in the tribe *Coccinellini.* Since specimens have not been seen, nothing definite can be said. The genus *Megillina* also exhibits characteristics of several groups. Weise (1909), in his description of the genus, states that it resembles quite closely the genus *Adalia.* Since this is so, this genus too will be placed tentatively in the Coccinella group of genera.

FOSSIL EVIDENCE

The earliest record of any of the Coccinellidae is reported from the mid-Jurassic Stonefield slates of Eyeford, England. The fossil was placed in the genus *Coccinellophane* and was a small, somewhat elongate beetle (Handlirsch, 1908). Westwood (see Handlirsch loc. cit.) records the remains of a beetle, from the late Jurassic of Durdlestone Bay, England, which he simply called 'Coccinellidae.' Handlirsch comments that these remains might be heteropteran. Fossils from the Tertiary can be identified with much greater certainty. The genus *Adalia* is reported from the mid-Oligocene in Germany and the Florissant beds (Miocene) in Colorado. *Coccinella* has been recorded from the lower Oligocene in Germany and from the Baltic amber deposits. Five other species of this genus are known from the upper Oligocene of Germany, and eleven species have been found in the upper Miocene deposits of Europe. *Sospita* has been reported from the upper Oligocene of Europe. The genus *Anatis* is reported from the Florissant beds, Colorado (Wickham, 1917). Finally, the genus *Coccinella* has been taken twice in the Pleistocene deposits of Lexden, England. There is some doubt about one specimen which may be a *Cassida* (Chrysomelidae).

Although meagre, this record indicates that the earliest recognizable forms were sub-ovoid in shape. In general features these forms resemble *Adalia*.

ARRANGEMENT AND PHYLOGENY OF THE GENERA

The genera which have been discussed in these pages can be placed in seven generic groups. These groups are not all of the same morphological value, but may be used to form three major units which are morphologically definite and which may be considered of equivalent value. For this reason these three major groups will be considered as tribes and will be given names accordingly. The following arrangement, then, is proposed:

Tribe COCCINELLINI

- *Adalia* group
  - *Adalia* Mulsant
  - *Hysia* Mulsant
  - *Nesis* Mulsant
- *Coccinella* group
  - ?*Aaages* Barovsky?
  - ?*Megillina* Weise?
  - *Chelonites* Mulsant
  - *Cissella* Weise
  - *Agrabia* Casey
  - *Coccinella* (sens. str.)
  - *Harmonia* Mulsant
  - *Coccinula* Dobzhansky
  - *Synharmonia* Ganglbauer
  - *Aphidecta* Weise
- *Anatis* group
  - *Propylaea* Mulsant
  - *Anatis* Mulsant
  - *Sospita* Mulsant
  - *Myrrha* Mulsant
  - *Calvia* Mulsant
  - *Anisocalvia* Crotch
  - *Neomysia* Casey
  - *Neocalvia* Crotch
  - *Neopalla* Chpn.
- *Tytthaspis* group
  - *Adaliopsis* Capra
  - *Tytthaspis* Crotch
  - *Isora* Mulsant
  - *Bulaea* Mulsant
  - *Buprestodera* Sicard

Tribe ANISOSTICTINI

Naemia group
- *Naemia* Mulsant
- *Paranaemia* Casey
- *Coleomegilla* Timberlake
- *Eumegilla* Crotch
- *Eriopis* Mulsant

Anisosticta group
- *Anisosticta* Dejean
- *Macronaemia* Mulsant

Tribe HIPPODAMIINI

Hippodamia group
- *Adonia* Mulsant
- *Spiladelphia* Sem. & Dobzh.
- *Semiadalia* Crotch
- *Hippodamia* Dejean
- *Ceratomegilla* Crotch

These three tribes and their attendant genera are related as shown in Plate VIII. From the slim fossil evidence that is available and from the assumptions which were made earlier, it may be considered that the tribe Coccinellini is the most primitive, all of its members retaining generally the sub-ovoid shape, the steep mesosternal face, the grooves in the legs, and the gently curved sipho of the male genitalia. From this tribe, through *Adalia* and *Hysia,* the Anisostictini has developed and can be characterized by an elongate body form, a gradual loss of the mesosternal face and the leg grooves; this tribe has retained the coccinelline form of the sipho and, because of this, should be considered more closely allied to the coccinelline genera. The Hippodamiini, although showing some affinities with the genus *Coccinella,* has developed several major variations in structure. They possess a definitely ovoid or linear ovoid form, complex development of the mesosternum, and an angulate, valve-bearing sipho. These characters are sufficient to consider the Hippodamiini as a divergent group of genera which have arisen at quite an early period from the basic coccinelline stock.

The term Anisostictini was used first by Jacobson (1916) as a synonym for Hippodamiini. This can hardly be considered as valid for the generic basis, for these terms refer to two genera which are only distantly related. As has been shown, *Anisosticta* and *Hippodamia* belong to two quite distinct tribes. It is therefore justifiable to construct tribal designations from these names without any conflict.

Whereas the relationships of the genera within the tribes Anisostictini and Hippodamiini are well-defined, the relationships of the genera in the tribe Coccinellini must be considered as tentative. Some of the genera are undoubtedly placed correctly; others exhibit characters that differ so slightly from the common form that they could be placed in several different positions. The genera have been related, as shown in Plate VIII, often on the basis of the quality of a character, its tendency to lead to something else, rather than on the character as it appears in the one genus. Such is certainly the case with *Propylaea.* This genus could as easily have been placed at the base of the *Tytthaspis* group of genera or, even, the *Coccinella* group, but because of the quality of some of the characteristics of the genus, it showed a tendency to lead more logically to the *Anatis* group than to any of the others. Before the position of these genera can be finally decided, detailed investigations should be undertaken on the specific level, and the primitive members of each genus should be related to each other or to a common progenitor.

Although the generic groups have been based upon anatomical characters, many of the genera can be separated also on the basis of distribution. Table I shows the general distribution of each genus. From this it can be seen that the tribe Coccinellini is mainly centred in the Old World; of the *Adalia* group only the genus *Adalia* is found in the New World; of the *Coccinella* group *Coccinella* is cosmopolitan whereas *Agrabia* is confined to North America and Mexico. In the *Anatis* group *Propylaea, Sospita, Myrrha,* and *Calvia* are found mainly in the palaearctic regions, *Neocalvia* and *Neopalla* are restricted to the neotropical region, whereas the other genera of this group are generally holarctic. The *Tytthaspis* group does not usually occur outside the palaearctic region although *Isora* and *Buprestodera* are found in adjacent territory to the south (India and southern Africa).

The tribe Anisostictini, on the other hand, is essentially neotropical with some genera such as *Naemia* and *Coleomegilla* extending into the nearctic regions, and with one group, the Anisosticta group, being wholly holarctic. Finally, the Hippodamiini is holarctic with few extensions, probably in mountainous areas, into other regions.

SUMMARY

From a study of the adult anatomy of the various genera contained in the tribe Coccinellini (sens. Korschefsky) it has been shown that these genera can more easily be placed in three tribes, Coccinellini (sens. str.), Anisostictini, and Hippodamiini. Thus genera which are obviously related can be grouped with each other, instead of being confused with genera which appear to be related only because they have undergone a form of parallel evolution. The Coccinellini is the most primitive tribe, with the genus *Adalia* representing the fundamental concept of this tribe. The Anisostictini have arisen from *Adalia,* possibly through the genus *Hysia.* The Hippodamiini have also arisen from the primitive Coccinellini, such as *Adalia,* even though some members do resemble *Coccinella* in certain structures. Whereas the Coccinellini exhibit a retention of many of the primitive characters and, for this reason, are difficult to arrange generically, the Anisostictini and the Hippodamiini are both much advanced and have become somewhat restricted in their geographic distribution. The Anisostictini

TABLE I

Distribution of the Genera of the Coccinellini, Hippodamiini, and Anisostictini

Genus	Distribution
COCCINELLINI	
Adalia	Cosmopolitan
Hysia	East Indies, Celebes, New Guinea
Nesis	unknown
Coccinella	Cosmopolitan
Agrabia	North America, Mexico
Cisella	Australia
Harmonia	Palaearctic regions
Synharmonia	Palaearctic regions
Coccinula	Palaearctic regions
Aphidecta	Eastern Europe and Asia Minor
Chelonitis	Central Europe
Megillina	Madagascar
Aaages	Mongolia
Anatis	Holarctic regions
Anisocalvia	Holarctic regions
Neomysia	Holarctic regions
Propylaea	Palaearctic regions (Eastern Asia)
Sospita	Europe, China
Calvia	Palaearctic regions, south to India
Myrrha	Palaearctic regions
Neopalla	Northern South America, Central America
Neocalvia	South America
Tytthaspis	Palaearctic regions, northern Africa, Nepal
Bulaea	Palaearctic regions, northern Africa, Nepal
Adaliopsis	Central and southern Europe
Buprestodera	India
Isora	Africa
HIPPODAMIINI	
Adonia	Palaearctic regions, central Africa, India
Hippodamia	Holarctic, South America
Semiadalia	Central Europe, China
Ceratomegilla	Arctic and sub-arctic North America
ANISOSTICTINI	
Naemia	Central North America, Central America, northern South America
Paranaemia	Central North America, Mexico
Coleomegilla	South, Central, North America
Eriopis	South America
Eumegilla	South America
Anisosticta	Holarctic regions
Macronaemia	Central North America, China

are mainly Neotropical, the Hippodamiini mainly Holarctic. Neither of these tribes has diverged so far from the original that their relationships are obscured, and it is not possible to say that one is more advanced than the other.

Appendix

TAXONOMIC CHANGES

As a result of the investigations which have been undertaken, the following taxonomic changes are suggested. All these changes are restorations of generic names which have, in the opinion of the author, been incorrectly placed either as synonyms or as subgenera in recent publications.

Coleomegilla Timberlake

Megilla Mulsant 1850, Spec. Trim. Securipalp, pp. 5,24; *see also* Crotch 1873, Trans. Amer. ent. Soc., 4:364; Casey 1899, N.Y. ent. Soc., 7:75,76; Leng 1903, N.Y. ent. Soc., 11:36,38.

Ceratomegilla Crotch, *see* Leng 1920, Catal. Col., p. 215; Korschefsky 1932, Col. Catal. pars 120, p. 312.

Coleomegilla Timberlake 1920, Proc. U.S. nat. Mus., 56: 139; *ibid.* 1920, Canad. Ent., 52:96; Leng and Mutchler 1927, Suppl. 1919–1924 to Catal. Col. (Leng), p. 33; Korschefsky 1932, Col. Catal. pars 120, p. 312 (*Ceratomegilla* Crotch); Blackwelder and Blackwelder 1948, 5th Suppl. Catal. Col. Leng), p. 27; Timberlake 1943, Hawaii. Plant. Rec., p. 9; Wingo 1952, Iowa St. Coll. J. Sci., pp. 15–53.

(Type: *C. maculata* DeGeer)

Although the name *Coleomegilla* has been used as a generic name since 1943 it has not been formally designated as such. Timberlake (1943) pointed out that this genus was different from *Ceratomegilla* Crotch, a fact that has been further emphasized here. The genus *Coleomegilla* includes the following species: *innotata* Muls., *maculata* DeG. and *quadrifasciata* Schon.

Ceratomegilla Crotch

Ceratomegilla Crotch 1873, Trans. Amer. ent. Soc., 4:363,365; *see also* Leng 1903, J. N.Y. ent. Soc., 11:37,39; Casey 1899, J. N.Y. ent. Soc., 7:75; Leng 1920, Catal. Col., p. 215; Korschefsky 1932, Col. Catal. pars 120, pp. 312, 315; Timberlake 1943, Hawaii. Plant. Rec., p. 9.

(Type: *C. ulkei* Crotch)

This genus is distinct from *Coleomegilla* as designated above, on the basis of general form and the structure of the male genitalia. The genus is, at present, monospecific.

Paranaemia Casey

Paranaemia Casey 1899, J. N.Y. ent. Soc., 7:75,76; *see also* Leng 1903, J. N.Y. ent. Soc., 11:37,38; Leng 1920, Catal. Col., p. 215 (sub-genus); Korschefsky 1932, Col. Catal. pars 120, pp. 312,315 (sub-genus).

(Type: *P. vittigera* Mannerheim)

This genus is very closely allied to *Coleomegilla* from which it may be distinguished by slight but constant differences in the structure of the genitalia and by the maculation.

Coccinula Dobzhansky

Coccinula Dobzhansky 1925, Zool. Anz., 67:244,249; *see also* Mader 1927, Z. Ver. NatBeob., Wien, pp. 19,25; Korschefsky 1932, Col. Catal. pars 120, p. 439 (sub-genus).

Harmonia Mulsant

Harmonia Mulsant 1850, Spec. Trim. Sercuripalp., pp. 74,75; *see also* Crotch 1873, Trans. Amer. ent. Soc., 4:375; Crotch 1874, Rev. Fam. Coccin. (=*Coccinella*); Dobzhansky 1925a, Zool. Anz. 67:244; Mader 1927, Z. Ver. NatBeob., Wien, pp. 19,24; Korschefsky 1932, Col. Catal. pars 120, p. 439 (sub-genus).

The two genera just mentioned must be considered quite distinct and quite apart from *Coccinella* (sens. str.). Dobzhansky (1927) has presented means whereby these genera can be separated on a sound structural basis.

Synharmonia Ganglbauer

Synharmonia Ganglbauer 1899, Die Käfer von Mittel-Europa III, pp. 994, 1002; *see also* Dobzhansky 1925, Zool. Anz., 67:241; Mader 1927, Z. Ver. NatBeob., Wien, pp. 19,24; Korschefsky 1932, Col. Catal. pars 120, p. 440 (sub-genus).

(Type: *S. conglobata* [Linnaeus])

This genus, although closely allied to *Coccinella,* may be distinguished from that genus both by the shape of the body and the form of the male genitalia.

Anisocalvia Crotch

Anisocalvia Crotch 1873, Trans. Amer. ent. Soc., 4:364,373; *see also* Casey 1899, J. N.Y. ent. Soc., 7:84,89; Leng 1903, J. N.Y. ent. Soc., 11:194,206; Leng 1920, Catal. Col., p. 217; Korschefsky 1932, Col. Catal. pars 120, p. 521 (sub-genus); Wingo 1952, Iowa St. Coll. J. Sci., pp. 15–54.

(Type: *A. quatordecimguttata* [Linnaeus])

Although this name has been used as a generic name since the work of Korschefsky, it has never been formally replaced as such, *Anisocalvia* with its many species, forms a discrete unit which can be separated from *Calvia* by the form of the male genitalia as well as the characters which Crotch (1873) assigns to its member species.

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